Development of Restoration and Scaling Options for Songbirds

Informing Restoration and Conservation of Songbirds that Breed in the South River Watershed, Virginia

THE INSTITUTE FOR
BIRD POPULATIONS

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James F. Saracco
The Institute for Bird Populations, PO Box 1346, Point Reyes Station, CA 94956
E-mail: jsaracco@birdpop.org

Viviana Ruiz-Gutierrez
Department of Fish, Wildlife, and Conservation Biology, Colorado State University, 136 Wagar Hall, Fort Collins, CO 80523-1474
E-mail: vruizg@colostate.edu

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Executive Summary

From 1929 to 1950 mercuric sulfate was released into the South River watershed (SRW) from an acetate fiber manufacturing plant in Waynesboro, Virginia. Recent research has quantified negative effects of this contamination on fish and wildlife. Breeding songbirds are one taxa for which negative effects of mercury have been well-documented, and restoration opportunities are being sought both on the breeding grounds along the SRW, as well as on over-wintering grounds of migratory species. Here we report on research aimed at informing restoration of overwintering habitats for Neotropical migratory songbird species. Specifically, we (1) summarize literature suggesting the importance of winter habitat in limiting populations of these species; (2) summarize data on migratory connectivity with emphasis on potential linkages between SRW breeding birds and wintering habitats in Belize (where opportunities for restoration are being evaluated); and (3) analyze data from the Monitoreo de Sobrevivencia Invernal (MoSI) program in conjunction with remote-sensed habitat data to identify features associated with high-quality overwintering habitats. We focus summaries and analyses on eleven species that commonly breed in the southeastern United States (typical of the non-agricultural portions of the Shenandoah Valley) and over-winter in Mexico and Central America. Restoration opportunities are specifically being sought in Belize, and we summarize data with this in mind.

A growing body of literature suggests the importance of the non-breeding season in affecting the survival, reproductive success and population dynamics of Neotropical migratory songbirds. We found some degree of migratory linkage between Virginia and Belize for most target species, particularly for Wood Thrush, Hooded Warbler, Kentucky Warbler, and Common Yellowthroat. Belize and Virginia are both within a major migration corridor, and restoration in either of these areas would also provide important stopover habitat for migrating birds. Most target species occurred more frequently in habitats with greater vegetation structure and higher plant productivity (higher values of remote-sensed Enhanced Vegetation Index [EVI]), such as in evergreen broadleaf forest, than in shrubland, pine, and drier deciduous forest habitats. Only one of our target species, Common Yellowthroat, a species typically found in shrubland and marsh habitats, was more frequently encountered at sites with lower EVI compared to nearby sites. Although plant productivity tends to decline across much of the winter ranges of target species during the overwintering period (which spans the end of the wet season through the dry season), sites with relatively positive changes in plant productivity during this time appear to be associated with higher quality winter habitat for many species. We found that relatively positive changes in plant productivity were strongly associated with relatively positive changes in body mass between captures for birds captured multiple times during a winter season. Relatively positive average changes in plant productivity during the overwintering period were also associated with higher overwintering survival rates for three of nine target species with sufficient data for analysis (Wood Thrush, Gray Catbird, Worm-eating Warbler). Two species that were associated with a broader array of habitat types (Yellow Warbler and the Yellow-breasted Chat) had higher survival at sites with more negative change in productivity. Overwintering survival declined over the nine years of study for six of nine target species, and overwintering survival appeared to be correlated with annual survival for many target species. This highlights the need for including winter habitat restoration as part of an effective conservation strategy for migratory birds.

1. Introduction

Between 1929 and 1950 mercuric sulfate was released into the South River (a tributary to the South Fork Shenandoah River) from an acetate fiber manufacturing plant in Waynesboro, Virginia, USA (Carter 1977). Birds around the South River have since been shown to have had high mercury exposure (Cristol et al. 2008), and species studied in detail (e.g., Tree Swallow [*Tachycineta bicolor*] and Carolina Wren [*Thryothorus ludovicianus*]) appear to have relatively low reproductive success and survival rates, as well as behavioral and physiological impairments (Brasso and Cristol 2008, Condon and Cristol 2009, Hawley et al. 2009, Wada et al. 2009, Brasso et al. 2010, Hallinger and Cristol 2010, Hallinger et al. 2010, 2011, Jackson et al. 2011). Restoration options aimed at offsetting injury to birds and other wildlife in the South River watershed (SRW) from mercury contamination are currently under consideration.

Much of the work in quantifying the levels and effects of mercury on SRW birds to assess injury has focused on birds of forest-pasture edges. However, intact deciduous forest is the dominant historical land cover type in the region and supports a variety of migratory and resident bird species of conservation concern (USFWS 2008; Partners in Flight Species Assessment Database [http://www.rmbo.org/pif/pifdb.html]). Targeting forest habitats as part of SRW restoration efforts is important within a larger conservation context because obligate forest birds of the eastern United States have declined sharply in recent decades (U.S. NABCI Committee 2009, Sauer and Link 2011).

Mitigating effects of mercury contamination on SRW birds through restoration or conservation is complicated by the fact that many bird species found in the region spend only a small portion of their life cycle there. For example, about half of the bird species that breed in temperate forests of North America migrate to the Neotropics where they spend more than half the year. Many of these species are of high conservation concern and have suffered recent population declines. North American Breeding Bird Survey (BBS) data show that in the Appalachians Bird Conservation Region (see http://www.nabci-us.org/bcr28.html), within which lies the South River contamination site, 46% of Neotropical migratory bird species significantly declined, while just 30% of short-distance migrants and 13% of permanent resident species declined between 1966 and 2009 (Sauer et al. 2011). Only 13% of Neotropical migratory species significantly increased in the region over this time period compared to about half of all short-distance migrant and permanent resident species surveyed. The importance of emphasizing migratory species for conservation action is further supported at a national scale, where BBS data suggest that permanent resident species have increased by about 20% over the past 40 years, while short-distance, and especially long-distance, migrants tended to decline over this time period (Sauer and Link 2011). Thus, it is reasonable that an effective restoration plan for SRW birds should consider opportunities for conserving or improving overwintering habitats as well as habitats near the impact site.

2. Objectives

To inform restoration of breeding habitat for songbirds along the SRW, D. Cristol submitted an earlier draft report (circulated on 2/1/12) that reviewed literature on habitat restoration on temperate breeding grounds, summarized bird surveys conducted in the SRW in 2011, and provided information on bird-habitat relationships deriving from those surveys. A possible currency for ranking habitat types based on counts of detected birds and regional conservation scores for each species (http://www.rmbo.org/pif/pifdb.html) was also suggested. We provide an updated version of this report here in the Appendix.

Here we report on research aimed at informing restoration of overwintering habitats for Neotropical migratory songbird species that breed along the SRW. Specifically, we (1) summarize literature on the potential importance of winter habitat in limiting populations of these species; (2) summarize data on migratory connectivity with emphasis on potential linkages between SRW breeding birds and wintering habitats in Belize (where opportunities for restoration are being evaluated); and (3) analyze data from the Monitoreo de Sobrevivencia Invernal (MoSI) program in conjunction with remote-sensed habitat data to identify features associated with high-quality overwintering habitats. We focus summaries and analyses on eleven species that commonly breed in the southeastern United States (typical of the non-agricultural portions of the Shenandoah Valley) and over-winter in Mexico and Central America (Table 1).

Table 1. Eleven focal migratory bird species that breed in bottomland or upland deciduous forests or in riparian or successional habitats of the southeastern United States with wintering ranges that include Mexico and Central America. All species were detected on breeding point counts conducted along the South and South Fork Shenandoah Rivers between Waynesboro and Front Royal during 2005, 2006, or 2011. A general description of overwintering habitats where they occur is also given.

Species	**Winter habitat**
Wood Thrush (*Hylocichla mustelina*)	Tropical moist/wet forests, forest edges, shade coffee.
Gray Catbird (*Dumetella carolinensis*)	Forested, shrub/successional, forest edges, and wooded agricultural habitats.
Black-and-white Warbler (*Mniotilta varia*)	Forests (dry to wet), but also successional/disturbed areas, parks, plantations, gardens.
Yellow Warbler (*Setophaga petechia*)	Forested, shrub/successional, wooded agricultural habitats, parks. Common in mangroves.
American Redstart (*Setophaga ruticilla*)	Variety of forest types and other habitats with woody vegetation.
Hooded Warbler (*Setophaga citrea*)	Successional, forested and riparian habitats.
Worm-eating Warbler (*Helmitheros vermivorum*)	Forested habitats, shade coffee.
Ovenbird (*Seiurus aurocapilla*)	Variety of forested habitat types.
Kentucky Warbler (*Geothlypis formosus*)	Forested habitats, primarily Caribbean lowlands.
Common Yellowthroat (*Geothlypis trichas*)	Variety of shrub, successional, and wetland habitats.
Yellow-breasted Chat (*Icteria virens*)	Scrub and successional habitats. Also savannahs and forests with patches of dense shrub cover.

These species, in addition to their importance in SRW habitats, are commonly captured as part of the MoSI program. Several of these species, including Wood Thrush (Fig. 1), Worm-eating Warbler, and Kentucky Warbler, have suffered severe recent population declines and are of high conservation concern (USFWS 2008; Partners in Flight Species Assessment Database [http://www.rmbo.org/pif/pifdb.html]). Many of the remaining species have declined at regional or continental scales and have been identified as conservation priorities in Partners in Flight Physiographic Strata Plans and state Wildlife Action Plans. Finally, we summarize remote-sensed habitat data for Belize to guide restoration decisions.

Figure 1. Wood Thrush being banded at a Monitoreo de Sobrevivencia Invernal (MoSI) station in Belize.

3. The Importance of Winter Habitat for Migratory Bird Populations

Many Neotropical migratory bird species, including species that typically use forested habitats during the breeding season, can be found in an array of habitats in winter (Greenberg 1992, Rappole 1995, Piaskowski et al. 2005). However, patterns of site occupancy and abundance may provide misleading indicators of habitat quality (Marra and Holberton 1998). Winter habitat quality can be better gauged with such metrics as over-wintering apparent survival rate (site persistence), annual apparent survival rate, and body condition. These parameters have been intensively studied for a few species within limited geographic areas (e.g., Marra and Holmes 2001, Latta and Faaborg 2002). Yet, few data exist for most species, regions, and habitats (Faaborg et al. 2010). This dearth of data is disturbing because most natural habitats in the northern Neotropics are "vulnerable, threatened, or endangered" due to direct human impacts (Olson and Dinerstein 1998).

Climatic conditions, and in particular, rainfall has been related to the abundance, survival, and recruitment rates of Neotropical migratory songbirds on their wintering grounds (Sillett et al. 2000, Dugger et al. 2004). Birds occupying low-quality winter habitat may be forced to leave winter home ranges and suffer increased risk of mortality (Rappole et al. 1989) or reduced physical condition (Latta and Faaborg 2002). Birds that persist in low quality winter habitat may have relatively high mortality rates during late winter (when resources are often at a minimum) or during spring migration (Sillett and Holmes 2002). Furthermore, birds occupying low-quality overwintering habitat could arrive late or in poor physical condition on their breeding grounds leading to low recruitment into the breeding population or low reproductive success (Marra et al. 1998, Nott et al. 2002). Conditions experienced during the non-breeding season can drive survival rates (Mazerolle et al. 2005, LaManna et al. in review), reproductive success (Nott et al. 2002, Norris et al. 2004), and likely play a key role in effecting population changes (DeSante et al. 2001, Saracco et al. 2008b, Wilson et al. 2011).

4. Migratory Connectivity: Virginia-Belize Linkages

Restoration options for overwintering Neotropical migratory birds that breed in the SRW are being pursued in Belize. With this in mind, we summarized geographical migratory linkages in terms of the potential strength of connections between breeding and wintering areas in these two specific geopolitical regions for target species and populations.

4.1. Winter distribution overlap in migratory bird species that breed in Virginia

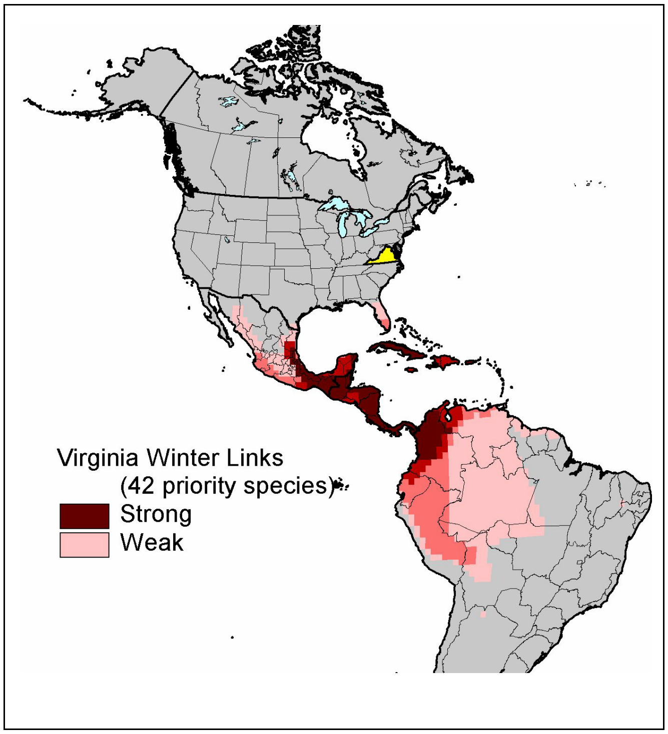

Figure 2. Migratory linkages represented as distributional overlap in winter ranges of migratory bird species of high conservation priority that breed in Virginia, USA (from Blancher et al. 2006).

