

# Associations of bobolink territory size with habitat quality

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Territory size generally varies with habitat quality, including vegetation structure, food abundance and available space. Bobolink (*Dolichonyx oryzivorus*), a semi-colonial species, is known to respond to these habitat quality factors individually, though no previous study has examined these factors simultaneously in relation to territory size. We examined the relationship between bobolink territory size and vegetation structure, prey abundance and patch size in hayfields of southern Ontario, Canada. All three factors were influential in explaining variation in territory size. Important prey items were more abundant in small territories. These small territories also had taller and denser vegetation, deeper litter, and less bare soil. Territory size was related to patch size, with smaller territories on smaller fields. We compared our results with other studies that have found links between territory size and individual variables, including factors not in our models.

## Introduction

Associations between animal distributions and available habitat have been studied for many species in terms of landscape features, macro- and micro-habitat characteristics, prey availability and inter- and intraspecific interactions. These factors are also known to influence breeding territory size and placement within available habitat. Bobolink (*Dolichonyx oryzivorus*) is an example of a species for which many of these associations have been studied singularly. Bobolinks are neotropical migratory grassland birds that breed predominantly in agricultural grasslands in North America, for which several characteristics of preferred habitat have been inferred from settlement patterns. Attempts to

better understand the requirements of this species have been made to inform conservation efforts, as bobolinks have experienced significant, widespread population declines along with many other grassland breeding birds in North America (Sauer *et al.* 2011).

Bobolink density generally increases with field or patch size (Herkert 1994, Johnson & Igl 2001, Renfrew & Ribic 2008), and is also influenced by the edge type enclosing the habitat, such as reduced density near woodland edges (Fletcher & Koford 2003, Bollinger & Gavin 2004), as well as the features and openness of the surrounding landscape, with more open landscapes related to greater abundance (Renfrew & Ribic 2002, Horn & Koford 2006, Shustack *et al.* 2010, Keyel *et al.* 2013). Vegetation structure and

composition also relate to bobolink density; they generally prefer grassland habitat with greater vegetation height and density when they arrive on the breeding grounds (Nocera *et al.* 2007), a greater grass to alfalfa (*Medicago sativa*) ratio (Bollinger 1988), moderate litter depth (Wiens 1969, Herkert 1994), a low proportion of bare soil (Schneider 1998, Warren & Anderson 2005) and greater coverage of forbaceous plants used by males for song perches and building nests beneath (Schneider 1998, Frei 2009), all of which are characteristics more common to older hayfields seeded several years prior to settlement by bobolinks. On the breeding grounds, adult bobolink diet consists mainly of invertebrates and some plant matter (Beal 1900, Martin & Gavin 1995) and breeding season invertebrate abundance may be associated with greater bobolink abundance and reproductive activity (Nocera *et al.* 2007). Invertebrate orders most consumed by adult bobolinks are Coleoptera, Lepidoptera, Hymenoptera and Orthoptera (Beal 1900, Martin & Gavin 1995), while bobolink young are fed Lepidopteran and Hymenopteran larvae almost exclusively, as well as occasional Orthoptera, Homoptera, Ephemeroptera, Aranea and adult Lepidoptera (Wittenberger 1980, Moskwik & O'Connell 2006, Little *et al.* 2009).

While many studies have explored how such features influence grassland bird distributions on the breeding grounds, information regarding territory size and usage by bobolink and other grassland birds remains scant (Ribic *et al.* 2009). Nocera *et al.* (2009) determined that distributions of bobolink territories followed that predicted by a "neighborhood model", where older males held smaller territories clustered in regions of higher quality habitat and younger males with less breeding experience aggregated around the periphery in larger, lower quality territories. Bobolink territory size has been suggested to vary with habitat quality (Wiens 1969, Martin 1971, Wittenberger 1980); however, this has yet to be examined with a broader and full suite of variables, considered indicative of quality, which may be involved in bobolink habitat selection and use.

We sought to identify links between vegetation characteristics, field characteristics, the abundance of prey items and bobolink territory size. We predicted that relatively smaller ter-

ritories would be of higher quality in terms of preferred hayfield vegetation and greater abundance of important prey items, compared to larger territories. We also expected that territory size would vary irrespective of field size if density dependent processes were the only factor to modify habitat use. We discuss how our multivariate approach compares with other studies that have found relationships between territory size and singular factors such as habitat variables, bobolink age, mating status, and conspecific attraction.

