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RESEARCH ARTICLE

Urban development reduces fledging success of Barn Owls in British Columbia, Canada

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ABSTRACT

The decline of Barn Owls (*Tyto alba*) in Europe and North America has been attributed to the loss and fragmentation of grassland foraging habitat and increased urbanization; both factors can reduce reproductive output and adult survival. We examined how the composition of the agricultural landscape influenced fledging success (defined as the number of young fledged per nesting attempt) of a threatened population of Barn Owls in the Fraser Valley, British Columbia, Canada. Among landscape variables, only amount of urban cover was correlated with fledging success of Barn Owls: Fledging success decreased with increasing urban cover within a 1-km radius of the nest site. This effect was driven by increased brood reduction: Individuals at sites with more urban cover fledged fewer young but did not lay smaller clutches or fledge young in poorer condition. Given that brood reduction is linked to food availability in Barn Owls and other species, this suggests that food availability was reduced in more urbanized landscapes. Fledging success was not influenced by grassland cover, grassland composition (number and distance to patches of grassland), or the length of highway within a 1-km radius of nest sites. The proportion of prey biomass consisting of voles varied considerably between nests (range: 0.41–0.92) but was not related to landscape composition surrounding a nest site. Because urban cover reduced fledging success but not diet composition, our data suggest that the amount of urban cover leads to indirect effects on the abundance of small mammals within the landscape.

Keywords: agricultural landscape, breeding success, diet quality, *Tyto alba*, urbanization

Le développement urbain réduit le succès à l'envol chez *Tyto alba* en Colombie-Britannique, au Canada

RÉSUMÉ

Le déclin de *Tyto alba* en Europe et en Amérique du Nord a été attribué à la perte et à la fragmentation de l'habitat de prairie où l'espèce s'alimente et à l'augmentation de l'urbanisation; ces deux facteurs peuvent réduire l'efficacité de la reproduction et la survie des adultes. Dans cette étude, nous avons examiné comment la composition du paysage agricole influence le succès à l'envol (défini comme étant le nombre de jeunes ayant atteint l'envol par tentative de nidification) d'une population menacée de *T. alba* dans la vallée du Fraser, en Colombie-Britannique, au Canada. Parmi les variables du paysage, seule la couverture urbaine était corrélée avec le succès à l'envol de *T. alba*. Le succès à l'envol diminuait avec l'augmentation de la couverture urbaine dans un rayon d'un kilomètre du site de nidification. Cet effet était dicté par une réduction croissante de la taille de la nichée: Les individus des sites ayant plus de couverture urbaine ont produit moins de jeunes à l'envol mais n'ont pas pondu moins d'œufs ou produit des jeunes à l'envol en moins bonne condition. Puisque la diminution de la taille de la nichée est reliée à la disponibilité de la nourriture chez *T. alba* et d'autres espèces, cela suggère que la disponibilité de la nourriture était réduite dans les paysages plus urbanisés. Le succès à l'envol n'était pas influencé par la couverture de la prairie, la composition de la prairie (le nombre et la distance aux îlots de prairie) ou la longueur d'autoroute dans un rayon d'un kilomètre des sites de nidification. La proportion de la biomasse de proies composée de campagnols variait considérablement entre les nids (0,41 à 0,92) mais n'était pas reliée à la composition du paysage autour d'un site de nidification. Puisque la couverture urbaine réduisait le succès à l'envol mais pas la composition de l'alimentation, nos données suggèrent que la couverture urbaine mène à des effets indirects sur l'abondance des micromammifères dans le paysage.

Mots-clés: paysage agricole, qualité de l'alimentation, succès reproducteur, *Tyto alba*, urbanisation

INTRODUCTION

Birds associated with agricultural landscapes have experienced strong population declines and range contractions across Western Europe and North America (Fuller et al. 1995, Brennan and Kuvlesky 2005, Donald et al. 2006). Declines have been attributed to habitat degradation due to agricultural intensification (Fuller et al. 1995, Donald et

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al. 2006) and the loss of agricultural land to urbanization (Filippi-Codaccioni et al. 2008, Ludwig et al. 2009). The value of agricultural land as wildlife habitat is degraded when small fields with rotational crop practices and hedgerows are converted to large, intensively utilized fields with monocultures (Fuller et al. 1995, Wilson et al. 2005). In addition to habitat loss, urbanization creates road networks that fragment habitat and expose wildlife to traffic (Underhill and Angold 2000, Borda-de-Água et al. 2014). These changes in landscape composition have been linked to the reduced reproductive output and survival of many farmland birds (Fuller et al. 1995).

Newton (2004) argued that most of the declines in populations of farmland birds in Britain (~70% of species) are associated with reduced reproductive output rather than reduced adult survival. Changes in agricultural practices can reduce the reproductive output of farmland birds in a variety of ways. Breeding habitat can be lost as a result of the drainage and conversion of grasslands for cultivation (Vickery et al. 2001, Wilson et al. 2005). Intense grazing regimes can reduce nest cover and increase nest predation rates (Chamberlain and Crick 2003). Increased herbicide and pesticide use can reduce food availability (Rands 1985, Taylor et al. 2006) and reduce the number of breeding attempts and breeding success (e.g., Browne and Aebischer 2004, 2005). Increased use of fertilizers also allows earlier and more frequent haying, which reduces the nesting success of ground-nesting birds (Green and Stowe 1993, Schekkerman et al. 2008).