Similarity in the distributions of priority (i.e., high Partners in Flight [PIF] ranking; Panjabi et al. 2001) migratory bird species between breeding grounds in Virginia and wintering grounds is strongest across a broad stretch that extends from Cuba and the Atlantic slope of Mexico through Central America, and northern Colombia (Fig. 2; Blancher et al. 2006). Although this community perspective does not distinguish migratory linkages of particular populations, it does provide a reasonable starting point for outlining the extent of the Neotropics within which conservation and restoration opportunities for South River birds might be sought out and effectively applied. From this perspective, Belize is well within the zone of strong species linkages with Virginia.

4.2. Band recoveries: a community-level view of migration

If we consider recoveries of banded individuals of migratory songbird species that breed in the South River region, very few data exist. Just 27 individuals banded during the breeding season (May-July) had been recovered south of the US during the winter months (October-April) as of 2009. Nevertheless, a general pattern emerges that suggests that birds that breed farthest east tend to overwinter in the Caribbean region (including eastern lowland Central America), while birds that breed farther west, tend to overwinter in Mexico and the Pacific Slope (Fig. 3).

Many of the species that winter in Belize migrate along the Eastern Flyway, which includes Virginia and other eastern states. Restoring wintering habitat in Belize will benefit the species that breed in Virginia (in the SRW), as well as birds that utilize the Eastern Flyway for migration, including those that stop in Virginia (and the SRW) to rest and feed en route to more northern breeding grounds. Conversely, restoring wintering habitat in Belize will also offer some benefit to Virginia-breeding species that are migrating to more southerly wintering habitats and stopping over in Belize.

4.3. Species-scale patterns of migratory connectivity

Technological advancements, principally the advent of small satellite transmitters, have greatly enhanced understanding of movements and migratory connectivity for large bird species. However, these transmitters are not yet lightweight enough for use on small songbirds. Nevertheless, basic understanding of linkages between breeding and wintering areas in these species can be obtained from a variety of sources, including band recoveries, stable isotope signatures in feathers, genetic characteristics (of birds or their avian parasites), and geolocators, as well as from geographical morphometric variation.

Below we summarize published information on migratory connectivity for each target species. In addition, we present results of analyses of wing-chord length data from birds banded as part of the Monitoring Avian Productivity and Survivorship (MAPS) program in temperate North America during 200-2006 (DeSante et al. 2004) and the MoSI program in the Neotropics during 2002-2011 (DeSante et al. 2005). Such analyses have been shown previously to be useful for lending insight into patterns of migration and migratory connectivity (Saracco et al. 2009). The specific approach used was a conditional spatial autoregressive (CAR) model (Besag et al. 1991) applied to wing-chord data from each monitoring program (1° resolution). Models were corrected for age-differences in wing-chord length as well as feather wear (Flinks and Salewski 2012). We analyzed models using Bayesian approach. We used uninformative prior distributions for all model parameters. We obtained posterior distributions of parameters by sampling full conditional distributions using Markov chain Monte Carlo (MCMC) methods (Gilks et al. 1996), as implemented in Posteriors were based on 30,000 iterations of two chains after discarding the first 10,000 iterations and thinning by 10. Models were run using the software program WinBUGS (Spiegelhalter et al. 2003) via the R2WinBUGS package (Sturtz et al. 2005) in R (R Development Core Team 2011).

The probability of population-level connections between Virginia and Belize seems to be high for many target species, particularly Wood Thrush, Hooded Warbler, Kentucky Warbler, and Common Yellowthroat. We feel that this finding makes a strong case for implementing restoration activities in Belize, as part of a larger program designed to offset injury to bird populations in Virginia.

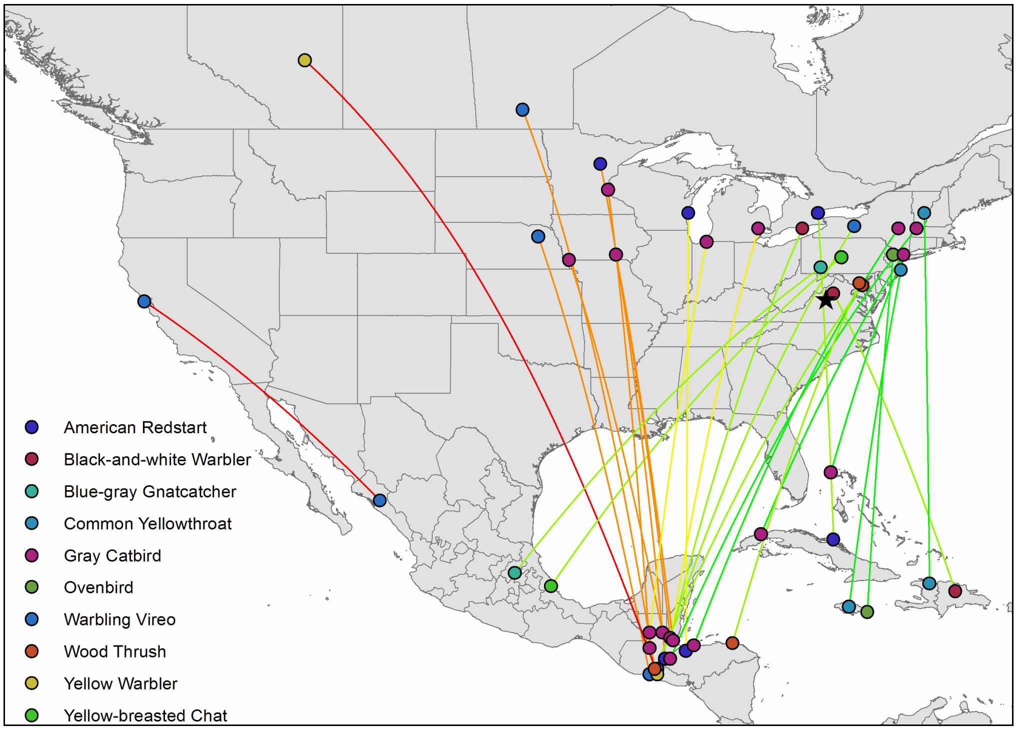

Figure 3. Band recoveries of 27 individuals of migratory bird species that breed in the South River, VA (indicated by black star) area that were banded during the breeding season in the US or Canada and recovered south of the US-Mexico border (data through 2008). Lines connecting banding and recovery sites are shaded along a color ramp that ranges from red (farthest west breeding site) to green (farthest east breeding site).

Wood Thrush.—Recent application of geolocator technology on this species have shown that breeding birds in north-central Pennsylvania overwinter in eastern Honduras and Nicaragua (Stutchbury et al. 2009). Analyses of MAPS and MoSI wing chord data suggest a leap-frog migration pattern with the longest-winged birds in the North/Northeast portion of the breeding range overwintering the farthest south and East in the winter (Fig. 4; note that wings were on average longer in the winter than in the breeding season). Unpublished geolocator data corroborate this pattern (B. Stutchbury pers. comm.) Collectively, these data support some degree of connectivity between SRW breeding birds and birds overwintering in Belize.

Gray Catbird.—Analyses of MAPS and MoSI wing chord data showed little evidence of spatial structuring of wing lengths of Gray Catbird that would suggest patterns of migratory connectivity. Based on analysis of band recoveries and geolocator data, Ryder et al. (2011) report linkages between breeding catbird populations in the Midwest U.S. and wintering populations in Guatemala and Belize. Birds of the Mid-Atlantic U.S. (north of Virginia) over-wintered in the Southeastern U.S., Bahamas, and Cuba.

Black-and-white Warbler. —Despite broad breeding and wintering ranges, this species is fairly monotypic across breeding and wintering ranges (Kricher et al. 1995). This suggests extensive mixing of populations (i.e. weak migratory connectivity). This is corroborated by analysis of MoSI and MAPS wing-chord data, which do not seem especially useful for resolving pattern in migratory connectivity.

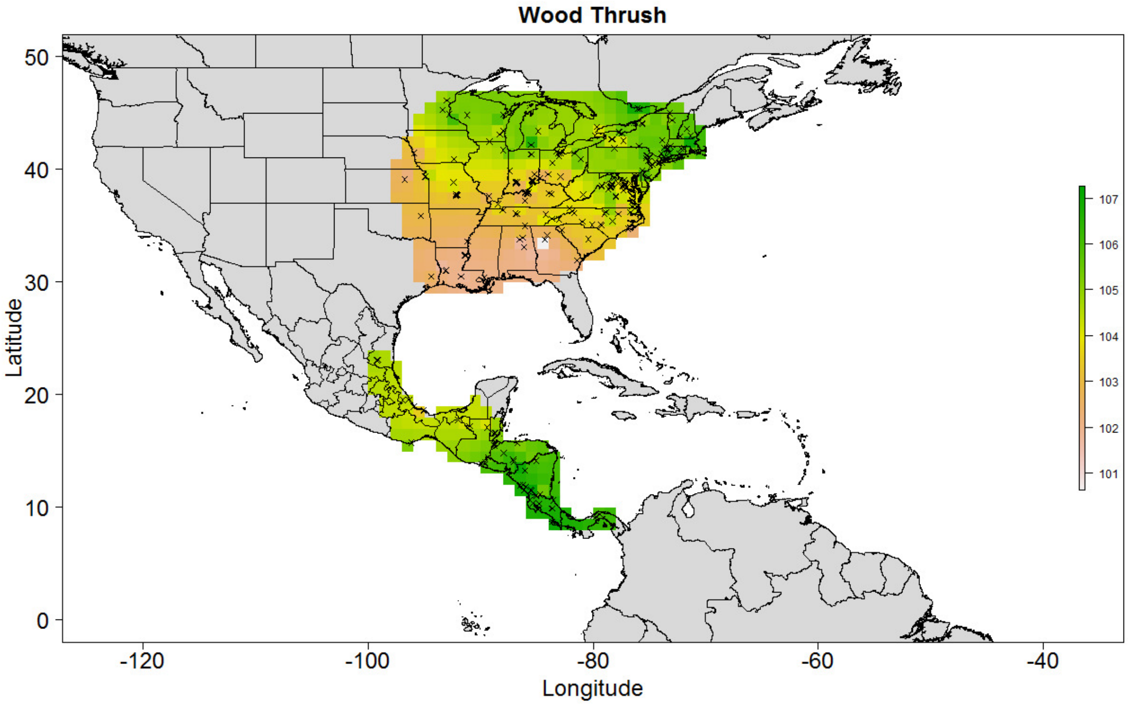

Figure 4. Predicted wing chord length for adult Wood Thrush based on spatial autoregressive models applied to 2000-2006 MAPS data (breeding range) and 2002-2010 MoSI data (winter range).

Yellow Warbler. —Yellow Warbler is comprised of a diverse assemblage of taxonomic groups and subspecies (Lowther et al. 1999). Breeding birds of the eastern U.S., including the SRW, are within the *D. p. aestiva* subspecies. The migration systems of the various subspecies are complex, and eastern birds (including *D. p. aestiva* subspecies) birds may overwinter anywhere from southern Mexico to northern South America (Boulet et al. 2006).

American Redstart. —Stable Hydrogen isotopic signatures suggest that American Redstarts that breed in central and southeastern U.S. likely overwinter in the Caribbean region (Norris et al. 2006). Samples collected in Belize suggested linkages most likely with the Midwest and Northeast U.S.

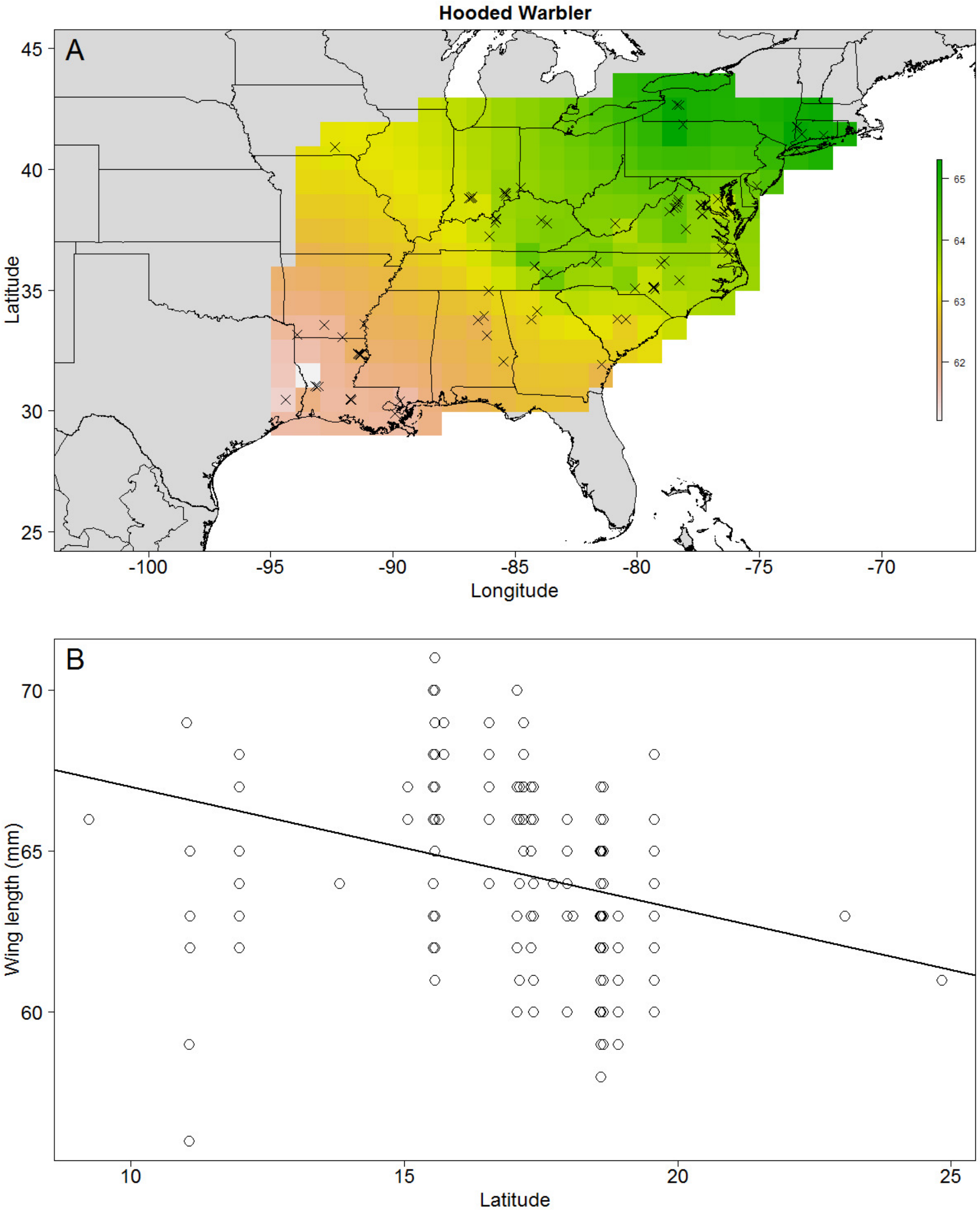

Figure 5. (A) Predicted wing chord length for Hooded Warbler across their breeding range based on spatial autoregressive model applied to MAPS data and (B) wing length by latitude on wintering grounds; line is fitted regression applied to these data. Predictions of winter wing length for a latitude within Belize (ca. 15°N) are similar to predicted values of breeding birds in Virginia (64-65 mm).