## Material and methods

### Study sites

Data were collected in May and June of 2012 from hayfields (composed primarily of cool-season grasses) prior to first harvest across six privately owned farms in Peterborough, Kawartha Lakes, and Hastings Counties in Ontario, Canada (centered on 44°18'N, 78°19'W). Hayfields varied in size (3.0–13.5 ha, mean = 6.0 ha,  $n = 6$ ), surrounding edge type, May vegetation height (which varies based on timing of final harvest in the previous year), and hay composition. Study fields were seeded from three to over 15 years prior to study.

### Territory mapping

Between late May and early June, we captured male and female bobolinks with mist-nets near male territories and marked them with a United States Fish and Wildlife band (issued by the Canadian Wildlife Service) on one leg and a unique combination of color bands on the other. We captured and handled all bobolinks according to procedures approved by the Trent University Animal Care Committee (protocol #12012). Not all male bobolinks occupying our study fields were caught and marked.

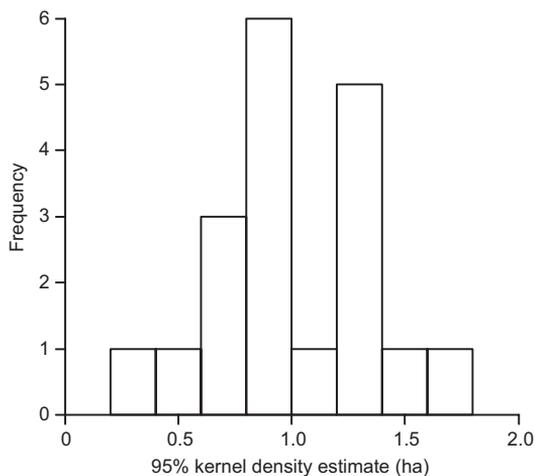
To determine the area of male territories, we used a flush-mapping technique designed for grassland birds (Wiens 1969), achieved by spotting and approaching marked birds to record

their location with a GPS unit (when positioning error was  $< \pm 5$  m), and following them to record subsequent locations as they flushed away to other spots in their presumed territory. We mapped the territories of marked males until the second or third week of June when dispersal from territories started following the fledging of young, or hay was harvested.

Territory size was determined using 95% kernel density estimation in R ver. 2.15.1 (R Development Core Team 2012) with the package *adehabitatHR* (Calenge 2006). We used  $h_{ref}$  as a smoothing parameter in our kernel density estimation over least-squares cross-validation methods, as it formed more realistic bobolink territory distributions and operated best with closely clustered points. Bobolink territory sizes showed a bimodal distribution with a natural break at 1 ha (Fig. 1). As such, and to facilitate multiple logistic regression, we classified territories  $< 1$  ha as small ( $n = 11$ ) and those  $> 1$  ha were classified as large ( $n = 8$ ).

### Data collection for predictive variables

We measured a total of 18 variables encompassing vegetation and field characteristics and abundance of invertebrates (Table 1). Vegetation variables were measured in mid-May, around the time of male bobolink territory establishment. From points approximately centered on  $\sim 0.4$  ha sub-plots of each field, we tossed a  $50 \times 50$  cm sampling frame (Daubenmire 1959), rotating the approximate cardinal direction of the toss for each point sampled. At these points we also used a Robel pole (Robel *et al.* 1970) to measure vegetation height and density by measuring visual obstruction in decimeters in each of the four cardinal directions and averaging the four measurements. Within the Daubenmire frame, we estimated percent cover of live vegetation, grass, alfalfa, forbaceous plants and bare soil; all proportional data were arcsine square-root transformed prior to analysis. We measured litter depth (in cm) in each of the four corners of the frame and averaged the measurements. The mean of each vegetation variable was calculated for each field. All vegetation sampling was done by one individual to reduce observer variability



**Fig. 1.** Frequency distribution of 95% kernel density estimates of male bobolink territory size ( $n = 19$ ) from a range of 10–31 (mean = 17) mapped points per individual. We classified territories  $< 1$  ha as small ( $n = 11$ ) and those  $> 1$  ha as large ( $n = 8$ ) about a natural break around  $\sim 1$  ha to facilitate multiple logistic regression.

