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Original Article

Do Singing-Ground Surveys Reflect American Woodcock Abundance in the Western Great Lakes Region?

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ABSTRACT The Singing-ground Survey (SGS) is the primary monitoring tool used to assess population status and trends of American woodcock (*Scolopax minor*). Like most broad-scale surveys, the SGS cannot be directly validated because there are no independent estimates of abundance of displaying male American woodcock at an appropriate spatial scale. Furthermore, because locations of individual SGS routes have generally remained stationary since the SGS was standardized in 1968, it is not known whether routes adequately represent the landscapes they were intended to represent. To indirectly validate the SGS, we evaluated whether 1) counts of displaying male American woodcock on SGS routes related to land-cover types known to be related to American woodcock abundance, 2) changes in counts of displaying male American woodcock through time were related to changes in land cover along SGS routes, and 3) land-cover type composition along SGS routes was similar to land-cover type composition of the surrounding landscape. In Wisconsin and Minnesota, USA, counts along SGS routes reflected known American woodcock-habitat relations. Increases in the number of woodcock heard along SGS routes over a 13-year period in Wisconsin were related to increasing amounts of early successional forest, decreasing amounts of mature forest, and increasing dispersion and interspersion of cover types. Finally, the cover types most strongly associated with American woodcock abundance were represented along SGS routes in proportion to their composition of the broader landscape. Taken together, these results suggest that in the western Great Lakes region, the SGS likely provides a reliable tool for monitoring relative abundance and population trends of breeding, male American woodcock. Published 2013. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS American woodcock, Minnesota, *Scolopax minor*, Singing-ground Survey, western Great Lakes region, Wisconsin.

The American woodcock (*Scolopax minor*; hereafter, woodcock) Singing-ground Survey (SGS) was designed to track woodcock abundance and population trends across its primary breeding range in the eastern United States and adjacent southern Canada (Tautin et al. 1983, Cooper and Parker 2011). The SGS has been conducted annually since 1968 and consists of approximately 1,500 5.4-km routes, each with 10 locations where observers count the number of singing (referred to as "peenting") male woodcock heard during a 2-minute period near dusk. When the SGS was initially implemented, survey routes were located along secondary roads within randomly selected 10-minute latitude–longitude geographic blocks (Tautin et al. 1983, Sauer and Bortner 1991, Straw et al. 1994) across the primary breeding range of woodcock. The starting location for routes was established at the secondary road intersection nearest the center of the 10-minute latitude–longitude block and the direction of travel was determined randomly. As with most large-scale wildlife surveys (Anderson 2001), the SGS has not been directly validated, and has been assessed indirectly in only a few locations and at relatively small spatial scales (e.g., Dwyer et al. 1983, Jentoft 2000, Klute et al. 2000, Morrison et al. 2006). Therefore, whether the existing SGS routes adequately represent woodcock relative abundance at broad spatial scales, and how well the SGS tracks changes in woodcock abundance are not known.

Between 1968 and 2011, the number of singing male woodcock heard on the SGS declined at a rate of ≈1.0%/year in the Eastern and Central Management regions (Cooper and Parker 2011). Concerns over declines in counts led to reductions in hunting bag limits and season length, delays of hunting-season opening dates, and the development of a

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management plan to increase woodcock population density (Kelley et al. 2008, Cooper and Parker 2011). In the past 10 years, there have been no statistically significant trends in counts of woodcock on the SGS in either the Eastern or Central Management regions, which has been interpreted as evidence of stationary woodcock populations (Cooper and Parker 2011). However, trends in the number of singing male woodcock counted during the SGS are difficult to interpret without additional information, especially an understanding of the relationship between woodcock abundance and land-cover composition along survey routes and how well existing SGS routes represent land-cover composition in the landscapes they were intended to represent.

Existing studies of woodcock–habitat relations are limited to a few locations and geographic extent, but suggest that woodcock abundance is related to amount, distribution, and availability of resources (e.g., food availability, amt and juxtaposition of cover important to reproduction and survival; Dwyer et al. 1983, Steketee et al. 2000). Thogmartin et al. (2007) used these woodcock–habitat relations to develop a model of woodcock abundance at a broad spatial scale, and Hale and Gregg (1976) postulated that as conditions change, abundance of woodcock (and therefore, counts) also changes. However, the relationship between change in woodcock counts along SGS routes and changes in land-cover composition along routes is not well-documented, and this relationship has not been assessed in the Central Management Region. Amount, distribution, and juxtaposition of land-cover types in the Central Management Region have changed since SGS routes were established. Whether SGS counts reflect the effects of changes in land-cover composition on woodcock abundance is not known.

Whether land-cover composition along SGS routes continues to appropriately represent the broader landscape the SGS was intended to represent is also not clear. Results of previous studies that examined how the broader landscape is represented by land cover along SGS routes have been inconsistent. In Pennsylvania, USA, Klute et al. (2000) found that the landscape along SGS routes differed from the broader landscape at several spatial scales. In Michigan, USA, Jentoft (2000) found that land-cover composition along SGS routes was generally similar to the broader Michigan landscape. In New Brunswick, Canada, Morrison et al. (2006) found that land cover changed along SGS routes differently than it changed in the broader landscape. Their (Morrison et al. 2006) results indicated that singing-grounds, nesting, and feeding habitat increased throughout the broader landscape, while it declined along SGS routes.