Hooded Warbler. —This species has relatively small breeding (mainly southeastern U.S.) and wintering (mainly Caribbean slope of Mexico and Central America and Cuba). Chiver et al. (2011) report little geographic variation in color or size. However, both MAPS and MoSI data show geographic variation in wing length. MAPS data show a gradient of increasing wing length from the southwest to northeast (Fig. 5A). MoSI data suggest that at the latitude of Belize (ca. 17°N), mean wing lengths are about the size predicted for bird in the SRW region (Fig. 5B). The species can be quite abundant in lowland wet gallery forest in Belize (Chiver et al. 2011, pers. obs.). Although sexes may segregate by habitat type (females more in scrub, successional; males more common in taller forest; Lynch et al. 1985, Morton et al. 1987, Conway et al. 1995), there does not seem to be larger scale geographic separation of sexes (J.F.S. unpublished data).

Worm-eating Warbler. —This species is reported to show little or no geographic variation (Hanners and Patton 1998), and we could find no information on migratory connectivity in the literature. The MAPS/MoSI wing chord map for Worm-eating Warbler suggests that birds that breed in the southern and western portions of the breeding range overwinter farthest north (Veracruz, Oaxaca, Chiapas) and that longer winged breeding birds of the Northeast overwinter on the Pacific Slope of northern Central America (Guatemala, El Salvador) and in the south (Panama). We lacked wing data from much of the Greater Antilles, however, where the species also overwinters (Fig. 6).

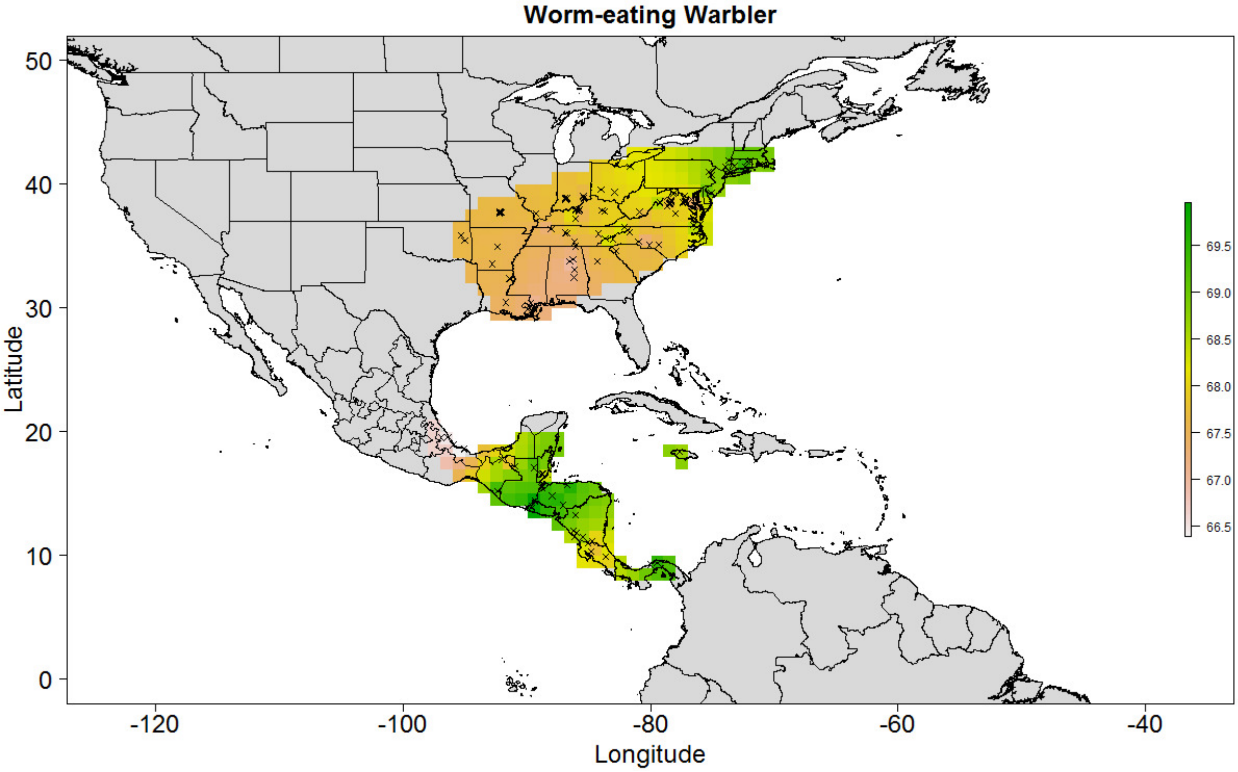

Figure 6. Predicted wing chord length for adult Worm-eating Warbler based on spatial autoregressive models applied to 2000-2006 MAPS data (breeding range) and 2002-2010 MoSI data (winter range).

Ovenbird. —Little is known about migratory connectivity in Ovenbirds. Three subspecies are recognized. Of these, the one that breeds in the SRW (*Seiurus aurocapilla aurocapilla*) may overwinter anywhere from Florida throughout the Greater Antilles, and in Middle America from the Yucatan Peninsula south through Panama and northern South America (Porneluzi et al. 2011). MAPS and MoSI wing-chord data do not seem to be especially helpful in adding insight into migratory connectivity in this species. The general pattern was for the shortest winged individuals to occur farthest west in the breeding range and northwest in the winter range and for the longest-winged individuals to occur in the northeast of the breeding range and on the Pacific Slope of Central America.

Kentucky Warbler. —Kentucky Warbler has a breeding and wintering range that is very similar to Hooded Warbler, and the two occupy very similar habitats during both the breeding and non-breeding seasons. MAPS and MoSI wing chord data suggest that breeding birds of the northeastern portion the breeding range likely overwinter in eastern portions of the winter range (Fig. 7). These data are consistent with migratory connectivity between Virginia and Belize.

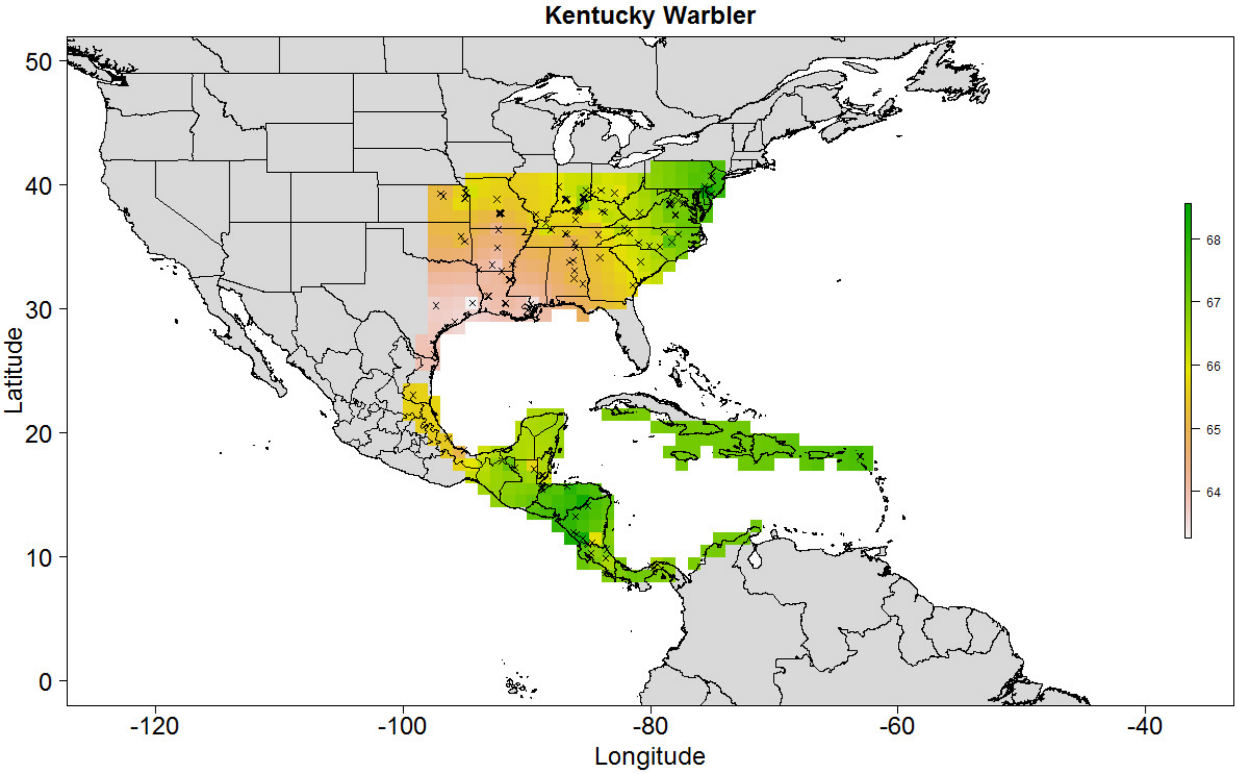

Figure 7. Predicted wing chord length for adult Kentucky Warbler based on spatial autoregressive models applied to 2000-2006 MAPS data (breeding range) and 2002-2010 MoSI data (winter range). These data are consistent with possible overwintering of SRW-breeding Wood Thrush in Belize.

Common Yellowthroat. —Genetic evidence of Common Yellowthroat and their malarial parasites show differentiation of lineages on the breeding grounds between the eastern and western U.S. (Ball and Avise 1992, Guzy and Ritchison 1999, Lovette et al. 2004, Pagenkopp et al. 2008). Southern populations are probably mostly sedentary; and migratory populations from eastern and western portions of the breeding range may overwinter in different areas. Mitochondrial DNA suggest that eastern breeding birds (likely including SRW populations) may overwinter in Central America, and 100% of 9 samples collected in Belize were from eastern breeding lineages (Lovette et al. 2004). Wing lengths from MAPS and MoSI data are consistent with the hypothesis that SRW, Virginia breeding birds overwinter from southern Mexico to at least Northern Central America (including Belize (Fig. 8; note that samples not available in southern-most parts of winter range), and possibly eastward in the Caribbean). Also of note, is that differences in wing lengths between breeding and migratory populations are consistent with differences in survival rates seen in MAPS data (Saracco et al. 2012).

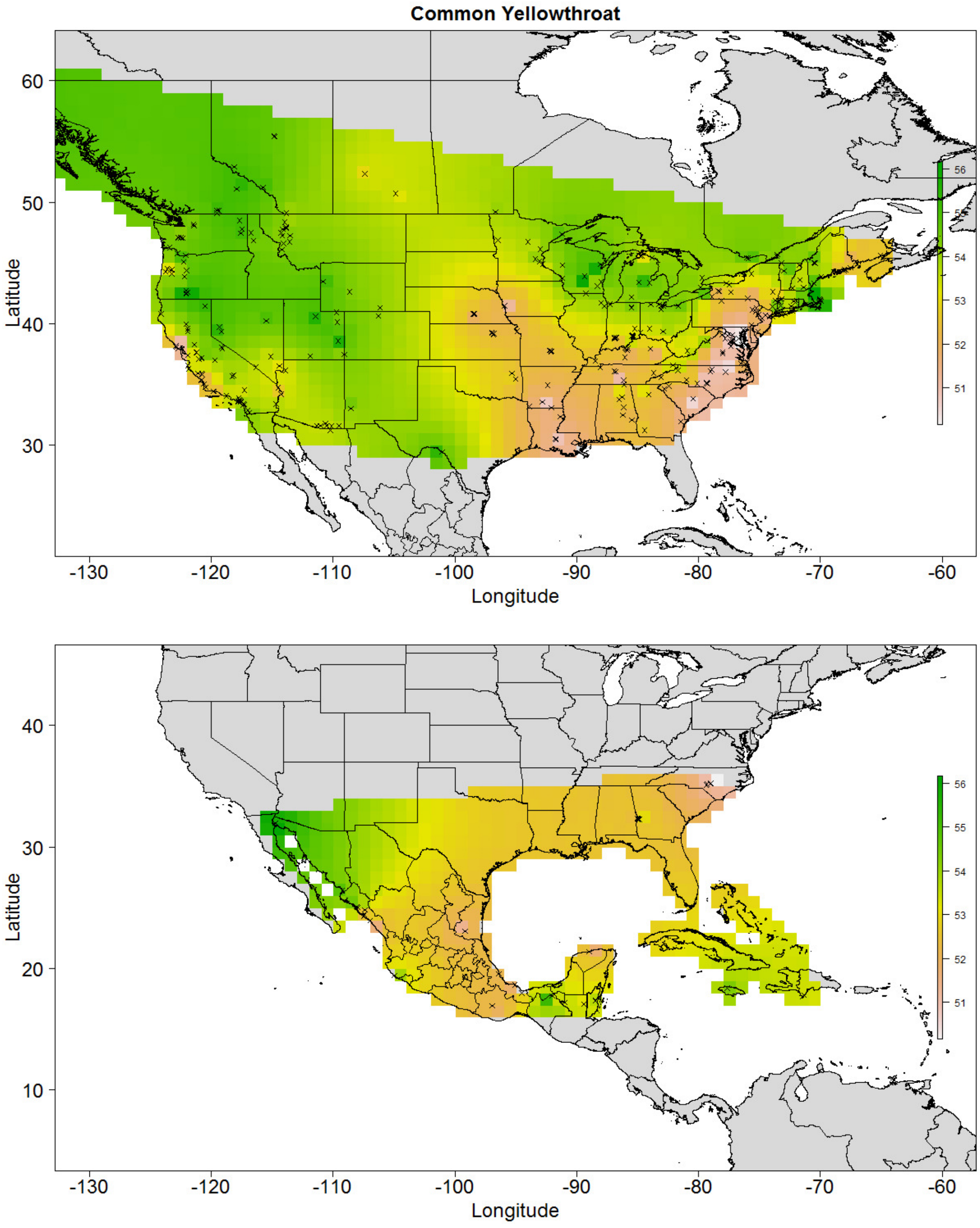

Figure 8. Predicted wing chord length for adult Common Yellowthroat based on spatial autoregressive models applied to 2000-2006 MAPS data (top; breeding range) and 2002-2010 MoSI data (bottom; winter range). Few samples were available from the wintering grounds, and no birds were recorded in the southern reaches of the winter grounds, which extend south through Costa Rica. These data suggest that SRW Wood Thrush likely winter southeast of Guatemala and Belize.