(KMD). Field size was also included as a variable and we estimated this using Google Earth Pro (Google Inc., Mountain View, CA).

We collected sweep net samples of invertebrates weekly between 10:00 and 15:00 in dry vegetation when wind speed was  $< 20$  km  $h^{-1}$ , near points approximately centered on  $\sim 0.4$  ha sub-plots of each field. Each sample consisted of two transects along which we swept a net 25 times, emptying the net between transects and alternating transects along an east–west or north–south axis for subsequent samples. Sweeps consisted of  $\sim 180^\circ$  arcs through the upper-most layer of vegetation, stepping forward with each sweep. Samples were frozen until processing, when all invertebrates  $> 3$  mm were classified to order and counted. We calculated mean abundance of each order for each field from four consecutive weeks of samples from May to June, prior to hay harvesting. We included, as predictive variables, mean abundances of Hemiptera, Homoptera (excluding aphids even if  $> 3$  mm), Aranaea, Opiliones, Diptera, Coleoptera, Orthoptera, Lepidoptera, Hymenoptera and larvae of Lepidoptera and Hymenoptera (collectively termed ‘caterpillars’). For consistency, sweep netting and invertebrate classification were each performed by one individual.

**Table 1.** Mean (SD) of invertebrate sample abundances and vegetation structure variables for each of the six study fields (A–F).

Variable	A	B	C	D	E	F
Hemiptera	206.5 (159.10)	161.28 (92.79)	11.39 (11.49)	14.3 (10.12)	23.33 (22.87)	153.54 (103.49)
Homoptera	12.69 (18.17)	9.63 (15.41)	1.28 (1.78)	3.15 (3.61)	8.38 (10.06)	4.00 (4.68)
Lepidoptera	0 (0)	0.08 (0.27)	0.06 (0.24)	0.03 (0.16)	0.29 (0.55)	0.13 (0.34)
Larvae	57.91 (48.39)	17.75 (16.30)	34.33 (31.25)	25.7 (28.48)	13.00 (15.53)	4.17 (3.81)
Aranaea	1.16 (1.39)	1.33 (1.62)	1.06 (1.51)	0.50 (0.82)	2.04 (1.90)	1.25 (1.36)
Opiliones	0 (0)	0.03 (0.16)	0 (0)	0.05 (0.22)	0.04 (0.20)	0 (0)
Diptera	0.28 (0.58)	0.98 (1.00)	0.22 (0.55)	0.75 (1.53)	0.92 (1.25)	0.88 (1.03)
Hymenoptera	2.91 (3.53)	2.20 (3.10)	3.17 (3.50)	0.48 (0.75)	3.54 (3.69)	1.04 (1.30)
Coleoptera	2.56 (2.09)	5.55 (8.71)	2.00 (1.24)	0.80 (0.85)	2.92 (3.57)	1.42 (1.38)
Orthoptera	0.16 (0.37)	0.05 (0.22)	0.06 (0.24)	0.08 (0.27)	0.54 (0.78)	0.04 (0.20)
Live vegetation cover (%)	69.38 (0.14)	57.00 (0.15)	69.17 (0.14)	57.00 (0.15)		
Grass cover (%)	41.88 (0.10)	32.00 (0.11)	41.67 (0.17)	36.00 (0.20)		
Alfalfa cover (%)	24.38 (0.09)	7.75 (0.10)	13.33 (0.13)	12.00 (0.12)		
Forb cover (%)	2.19 (0.03)	0 (0)	0 (0)	1.00 (0.02)		
Soil cover (%)	2.19 (0.04)	3.75 (0.05)	5.42 (0.06)	9.50 (0.09)		
Vegetation height and density (dm)	2.58 (0.64)	1.49 (0.35)	2.13 (0.45)	1.34 (0.54)		
Litter depth (cm)	3.44 (1.09)	1.58 (0.96)	1.67 (0.85)	0.80 (0.47)		