Range contraction and population declines of Barn Owls (*Tyto alba*) in Europe and North America have also been attributed to changes in agricultural landscapes that reduce both adult survival and reproductive output (Bunn et al. 1982, Colvin 1985, Taylor 1994, Toms et al. 2001, Ramsden 2003). For example, increases in road networks are associated with reduced survival of Barn Owls because the owls hunt on grassy verges along roads, making them vulnerable to collisions with vehicles (Ramsden 2003, Preston and Powers 2006, Boves and Belthoff 2012, Borda-de-Água et al. 2014). Increased use of second-generation anticoagulant rodenticides, which are lethal to Barn Owls, may also contribute to population declines by poisoning adults and young (Newton et al. 1990, Albert et al. 2010). Agricultural intensification reduces the number of potential breeding sites by removing wooden barns and old trees (Taylor 1994, Ramsden 1998). Finally, conversion of grasslands used by Barn Owls for foraging is linked to lower breeding success (Colvin 1985, Butet and Leroux 2001).

In the Fraser Valley of British Columbia, Canada, 30% of the nest sites used by Barn Owls in the 1990s are no longer available because old buildings were removed or replaced with structures unsuitable for owls (Hindmarch et al. 2012). The occupancy of remaining nest sites is negatively affected by the presence of highways (Hindmarch et al. 2012). The composition of the agricultural landscape could also influence the breeding success of Barn Owls in this region. Breeding success may vary with the amount and location of grasslands within a home range, because these are expected to influence prey availability. Breeding success could also vary with the amount of urban cover or roads within a home range. Finally, the amount of grassland, urban cover, or roads could influence breeding success by altering the composition of the prey community. Barn Owls are vole specialists, and breeding success increases with the proportion of voles (*Microtus* spp.) in the diet (Gubanyi et al. 1992, Taylor 1994).

We investigated the influence of landscape composition on fledging success of Barn Owls in the Fraser Valley. We described the landscape composition surrounding nest sites occupied by Barn Owls, quantified their diet composition during the nestling period, and monitored fledging success (number of young fledged per nesting attempt). We examined the relationship between landscape composition and (1) fledging success, (2) brood condition (the mean standardized asymptotic mass of chicks in a brood), and (3) diet composition (the proportion of prey biomass consisting of voles). We also assessed whether landscape effects on fledging success were a consequence of landscape effects on clutch size and/or brood reduction.

METHODS

Study Area

We monitored the breeding and diet of Barn Owls within the municipalities of Delta and Surrey, an area of 681 km^2 within the Fraser Valley, British Columbia, Canada (49°8′0″N, 122°18′0″W; Figure 1). Our study area is bounded by the Fraser River to the north, the U.S. border to the south, Georgia Strait to the west, and the municipality of Langley to the east. Agricultural land in the Fraser Valley was traditionally used for pasture and hay production. Over the past 50 yr, first vegetable production and then berry production have increased (Elliott et al. 2011). These changes have resulted in a net loss of grasslands (Hindmarch et al. 2012).

Monitoring of Breeding

Breeding pairs were located by surveying all known sites documented as being occupied by Barn Owls in the 1990s (Andrusiak 1994), all old wooden barns or other tall structures with suitable openings near the roof and single, and old standing trees on farm properties. Pairs were monitored in 2007 and 2008 from early March until the end of August, when the majority of breeding occurs in British Columbia (Campbell et al. 1990). We obtained data on the breeding success of pairs occupying 40 nest sites (2007, $n = 29$; 2008, $n = 34$);