As with most large-scale surveys (Anderson 2001), there has not been an assessment in the western Great Lakes region of how well the SGS tracks woodcock abundance and trends, and it is likely not feasible to independently estimate woodcock abundance at a regional scale to directly evaluate how well SGS counts track woodcock abundance. In addition, the SGS counts only singing male woodcock, and the relationship between counts of singing male woodcock and overall woodcock abundance is unclear. In the absence of independent estimates of population size or trend, however, it may be possible to indirectly validate large-scale surveys of animal abundance or population trends by assessing whether survey results correspond with established habitat-use relations, reflect changes in abundance and distribution of land-cover types through time, and accurately sample land-cover types used by the species of interest. Therefore, our objective was to indirectly assess whether counts of singing male woodcock on the SGS reflect woodcock relative abundance and trends in abundance in the western Great Lakes region by evaluating whether 1) woodcock counts were related to land-cover types found along SGS routes in Minnesota and Wisconsin, USA; 2) changes in woodcock counts along SGS routes in Wisconsin were related to changes in amount of land-cover types along routes over a 13-year period; and 3) land-cover types along SGS routes in Minnesota and Wisconsin currently reflect the land-cover type composition of the landscape. If counts of woodcock from the SGS are useful indices of woodcock abundance and population trends at a regional scale, we expected that counts would be positively related to amount of preferred woodcock habitat, that changes in counts through time would be related to changes in amount of land-cover types used by woodcock during the spring, and that land-cover types used by woodcock were represented similarly along surveys routes and in the landscapes these routes were intended to represent. In combination, these evaluations allowed us to assess whether counts and trends in counts of woodcock resulting from the SGS provide a reasonable measure of singing male woodcock relative abundance and trends in abundance in the western Great Lakes region.

STUDY AREA

We defined our sample universe using existing SGS routes in the Central Management Region in Minnesota ($n = 123$) and Wisconsin ($n = 117$), distributed throughout the woodcock breeding range in these states. We used a subset of SGS routes that represented the primary forested areas of each state based on the U.S. Environmental Protection Agency's (U.S. EPA) ecoregions in our analysis relating SGS to land cover. The area these routes represent consisted of deciduous forest that gradually transitioned to coniferous forest and was interspersed with lakes and wetlands over gradual elevation changes (U.S. EPA 2007). For our analysis comparing the change in SGS counts with changes in land cover through time, we used a subset of routes that represented the primary forested area of Wisconsin (Fig. 1). Finally, for our analysis comparing land cover of the broader landscape with the land cover along SGS routes, we used all SGS routes with verified locations (see below) in Minnesota ($n = 120$) and Wisconsin ($n = 62$). Land-cover types and vegetation associations for Minnesota are described in Tester (1995) and for Wisconsin are described in Curtis (1971).

METHODS

We used 3 evaluations to meet our objectives. These evaluations were based on models that required accurate SGS stop locations, SGS stop-level count data, land cover of the

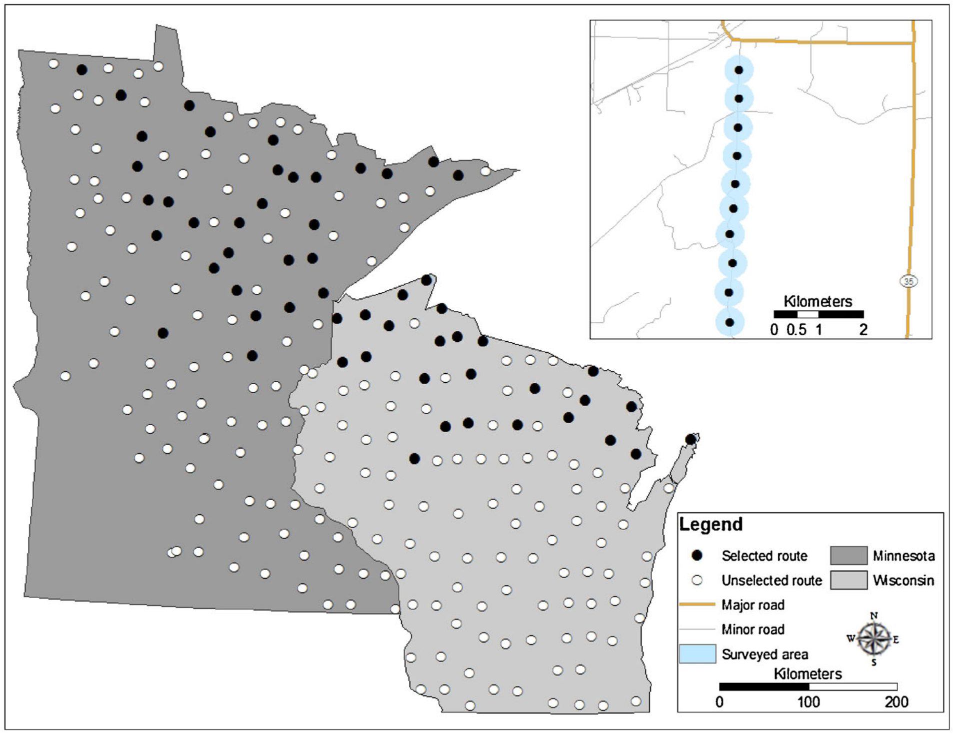

Figure 1. Distribution of American woodcock Singing-ground Survey routes in Minnesota and Wisconsin, USA, and an example of the area surveyed by a single route (10 stops/route). Routes selected for analyses of relationships between land-cover type and woodcock counts are in black; all other routes are indicated in white.

surrounding SGS stop locations for 2 periods, and land-cover composition of the broader landscape. The U.S. Fish and Wildlife Service provided SGS stop location and stop-level count data. For routes with duplicate counts in a single year ($n = 12$), we used the highest count for that year. To minimize the influence of annual variation in counts at each stop, we used the average count for 2007–2009 from Minnesota and 1991–1993 and 2004–2006 from Wisconsin in models relating counts of woodcock to land-cover composition (see below).

We quantified stop-level land-cover data through classification and delineation of aerial photographs. We classified land cover based on habitat attributes important to woodcock (based on Dwyer et al. [1983] and Steketee et al. [2000]) using U.S. National Agriculture Imagery Program color aerial photographs (1-m resolution, 2005 photos) and a mosaic of early 1990s black and white, 1-m-resolution aerial photographs (primarily consisting of 1992 photographs obtained from Wisconsin View [2009]) to delineate land-cover types for Wisconsin and color infrared aerial photographs (1-m resolution, 2008 photos) to delineate land-cover types for Minnesota. We delineated land-cover types under a modified Anderson Land-cover Classification scheme (Anderson et al. 1976) and included estimates of canopy height for the area within a 330-m radius around each listening stop, which is the presumed maximum detection distance for woodcock (Duke 1966).