## Statistical analysis

We did not measure vegetation variables from two study sites that we acquired in late May, as measurements would not have been comparable to those we made in mid-May during male territory establishment. Due to these unavailable data which created restrictions with degrees of freedom, multiple logistic regressions with the binary dependent variable for small (0) and large (1) territories were performed separately for the vegetation variables (from four fields) and invertebrate variables (from six fields). Each model also included the variable field size. All analyses were performed with R ver. 2.15.1 (R Development Core Team 2012). Due to multicollinearity within both sets of predictive variables, we performed a principal components analysis (PCA) for each set, and we retained all principal components (PC) explaining > 10% of total variance. We included a random effect of study field and developed two mixed-effects logistic regression models, modeling territory size (large or small) with the predicted principal components retained from the vegetation variables and field size, and the invertebrate variables and field size (function *glmer* in the package *lme4* in R; Bates *et al.* 2012). We used the Bayesian Information Criterion (BIC) to select the model(s) that best fit the data (using package ‘MuMIn’; Barton 2012) from all combinations of variables in the candidate sets (16 competing models with invertebrate variables and 8 with vegetation variables; Tables 2 and 3). We chose BIC as our model selection tool due to the large number of correlated predictive variables and the use of principal components, as well as a modest sample size, to reduce model complexity and focus on interpreting the main effects. Further, we considered the costs and benefits of the bias-variance tradeoff in choosing BIC over other available model selection criteria, and saw greater benefit in reducing variance given the large number of variables we assessed. Model accuracy was assessed with receiver operating characteristic (ROC) curves and area under curve (AUC) estimates (package *epicalc*; Chongsuvitwong 2012). An AUC estimate of 0.5 indicates the model offers no discrimination while 1.0 is perfect predictability (Hosmer & Lemeshow 2000). Although AUC has received some criti-

cism (e.g., Lobo *et al.* 2008), largely in the context of biogeography and species distributions, AUC is still a viable tool for measuring the performance of non-competing models (Elith & Graham 2009) as in this study.

## Results

A range of 10–31 points (mean = 17) were

mapped for each of 19 male bobolinks across six fields. Mean  $\pm$  SE bobolink territory size was 1.01 ha  $\pm$  0.08, and ranged from 0.38–1.67 ha. The number of points mapped per male did not correlate with territory size ( $r = -0.12$ ,  $t_{17} = -0.49$ ,  $p = 0.63$ ) indicating that territory size is unbiased by potential differences in our effort.

The first four principal components were retained from PCA of the predictive variables in the invertebrate data (explaining 39%, 28%,

**Table 2.** Top 10 of 16 candidate models for the logistic regression of small (0) and large (1) male bobolink territories with four principal components representing variation in the variables for field size and mean abundance of invertebrate orders (Hemiptera, Homoptera, Aranaea, Opiliones, Diptera, Coleoptera, Orthoptera, Lepidoptera, Hymenoptera and larvae of Lepidoptera and Hymenoptera). Model coefficients are given for these models representing the logistic link function in a linear combination of the parameters. Models are sorted and ranked in order of increasing  $\Delta$ BIC (Bayesian Information Criterion). Model weight is represented by  $w_i$  and  $K$  represents the number of model parameters.

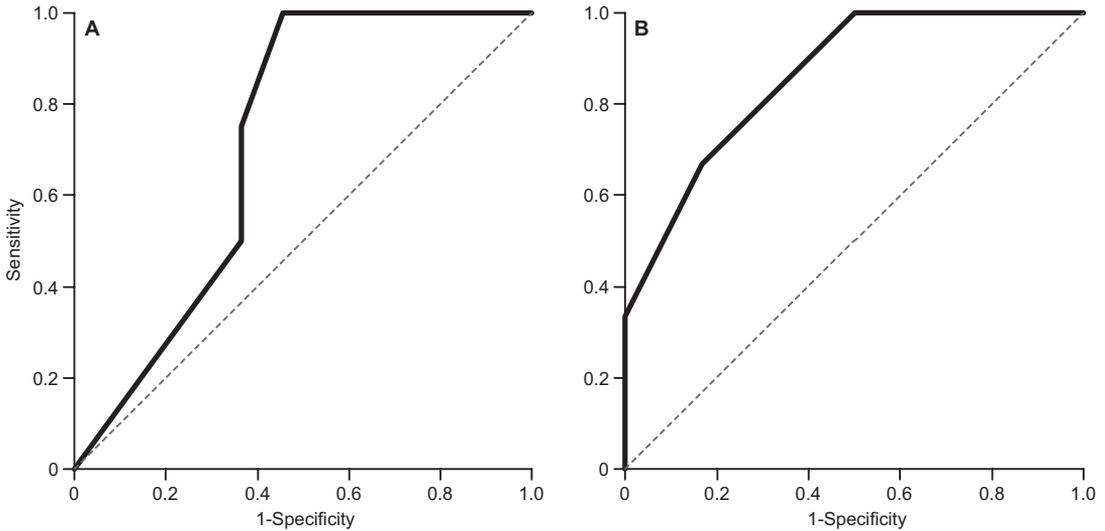
Rank	Parameter estimates						$\Delta$ BIC <sup>a</sup>	$w_i$
	Intercept	PC1	PC2	PC3	PC4	$K$		
1	-0.32					1	0.00	0.31
2	-0.34	-0.28				2	1.56	0.14
3	-0.33			-0.44		2	1.60	0.14
4	-0.32		-0.08			2	2.85	0.07
5	-0.32				-0.08	2	2.90	0.07
6	-0.41	-0.33		-0.50		3	2.94	0.07
7	-0.34	-0.28	-0.07			3	4.44	0.03
8	-0.34		-0.09	-0.44		3	4.45	0.03
9	-0.35	-0.28			-0.09	3	4.46	0.03
10	-0.33			-0.43	-0.08	3	4.51	0.03