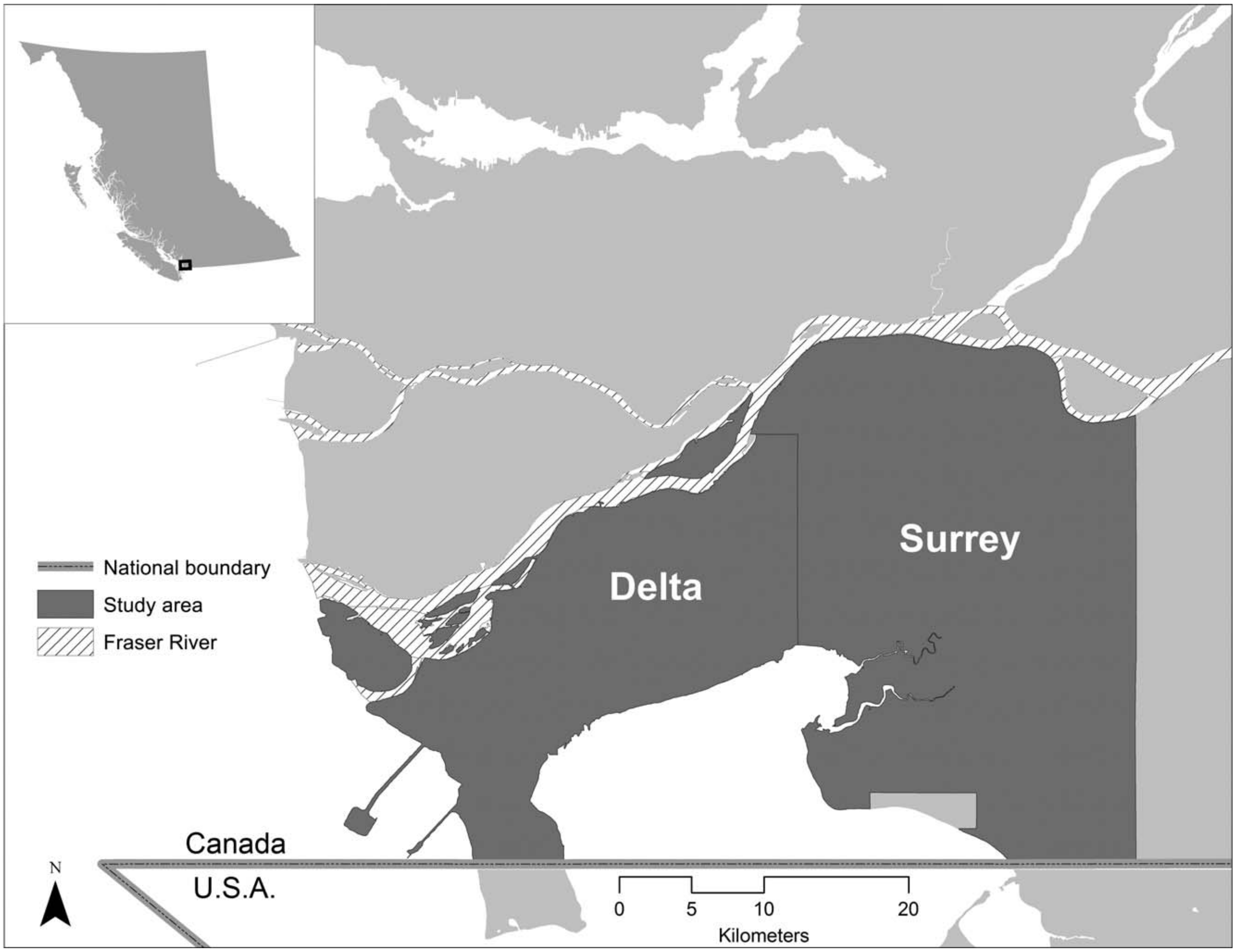

FIGURE 1. Map showing the study area in the Fraser Valley, British Columbia, Canada. Dark shading indicates the study area in the municipalities of Delta and Surrey located south of the city of Vancouver.

23 nest sites were monitored in both years. No pairs raised >1 brood at a nest site during the 6-mo observation period.

Sites were visited every month at the start of the season, every 10–15 days after clutches were initiated, and every 6–10 days from hatching until chicks were 45–55 days old. To minimize disturbance, we visited at night until the females no longer roosted with the chicks. Visits ceased when the oldest chick in the brood was ~55 days, so that chicks would not fledge prematurely (Smith et al. 1974, Bunn et al. 1982). Where the condition of the building allowed, nests were accessed during each visit and any chicks present were weighed. Prior to banding, chicks within each brood were identified by marking them on the back of their heads with nontoxic colored paint. A blood sample (100 μL) was collected by puncturing the brachial vein when chicks were ~35 days old. Where possible, we recorded clutch size, brood size at hatch, and brood size at fledging.

Estimating Sex-specific Nestling Condition

When first measured, nestlings were aged on the basis of their mass in one of two ways. If nestlings weighed ≤20 g, they were considered to have hatched within the past 24 hr (Howell 1964, Rich and Carr 1999). Nestlings that weighed >20 g were aged using the predicted age–mass relationship for chicks. We determined this relationship using a logistic growth curve estimated from 11 nestlings monitored from hatching (for details, see Hindmarch 2010).

The growth of Barn Owl chicks can be approximated using a logistic growth curve, which reaches an asymptotic mass at ~40 days (Ricklefs 1968, Taylor 1994, Durant and Handrich 1998). To estimate chick size and quality at fledging, we estimated the asymptotic (maximum) mass for each chick that survived to fledging and was measured ≥4 times over the nestling period (mean = 6), by fitting a logistic growth curve.

We determined the sex of 23 nestlings using a molecular technique based on polymerase chain reaction. Molecular

TABLE 1. Definition of landscape variables assessed within the estimated home range (1-km radius from the nest) of Barn Owls in the Fraser Valley, British Columbia, Canada.

Landscape term	Code	Variable definition
Grassland cover	Grass	High-quality grass cover (km^2) = area in old fields (>4 yr since mowed), young fields (>2 yr since mowed), and native grassland Other grass cover (km^2) = area in hay fields, pastures, grass verges along roads and between fields
Grassland composition	Patches	Patch number = number of continuous patches of grass >0.1 ha Distance to patches = average distance from nest to grass patch
Urban cover	Urban	Impermeable surface cover = residential, industrial, greenhouses, and commercial land (km^2)
Highways	Highway	Highways = length of highways and connecting ramps (km)

sexing was conducted using the primers P2 and P8, which bind to the Z and W chromosomes (Griffiths et al. 1998). Female nestlings had a higher asymptotic mass than males (females: mean = 539.3 g, 95% confidence interval [CI]: 503.7–575.0 g, $n = 12$; males: mean = 474.8 g, 95% CI: 443.0–506.7 g, $n = 11$). The remaining nestlings ($n = 106$) were assigned a sex on the basis of this variation in asymptotic mass. One chick had an asymptotic mass that fell between 503.7 and 506.7 g; it was sexed on the basis of its relative size within the brood.

We calculated a standardized mass score for each chick using the deviation from the mean sex-specific asymptotic mass during the nestling period divided by the sex-specific standard deviation. The mean score for all the chicks within each brood was then used to determine the condition of a brood.

Assessing Diet Composition of Females and Their Broods

We collected regurgitated pellets from nest sites visited every 6–10 days during the late incubation and nestling periods (March–August, 2007–2008). Prey items in each pellet were identified using bone remnants, and the number of individuals of each prey type was determined by pairing each skull with the correct numbers of ischia, left and right mandibles, and tibiae–fibulae; or, in the case of birds, of each skull with sternum, gizzard sac, and feet. The remaining bones contained within the pellet were assembled to determine the minimum number of additional individuals whose skulls may have been crushed. We used the proportion of prey biomass consisting of voles as an index of diet composition (Otteni et al. 1972, Meek et al. 2009) for each breeding attempt where we had collected $\geq$16 pellets during $\geq$4 visits to the nest site (2007, $n = 18$, 2008, $n = 21$). Information on body mass for the different species of prey was obtained from British Columbia field guides on rodents, lagomorphs, and birds (Nagorsen 1996, Sibley 2003, Nagorsen 2005).