Yellow-breasted Chat. —Mitochondrial DNA data show broad separation of the disjunct eastern and western breeding populations of Yellow-breasted Chat (Lovette et al. 2004). Eastern breeding birds may overwinter largely in eastern and southern parts of the winter range, from Veracruz south through Central America, while western breeding birds may overwinter along the Pacific slope of Mexico from Baja California and Sinaloa south through Oaxaca.

5. Leveraging MoSI and Remote-sensed Habitat Data to Evaluate Winter Habitat Quality

In an unprecedented international effort to provide broad-scale data on migratory landbird habitat quality in the northern Neotropics, The Institute for Bird Populations (IBP) and partners across Mexico, Central America, and the Caribbean established the Monitoreo de Sobrevivencia Invernal (MoSI) program in 2002 (DeSante et al. 2005). MoSI consists of a spatially extensive network of mist-netting and bird-banding stations across the Neotropics that utilizes a standardized field protocol and state-of-the-art analytical techniques to make inferences about spatial and habitat-related variation in winter site persistence, annual survival, body condition, and migratory connectivity (Saracco et al. 2008a, 2009). More than 60 collaborators representing 14 countries have contributed data from > 180 MoSI stations during the first eight years of the MoSI program (Fig. 9). Many MoSI stations have been established and operated on sites designated as Important Bird Areas (IBAs), within state or national protected areas, and within various private reserves and agro-ecosystems (e.g., coffee plantations). This network of banding stations complements the highly successful Monitoring Avian Productivity and Survivorship (MAPS) program (Saracco et al. 2009), which since its establishment in 1989, has relied on a similar network of bird-banding stations to estimate avian demographic parameters of breeding birds in temperate North America (DeSante et al. 2004, DeSante and Kaschube 2009).

Here we present results of analyses of MoSI capture-recapture data in conjunction with remote-sensed habitat data to provide information on spatial variation in winter habitat quality for target SRW-breeding migratory landbird species. For habitat covariates, we used summaries of data derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument of NASA's Terra satellite, principally the enhanced vegetation index (EVI; MODIS product MOD13A2) summarized at 1-km^2 resolution (Glenn et al. 2008). EVI is a metric of plant productivity; it is particularly useful as it captures both structural (e.g., canopy architecture) and seasonal components of habitat quality. In contrast to other vegetation indices, such as the Normalized Difference Vegetation Index (NDVI), it exhibits improved properties of less saturation at high values (Huete et al. 2006, Xiao et al. 2004) and less sensitivity to clouds and smoke (Miura et al. 1998; Xiao et al. 2003). The exact relationship between MODIS EVI and vegetation conditions on the ground has not been studied extensively, but case studies have shown a tight relationship between EVI and vegetation conditions measured in the field, such as leaf area index (Glenn et al. 2008, Potithepa et al. 2010). We also included MODIS-derived International Geosphere-Biosphere Programme (IGBP) land cover type (MODIS product MOD12Q1; Friedl et al. 2002) as a covariate of detection probability in capture-recapture analyses and in body condition (mass-change analyses).

Summaries and analyses presented below include: 1) a comparison of mean January (i.e., mid-winter) EVI and mean early-to-late season EVI differences (EVI change) among sites with captures of a target species, capture sites where recaptures (between months or years) were also recorded, and nearby sites without captures recorded; 2) a summary of capture-recapture models that provide annual and within-winter survival for nine target species and relate within-winter survival to mean EVI change; and 3) an analysis of change in mass between captures in habitat covariates. To calculate mean EVI change, we subtracted the mean Feb-Apr EVI from the mean Oct-Dec EVI for each year and then averaged across years. Positive values of EVI change represent sites that become greener (i.e., have increasing productivity) over the winter period, while negative values represent sites that have declining plant productivity over the winter period. EVI change values for the entire MoSI region tended to be negative (mean = -0.040; intraquartile range = -0.071–0.002), as the overwintering period extends from the beginning to end of the dry season, and leaf-loss during the dry season can be high, especially in largely deciduous habitats. EVI does increase during the dry season in some regions, particularly in habitats that are not water limited and that might have persistent cloud cover during the wet season (e.g., some cloud forests, riparian rain forests). Mean January EVI was relatively high, and the mean winter EVI change was relatively positive, in Belize compared to much of the rest of Central America and Mexico (Fig 10).

Figure 9. Distribution of Monitoreo de Sobreviencia Invernal (MoSI) bird monitoring stations established and operated between 2002 and 2011.

5.1. EVI variation among no-capture, capture, and recapture sites

We examined mean EVI for the month of January and mean early-to-late season EVI differences (mean monthly Feb-Apr EVI - mean monthly Oct-Dec EVI) for each target species at all MoSI stations with at least 15 pulses of data (to minimize effects of imperfect detectability). We

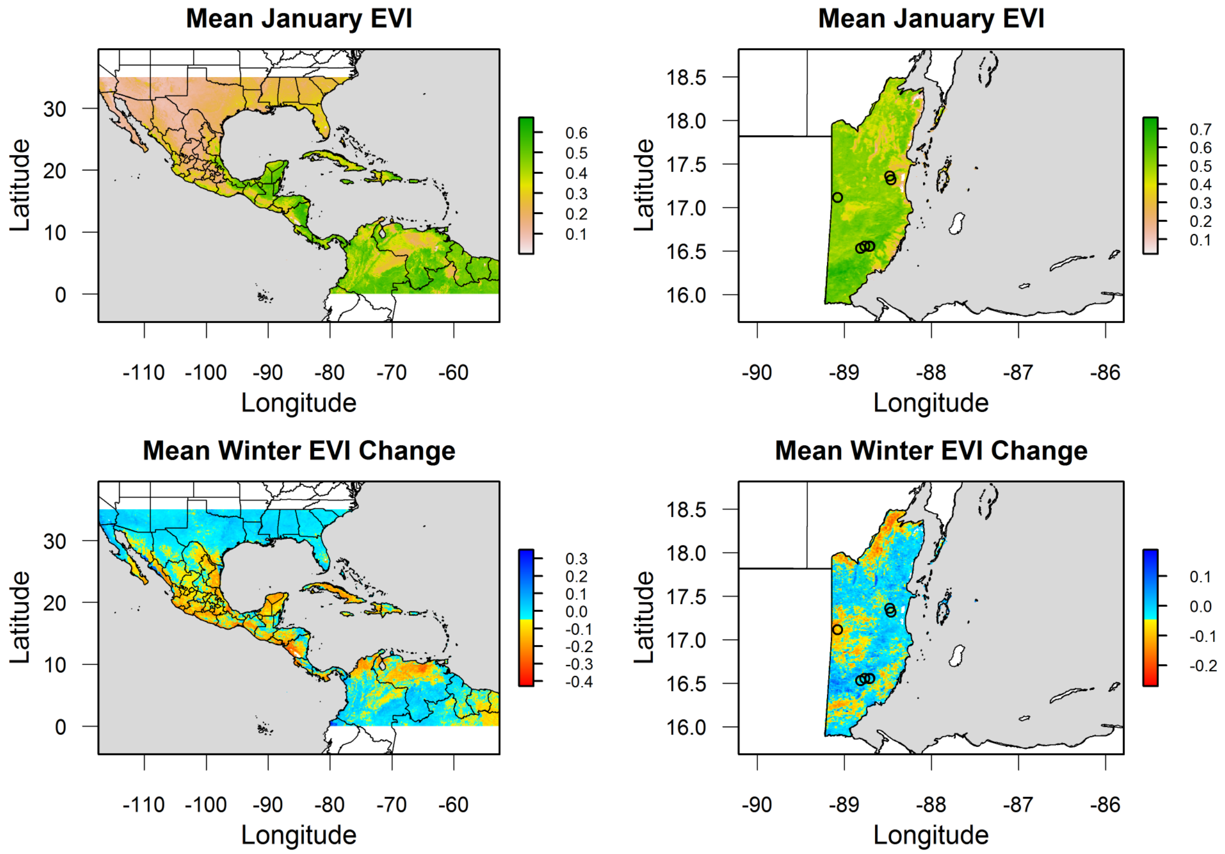

***Figure 10.** Enhanced Vegetation Index (EVI) data derived from the Moderate Resolution Imaging Spectroradiometer [MODIS] sensor on the NASA Terra satellite. Top panels show mean January EVI for 2003-2011 across the region (left) and for Belize (right). Bottom panels highlight spatial variation in seasonal change in EVI at the regional level (left) and for Belize (right). Dry forests and other arid habitats (red areas) lose leaves and so become less 'green' over the winter, while some humid areas that are not water-limited become greener during this time. Open circles on Belize map show locations of banding stations that contributed data to the MoSI program that were included in analyses presented here.*

summarized EVI mean values for 1) stations without captures, but located less than 160 km from a station where one or more individuals were captured (*No captures*), 2) all stations with one or more individual captures (*Captures*), and 3) all stations where one or more individuals were recaptured (*Recaptures*).

Plant productivity and vegetation conditions were typically poorer at sites without captures relative to nearby sites with captures for species common in evergreen broadleaf forests (e.g. Wood Thrush, Yellow Warbler, American Redstart, Worm-eating Warbler, Ovenbird, Kentucky Warbler, and Hooded Warbler; Fig. 11). Conditions did not differ between ‘No captures’ and ‘Captures’ sites for species more closely associated with edge, shrub, or more open wooded habitats (e.g. Gray Catbird, Black-and-White Warbler, Yellow-breasted Chat). Vegetation conditions were relatively poor in ‘captures’ relative to ‘No captures’ sites only for the Common Yellowthroat, a species that primarily inhabits shrub and early successional habitats. Mean EVI values for January between ‘Captures’ and ‘Recaptures’ sites differed mainly in variability, but mean values for each site category largely overlapped for all species (Figure 11).

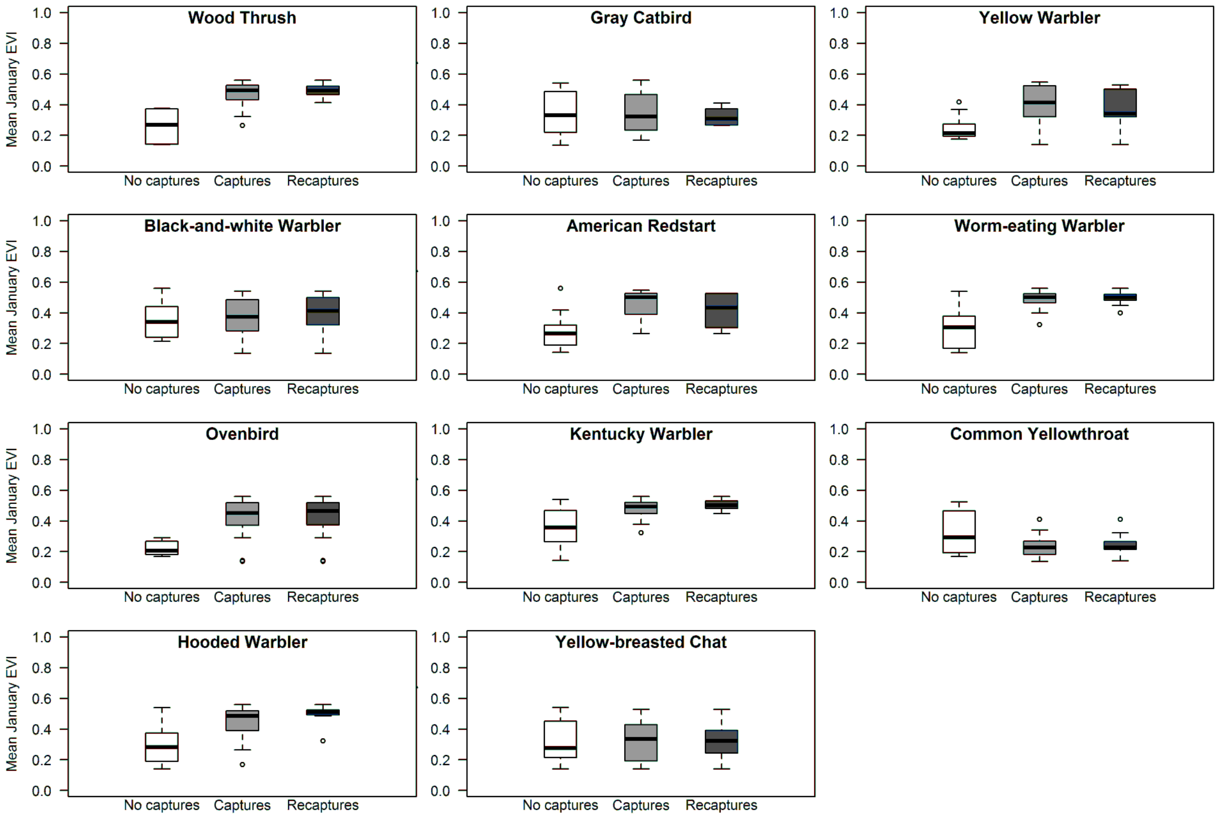

Figure 11. Mean January EVI across years for each target species at MoSI stations without captures but < 160 km (ca. 100 mi.) of a site with ≥ 1 capture ('No captures'), sites with ≥ 1 capture ('Captures'), and sites with ≥ 1 recapture ('Recaptures'). We only considered stations with at least 15 pulses of data.