<sup>a</sup> lowest value of BIC = 28.8.

**Table 3.** Eight candidate models for the logistic regression of small (0) and large (1) male bobolink territories with three principal components representing variation in the variables for field size and vegetation characteristics (percent cover of live vegetation, grass, alfalfa, forb, and bare soil, vegetation height and density, and litter depth). Model coefficients are given for these models representing the logistic link function in a linear combination of the parameters. Models are sorted and ranked in order of increasing  $\Delta$ BIC (Bayesian Information Criterion). Model weight is represented by  $w_i$  and  $K$  represents the number of model parameters.

Rank	Parameter estimates					$\Delta$ BIC <sup>a</sup>	$w_i$
	Intercept	PC1	PC2	PC3	$K$		
1	-2.89	4.86	7.28		3	0.00	0.37
2	0.05		0.94		2	1.67	0.16
3	-0.03	0.45			2	2.25	0.12
4	0.00				1	2.30	0.12
5	-1.46	4.12	6.93	1.23	4	2.48	0.11
6	0.05		0.93	-0.06	3	4.15	0.05
7	-0.05	0.46		-0.18	3	4.67	0.04
8	0.00			-0.12	2	4.75	0.04

<sup>a</sup> lowest value of BIC = 16.8.



**Fig. 2.** Receiver operating characteristic (ROC) curves depicting model accuracy and the area under the curve (AUC) for the averaged logistic regression models representing **(A)** the invertebrate prey model (AUC = 0.72, 95%CI = 0.47–0.96), and **(B)** the vegetation characteristics model (AUC = 0.86, 95%CI = 0.56–1), which describe the differences between small (0) and large (1) territories for a suite of variables.

15%, and 12% of variance respectively, 95% cumulatively), and the first three components were retained from the vegetation data (explaining 69%, 20%, and 11% of variance respectively, 100% cumulatively) to be included in the logistic regression models to predict territory size. Variance attributed to the study field random effect approached zero (indicating little effect) for both models and was removed.

There was no clear top model for either the invertebrate or vegetation model, so we used model averaging on models with  $\Delta\text{BIC} < 2$ . The distribution of small (0) and large (1) bobolink territories with principal components 1 and 3 extracted from the invertebrate model predictive variables was best described by the model-averaged logistic regression equation:

$$g(x) = -0.3285 - 0.0681(\text{PC1}) - 0.1026(\text{PC3})$$

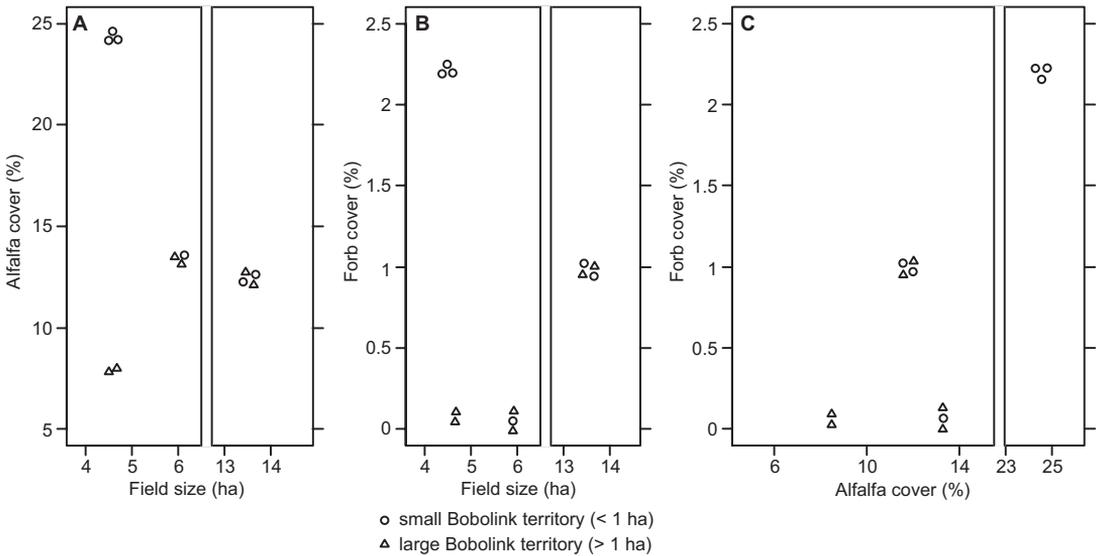
The area under the ROC curve estimate (AUC = 0.72, 95%CI = 0.47–0.96; Fig. 2A) indicates that model accuracy is adequate, as AUC estimates from 0.7 to 0.8 indicate reasonable accuracy (Hosmer & Lemeshow 2000). PCs 1 and 3 are equally weighted in the averaged model (Table 2). Several invertebrate Orders had moderate loadings on PC1 (Table 4) and the

positive eigenvector coefficients indicate these Orders were more abundant on small territories, particularly Araneae, Hymenoptera, Orthoptera, Lepidoptera and Coleoptera (arbitrarily those with eigenvector coefficients  $> 0.3$ , in descending order). Field size also loads moderately on PC1, indicating large territories were associated with larger field size. PC3 is of equal model importance, and moderate loadings with negative coefficients for Hemiptera and Diptera indicate that these items were more abundant in large territories, while Lepidoptera and Hymenoptera larvae, Hymenoptera and Orthoptera were more abundant in small territories.

The distribution of small (0) and large (1) territories with principal components 1 and 2 extracted from the vegetation model predictive variables was best described by the model-averaged logistic regression equation:

$$g(x) = -2.0041 + 3.3887(\text{PC1}) + 5.3598(\text{PC2})$$

The area under the ROC curve estimate (AUC = 0.86, 95%CI = 0.56–1; Fig. 2B) indicates the model has high accuracy (AUC  $> 0.8$ ) when discriminating between small and large territories with PCs 1 and 2. PC2 is weighted slightly greater than PC1 in the averaged model



**Fig. 3.** Jittered plots depicting the amount of (A) alfalfa cover (%) across field size (ha), (B) forb cover (%) across field size (ha), and (C) forb and alfalfa cover (%), on four hayfields with small (circle symbols) and large (triangle symbols) individual male bobolink territories, to illustrate the relationships of these three variables of interest in PC2 in the vegetation logistic regression model.

(Table 3). All variables but forb cover had similar moderate loadings on PC1 (Table 4), and large territories were associated with more bare soil and larger field size, while small territories were associated with higher values of the remaining variables, including vegetation height and density, litter depth and live vegetation cover (in decreasing order of eigenvector coefficients).

Forbaceous plant cover loaded highest on PC2, followed by field size and alfalfa, all with negative eigenvector coefficients. The relationship of these variables in PC2 (Fig. 3) indicates that generally, large territories on a small field had the least forb and alfalfa cover, and small territories on a small field had the highest amounts of forb and alfalfa cover.

**Table 4.** Percentage of variation explained and eigenvector coefficients for principal components retained in the averaged models for the logistic regressions of small (0) and large (1) territories with the invertebrate predictive variable set [ $g(x) = -0.3285 - 0.0681(\text{PC1}) - 0.1026(\text{PC3})$ ] and the vegetation predictive variable set [ $g(x) = -2.0041 + 3.3887(\text{PC1}) + 5.3598(\text{PC2})$ ].