Land-use Characteristics and Spatial Analysis

We created digitized data layers of current land use in Delta and Surrey using information from several sources. Data on housing and commercial and industrial land use were obtained from a 2006 Vancouver Regional District land-use layer map for the entire study area. This map characterizes all land-use polygons to a minimum land area of 0.2 ha (Metro Vancouver 2008). Data on grassland and crop cover in Delta were obtained from an individual field layer from 2007 that contained information on crop types (Ducks Unlimited personal communication). A similar data layer was not available for Surrey, so we created a data layer by visually inspecting individual fields for land use or crop type and digitizing these data ($n =$ 1,747 fields). Finally, data on highways, connecting ramps, and roads within the study area were obtained from a 2007 British Columbia road layer map.

We queried these data layers using ArcGIS version 9.2 (ESRI, Redlands, California, USA) to quantify 7 features of the agricultural landscape within a 1-km radius of each nest site. We used a 1-km radius around each site because this results in an area that approximates the home range of a Barn Owl (3 km^2; Taylor 1994, Shawyer and Shawyer 1995). The 7 features were (1) area of high-quality grass, (2) area of other grass, (3) number of grass patches (where a "patch" is any area of grass >0.1 ha), (4) average distance to these grass patches, (5) area of urban cover, (6) length of highways, and (7) length of secondary roads (for definitions and additional description of variables, see Table 1 and Hindmarch 2010). The length of secondary roads within a 1-km radius of a nest site was strongly correlated with the length of highways ($r_p = 0.59$) and the area of urban cover ($r_p = 0.73$), so this variable was excluded from analyses. We subsequently grouped variables related to grassland cover and fragmentation into 2 composite terms (see Table 1) that were entered or excluded from models together in order to minimize the number of models in the candidate model sets (see below).

Statistical Analyses

We calculated standardized estimates of fledging success (total number of young fledged per nesting attempt), brood condition, clutch size, brood reduction (proportion of hatched young that failed to fledge), and diet composition (proportion of prey biomass consisting of

TABLE 2. Summary of composition of foraging habitat within a 1-km radius of Barn Owl nest sites in the Fraser Valley, British Columbia, Canada ($n = 40$ sites). For a comparison of land use at occupied and unoccupied sites, see Hindmarch et al. 2012.

Land-use variable	Mean ± SD	Minimum	Maximum
High-quality grassland (ha)	11 ± 15	0	55
Other grassland (ha)	35 ± 34	3	147
All grassland (ha)	46 ± 36	6	148
Number of grassland patches	5.3 ± 2.8	1	13
Average distance to patches (m)	523 ± 105	252	708
Length of highway (km)	0.95 ± 1.58	0	6.88
Length of other roads (km)	5.61 ± 3.31	1.19	14.73
Urban cover (ha)	27 ± 33	0	121

voles) for each year by subtracting the mean and dividing by the standard deviation for each year to remove interannual variation. For nests monitored in both years, we then used averages of these standardized estimates in subsequent analyses.

We analyzed the data in 3 steps because we had a larger sample of nests with associated landscape data ($n = 40$ nest sites) than of nests with diet composition data ($n = 28$ nest sites). First, we used the larger dataset to examine the relationship between each of our landscape terms (grassland cover, grassland composition, urban cover, and highways) and 4 dependent variables (fledging success, brood condition, clutch size, and brood reduction). We did not include brood size as a variable in models exploring variation in brood condition because there was no relationship between brood size and brood condition (Hindmarch 2010). Second, we used the smaller dataset to examine the relationship between each of our landscape terms and diet composition at nests. Finally, we examined whether variation in fledging success, clutch size, brood condition, and brood reduction were best described by models that included only a landscape term, only a diet composition term, or both a landscape term and a diet composition term. Collinearity was generally low among landscape variables (Pearson's correlation coefficients <0.50). The strongest correlation was between urban cover and highways ($r_p = 0.47$).

Candidate model sets examining landscape effects on fledging success, brood condition, clutch size, brood reduction, and diet composition included a model representing each a priori hypothesis (see Table 1) and a null model (intercept only; $n = 5$ models). Candidate model sets assessing the relative importance of landscape effects and diet composition in explaining variation in fledging success, brood condition, clutch size, and brood reduction included a null model, the best landscape model (if it had more support than the null model in our first candidate model set), a model with only a diet composition term, and, where there was evidence of landscape effects, a model with both a landscape term and a diet composition term (maximum $n = 4$ models).

We used an information-theoretic approach to rank and identify the best-supported models within each model set (Burnham and Anderson 2002). We calculated Akaike's Information Criterion adjusted for small sample sizes (AIC_c) and AIC_c weights (w_i) for each model. Models with AIC_c scores within 2 of the best model and with high w_i values were considered to have strong support (Burnham and Anderson 2002). We calculated the weighted averages of parameter estimates, their unconditional standard errors, and 95% CIs using all models in the 95% confidence set (Burnham and Anderson 2002, Mazerolle 2013). Unconditional standard errors account for model uncertainty when averaging across models. We used the Akaike model weights and the weighted parameter estimates, standard errors, and confidence intervals to draw inferences about the ecological importance of the variables (Arnold 2010). Analyses were conducted in R version 3.0.2 (R Core Team 2013) using the AICcmodavg package (Mazerolle 2013). We report all values as means ± SD.