Patterns of seasonal EVI change among sites without captures vs. sites with captures and recaptures were not as clear as for the mean January EVI (Fig. 12). Few species showed any indication that EVI change was more positive for sites with captures or recaptures compared to nearby sites without captures. Indeed, for several species, EVI change tended to be more negative at sites with captures and recaptures compared to nearby sites without captures (e.g., Yellow Warbler, Black-and-white Warbler, Ovenbird, Hooded Warbler). This could simply reflect the fact that sites with captures and recaptures for these species (at least all but Black-and-white Warbler) had much higher EVI values overall, and so change in EVI (which was largely negative) was also probably relatively greater.

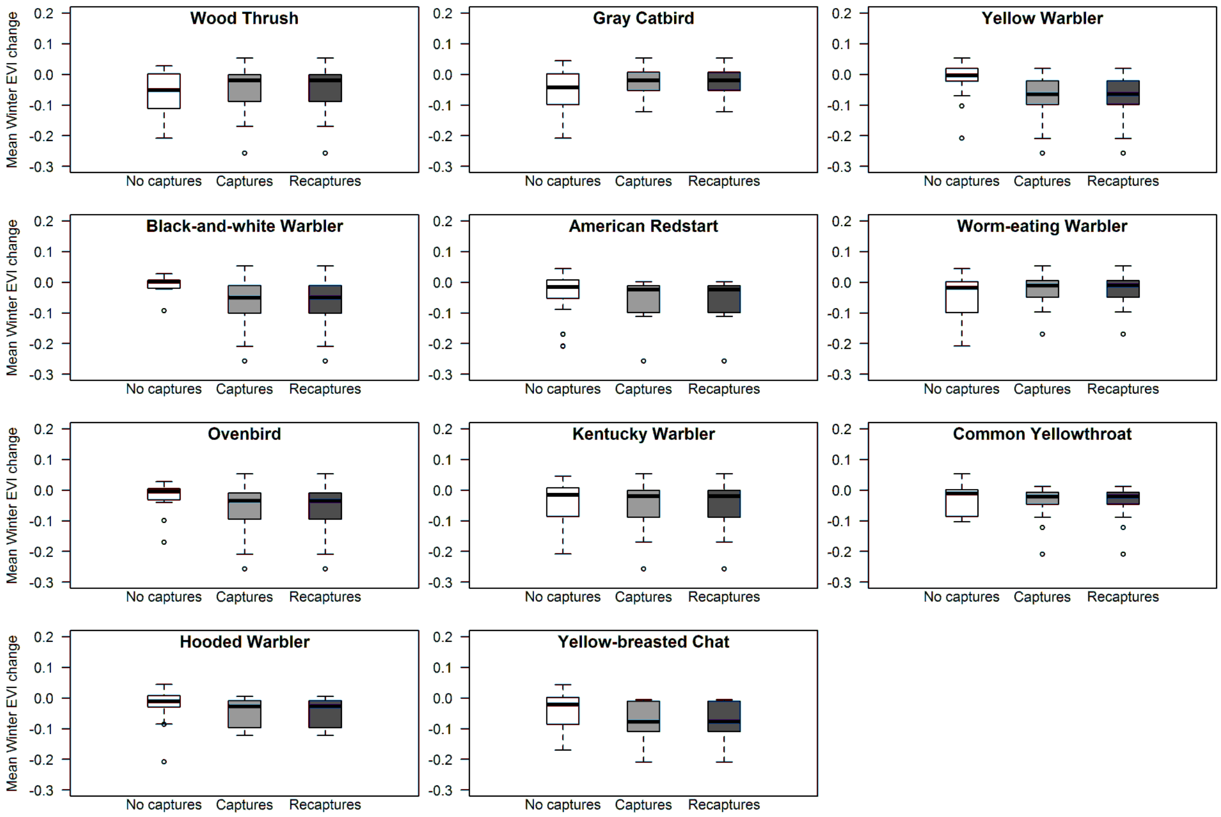

Figure 12. Mean change in EVI over the winter period for each target species at MoSI stations without captures but < 160 km (ca. 100 mi.) of a site with ≥ 1 capture ('No captures'), sites with ≥ 1 capture ('Captures'), and sites with ≥ 1 recapture ('Recaptures'). We only considered stations with at least 15 pulses of data.

5.2. Capture-recapture modeling

A core focus of our efforts to assess winter habitat quality has been the development of appropriate capture-recapture models to estimate apparent annual and within-winter survival rates and related parameters (e.g. probability of capture, probability of birds entering or leaving study areas between sampling occasions), and to model these parameters as functions of habitat variables. Previous efforts that made a variety of simplifying assumptions have suggested the potential importance of remote-sensed habitat features in affecting survival rates (e.g., Saracco et al. 2008a). However, our ability to apply more realistic and complex models has been limited by restrictions on the format and quality of banding information that these models require. Nevertheless, with assistance from experts and software developers in the field of capture-recapture data analysis, we now have working population models that can represent both open and closed population parameters, and are thus better-suited to the many complexities unique to our data set, including large spatial replication, missed visits, movements of individuals between our monthly sampling occasions, sparse data for many species and sites, and our hierarchical sampling design that includes both within- and between-season replication.

At this point, we have estimated annual and within-winter survival for all target species with a large-enough sample size using our most recent version of an open population survival model, called the Open Robust Design (ORD) model in Program MARK (White and Burnham 1999). This model has been successfully applied to estimate annual and within season survival of nesting sea turtles (Kendall and Bjorkland 2001) and survival of pond-breeding amphibians (Bailey et al. 2004), but has never been applied to estimate survival of migratory bird species. We modeled annual survival and recapture probabilities using the ORD model as constant or varying by year, and within-winter survival as constant, but modeled the rates during the first interval (e.g. Nov-Dec) as separate from all subsequent sampling intervals. In a second analysis, we focused specifically on estimating within-winter survival rates, and we were successful at incorporating remote-sensed habitat covariates by using a more sophisticated version of the ORD model. This version estimates within-winter apparent survival (e.g. probability that resident individuals will persist on the wintering grounds) and the initial proportion of resident and transient individuals at the start of sampling, including the subsequent probabilities of residents and transients to enter the study site between the monthly sampling occasions. Support for both analyses was evaluated using Akaike's Information Criterion for small sample sizes (AICc) in Program MARK.

5.2.1. Annual and overwintering survival.—Annual survival estimates for several target species were successfully estimated. Models which included time variation received more support from the data relative to models where survival was constant; time-dependent models received the lowest AICc values and were more than 2 AICc units away from constant models (Burnham and Anderson 2002). More importantly, these results show that annual and within-winter survival tends to be correlated, providing a strong argument for the importance of including winter restoration as part of a larger restoration effort (Fig. 13). In this analysis, we used a broad correction for differences in capture probabilities between habitats by including MODIS land cover type as a covariate. Future analyses will include remote-sensed EVI habitat covariates on capture probabilities, and more advanced optimization methods (e.g. Bayesian estimation) will be tried in order to model annual survival as a function of habitat covariates, which will make the best use of available data.

5.2.2. Within-winter survival for 'resident' birds and relationship to mean EVI change.—We estimated overwintering survival rates for resident individuals of nine target species (Table 2, Fig. 14) using a more flexible and advanced version of the Open Robust Design model described above in Program MARK. This model has the option to model "unobservable" states, and we defined two states in this analysis: "transient" and "resident" birds. Transient birds can be thought of as those passing through a station, either as a passage migrant or wanderer (i.e. non-sedentary overwintering bird), while residents would be defined as those individuals attempting to over-winter at the station. Because we are not able to assign individuals with certainty to either state (e.g. unobservable), all individuals are designated as "unknown", and the model itself decides the probability that each individual is a transient or a resident bird. This allows us to model within-winter survival rates for individuals designated as residents, and provides a more robust measure of survival because it corrects for the fact that transients might be captured more than once during a season. We modeled within-winter survival as a function of the mean difference in EVI values between the early and late sampling season, and include fixed-effects to correct for differences between years and broad IGBP habitat classifications. We also included an additive effect of year of sampling and mean difference in EVI values, in order to see if the effect of EVI varied slightly by year. We did not have enough data to test for an interaction across years, but we hope to model this in the future. We modeled the probability of entry to a study site for transient and resident individuals as a function of latitude, MODIS land cover type, and the mean difference in EVI values used previously in the survival parameters. Recapture probabilities were modeled using the same covariates as probabilities of entry, with the exception of latitude. The estimate of proportion of resident individuals was not modeled using covariates, but a fixed effect of station and year will be included in future analyses, as well as remote-sensed habitat covariates.

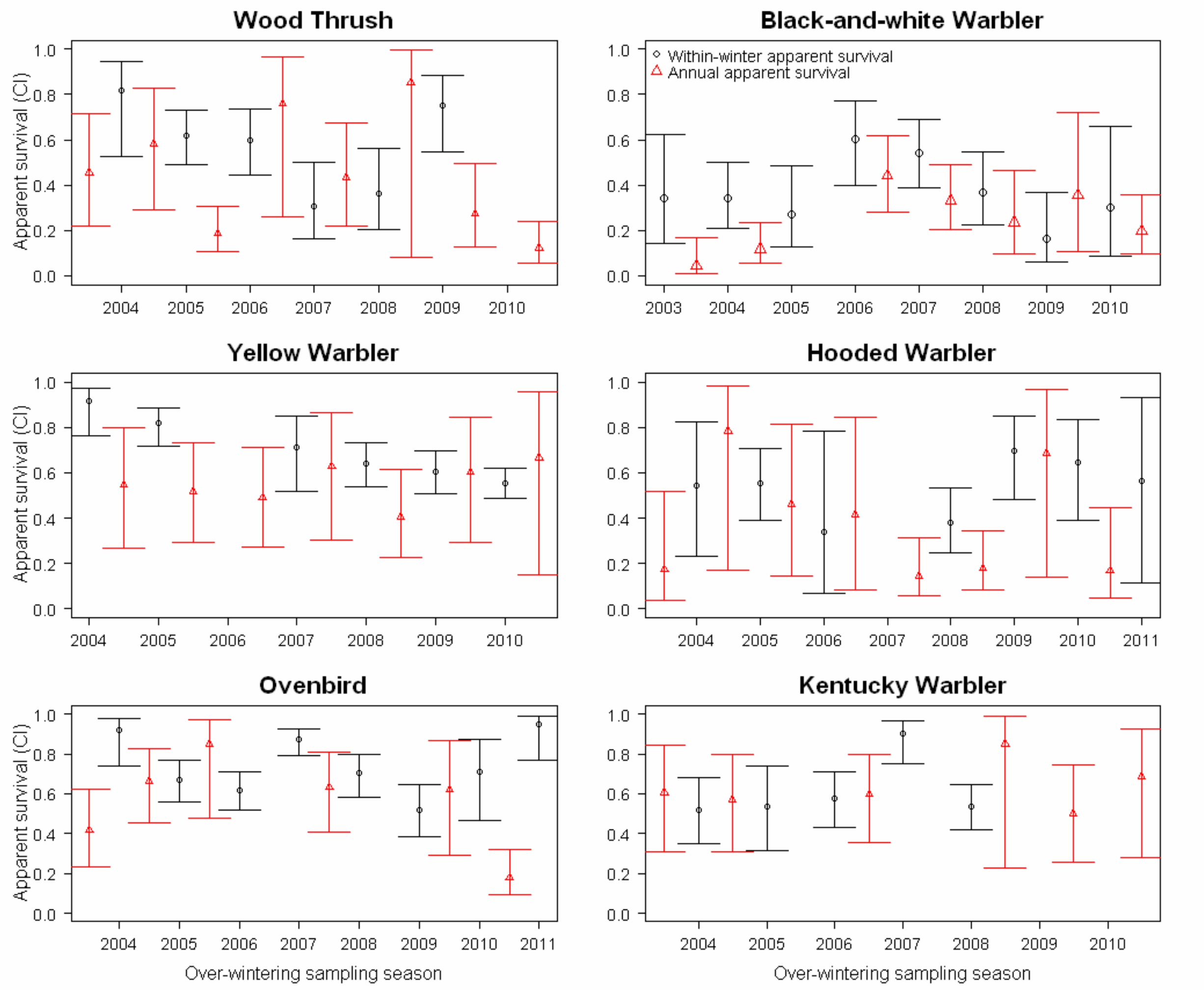

Fig. 13. Estimates of annual and within-winter apparent survival from the MoSI program for six target species from winter 2003-04 through 2010-11. Estimates of within-winter survival (red) are for each winter sampling season (2003-2010), and apparent annual survival (black) is estimated at intervals between sampling seasons (e.g. 2003 to 2004). Missing values indicate that not enough recaptures were generated across stations during that sampling period to estimate survival probabilities.