Invertebrate variables	PC1	PC3	Vegetation variables	PC1	PC2
Percentage explained	39.2	15.1	Percentage explained	68.6	20.2
Eigenvector coefficients			Eigenvector coefficients		
Hemiptera	0.12	-0.53	Live vegetation cover	-0.39	0.08
Homoptera	0.29	-0.04	Grass cover	-0.34	-0.15
Aranaea	0.47	0.00	Alfalfa cover	-0.37	-0.39
Opiliones	-0.06	0.25	Forb cover	-0.14	-0.69
Diptera	0.11	-0.40	Soil cover	0.36	-0.29
Coleoptera	0.32	-0.13	Vegetation height and density	-0.42	0.02
Orthoptera	0.35	0.38	Litter depth	-0.41	-0.02
Lepidoptera	0.35	0.03	Field size	0.32	-0.50
Hymenoptera	0.36	0.39			
Larvae	-0.07	0.39			
Field size	-0.42	0.19			

## Discussion

Our study showed that bobolinks modify territory size on the basis of multiple environmental characteristics. The smallest territories were those that had the highest abundance of potential prey, especially Aranea (spiders), Hymenoptera (primarily larvae) and Orthoptera (grasshoppers). Smaller territories also tended to have greater vegetation height and density, litter depth and ground cover. Field size was an important factor; smaller territories were associated with smaller fields, which by extension, indicates that small fields in our study were generally of higher quality and contained sought-after vegetation and field characteristics and abundance of important prey orders. Previously, many of these habitat quality features have been related to territory size in isolation; our study looked at all of these variables in a multivariate approach that identified linkages among some of the features by including them in two models.

Our 95% kernel density territory size estimates (range = 0.38–1.67 ha) are within the range of those estimated previously for bobolinks (Wiens 1969, Martin 1971, Wittenberger 1980, Bollinger 1988, Fletcher & Koford 2003). The wide range in territory size suggests a measurable disparity in habitat quality. In general, invertebrate abundance had a negative relationship with territory size, as small territories had greater abundance of prey orders important to adult diet (Table 4; Beal 1900, Martin & Gavin 1995), as well as caterpillars (Lepidopteran and Hymenopteran larvae) which may be most important to the diet of young (Wittenberger 1980, Moskwik & O'Connell 2006). Also, smaller territories had higher measurements of vegetation structure variables that have been shown to correlate positively with bobolink density, such as forbaceous plant cover and vegetation height and density (Table 4; Schneider 1998, Nocera *et al.* 2007), while larger territories had more bare soil cover, a known negative correlate of bobolink density (Schneider 1998, Warren & Anderson 2005). Smaller territories were related to greater amounts of alfalfa, although alfalfa was not dominant on any study field so as to expect it rendered habitat unfavorable (Bollinger 1988), as all fields had < 25% average alfalfa cover.

Further, percentage of forb and alfalfa cover may be positively correlated on some fields because alfalfa can be considered forbaceous (Fig. 3). Forbs are important habitat for males as song perches that increase their visibility (Moskwik & O'Connell 2006). Furthermore, most nests are built under forbs for improved concealment and stability (Martin 1971, Frei 2009). Our and other studies (e.g., Wittenberger 1980) thus showed that vegetation characteristics may influence the abundance of certain invertebrates, as caterpillars have been shown to correlate with the presence of forbaceous plants.

The model containing vegetation variables was more accurate (having a higher AUC estimate) at discriminating small and large territories than the invertebrate prey model (Fig. 2). However, it is difficult to compare the effect of both models on influencing bobolink territory size. Prey variables consisted of mean abundance of orders from a given field, counting all invertebrates > 3 mm, whereas higher resolution classification of important prey items or the use of biomass estimates may have led to a higher AUC estimate. Further, we are not able to discern from these data whether male bobolinks directly monitor food availability to decide on the size of territory they will defend or if they simply use structural cues that correlate with increased prey abundance. Previous work on other territorial birds, such as Lapland longspurs (*Calcarius lapponicus*) and ovenbirds (*Seiurus aurocapilla*), has suggested that structural cues may have a larger role (Seastedt & MacLean 1979, Smith & Shugart 1987).