RESULTS

Landscape Composition Surrounding Barn Owl Nest Sites

Grassland habitat made up, on average, 15% of the area within a 1-km radius of Barn Owl nest sites (high-quality grassland: 4%; other grasslands: 11%). Urban cover made up an additional 9%. The remaining habitat included grain (wheat, barley, and rye), berries (blueberries and cranberries), vegetables (corn, potatoes, beans, and leafy vegetables), nursery crops, and shrub habitat. There was considerable variation in the amount of grassland habitat, urban cover, and length of highways and secondary roads within 1 km of the nest sites used by Barn Owls (Table 2).

Does Landscape Composition Influence Fledging Success, Brood Condition, Clutch Size, or Brood Reduction?

The fledging success of Barn Owls at the 40 monitored nest sites was 2.7 ± 1.0 fledged young per nesting attempt (range: 0–5). Fledging success was higher in 2007 (3.3 ± 1.1, $n = 23$) than in 2008 (2.3 ± 1.0, $n = 23$; paired t-test, $t_{22} = 3.39$, $P = 0.03$).

Standardized fledging success declined as the amount of urban cover increased (Figure 2). The model including the urban cover term received 6.8× the support of the null model, and the weighted parameter estimate for the urban cover term had 95% CIs that did not bound zero (Tables 3 and 4). All other landscape models received less support than the null (intercept only) model, and the weighted parameter estimates for the remaining landscape terms

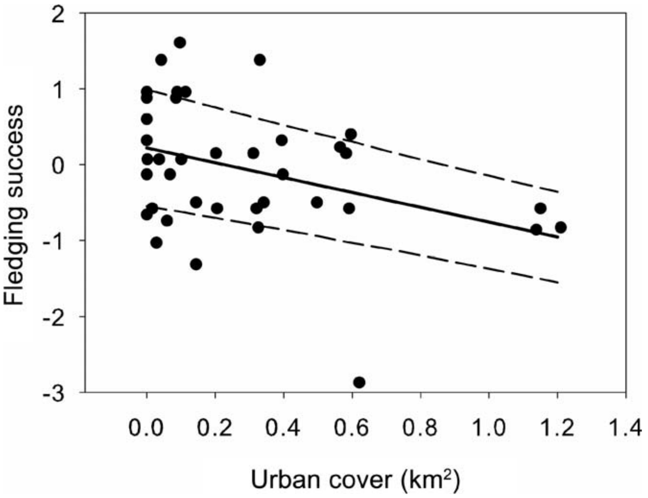

FIGURE 2. Relationship between urban cover (km^2) within a 1-km radius of a nest site and average fledging success of Barn Owls in the Fraser Valley, British Columbia, Canada (1.2 km^2 of urban cover represents 38% of the area within a 1-km radius of the nest). Fledging success (total number of young fledged per nest attempt) was standardized by subtracting the mean and dividing by the standard deviation for any given year. Solid and dashed lines show the predicted relationship (± 95% CI) from the best-supported model in the candidate model set (fledging success = 0.22 [0.17 SE] – 0.98 [0.39 SE] * urban cover).

TABLE 3. Summary of AIC$_c$ statistics for models examining the relationship between landscape composition and standardized measures of (A) fledging success (total number of fledged young per nest attempt), (B) brood condition, (C) clutch size, (D) brood reduction (proportion of hatched young that failed to fledge), and (E) diet composition (proportion of prey biomass consisting of voles) of Barn Owls breeding in the Fraser Valley, British Columbia, Canada. For definitions and abbreviations of variables, see text and Table 1. The results for all strongly supported models (ΔAIC$_c$ < 2.0) and the null model are presented (K = number of parameters estimated, n = sample size, ΔAIC$_c$ = differences between the AIC$_c$ of each model and the model with the highest AIC$_c$ score, and w_i = AIC$_c$ weight for that model).

Model	K	n	AIC$_c$	ΔAIC$_c$	w_i
(A)					
Fledging success = urban	3	40	100.48	0.00	0.68
Fledging success = intercept only	2	40	104.23	3.75	0.10
(B)					
Brood condition = intercept only	2	31	80.39	0.00	0.45
Brood condition = highway	3	31	81.13	0.74	0.31
(C)					
Clutch size = intercept only	2	25	73.63	0.00	0.50
(D)					
Brood reduction = urban	3	25	65.61	0.00	0.98
Brood reduction = intercept only	2	25	75.86	10.24	0.01
(E)					
Diet composition = intercept only	2	27	74.87	0.00	0.46
Diet composition = urban	3	27	76.06	1.18	0.25
Diet composition = highway	3	27	76.50	1.63	0.20

had confidence intervals that bounded zero (Tables 3 and 4).

Brood condition (mean standardized asymptotic mass) was unrelated to the landscape composition surrounding a Barn Owl nest. The null model in this candidate model set received 1.5× the support of the best landscape model that included the highways term (Table 3). Weighted parameter estimates of the landscape terms all bounded zero (Table 4).

Barn Owl clutches contained 2–8 eggs (5.4 ± 1.6, $n = 37$). Clutch sizes at nests monitored in both years were similar in 2007 (5.5 ± 1.6) and 2008 (4.6 ± 1.4, paired t-test, $t_{10} = 1.02$, $P = 0.33$). Standardized clutch size did not vary with landscape composition. The null model was the best model in the candidate model set; no models with landscape variables received strong support (Table 3). Weighted parameter estimates of the landscape terms all bounded zero (Table 4).