To estimate canopy height, we used a variety of visual cues in aerial photographs (e.g., texture, shadows, additional land-cover data, etc.), trained the person who conducted delineations using photographs with areas of known canopy height, utilized photos of various land-cover types with known heights as reference photos, and ensured that only one person completed all photo interpretation to maintain consistency. We subsequently evaluated accuracy of canopy-height estimates by visiting random points along SGS routes (see below). Based on the modified Anderson et al. (1976) classification scheme, we used 6 land-cover types in our analysis: urban or developed land, open space, mature forest, water, wetlands, and early successional forest (for a full description of these categories, see Nelson 2010).

For the Wisconsin 2005 and Minnesota 2008 land-cover classification, we evaluated accuracy of land-cover type delineation by comparing classification resulting from photo interpretation with land-cover type and height determined by visits to random points along SGS routes. We calculated accuracy of our air-photo classifications using error matrices and the κ statistic (Congalton and Green 1999). For Wisconsin, 1992 historical stand data did not exist. Therefore, we could not determine accuracy of the Wisconsin 1992 delineation directly. However, historical stand data from 1992 for Minnesota were available from the Minnesota Department of Natural Resources (MN DNR), and we used these data to indirectly evaluate accuracy of land-cover classification from 1990s Wisconsin aerial photos. We classified random points in Minnesota using the same method we used to classify points in Wisconsin. We then compared the land-cover type classification and delineations in Minnesota with historical stand data using error matrices and the κ statistic (Congalton and

Green 1999). We used this assessment of classification accuracy as a surrogate for classification accuracy of our early 1990s Wisconsin land-cover classification (for a full description of land-cover delineations and assessment of their accuracy, see Nelson 2010). To represent land cover of the broader landscape, we used LANDFIRE data obtained through the LANDFIRE website (http://www.landfire.gov/). LANDFIRE model accuracy, as determined by cross-validation (http://www.landfire.gov/), ranged from 66% to 98% for land-cover types and from 80% to 90% for forest height (LANDFIRE 2006). The LANDFIRE data have 37 categories of land-cover type across Minnesota and Wisconsin. We reclassified LANDFIRE categories into 6 land-cover types to represent similar land-cover types included and described in previous woodcock studies (Dwyer et al. 1983, Steketee et al. 2000, Nelson 2010). These 6 land-cover types included urban or developed land, open space, mature forest, water, wetlands, and early successional forest (for a full description of category mapping of LANDFIRE data, see Nelson 2010).

To develop models relating counts of woodcock to land-cover composition, we randomly selected a subset of 60 routes (30 in MN and 30 in WI; Fig. 1) located in the predominantly forested area of Minnesota and Wisconsin (110 forested routes: 68 in MN and 42 in WI; Fig. 1). We only considered routes where woodcock had been detected consistently during the period for which we had land-cover data. We could only use 26 of the 30 randomly selected routes from Wisconsin in our analysis because we were unable to complete land-cover type delineation for 4 routes (Fig. 1).

Statistical Analyses

Based on hypothesized variables thought to affect woodcock abundance (Table 1), we used 6 land-cover types and 3 landscape metrics to create 19 *a priori* models relating land-cover or landscape metrics at listening stops along SGS routes to woodcock counts at those stops. We assessed these models using an information-theoretic framework (Burnham and Anderson 2002) and used Akaike's Information Criterion (AIC; Akaike 1973) to identify models best supported by the data. We evaluated these models relating woodcock counts to land-cover data using PROC GLIMMIX in Program SAS v.9.2 (The SAS Institute, Inc.© 2007; Table 2). All models related land cover within 330 m (Duke 1966) of SGS stops to the average SGS count for a 3-year period (WI 2004–2006, MN 2007–2009). The general linear mixed, single-parameter model was

$$\mathrm{Log}(Y_{ij}) = \beta_0 + \log(X_{ij} + 1) + U_i$$

where Y_{ij} is the average SGS count for stop i at time j. For Minnesota, time j was the period 2007–2009, and for Wisconsin j was 2004–2006. We log-transformed counts to reflect a Poisson distribution associated with count data. X_{ij} is the proportion of a land-cover type at stop i and time j, which we log + 1-transformed to convert to a Poisson distribution to allow inclusion of land-cover types with 0% coverage at a stop. U_i allowed for correlation within routes at

Table 1. Land-cover variables included in the suite of *a priori* models and their hypothesized relationship to American woodcock Singing-ground Survey counts (SGS) in Minnesota and Wisconsin, USA.

Acronym	Variable	Hypothesized relationship to SGS counts	Rationale
DU	Proportion of area within 330 m of an SGS listening stop categorized as urban or developed land cover	Lower counts associated with higher proportion of urban land cover	Dwyer et al. (1983), Thogmartin et al. (2007)
OS	Proportion of area within 330 m of an SGS listening stop categorized as open space	Higher counts associated with intermediate proportion of open space; modeled as OS-OS^2	Dwyer et al. (1983), Steketee et al. (2000)
ES	Proportion of area within 330 m of an SGS listening stop categorized as early successional forest	Higher counts associated with higher proportion of early successional forest	Gutzwiller et al. (1983), Steketee et al. (2000), Thogmartin et al. (2007)
MF	Proportion of area within 330 m of an SGS listening stop categorized as mature forest (i.e., not early successional forest)	Lower counts associated with higher proportion of mature forest	Dobell (1977), Keppie and Whiting (1994)
OW	Proportion of area within 330 m of an SGS listening stop categorized as open water	Lower counts associated with higher proportion of open water	Lakes and rivers are non-habitat for woodcock
WL	Proportion of area within 330 m of an SGS listening stop categorized as wetlands	Higher counts associated with higher proportion of wetlands	Klute et al. (2000)
CONTAG[a]	Contagion Index (McGarigal and Marks 1995) calculated for the area within 330 m of an SGS listening stop, representing both interspersion and dispersion of habitat types	Higher counts associated with lower values of CONTAG (indicating interspersion but not clumping)	Gutzwiller et al. (1983), Thogmartin et al. (2007); landscapes that provide access to a variety of habitats in close proximity
IJI[a]	Interspersion and Juxtaposition Index (McGarigal and Marks 1995) calculated for the area within 330 m of an SGS listening stop, representing interspersion	Higher counts associated with higher values of IJI	Gutzwiller et al. (1983), Thogmartin et al. (2007); heterogeneous landscapes
FRAC_MN[a]	Mean Fractal Dimension Index (McGarigal and Marks 1995) calculated for the area within 330 m of an SGS listening stop, representing the complexity of patch shapes	Higher counts associated with higher values of FRAC_MN	Steketee et al. (2000), Thogmartin et al. (2007); landscapes with high amounts of edge