Contrary to expectations (based on the Ideal-Free Distribution; Fretwell & Lucas 1970), territory size had a positive relationship with field size in all models, which suggests that patch size is not as limiting to habitat selection as habitat quality. Small fields (~3 ha) of high, relatively homogenous quality supported several small territories, while larger fields of lower quality hosted mainly large territories at a much lower density. This pattern may result from the tendency of farms with several smaller fields to have older hayfields with more mixed grasses, while intensively-managed modern farms increasingly have newer and more homogenous hayfields, often forming near-monocultures of

recently seeded alfalfa, creating lower quality breeding habitat. It is unclear how intraspecific competition and density dependence further affects territory size as we did not monitor interference competition, however bobolinks settle relatively synchronously and we do not expect competition to have a larger overall effect on territory size than habitat quality. Despite that our sample size of territories was modest ( $n = 19$ ), a strong pattern emerged from both models relating territory size and habitat quality that is consistent with predictions. Further, though variables were sampled at the field (not territory) level, variance explained by the random effect of field approached zero in both models. This result may be a product of our study populations being below a density dependence threshold; it would be beneficial to replicate this study in areas of both higher and lower bobolink density than we studied here.

Information is limited regarding territory size and habitat usage of grassland birds (Ribic *et al.* 2009) and has been examined little for the bobolink, and usually in relation to only a few regionally-relevant factors at a time. Bobolink density on the breeding grounds has been related to vegetation characteristics (Wiens 1969, Wittenberger 1980, Bollinger 1988, Nocera *et al.* 2007) and invertebrate abundance (Bollinger 1988, Nocera *et al.* 2007), and though differences in quality between small and large territories have been suggested (Wiens 1969, Martin 1971, Wittenberger 1980), this has not been fully explored until now. Moskwik and O'Connell (2006) found that territories of monogamous bobolink males tended to be smaller and had significantly greater grass height, forbaceous plant cover and caterpillar density compared to the territories of polygynous males. They found that older females arrived first and were generally monogamous on smaller territories, followed by primary, then secondary females that settled on larger territories held by polygynous males. This result is unintuitive and counter to the Ideal-Free Distribution theory (Fretwell & Lucas 1970) where females should crowd into the higher quality habitat first, and settle in lower quality territories only when the payoff for doing so is larger. In contrast, Wittenberger (1980) found that densities of caterpillars and grasshoppers were greater

on the territories of polygynous bobolink males, and mated males had greater forb cover on their territories than unmated males. He also found that on what seemed to be primary habitat where bobolinks settled earlier and were more abundant, territories were smaller, and polygyny was more common (Wittenberger 1980). Martin (1971) also found a relationship between territory vegetation characteristics and mating status, as more females were attracted to territories with higher forb cover.

Nocera *et al.* (2009) examined the influence of social information on the aggregation of breeding bobolink territories on several large, contiguous patches of hayfields, and compared settlement to competing models describing habitat selection patterns. Territory settlement matched a "neighborhood model", in which older, more experienced males settled onto smaller territories clustered in areas of higher quality and paired with more females. Alternatively, younger, less experienced males were attracted by conspecifics and settled nearby in clusters of larger territories that did not coincide with higher quality and paired with fewer females. Resources were significantly greater within clusters of smaller territories in terms of May vegetation height and density, percentage forb cover and beetle abundance from pitfall traps (Nocera *et al.* 2009).

The models we present give a detailed assessment of how variables involved in bobolink habitat selection that are direct or latent indicators of habitat quality are related to bobolink territory size, and are relevant for plans to conserve and manage this at-risk species (classified as Threatened in Canada; COSEWIC 2010). In our study we looked at the effects of patch size, vegetation structure and prey as determinants of territory size. However, we did not monitor other potentially important factors, such as age of the birds or mating patterns, wherein we might expect that the smaller, higher quality bobolink territories we observed supported more mates consistent with the "polygyny threshold theory" (Martin 1971, Wittenberger 1980), and were held by older males (Nocera *et al.* 2009). It would be informative to extend our models to include more life-history details about the territory holders, such as age and settlement timing,

the number of mates and their success, and estimates of intraspecific competition. This could further enhance knowledge about the adaptation of different habitat selection and mating strategies for both male and female bobolinks and how they vary with age and experience.

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