Brood reduction was common and, on average, 41 ± 25% of hatched young failed to fledge (n = 28 broods). Levels of brood reduction did not vary between years at nest sites monitored in both 2007 and 2008 (paired t-test, $t_{12} = 0.06$, $P = 0.95$). Standardized levels of brood reduction increased as the amount of urban cover increased (Figure 3). The model including the urban cover term received more than 90× the support of the null model. The weighted parameter estimate for the urban cover term (2.04 ± 0.52) had 95% CIs that did not bound zero (Tables 3 and 4). The remaining models all received less support than the null model, and weighted parameter estimates for the remaining landscape terms all bounded zero (Tables 3 and 4).

Barn Owl Diet and Landscape Composition

Barn Owls ate a variety of prey; a total of 17 different species were found in the 1,524 pellets collected during the study. Voles, primarily field voles (*Microtus townsendii*) but also creeping voles (*M. oregoni*), were the main prey; the proportion of prey biomass consisting of voles was 0.70 ± 0.16 (range: 0.41–0.92, $n = 40$). The proportion of voles in the diet was correlated between years ($r_p = 0.58$, $P < 0.05$, $n = 12$) but was higher in 2007 (0.77 ± 0.14) than in 2008 (0.64 ± 0.19; paired t-test, $t_{11} = 4.04$, $P < 0.001$). Additional prey species found in pellets included rats (*Rattus rattus* and *R. norvegicus*), mice (*Peromyscus maniculatus* and *Zapus trinotatus*), shrews (*Sorex cinereus*, *S. monticolus*, and *S. vagrans*), moles (*Scapanus orarius* and *Neurotrichus gibbsii*), rabbits (*Sylvilagus floridanus*), and several bird species (including *Sturnus vulgaris*, *Colaptes auratus*, *Columba livia*, and *Calidris mauri*).

There was limited evidence that the landscape composition surrounding a nest site influenced diet composition during the breeding season. The null model received almost twice the support of the next best model, which included the urban cover term. None of the other

TABLE 4. Weighted parameter estimates, unconditional standard errors, and 95% confidence intervals (CI) for all variables included in models examining the relationship between landscape composition and standardized measures of (A) fledging success, (B) brood condition, (C) clutch size, (D) brood reduction, and (E) diet composition of Barn Owls breeding in the Fraser Valley, British Columbia, Canada. For definitions and abbreviations of variables, see text and Table 1.

Response variable	Land-use variable	Weighted parameter estimate	95% CI
(A) Fledging success	High-quality grass cover	1.43 ± 0.90	−0.33 to 3.19
	Other grass cover	0.46 ± 0.39	−0.30 to 1.23
	Distance to grass patch	0.0 ± 0.0	0 to 0
	Patches	0.0 ± 0.05	−0.10 to 0.10
	Urban cover	**−0.95 ± 0.39**	**−1.75 to −0.21**
	Length of highway	−0.13 ± 0.07	−0.27 to 0.02
(B) Brood condition	High-quality grass cover	−0.50 ± 1.0	−2.46 to 1.47
	Other grass cover	−0.12 ± 0.42	−0.96 to 0.71
	Distance to grass patch	0.0 ± 0.0	0 to 0
	Patches	−0.02 ± 0.05	−0.12 to 0.09
	Urban cover	0.11 ± 0.49	−0.85 to 1.07
	Length of highway	0.12 ± 0.10	−0.06 to 0.31
(C) Clutch size	High-quality grass cover	1.28 ± 1.34	−1.34 to 3.90
	Other grass cover	0.22 ± 0.51	−0.78 to 1.23
	Distance to grass patch	0.0 ± 0.0	−0.01 to 0
	Patches	0.09 ± 0.06	−0.03 to 0.06
	Urban cover	−0.39 ± 0.55	−1.47 to 0.7
	Length of highway	−0.03 ± 0.10	−0.22 to 0.21
(D) Brood reduction	High-quality grass cover	−1.85 ± 1.28	−4.35 to 0.66
	Other grass cover	−0.22 ± 0.51	−1.19 to 0.75
	Distance to grass patch	0.0 ± 0.0	−0.01 to 0
	Patches	0.0 ± 0.06	−0.12 to 0.12
	Urban cover	**2.04 ± 0.52**	**1.01 to 3.06**
	Length of highway	0.17 ± 0.08	−0.01 to 0.33
(E) Diet composition	High-quality grass cover	0.61 ± 1.40	−2.15 to 3.36
	Other grass cover	0.24 ± 0.52	−0.78 to 0.1.25
	Distance to grass patch	0.0 ± 0.0	0 to 0
	Patches	−0.03 ± 0.06	−0.15 to 0.09
	Urban cover	−0.61 ± 0.54	−1.66 to 0.44
	Length of highway	−0.10 ± 0.11	−0.31 to 0.11

landscape models received strong support (Table 3). Weighted parameter estimates of all the landscape terms also had confidence intervals that bounded zero (Table 4).

Does Diet Composition Influence Fledging Success, Brood Condition, Clutch Size, or Brood Reduction?

There was little evidence to indicate that landscape effects on fledging success and brood reduction were due to differences in diet composition. In the candidate model sets examining variation in fledging success and brood reduction, models that included the diet composition term had less support than the null models. By contrast, the best landscape models (the urban cover models) had 2.7 and 81 times more support than the null models (confirming the results of the previous analysis), and 3.4 and 4.5 times the support of models that also included the diet composition terms (Table 5). There was also little evidence that diet composition influenced clutch size and brood condition. In candidate model sets examining variation in clutch size and brood condition, the null models received 4 times and 3 times the support of models with the diet composition term (Table 5).