[a] Landscape indices calculated using FRAGSTATS (http://www.umass.edu/landeco/research/fragstats/fragstats.html); McGarigal and Marks (1995).

Table 2. Number of parameters (K), Akaike's information criterion (AIC), and model weights (w_i) for *a priori* models with ΔAIC values lower than the null model of American woodcock counts (3-yr average of Singing-ground Survey count) in Minnesota and Wisconsin, USA, developed based on documented or presumed relationships between woodcock abundance and landcover.

Model[a]	K	AIC value	ΔAIC	w_i
Minnesota				
OS, WL, ES	4	536.88	0	0.20
OW	2	537.18	0.30	0.17
OS, WL, ES, OS × WL × ES	5	537.63	0.75	0.14
DU, OS, MF, OW, WL, ES	7	538.13	1.25	0.11
MF	2	538.60	1.72	0.08
OS, WL, OS × WL	4	539.51	2.63	0.05
OS, ES	3	539.81	2.93	0.05
DU, MF	3	539.99	3.11	0.04
ES	2	540.00	3.12	0.04
DU, MF, DU × MF	4	541.54	4.66	0.02
CONTAG	2	541.56	4.68	0.02
(.)	1	541.61	4.73	0.02
Wisconsin				
ES	2	459.21	0	0.25
IJI	2	459.44	0.23	0.22
OS, ES	3	459.61	0.40	0.21
OS, WL, ES	4	461.24	2.03	0.09
OS, ES, OS × ES	4	461.61	2.40	0.08
OS, WL, ES, OS × WL × ES	5	462.77	3.56	0.04
DU, MF, DU × MF	4	463.46	4.25	0.03
CONTAG	2	463.50	4.29	0.03
DU, MF	3	465.03	5.82	0.01
DU, OS, MF, OW, WL, ES	7	465.45	6.24	0.01
MF	2	465.83	6.62	0.01
(.)	1	467.44	8.23	0.00

[a] CONTAG, contagion index; IJI, interspersion and juxtaposition index; DU, developed or urban; OS, open space; MF, mature forest; ES, early successional forest; OW, water; WL, wetland; (.), null (random intercept) model, see text for descriptions.

the stop level and assumed that route-level data were independent and normally distributed. We also included multiple-parameter models in the suite of *a priori* models as linear combinations (see Table 1 for description of *a priori* model development).

We included all single-variable models in our *a priori* model set, and we incorporated non-correlated variables into multiple-variable models based on biological plausibility (Nelson 2010). We evaluated models independently for Minnesota and Wisconsin because the land-cover data were derived from aerial photographs taken during different years. The *a priori* suite of models included 9 single-factor models, 6 two-factor models, 2 three-factor models, the full model, and the null model (Table 2). The full model included all land-cover types, but no landscape metrics. We did not include landscape metrics in the full model to avoid duplicate measurements within a single model (e.g., CONTAG and IJI both measure landscape interspersion). We included single-factor models to assess the relationship of each land-cover type or landscape metric to SGS counts. Two-factor and 3-factor models combined land-cover types that related similarly to woodcock counts (e.g., positively or negatively), which allowed us to determine whether a combination of similar land-cover types had an additive effect on woodcock counts (e.g., woodcock counts were greater if open space and early successional forest were both present than if only one of these land-cover types was present). We represented these multiple-factor models as pairs to assess whether factors were additive; 1 model included the additional land-cover type as an additive term and the second included the additive term and an interaction term.

We also assessed models relating changes in woodcock counts to changes in land-cover type along survey routes within an information-theoretic framework for the 26 randomly selected routes in Wisconsin. We considered change to and from 6 land-cover types and change in the landscape parameter Contagion Index (Table 3) as covariates in our *a priori* models. Using these covariates, we created general linear mixed models to assess the change in counts of woodcock between periods relative to the changes in land-cover type between those 2 periods (Table 4). Models related change in land-cover type from 1992 to 2005 within 330 m (Duke 1966) of SGS stops to the change in the average SGS counts for 3-year periods centered on 1992 and 2005. The general linear mixed model was

$$Y_i = \beta_0 + \log(X_i + 1) + U_i$$

where

$$Y_i = Y_{iT_2} - Y_{iT_1}$$

and Y_i is assumed to have a normal distribution. Y_{iT_1} is the average SGS count for stop i at the initial period T_1 (1991–1993). Y_{iT_2} is the average SGS count for stop i at the final period T_2 (2004–2006). X_i is the proportion of a land-cover type for each change in land-cover type (e.g., the amt of land that changed from early successional forest to mature forest) at stop i between 1992 and 2005, and is log + 1-transformed to allow the inclusion of changes in land-cover type with 0%

Table 3. Classes of variables related to change in land cover and the hypothesized relationship to American woodcock Singing-ground Survey (SGS) counts in Minnesota and Wisconsin, USA.