We found support for a positive relationship between within-winter survival and changes in EVI values over a sampling season for three of the nine species we were able to analyze (Table 2); AICc values for models that incorporated changes in EVI were lowest and greater than 2 AICc units away from models without this effect. For two of the three species, we found support for an additive effect of year and mean EVI differences (Fig. 14). These three species- Wood

Thrush, Gray Catbird and Worm-eating Warbler- are considered to depend mainly on forested habitats and wooded agricultural land uses (e.g. shade coffee) on their wintering grounds.

Table 2. Summary of results for annual and within-winter survival of resident individuals for 9 target species from winter 2003-04 through 2010-11. The second column summarizes the effects of habitat (difference in mean EVI) and sampling season (Year) for within-winter survival. Effects are defined as positive (+), no effect (N), and negative (–). For mean EVI change, "+" indicates that survival increases as EVI change becomes more positive, and "–" indicates that survival declines with more positive EVI change. The "Annual survival" indicates if annual apparent survival estimates were also estimated for that species (Y) or if there was not enough information to estimate survival and recapture probabilities (n/a).

	Within-winter survival		**Annual survival**
Species	*Mean EVI change*	*Year*	
Wood Thrush (*Hylocichla mustelina*)	+	–	Y
Gray Catbird (*Dumetella carolinensis*)	+	–	n/a
Black-and-white Warbler (*Mniotilta varia*)	N	–	Y
Yellow Warbler (*Setophaga petechia*)	–	–	Y
Hooded Warbler (*Setophaga citrea*)	N	–	Y
Worm-eating Warbler (*Helmitheros vermivorum*)	+	N	n/a
Ovenbird (*Seiurus aurocapilla*)	N	–	Y
Kentucky Warbler (*Geothlypis formosus*)	N	+	Y
Yellow-breasted Chat (*Icteria virens*)	–	N	n/a

Therefore, winter restoration efforts are very likely to have a positive effect on migratory bird populations if priority is given to forested habitats for which EVI is high, consistent, or tends to increase during the wintering season. Because our results have shown that annual survival appears to be linked to within-winter survival (Fig. 14), an increase in within-winter survival driven by habitat restoration is likely to positively influence annual survival rates for these and other species with similar habitat affinities. We did not have enough support for an effect of vegetation conditions for four species. We found a negative effect of EVI change on survival for two species- the Yellow Warbler and the Yellow-breasted Chat. These results do not come as a surprise given that they are associated with a wide-range of habitat types, from forested to more open-habitat types (e.g. shrubs, savannahs, and succession habitats), creating a broad range of EVI values for which they are found to persist in their wintering grounds. In addition, for Yellow Warbler at least, which seem to occupy areas with much higher EVI values relative to nearby sites (see Fig. 11), sites with large negative EVI change might reflect large increases in EVI at these sites during the rainy season rather than relatively large amounts of leaf loss.

An interesting finding was the negative effect of year of sampling for six of the nine species (Table 2). This trend of decreasing survival over time is also evident, to a lesser extent, in our results on annual survival rates (Fig. 11). The declining trend is most evident in the Wood Thrush and Yellow Warbler. Both of these species appear to be suffering population declines on their breeding grounds, both over the duration of the MoSI data set and over the past 40+ years (Sauer et al. 2011). Both Black-and-white Warbler and the Ovenbird appeared to have declining survival after 2006. Future analyses will test for the significance of a trend effect on annual survival for both annual and within-winter survival, and quantify the extent to which these trends are linked temporally.

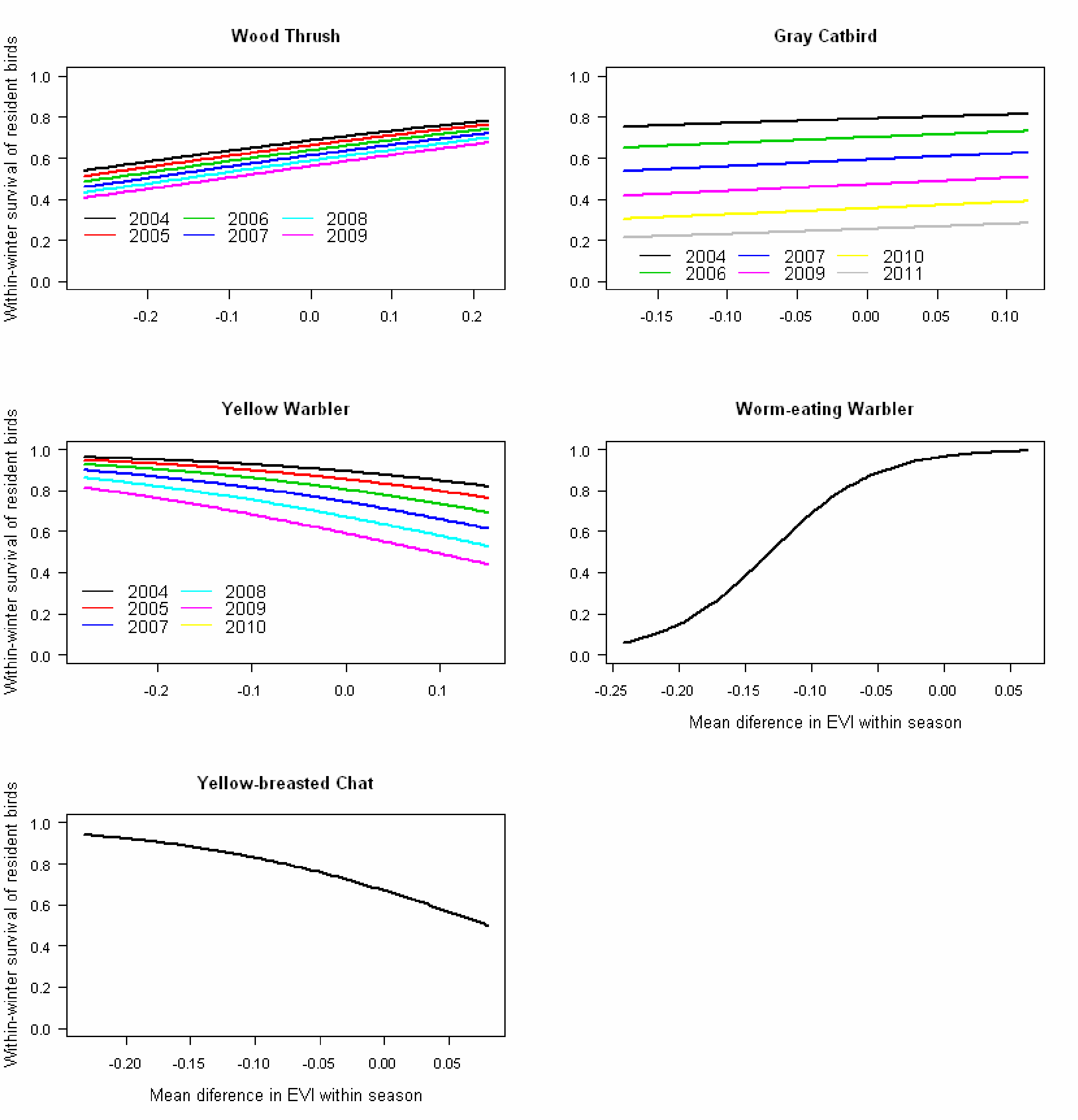

Fig. 14. Estimates of within-winter apparent survival from the MoSI program for six target species from winter 2003-04 through 2010-11. Within-winter survival was modeled as a function of the mean difference in EVI scores between early (October, November and December) and late season (January, February, March) during a sampling season. Predictions for each overwintering sampling season (e.g. 2004 = 2003-2004) are shown for those species where an additive effect between mean difference in EVI and sampling season was supported by the data.

5.3. Analysis of mass-change data

For each individual that was captured multiple times and at least one day apart within a season, we estimated change in mass as the difference between the current capture mass and the closest prior capture mass. We standardized mass changes by dividing the total change in body mass by the number of days between captures, to get a daily rate of mass change. We modeled average daily mass change (*Δmass*) as a function of environmental covariates, including the mean (*Mean.EVI*) and standard deviation of EVI (*SD.EVI*) in the month and station of recapture across years, change in these variables between month of recapture and closest previous capture (*Mean.EVI.change* and *SD.EVI.change*), EVI score for the month, year, and station of first capture (EVI.month), and the change in EVI between the month, year, and station of first capture, and the month, year, and station of recapture (*EVI.month.change*). We also included log(elevation), as well as fixed effect to control for variation among species (*spec*), and covariates to control for time of day (*t.day*) and day of season (*dos*) of the recapture. All continuous covariates were scaled to mean 0 and unit variance to facilitate estimation and interpretation of effects. We ran all possible additive combinations of these variables by applying the ’dredge' function of the multi-model inference (MuMIn) package (Kamil 2012) to regression models run using the 'lm' function in R (R Development Core Team 2011). We evaluated the relative importance of each of the remote-sensed habitat covariates by summing AICc model weights across all models in which the factor of interest was present (Burnham and Anderson 2002). Regression coefficients for each covariate were also model-averaged across all evaluated models.

We estimated 1,703 differences in body mass for 1,032 individuals from 2002-2009. For most recapture events, we did not detect a change in mass (*n* = 961), and we detected marginally more average daily mass gain events (*n* = 425) relative to mass loss events (*n* = 317). Our results could be influenced by the precision of the equipment used to weigh individuals, as well as the fact that we had to exclude 1,032 capture records because body mass at capture was not recorded. These factors could potentially limit our ability to fully characterize the habitat covariates that most influence changes in mass in migratory birds on their wintering grounds.

All of the remote-sensed habitat covariates had a positive effect on daily change in body mass, corrected for species, latitude, time of day, and day of sampling. The change in EVI score between the month of recapture and the month of initial capture (*EVI.month.change*) received the most support from the data, with a cumulative AIC score of 0.99, and a coefficient of 0.0616 (Fig. 15). None of the other factors received more than 50% support (cumulative AIC weights > 0.5), and the data did not indicate any support for an effect on average daily change in mass.

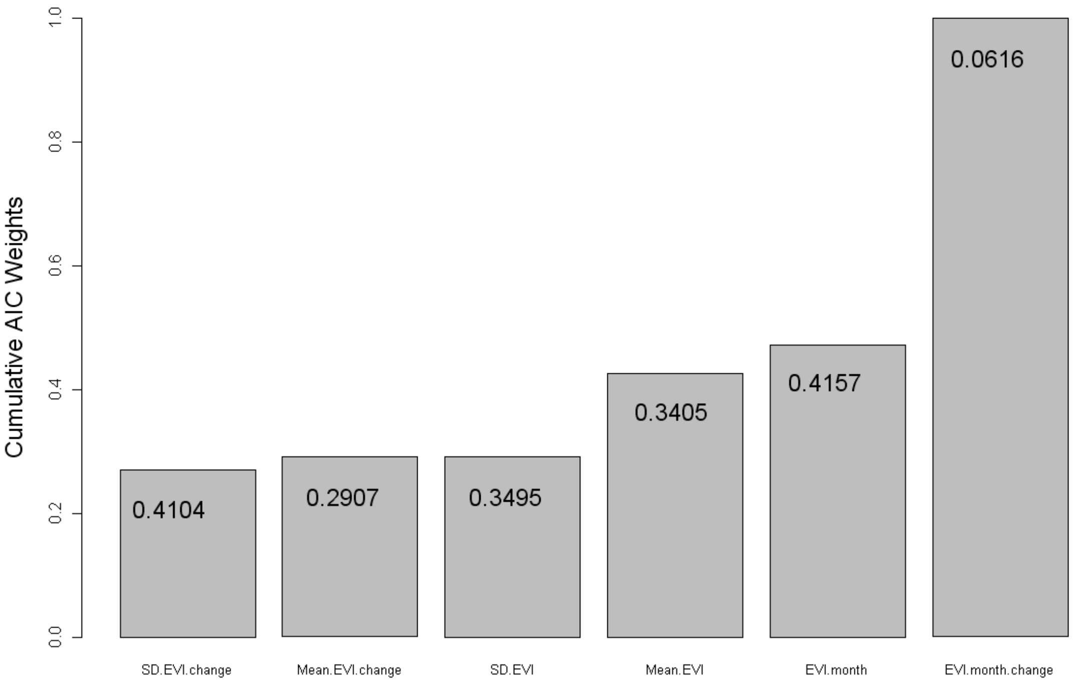

Figure 15. Relative support (Cumulative AIC weights) for each remote-sensed habitat covariate on change in body mass, across 11 migratory bird species that breed in the Shenandoah Valley region of Virginia, USA. Habitat variables are for the month and/or year each individual was recaptured, and changes in these variables (e.g. EVI.month.change) were estimated between the current recapture month, and the previous month of recapture, within a season. The model averaged coefficient for each variable is presented in bold.

As an example of the expected daily rate of change in body mass as a function of change in EVI between captures we present a predictive plot for change in body mass for Wood Thrush as a function of EVI change in Figure 16. One aspect of interest is that the predicted change in body mass across a broad range of EVI change is positive. This is not surprising, as birds captured early in the season are likely recovering from diminished body condition following migration, while birds recaptured later may have replaced reserves after a sedentary period on the wintering grounds. Figure 16 suggests that a -0.1 change in EVI over a period of 2 months (between January and March) would yield an increase in body mass of about 6 g (ca. 13% of mean body mass for this species), whereas a +0.1 change would yield an increase of ca. 7 g (ca. 15% of mean body mass). Although a seemingly a small difference, small changes in body mass over the wintering period have been shown to affect departure dates and subsequent productivity in American Redstarts (Marra et al. 1998), and such effects might be expected for other species as well.