DISCUSSION

Barn Owls, as a top predator in grassland habitats, are predicted to be indicators of changes in ecosystem quality (Fajardo 2001, Askew et al. 2007). Agricultural intensification and urbanization in the Fraser Valley of British Columbia, as in many parts of the world, has led to the loss and fragmentation of pasture and other grassland habitats, presumably reducing the ability of the landscape to support species like Barn Owls. Nevertheless, we did not find a link between the fledging success of Barn Owls and the amount of grassland habitats within their home range. The amount of urbanization was the key landscape predictor of Barn Owl fledging success and the level of brood reduction. In the mixed landscape of the Fraser Valley, the level of urbanization appears to be a better predictor of the health of local Barn Owl

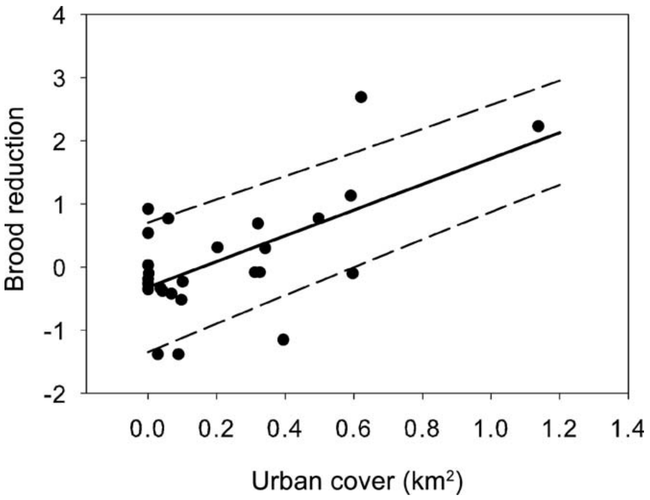

FIGURE 3. Relationship between urban cover (km^2) within a 1-km radius of a nest site and average standardized level of brood reduction in Barn Owls in the Fraser Valley, British Columbia, Canada. Brood reduction (the proportion of hatched young that failed to fledge) was standardized by subtracting the mean and dividing by the standard deviation for the year. Solid and dashed lines show the predicted relationship (± 95% CI) from the best-supported model in the candidate model set (brood reduction = –0.32 [0.18 SE] + 2.04 [0.52 SE] * urban cover).

TABLE 5. Summary of AIC$_c$ statistics for models examining diet-composition and landscape-composition effects on standardized measures of (A) fledging success, (B) brood condition, (C) clutch size, and (D) brood reduction of Barn Owls breeding in the Fraser Valley, British Columbia, Canada. Candidate model sets include only landscape models in which there is evidence of landscape effects (see Table 3). We present the results for all models in each candidate set. Variable definitions and abbreviations are provided in Tables 1, 2, and 3.

Model	K	n	AIC$_c$	ΔAIC$_c$	w_i
(A)					
Fledging success = urban	3	27	56.45	0.00	0.53
Fledging success = intercept only	2	27	58.35	1.90	0.20
Fledging success = urban + diet	4	27	58.75	2.30	0.17
Fledging success = diet composition	3	27	59.75	3.30	0.10
(B)					
Brood condition = intercept only	2	26	70.55	0.00	0.75
Brood condition = diet composition	3	26	72.74	2.20	0.25
(C)					
Clutch size = intercept only	2	20	58.03	0.00	0.80
Clutch size = diet composition	3	20	60.77	2.74	0.20
(D)					
Brood reduction = urban	3	21	46.66	0.00	0.81
Brood reduction = urban + diet	4	21	49.63	2.98	0.18
Brood reduction = intercept only	2	21	56.24	9.59	0.01
Brood reduction = diet composition	3	21	58.93	12.27	0.00

populations than the area of grassland that provides foraging habitat.

Barn Owls could be negatively affected by the amount of residential, commercial, and industrial land within their home range because urbanization reduces the quality or quantity of prey in surrounding foraging habitat. Diet composition, specifically the proportion of prey biomass consisting of voles, has been argued to be an indicator of diet quality for Barn Owls (Fast and Ambrose 1976, Derting and Cranford 1989, Taylor 1994). In the Fraser Valley, we found that Barn Owl fledging success and levels of brood reduction were negatively affected by the amount of urban cover within their home range, but that individuals breeding in areas with more urban cover did not have a lower proportion of voles in their diet. Barn Owls delivered a diet averaging 70% voles to their young, regardless of the amount of urbanization within their home range. However, fledging success was reduced at sites with more urban cover because these sites had higher levels of brood reduction. Brood reduction in birds is frequently influenced by food availability (Boland et al. 1997, Valkama et al. 2002). Given that urban cover reduced fledging success by increasing the levels of brood reduction at a nest site but did not influence diet composition, our data suggest that urbanized landscapes affect the availability of prey.

Urbanization also increases the exposure of wildlife to a range of contaminants. For example, rodenticides are widely used to suppress invasive rodent species; and the second-generation rodenticides, in particular, have been shown to result in secondary poisoning of nontarget species, including owls in the Fraser Valley and elsewhere (Albert et al. 2010, Christensen et al. 2012, Sanchez-Barbudo et al. 2012). Therefore, the higher risk of secondary exposure to rodenticides could increase adult or chick mortality in Barn Owls. Although we have not measured rodenticide exposure in these Barn Owls directly, 2 lines of evidence suggest that this is unlikely to have significantly reduced chick survival and, therefore, fledging success in our study. First, rodenticides are applied in locations that target rats (*Rattus* spp.) and house mice (*Mus musculus*) (Elliott et al. 2014), neither of which formed a large part of the Barn Owls' diet (Pimentel et al. 2000, Hindmarch 2010). Second, mortality within broods was nonrandom and was correlated with size and hatching order, which suggests that food availability, rather than rodenticide exposure, reduced fledging success (Hindmarch 2010). Nevertheless, exposure to rodenticides and other pest-control products are likely to continue to increase in the Fraser Valley, and the cumulative impacts on Barn Owls and other raptors need further examination (Elliott et al. 2011).