Classes of variables related to change in land cover	Variables	Hypothesized relationship to SGS counts	Rationale
Land cover that did not change	Area within 330 m of an SGS listening stop that remained classified as developed or urban (DU), mature forest (MF), open water (OW), open space (OS), early successional forest (ES), or wetlands (WL) between periods	No relationship beyond that between woodcock abundance and land cover (e.g., Dwyer et al. 1983, Steketee et al. 2000)	Land cover that remains in the same category through time is unlikely to be related to changes in counts of woodcock, unless habitat quality decreases (e.g., maturing forest)
Change from DU	Area within 330 m of an SGS listening stop categorized as DU that changed to OS or MF	Higher counts associated with change to OS, no change in counts associated with change to MF	Increase in amount of OS could provide singing grounds; change from DU to MF would not increase woodcock use; Dwyer et al. (1983)
Change to DU	Area within 330 m of an SGS listening stop categorized as MF, ES, or OS that changed to DU	Lower counts associated with change to DU, except no change in counts with change from MF to DU	Low or no woodcock abundance in DU; Dwyer et al. (1983)
Change from OW	Area within 330 m of an SGS listening stop categorized as OW that changed to MF, WL, or ES	Higher counts associated with change from OW	Transition from OW to terrestrial habitats likely increases use by woodcock
Change to MF	Area within 330 m of an SGS listening stop categorized as OS, ES, or WL that changed to MF	Lower counts associated with change to MF	Lower woodcock abundance in MF compared with OS, ES, or WL; Dobell (1977), Keppie and Whiting (1994)
Change from MF	Area within 330 m of an SGS listening stop categorized as MF that changed to OS, ES, or WL	Higher counts associated with change from MF	Higher woodcock abundance in OS, ES, or WL than in DU; Hale and Gregg (1976), Dwyer et al. (1983), Steketee et al. (2000)
Change among OS, ES, or WL	Area within 330 m of an SGS listening stop that changed from OS, ES, or WL to OS, ES, or WL	Counts may change but direction and magnitude not known	Woodcock use all 3 of these land-cover types; (Dwyer et al. 1983, Steketee et al. 2000)
ΔCONTAG[a]	Change in Contagion Index (McGarigal and Marks 1995) for the area within 330 m of an SGS listening stop	Higher counts associated with increased interspersion (decrease in CONTAG)	Gutzwiller et al. (1983)

[a] Landscape indices calculated using FRAGSTATS (http://www.umass.edu/landeco/research/fragstats/fragstats.html); McGarigal and Marks (1995).

Table 4. Number of parameters (*K*), Akaike's Information Criterion (AIC), and model weights (w_i) for *a priori* models with ΔAIC values lower than the null model of change of American woodcock counts at points along Singing-ground Survey routes related to change in land-cover types in Wisconsin, USA, from 1991–1993 to 2004–2006.

Model[a]	*K*	AIC value	ΔAIC	w_i
ΔCONTAG	2	511.73	0	0.17
MF	2	512.51	0.78	0.12
MF to ES	2	512.74	1.01	0.10
DU to OS	2	513.19	1.46	0.10
WL	2	513.21	1.48	0.09
ES to MF	2	513.43	1.70	0.07
OS to ES	2	513.90	2.17	0.03
DU to MF	2	515.45	3.72	0.03
(.)	1	515.57	3.84	0.03

[a] CONTAG, contagion index; DU, developed or urban; OS, open space; MF, mature forest; ES, early successional forest; WL, wetland; (.), null (random intercept) model.

coverage at a stop. U_i allows for correlation within routes at the stop level and assumes that route-level data were independent and normally distributed.

We did not consider land-cover changes summed across all 26 routes that comprised <10% (3.42 ha) of a single stop because we felt these changes were not observed enough to draw meaningful conclusions. Because there is very little published literature that relates change in land cover over time to change in woodcock counts, we included all 1-variable models (25 land-cover type changes, 1 landscape covariate, and the null model) in our suite of *a priori* models. We evaluated these 27 *a priori* models using SAS v.9.2 (The SAS Institute, Inc.© 2007) PROC GLIMMIX (Table 4) and ranked them using AIC. We expected several *a priori* models to relate to SGS counts similarly, and we grouped these into 8 categories (Table 3).

We then used the results of the single-variable *a priori* models as a guide in developing models *post hoc* that included multiple biologically relevant variables (Table 5). Prior to creating multiple-variable models, we evaluated collinearity between all possible pairs of land-cover type change variables and the contagion metric by calculating a correlation matrix

Table 5. Number of parameters (*K*), Akaike's information criterion (AIC), and model weights (w_i) for *post hoc* and *a priori* models with ΔAIC values lower than the null model of change of American woodcock counts at points along Singing-ground Survey routes related to change in land-cover types in Wisconsin, USA, from 1991–1993 to 2004–2006.

Model[a]	*K*	AIC value	ΔAIC	w_i
MF to ES, ES to MF[b]	3	511.09	0	0.19
ΔCONTAG	2	511.73	0.64	0.14
MF	2	512.51	1.42	0.09
MF to ES	2	512.74	1.65	0.08
DU to OS	2	513.19	2.10	0.07
WL	2	513.21	2.12	0.07
ES to MF	2	513.43	2.34	0.06
OS to ES	2	513.90	2.81	0.05
DU to MF	2	515.45	4.36	0.02
(.)	1	515.57	4.48	0.02

[a] CONTAG, contagion index; DU, developed or urban; OS, open space; MF, mature forest; ES, early successional forest; WL, wetland; (.), null (random intercept) model.
[b] *Post hoc* model.

(see Nelson 2010). We then combined non-correlated variables into a single model, and evaluated support for models using AIC.