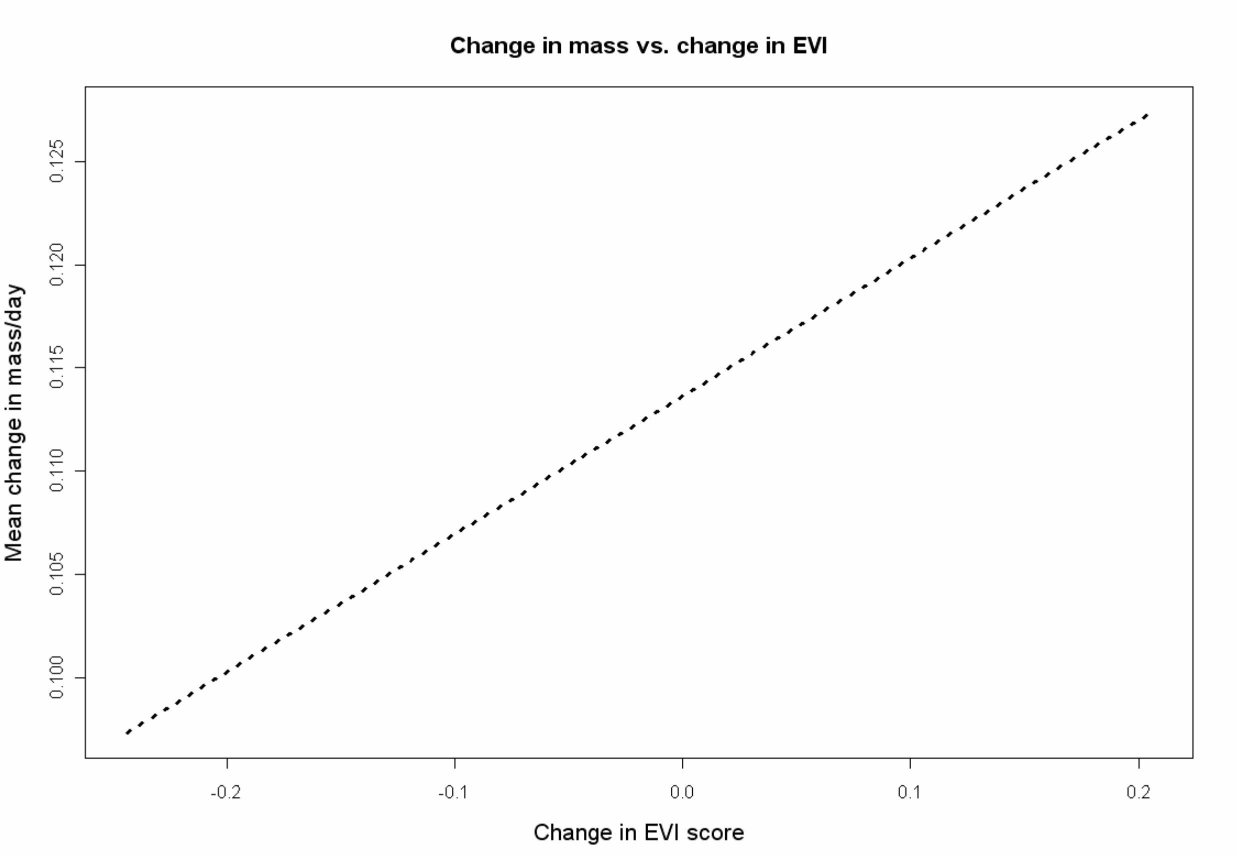

Figure 16. Predicted daily mass change for Wood Thrush as a function of change in the enhanced vegetation index (EVI) between captures for the month of initial capture of January at a central latitude in Belize and for mean values of all other covariates.

6. MODIS EVI Variation and Land Cover in Belize

To aid in selection of potential sites for land acquisition and to provide guidance for identifying appropriate target land cover types as endpoints for restoration, we show the distribution of mean January EVI as a function of landcover types based on two land cover classification systems. The first land cover classification system follows International Geosphere-Biosphere Programme (IGBP) and was based on data collected from the MODIS sensor on the NASA Terra satellite (Friedl et al. 2002). The second classification system is based on UNESCO ecosystems modified for application to Central America and was based on a combination of remote-sensed data and data collected in the field (Meerman and Sabido 2001, Vreugdenhil et al. 2002). UNESCO-Central America vegetation classes were updated for Belize in 2004 and those are the data that we report here (downloaded from http://biological-diversity.info/Ecosystems.htm). Transformations of spatial projections, data manipulations, and summaries were accomplished using functions in the 'raster' (Hijmans and van Etten 2012), 'rgdal' (Keitt et al. 2012), and 'sp' (Pebesma and Bivand 2005, Bivand et al. 2008) packages in program R (R Development Core Team 2011).

Maps showing the distribution of land cover and ecosystem types for Belize are presented in Figure 17. Belize is the most forested nation in Central America, and based on IGBP land cover categories, 88% of classified 1-km2 cells in the country were classified as evergreen broadleaf forest. This land cover type had a higher mean January EVI value than all other IGBP land cover classes (Fig. 18). Needleleaf forest and shrubland habitats had relatively low mean January EVI values. The cropland/natural mosaic land cover type had a similar (albeit slightly lower) distribution of EVI values to evergreen broadleaf forest. However, cropland/natural mosaic had the most negative EVI change over the winter period. Croplands, savannas and grasslands also had relatively more negative mean winter EVI changes compared to shrubland, wetland, and forested habitats. Other habitat types had similar distributions of EVI change (all close to zero).

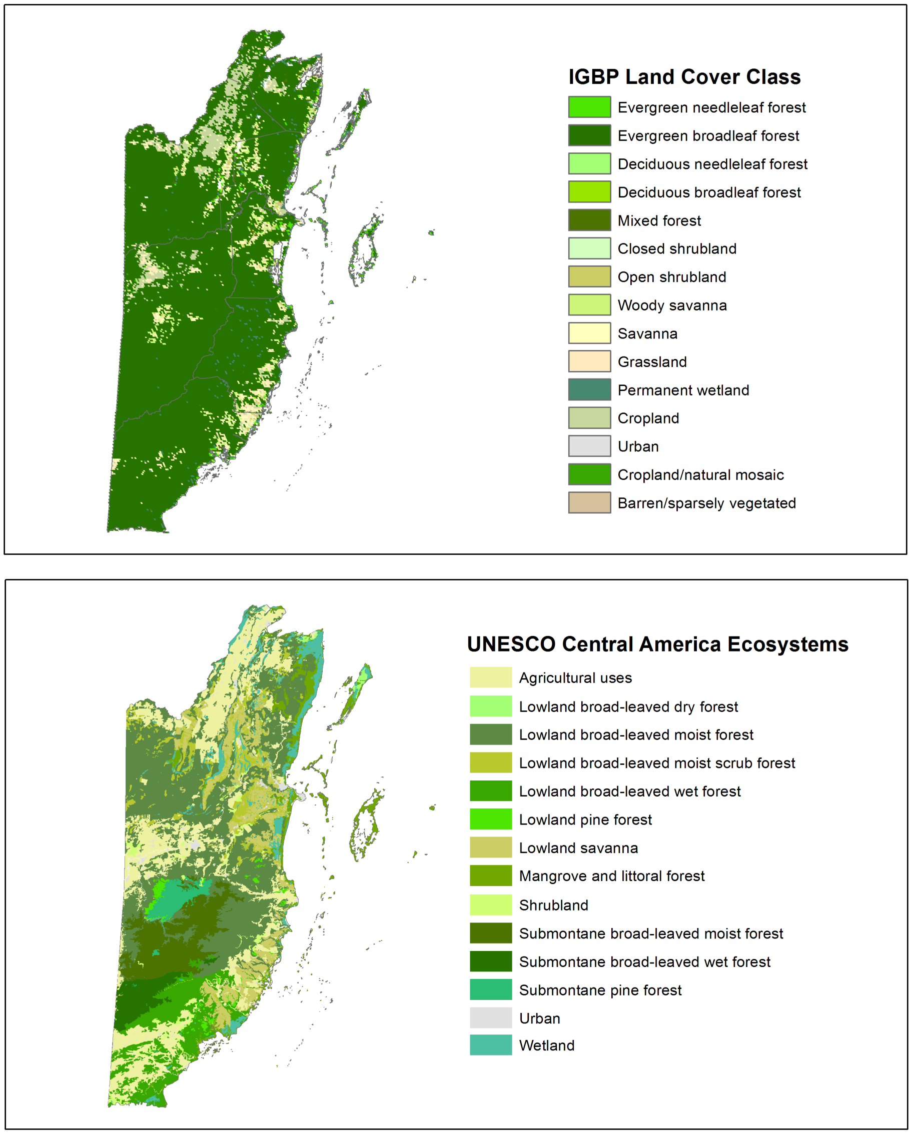

Figure 17. Spatial distribution of land cover in Belize based on International Geosphere-Biosphere Programme (IGBP) land cover class (top) and UNESCO Central America ecoysystem types.

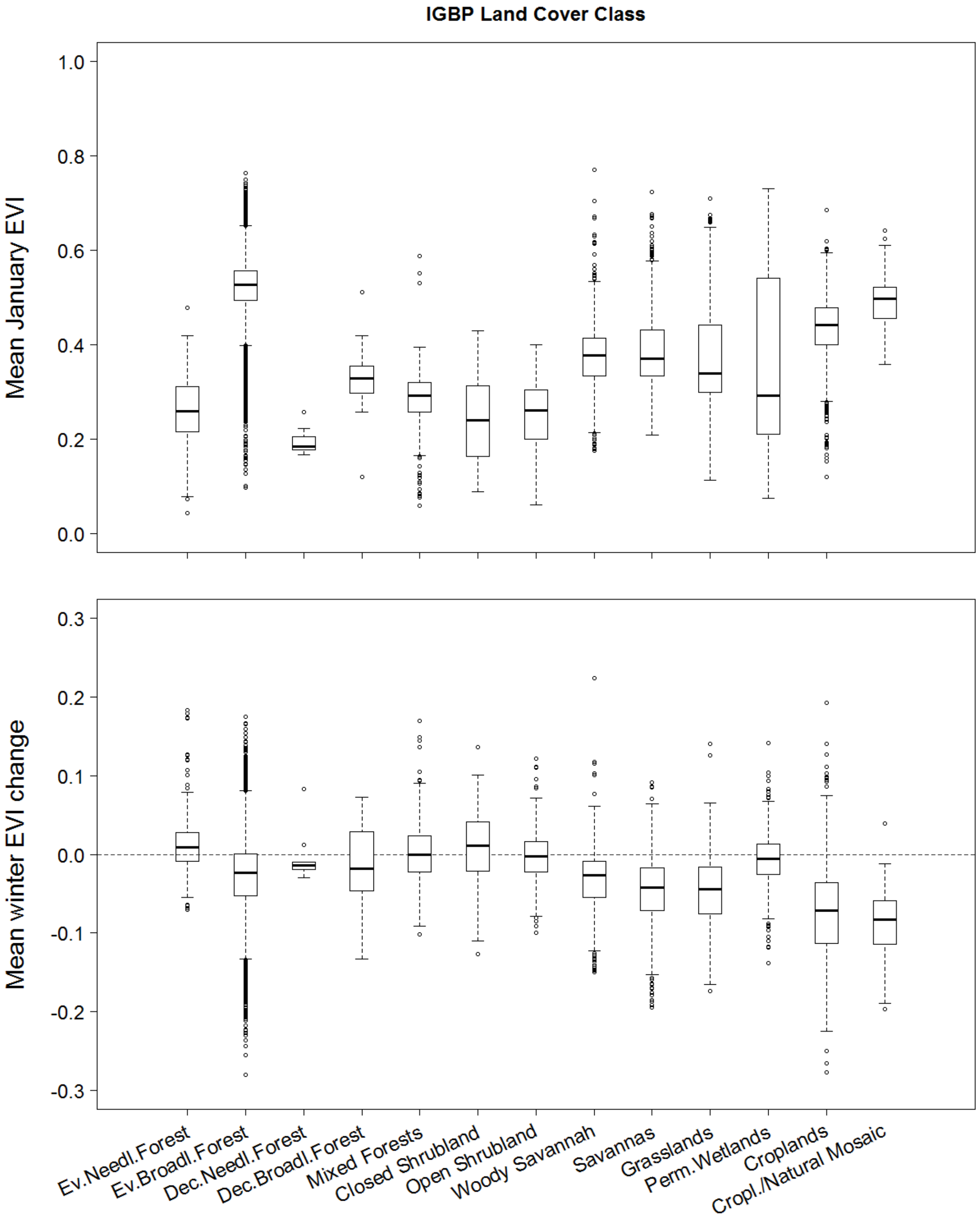

Figure 18. Distribution of mean January EVI and mean winter EVI change in relation to International Geosphere-Biosphere Programme (IGBP) land cover class based on 1-km^2 MODIS data for Belize.

If we consider UNESCO Central America vegetation classes, mangrove/littoral forests had the highest mean January EVI values and shrubland habitat had the lowest mean January EVI value (Fig. 19). Most positive mean winter EVI changes were observed for submontane broadleaf wet forest, while the most negative changes were for agriculture and lowland broadleaf dry forest habitats.

7. Discussion

A large number of species that breed in the Shenandoah Valley of Virginia overwinter in Belize. At the population level, we found strong support for connectivity between Virginia and nearby states and Belize for most target species considered. In addition to linkages between Virginia's breeding bird populations and birds overwintering in Belize, it should be stressed that Belize is also a major migration route for many Neotropical migratory songbird species (Bayly and Gómez 2011), and a variety of habitats in Belize are used by large numbers of passage migrants for resting and refueling during their migratory journeys (Gómez-Montes and Bayly 2010). The Appalachian Mountain region of Virginia is also along a major migration corridor of the Eastern U. S. and many birds that over-winter or migrate through Belize may also stopover in habitats in Virginia.