Urbanization is associated with increases in subsidized predators, particularly cats (*Felis catus*) and Norway rats (*Rattus norvegicus*). Urban-associated predators are likely to alter the composition of the rodent community in areas adjacent to urban developments. Bock et al. (2002), for example, demonstrated that the abundance of native rodents was reduced in grasslands where suburban habitat made up >10% of the landscape. However, we found that urbanization did not influence the proportion of voles in the diet, which suggests that owls are able to compensate and maintain their preference for voles even within a heterogeneous landscape (Fast and Ambrose 1976). Alternatively, any effects of urbanization on the prey community may be masked by the inability of Barn Owls to catch alternative prey, such as adult rats that are abundant in urban areas (Taylor 1994). This seems unlikely in our study, because Barn Owls captured a wide diversity of prey, including rats, but nevertheless primarily consumed voles.

A secondary consequence of urbanization is increased exposure to traffic. Barn Owls are particularly vulnerable to traffic mortality because they frequently hunt in open areas near roads or highways (Ramsden 2003, Preston and Powers 2006, Boves and Belthoff 2012). We predicted that increased exposure to roads would be associated with reduced fledging success of Barn Owls if this led to higher rates of parental mortality. However, similar to the results of Martin et al. (2010), we found no relationship between fledging success and the length of highways within the home range of breeding owls. Although mortality of breeding adults may be relatively rare, the death of 1 parent may have caused the remaining parent to abandon their brood on 2 occasions in our study. Barn Owls breeding at sites with increased exposure to highways also initiated clutches later than birds at less exposed sites (Hindmarch 2010). Because sites with increased traffic exposure are less likely to be occupied and experience higher turnover (Frey et al. 2011, Hindmarch et al. 2012), those sites may be occupied by younger breeding owls that generally initiate clutches later than older, more experienced birds (Frey et al. 2011).

The amount, quality, and location of grassland habitat should directly increase the abundance and availability of small mammals and should be correlated with the breeding success of Barn Owls. For example, Shawyer and Shawyer (1995) calculated that Barn Owls require ≥40 ha of high-quality grassland to breed successfully in southern England. In the Fraser Valley, Barn Owls bred at nest sites surrounded by substantially less grassland foraging habitat; 53% of nest sites had <40 ha of grassland within 1 km. In addition, the number of, or distance to, grassland patches within an owl's home range did not influence diet composition or the fledging success of Barn Owls. Our results are consistent with other studies that found that grassland cover does not strongly influence Barn Owl fledging success (e.g., Meek et al. 2009, Frey et al. 2011).

Landscape variables may not correlate with the breeding success of some bird species because they do not capture important features of the foraging habitat. If diet composition or prey abundance is strongly linked to an easily quantified habitat type (e.g., grasslands), the fledging success of Barn Owls should be correlated with the availability of grasslands. However, if prey abundance or availability is linked to microhabitat variation, broader habitat categories may not correlate with breeding success. Studies using broad or composite categories of habitat often do not observe the predicted correlations with breeding. For example, Frey et al. (2011) and Bond et al. (2005) found no association between the fledging success of Barn Owls and habitat composition within home ranges. Similarly, the fledging success of Barn Owls in urban and rural territories in Italy did not differ, although occupied sites contained less urban development and more open areas than random sites (Salvati et al. 2002). Regardless, all these studies emphasized the importance of open habitats for foraging Barn Owls, which suggests that (1) studies to assess landscape-level effects on breeding success need to be carefully compared and (2) landscape-level effects should be evaluated at coarse and fine spatial scales.

If landscape composition alters the availability of prey, owls breeding in areas with less grassland or increased urban cover may produce broods in poorer condition. However, we found no evidence that any of the landscape variables we measured influenced the condition of Barn Owl broods. Food availability may have little impact on brood condition because large competitive asymmetries within Barn Owl broods facilitate brood reduction when food is limited (Andrusiak 1994, Taylor 1994, Roulin et al. 1999). Consistent with this hypothesis, Barn Owls in our study had high hatching success (85%; Hindmarch 2010), but brood reduction of later-hatched nestlings occurred in 90% of successful broods. The level of brood reduction increased as the area of urban cover increased within a home range, which suggests that broods in more urbanized areas are more food limited than broods in areas with less urban development. The matching of brood size to food availability experienced by parents may therefore allow the condition of Barn Owl chicks to be maintained even when territories vary in quality (Lack 1947, Roulin et al. 1999).

Multiple landscape features may influence the distribution and demography of Barn Owls. Our results suggest that changes associated with urbanization, rather than the amount of high-quality foraging habitat within the agricultural landscape, reduces Barn Owl breeding success, possibly because urbanization reduces prey abundance and accessibility. Further work is needed to understand how landscape features influence the foraging behavior of Barn Owls, in order to assess how urban development will affect populations. However, if artificial nest boxes are used as a strategy to counteract the loss of suitable nesting habitat for Barn Owls in mixed agricultural habitats, nest boxes should be located in areas with less urban development and away from major roads.

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