Finally, to compare land-cover composition along SGS routes with land-cover composition of the broader landscape we used compositional analysis (Aebischer et al. 1993). Aebischer et al. (1993) described compositional analysis as an approach for assessing habitat selection of animals based on used and available habitat. For our purposes, habitat use was analogous to land-cover composition along routes and available habitat was analogous to land-cover composition of the broader landscape, and is represented mathematically by

$$y_R = y_L$$

where y_R is the land-cover composition along SGS routes and y_L is the land-cover composition of the broader landscape. We defined the land-cover types surveyed by SGS routes as the area within a circle of 330-m radius (i.e., the presumed max. detection distance of a displaying woodcock [Duke 1966]) around each listening stop; we used ArcMap to create these 330-m-radius circles. We represented the surrounding landscape for each route by placing a 10-minute latitude–longitude block centered on each route (e.g., Sauer and Bortner 1991, Straw et al. 1994), except when blocks for adjacent routes overlapped. In that case, we adjusted blocks so that they did not overlap, to avoid including the same landscapes for different routes.

Following Aebischer et al. (1993), we transformed the proportion of each land-cover type at the route (y_{Ri}) and landscape (y_{Li}) levels to ensure that each land-cover type was linearly independent. Our transformation for the route level was

$$y_{Ri} = \ln\left(\frac{x_{Ri}}{x_{RD}}\right)$$

and for landscape level was

$$y_{Li} = \ln\left(\frac{x_{Li}}{x_{LD}}\right)$$

where x_{Ri} and x_{Li} are the proportions of land-cover type i along a single route and corresponding landscape, and where x_{RD} and x_{LD} are the proportions of the Dth land-cover type along a single route and corresponding landscape, to which all other land-cover types are compared. We used the land-cover types "mature forest" and "urban or developed" as the Dth term, to allow ranking of all land-cover types (*sensu* Aebischer et al. 1993; see Nelson 2010 for details).

We used Hotelling's T-test to test the null hypothesis that land-cover composition along SGS routes was equivalent to land-cover composition of the landscape. Hotelling's T-test (calculated using Program R; R Development Core Team 2009) simultaneously tests whether all of the land-cover types are proportionally represented between the broader landscape and SGS routes. To determine whether a single land-cover type along SGS routes comprised a similar proportion of that land-cover type in the broader landscape, we followed the approach of Aebischer et al. (1993) and conducted Student's t-tests for each land-cover type, again using Program R. We then ranked land-cover types from most over-represented to most under-represented.

We tested for proportional representation of land-cover composition between SGS routes and the broader landscape for 4 subsets of SGS routes. We included Minnesota and Wisconsin together as a full data set using all 181 verified routes. We also separated Minnesota (119 routes) and Wisconsin (62 routes) because they represent administrative units that may be managed differently with respect to woodcock. Finally, we combined the forested area of Minnesota and Wisconsin (based on EPA ecoregions [Fig. 1; 139 routes]) to represent woodcock habitat in which woodcock might be expected to respond to changes in a similar way (i.e., as representative of a portion of the Central Management Region).

Use of trade names does not imply endorsement by the U.S. Federal Government or the University of Minnesota.

RESULTS

In Minnesota during 2007–2009, counts of woodcock at listening points on our subset of SGS routes ($n = 30$) ranged from 0 to 4 with a 3-year average that ranged from 0 to 3.33, with 488 woodcock detections across routes over the 3-year period. In Wisconsin for the period 1991–1993, counts ranged from 0 to 4 at listening stops with a 3-year average that ranged from 0 to 2.33, with 349 woodcock detections across routes over the 3-year period. In Wisconsin for the period 2004–2006 ($n = 26$ routes), counts at individual listening points ranged from 0 to 5 with a 3-year average that ranged from 0 to 3.66, with 414 woodcock detections across routes over the 3-year period. Accuracy of land-cover type delineation was 74% for Minnesota and 86% for Wisconsin with κ values of 0.69 and 0.83, respectively. Classification accuracy of individual land-cover types in Minnesota ranged from 40% to 100% as follows: developed land (96%), open space (86%), mature forest (88%), permanent water (100%), wetland (51%), and early successional forest (40%). In Wisconsin, the accuracy of individual land-cover types was developed (90%), open space (44%), mature forest (94%), permanent water (100%), wetland (68%), and early successional forest (48%). Accuracy of land-cover type classification from 1992 aerial photographs from Minnesota was 87% (κ value $= 0.84$), with accuracy of individual land-cover type classification ranging from 56% to 100% (see Nelson 2010 for a more detailed assessment of classification accuracy). About 25% of the area around SGS stops in Wisconsin changed land-cover type between 1992 and 2005, with the change in individual land-cover types ranging from -4.13% to 3.08% (Nelson 2010).

Models Relating Woodcock Counts to Land-Cover Composition

Among the models relating counts of woodcock to land-cover composition in Minnesota that we considered (Table 2), the best-supported model of woodcock counts at stops along SGS routes ($w = 0.20$) included the proportion of open space, wetlands, and early successional forest in the landscape surrounding listening stops. There were 4 other competing land-cover models (ΔAIC ≤ 2; Table 2): 1) the single-variable model including the proportion of water in the landscape surrounding listening stops ($w = 0.17$), 2) the 3-factor model including the proportion of water, open space, early successional forest, and their 3-way interaction term ($w = 0.14$), 3) the full model including the proportion of developed land, wetlands, open space, regenerating forest, and mature forest ($w = 0.11$), and 4) the single-factor model including the proportion of mature forest ($w = 0.08$). Based on single-variable models, both wetlands ($\beta = 0.82$, 95% Confidence Interval [CI] = -0.38–2.02) and early successional forest ($\beta = 1.14$, 95% CI = 0.00–2.28) were positively associated with woodcock counts, although the 95% CI for wetlands overlapped zero. Developed land ($\beta = -1.12$; 95% CI = -5.51–3.27), mature forest ($\beta = -1.18$; 95% CI = -2.22 to -0.14), and water ($\beta = -10.89$; 95% CI = -21.40 to -0.38) all were related negatively to counts, although 95% CI for developed land overlapped zero. Open space ($\beta = 0.87$; 95% CI = -1.25–2.99) was positively related to counts, but because open space was included in the model as a negative squared term (Table 1), it indicated an increase followed by decrease that was not statistically significant (i.e., 95% CI overlapped zero). The best-supported model of woodcock counts in Minnesota received 10 times the weight of the null model, and was slightly under-dispersed ($\chi^2/df = 0.44$), indicating reasonable model fit.

In Wisconsin, the best-supported model relating counts of woodcock to land-cover composition included only the proportion of early successional forest surrounding listening stops and had a model weight of 0.25 (Table 2). There were 2 additional competing models (ΔAIC ≤ 2; Table 2): 1) a model including only the Interspersion and Juxtaposition Index ($w = 0.22$; Table 1), and 2) a 2-factor model that included the proportion of early successional forest and open space ($w = 0.21$; Table 2). In single-variable models, wetlands ($\beta = 0.75$; CI = -2.03–3.53) and early successional forest ($\beta = 2.25$; CI = 0.96–3.54) both related positively to counts, although the 95% CI for wetlands overlapped zero. Developed land ($\beta = -2.01$; CI = -6.38–2.36), mature forest ($\beta = -1.19$; CI = -2.39–0.01), and water ($\beta = -2.31$; CI = -10.27–5.65) all related negatively to counts, but CIs for these parameter estimates all overlapped zero. Open space ($\beta = 0.44$; CI = -1.97–2.85) was positively related to counts, but because open space was included in the model as a negative squared term, it indicated an increase followed by decrease that was not statistically significant. The best-supported model of woodcock counts in Wisconsin received >20 times the weight of the intercept-only model and was slightly under-dispersed ($\chi^2/df = 0.55$), indicating reasonable model fit.

Models Relating Change in Woodcock Counts to Change in Land-Cover Composition

Nine models relating change in woodcock counts along SGS routes to change in land-cover composition along SGS routes in Wisconsin from 1992 to 2005 had lower AIC values than the null model (Table 4). The best-supported *a priori* model of change in woodcock counts between periods included ΔCONTAG (Table 1) with a model weight (w) of 0.17, which was 5 times greater than the weight (0.03) of the null model (Table 4). There were 5 additional competing models (ΔAIC ≤ 2; Table 4), including the following: unchanged mature forest ($w = 0.12$), change from mature to early successional forest ($w = 0.10$), change from developed or urban to open space ($w = 0.10$), unchanged wetland ($w = 0.09$), and change from early successional to mature forest ($w = 0.07$). Three of the variables in these competing models (ΔCONTAG: $\beta = -0.008$, 95% CI = -0.014 to -0.002; mature forest: $\beta = -0.679$, 95% CI = -1.268 to -0.092; change from early successional to mature forest: $\beta = -0.944$, 95% CI = -1.842 to -0.038) were related to decreases in SGS counts from 1991–1993 to 2004–2006. Four of the variables in these competing models were related to increases in SGS counts between periods (change from mature to early successional forest: $\beta = 1.048$, CI = 0.129–1.971; change from developed or urban to open space: $\beta = 22.004$, 95% CI = 1.498–42.502; wetlands: $\beta = 1.956$, 95% CI = 0.137–3.783; change from open space to early successional forest: $\beta = 1.967$, 95% CI = -0.029–3.969). Combining single-variable models *post hoc* resulted in one additional model, which included land-cover type change from mature to early successional forest and from early successional to mature forest ($w = 0.19$). Including this model reduced the number of competing models (ΔAIC ≤ 2) to 3, including the following: ΔCONTAG ($w = 0.14$), mature forest ($w = 0.09$), and change from mature to early successional forest ($w = 0.08$; Table 5). The best-supported *post hoc* model comparing the change in woodcock counts with change in land-cover composition received >10 times the weight of the intercept-only model and was slightly under-dispersed ($\chi^2/df = 0.37$), indicating reasonable model fit.

Models of Land-Cover Composition Along SGS Routes Versus Land-Cover Composition of the Broader Landscape

Composition of land-cover types along SGS routes in Minnesota and Wisconsin differed from that of the broader landscape in each subset we considered (Hotelling's T ranged from 210 to 548, all P-values < 0.001). Developed or urban land cover was significantly over-represented and wetlands and water were both under-represented on SGS routes relative to the broader landscape for all the comparisons we considered (Table 6). Rank-order of representation of land-cover types along SGS routes was the same for routes in Minnesota, Wisconsin, and Minnesota and Wisconsin combined (Table 6). For the forested portions of Minnesota and Wisconsin, rank-order differed from rank-order based on state boundaries in that early successional forest ranked second (rather than third) and open space ranked third (rather than second; Table 6).

DISCUSSION

We indirectly assessed the validity of the SGS in Minnesota and Wisconsin by evaluating whether counts of singing male

Table 6. Comparison of land-cover type along American woodcock Singing-ground Survey routes in Minnesota and Wisconsin, USA, in relation to their abundances in the broader landscape, based on compositional analysis (Aebischer et al. 1993). LANDFIRE (2006) data were used to determine land-cover type. The rank of each land-cover type is from high to low and is based on confidence intervals calculated from individual Student's *t*-tests and indicates over- (+) and under- (−) representation.

Data set	Land-cover type rank
MN and WI	DU[a,*](+) > OS = ES = MF > WL*(−) > OW*(−)
MN	DU*(+) > OS = ES = MF > WL*(−) > OW*(−)
WI	DU*(+) > OS = ES = MF > WL*(−) > OW*(−)
Forested area	DU*(+) > ES = OS = MF > WL*(−) > OW*(−)

[a] DU, developed or urban; OS, open space; MF, mature forest; ES, early successional forest; OW, water; WL = wetland.
* Ranking significantly different from all other rankings.

woodcock were related to abundance of land-cover types used by woodcock, whether changes in land-cover abundance through time were reflected in woodcock counts, and whether fixed survey-route locations sampled land-cover types used by woodcock in proportion to their availability. We concluded that counts of singing male woodcock at stops along SGS routes in Minnesota and Wisconsin were related to land-cover type and a landscape metric related to interspersion and amount of edge, which is consistent with hypothesized woodcock–habitat relations (e.g., Dwyer et al. 1983, Steketee et al. 2000, Thogmartin et al. 2007). Early successional forest and open space were the only 2 land-cover types included in the competing models in both Minnesota and Wisconsin (ΔAIC ≤ 2; Table 2), which suggests that these were the 2 land-cover types that best explained counts across broad regions, consistent with woodcock habitat use (i.e., use of open areas for singing grounds and early successional forest for nesting). The accuracy of our land-cover classification of early successional forest in Minnesota (40%) and Wisconsin (48%) was relatively low, due to the difficulty in determining forest height from aerial photographs. However, we mainly (MN 91% and WI 100%) misclassified early successional forest as mature forest (Nelson 2010), which resulted in an underestimation of the magnitude of the relationship between early successional forest and counts of woodcock on SGS routes because mature forest relates inversely to SGS counts when compared with early successional forest.

Several land-cover variables we considered exhibited unexpected relationships with woodcock counts on SGS routes. In Minnesota, the proportion of water in the landscape was inversely related to woodcock counts (ΔAIC $= 0.3$, $w = 0.17$; Table 2). Several studies have considered distance to water (e.g., Gutzwiller et al. 1983, Steketee et al. 2000) as a factor related to woodcock abundance, but we speculate that in Minnesota, as the proportion of the area surrounding SGS stops was increasingly open water (max. of 38%), the area available that could support woodcock decreased. In both Minnesota and Wisconsin, the amount of urban or developed land was not strongly related to woodcock counts at SGS stops (Table 2). This differed from the negative relationship reported by Dwyer et al. (1983) in the northeastern United States and by Thogmartin et al. (2007) for the U.S. portion of the primary woodcock breeding range. In the Eastern Management Region, conversion of other land-cover types to urban or developed land is thought to have contributed to declining woodcock population trends (Owen et al. 1977, Steketee et al. 2000). In Minnesota and Wisconsin, we did not observe a similar relationship, although only a small number of SGS stops in our sample (7 in MN and 8 in WI) included a large portion (>20%) of this land-cover type, and the majority of area we classified as urban or developed consisted of roads (M. R. Nelson and D. E. Andersen, unpublished data). The amount of developed land cover along SGS routes in our study was relatively low (<7% of the landscape during both periods) but increased by 36% from 1992 to 2006. This proportional increase in the amount of developed land cover is comparable to the average proportional increase reported by Dwyer et al. (1983) of 33.4% (range = 13.4–41.1%). However, Dwyer et al. (1983) did not report the proportion of the landscape they evaluated that consisted of developed land, making it difficult to directly compare our results with theirs.

Based on the results of previous studies (e.g., Dwyer et al. 1983), we expected to find a relationship between land-cover type change and woodcock counts in our assessment of Wisconsin SGS routes. When we included our *post hoc* model, we found the strongest support for models of change in woodcock counts along SGS routes in Wisconsin from 1992 to 2005 related to the change to and from mature and early successional forest, the change in measures of contagion (ΔCONTAG), and land cover that remained as mature forest. Dwyer et al. (1983) found that only change to developed land cover was significantly related to woodcock counts in the Eastern Management Region; however, they did not consider initial land-cover type in their analyses. We considered each possible initial and final land-cover type separately and therefore included considerably more land-cover types in our analyses than Dwyer et al. (1983), which may explain some of the differences between our results and theirs.

Our assessment of how well land-cover composition along SGS routes in Minnesota and Wisconsin currently reflect land-cover composition in the broader landscape produced results similar to those of Klute et al. (2000) and Morrison et al. (2006) in that not all land-cover types are represented along SGS routes in the same proportions that comprise the broader landscape (Table 6). Urban or developed land cover is over-represented on Minnesota and Wisconsin SGS routes, whereas water and wetlands are under-represented compared with their abundance within the broader landscape (Table 6). These land-cover types were also identified by Klute et al. (2000) in Pennsylvania to be significantly different between SGS and random routes. Similarly, Morrison et al. (2006) concluded that land-cover composition along SGS routes in New Brunswick was not the same as in the broader landscape that SGS routes were intended to represent. In contrast, Jentoft (2000) reported that in

Michigan, land-cover composition along SGS routes was similar to land-cover composition of the entire state.

Even though our compositional analysis indicated that not all land-cover types along SGS routes in Minnesota and Wisconsin are represented proportionally to land-cover composition in the broader landscape, composition of open space, early successional forest, and mature forest were similar between SGS routes and the broader landscape. These land-cover types were related to woodcock counts along SGS routes in Minnesota and Wisconsin, and based on other evaluations of woodcock–habitat relations (e.g., Dwyer et al. 1983, Steketee et al. 2000), are thought to influence woodcock abundance. Therefore, our analyses suggest that land-cover types most strongly related to woodcock abundance (e.g., open space and early successional forest) were represented on SGS routes similarly to their abundance in the broader landscape.

MANAGEMENT IMPLICATIONS

The American woodcock conservation plan (Kelley et al. 2008) is based on the premise that the best way to return woodcock densities to those observed in the early 1970s and to halt the apparent decline in woodcock population abundance is to increase the amount of woodcock habitat in the landscape. We demonstrated that across broad regions (MN and WI) SGS counts relate most strongly to early successional forest and open space, consistent with the premise of the woodcock conservation plan. Furthermore, our results indicated that increasing the amount of early successional forest and decreasing the amount of mature forest while increasing the interspersion of land-cover types are likely to increase counts of singing male woodcock, and that SGS counts do track changes in land-cover composition. Finally, in Minnesota and Wisconsin, SGS routes do not represent all land-cover types in proportion to their occurrence in the broader landscape, but do proportionally represent the land-cover types associated with woodcock abundance. Consequently, it is likely that counts resulting from the SGS provide a reasonable source of information for tracking changes in abundance of singing male woodcock at the landscape scale in the western Great Lakes region.

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