Although target species considered in our analyses occupy a variety of habitats during the non-breeding season, we found some consistent patterns that should guide coarse-grained restoration decisions for application on the wintering grounds. First, most target species occurred more frequently in habitats with greater vegetation structure and higher plant productivity (higher EVI values), such as in evergreen broadleaf forest, than in shrubland, pine, and drier deciduous forest habitats. Only one of our target species, Common Yellowthroat, a species typically found in shrubland and marsh habitats, was more frequently encountered at sites with lower EVI compared to nearby sites.

Second, relatively positive changes in body mass during winter were associated with sites that were stable or that increased in EVI over the winter period; e.g., wetter forests such as riverine habitats that retain moisture well and wetland habitats. Dry habitats that experience high leaf loss during the overwintering period may be of relatively poor quality, as birds may not be able to put on adequate fat prior to spring migration. This could cause delayed departure from wintering grounds and negatively affect reproductive success in the subsequent breeding season (Marra et al. 1998, Smith et al. 2010).

Drying and lowered plant productivity over the winter period can also negatively affect survival. We found a strong positive relationship between change in EVI over the winter and winter survival rates of resident birds for three of nine species examined (Wood Thrush, Gray Catbird, and Worm-eating Warbler). Winter survival rates tended be correlated with annual survival rates (although covariation was not specifically modeled). Annual adult survival rates can be a key demographic driver of population dynamics in Neotropical migratory species (Noon and Sauer 1992, Woodworth 1999, DeSante et al. 2001, Saracco et al. 2008b). There are existing data for a few species that suggest the importance of winter precipitation and plant productivity in affecting

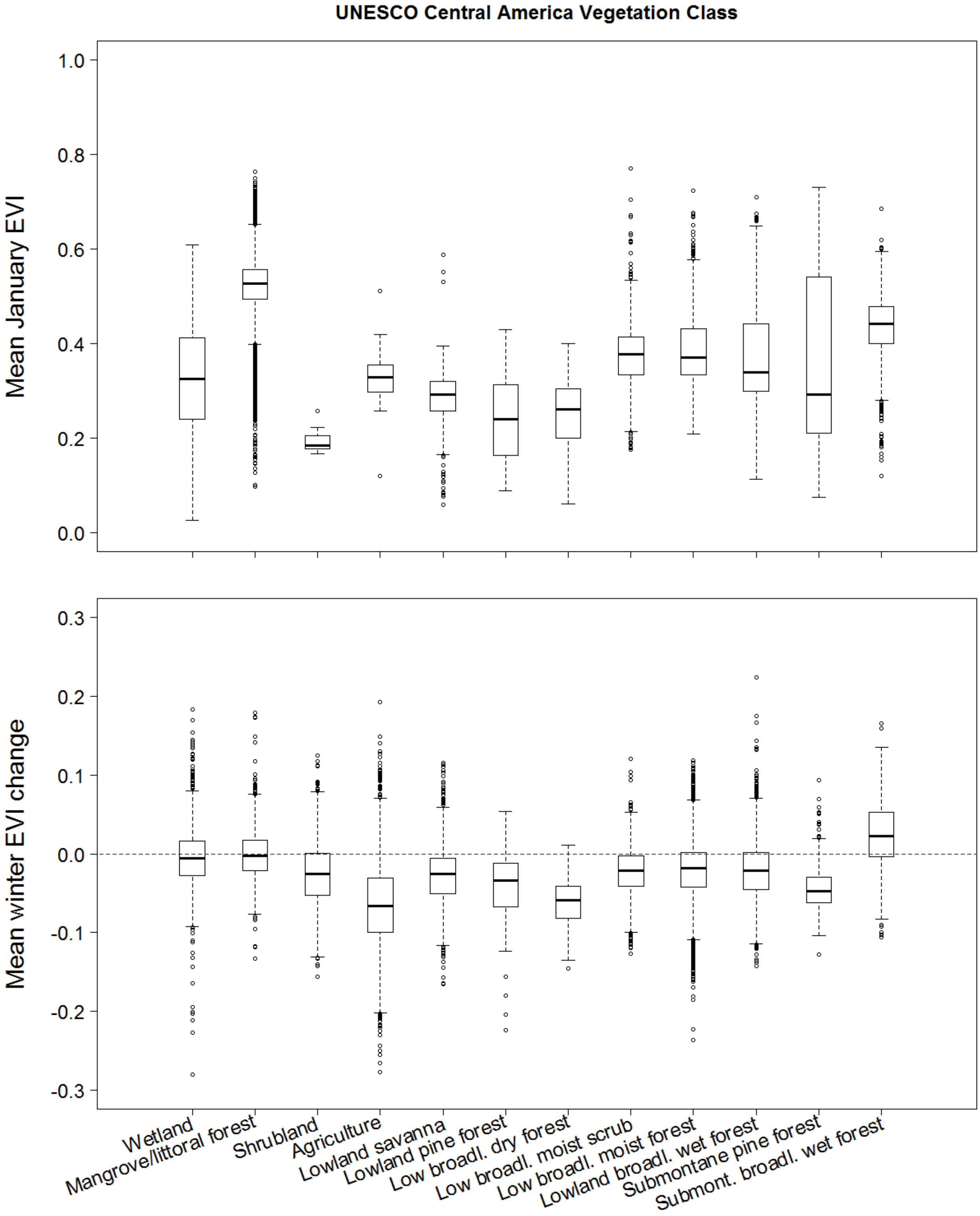

Figure 19. Distribution of mean January EVI and mean winter EVI change in relation to UNESCO Central American vegetation classes for Belize.

survival rates (Mazerolle et al. 2005, LaManna et al. in review) and the abundance of birds on the breeding grounds (Wilson et al. 2011), and our findings further support this growing body of literature.

Wet evergreen broadleaf forests, particularly within riparian corridors that may be more resilient to seasonal drying, provide good overwintering habitat for several of our target species, including Wood Thrush, Gray Catbird, Hooded Warbler, Kentucky Warbler and Ovenbird (Piaskowski et al. 2005, 2006). These forests may be a variety of ages and still provide suitable habitat. For example, Conway et al. (1995) found similar overwintering survival rates for these bird species between mature evergreen broadleaf forest and regenerating (4-10 year) forest in Toledo District, southern Belize. Thus, allowing or assisting forest regeneration on disturbed sites may yield benefits for overwintering migrant birds within a relatively short time-window. Establishment of regeneration sites within a largely forested landscape (as is commonly found in Belize) may be especially effective because it will increase landscape connectivity and the overall amount of habitat for resident forest bird species as well. Some heterogeneity of forest ages may also benefit sex-based differences in habitat preferences (Morton et al. 1987, Conway et al. 1995; but see e.g., Marra and Holmes 2001), and some degree of habitat heterogeneity on landscape scale may also allow for varied habitat preferences among species during winter and on migration (Piaskowski et al. 2005, Gómez-Montes and Bayly 2010).

The importance of protecting sites that are resilient to the seasonal winter drying in Mexico and Central America must also be stressed in the context of climate-change predictions, which suggest temperature increases and sharp declines in annual precipitation in the region during the coming decades (Parry et al. 2007, Karmalkar et al. 2011). Wet-season precipitation declines might be expected to limit early winter increases in EVI, while declines in dry-season precipitation might be expected to increase leaf loss over the winter period (resulting in more negative EVI change values). Both of these changes would be expected to diminish habitat quality for migratory birds throughout the region.

We see research reported on here as a first step in developing a sound science-based strategy for restoration of migratory SRW birds on their wintering grounds. A significant step that still needs to be accomplished is the development of a standard, or at least comparable currency for valuating and comparing restoration options on breeding and wintering grounds. D. Cristol (Appendix) proposed one potential metric for evaluating breeding habitat quality in the SRW, however other options might be considered. A similar scoring system could be developed for winter habitats. Nevertheless, it should be stressed that any habitat restoration end goal will not be optimal for all species, and so options will be limited to some extent by subjective priorities and available opportunities. We look forward to continuing to work with the larger South River Science Team to develop and apply appropriate metrics for this restoration effort. Finally, we strongly recommend that regardless of which currencies are applied or which restoration alternatives are pursued, an appropriate monitoring program should be developed and implemented to ensure that restoration goals are met.

8. Acknowledgements

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Appendix. Results of Preliminary Songbird Restoration Study, South River, Virginia. Prepared by Daniel Cristol, May 8, 2012.

Background on songbird habitat restoration. Songbirds are in trouble in North America. The number of birds found on breeding bird surveys in the US and Canada (most of which are songbirds) has declined by 10-20% since the 1960s (Sauer and Link 2011, Valiela and Martinetto 2007). Birds are experiencing well-known challenges in the tropical wintering grounds and along migration routes, while the degradation and fragmentation of breeding habitat by suburban sprawl and development in eastern North America is also an undeniable force in songbird declines. The hardest hit species depends on which region and time period is being examined, but in general the fastest declining songbird populations are those nesting in aridlands/grasslands and Eastern forests, and those that migrate to the tropics (Sauer and Link 2011, but see Valiela and Martinetto 2007).

I carried out a literature review on songbird habitat restoration to provide background as it applies to the South River watershed (SRW). The literature on avian response to habitat variables is immense, and hundreds of studies have described the avian response to habitat restoration and habitat-management, so I have included only the most recent and relevant studies here. Before considering a songbird habitat restoration program, it is essential to determine 1) whether habitat restoration actually changes bird communities, and 2) what we already know about responses of eastern North American avian communities to restoration of agriculturally disturbed riparian habitat like that in the SRW.

Do songbird communities change after habitat restoration? In other words, if you build it will they come? The answer is a resounding “yes”. While it is important to remember that it is likely that studies finding negative results might be harder to publish than those with positive results, I encountered almost no studies that failed to detect changes in bird communities after restoration (but see Kalies et al. 2010 for a meta-analysis that uncovered some negative results for southwestern pine forest restoration). Most studies examined the effect of a particular forestry technique or range management practice on abundance of one or a few species of birds, usually in coniferous forests or prairie grasslands, and thus have little direct relevance for the SRW (e.g., Bajema et al. 2001, but see Duguay et al. 2001 for effects of deciduous forestry techniques on songbirds in West Virginia). Some studies of specific restoration techniques may have high relevance for SRW projects at a later date when options are clarified (e.g., playing birdsongs to attract immigrants to restored habitat: Ward & Schlossberg 2004; streamside filter strips as grassland bird habitat in Maryland: Blank et al. 2011; bird abundance in riparian forests of different widths in Maryland and Delaware: Keller et al. 1993; managing Conservation Reserve Program grasslands for birds in Maryland: Gill et al 2006; strategies for managing early successional habitat for wildlife: Harper 2007; grassland songbird response to hayfield mowing rotation in West Virginia: Warren & Anderson 2005).

Because the SRW includes a large amount of residential development, I paid special attention to findings particular to forest songbirds of developed landscapes. For example, one study found that although larger woodlots have higher diversity and abundance of neotropical migrant songbirds, the presence of homes within 100 m of the edge of the forest undermines this relationship, such that a 4 ha woodlot in a non-residential area has the same diversity and higher abundance than a 25 ha woodlot with nearby houses (Friesen et al 1995). A general framework for restoring fragmented, urbanized landscapes for birds has been developed and provides many specific recommendations such as maintaining dead trees and native plants, integrating urban parks into the restoration plan, and actively managing mammalian species (Marzluff & Ewing 2001).

One of the best-studied cases of songbird habitat restoration is that of the Sacramento River in California. This watershed has lost 98% of its original riparian forest, and suffers from pollution and altered hydrology. A joint venture between The Nature Conservancy, USFWS and other foundations and agencies replanted native trees and shrubs on agricultural land adjacent to remnant riparian fragments. Detailed bird surveys were performed annually from 1993-2003 on 10 plots and results compared to remnant fragments (Gardali et al. 2006). Songbirds have increased steadily (3-10% on both restored and remnant plots) despite continued declines in other parts of the region. Colonization occurred quickly although a few species (house wren, Bewick's wren) did not colonize for 5-10 years after restoration. One species of serious conservation concern (lazuli bunting) has continued to decline due to brown-headed cowbird parasitism. One endangered and several threatened species have increased, and it appears that they spread from remnant fragments to adjacent restored sites as hoped. Overall, "riparian restoration in the Sacramento Valley has been largely successful in terms of providing habitat for a diverse community of breeding landbirds", including the federally endangered least Bell's vireo (Kus 1998).

Another relevant study, of deciduous forest restoration (oak savanna) in Illinois, found that after restoration, regardless of plot size, 12 species increased while five decreased, nesting success was enhanced or unchanged, and the avian community of the restored habitat was distinctly different from nearby unrestored oak forest. Authors concluded that "small patches of forest habitat that regularly function as population sinks may offer far better prospects for birds if they are subjected to … ecosystem restoration" (Brawn 2006). Note that a "population sink" is an area in which reproductive success is lower than that needed to maintain the population, which would thus disappear without immigration from "population sources" where reproduction exceeds mortality. In summary, there is solid evidence that restoring habitat for songbirds works; changes in abundance, diversity and reproductive success of numerous species have been documented for a wide variety of habitats and spatial scales, including on riparian deciduous habitats most applicable to the SRW (e.g., see these meta-analyses: conservation reserve program grasslands, Herkert 2009; deciduous forest regeneration after uniform partial harvest, Vanderwel et al. 2007; plot size and edge as predictors of nest predation: Hartley & Hunter 1998).

Only a few studies have examined restoration of eastern deciduous forest habitat in an agriculturally disturbed landscape, although there are countless papers comparing avian response to different methods of logging, which is related to habitat restoration (e.g., Annand & Thompson 1997). One of the most relevant is an examination of bird densities and reproductive success on 36 sites in the Mississippi Alluvial Valley in Louisiana and Missississipi, where >200,000 acres of agricultural floodplain has been reforested for conservation in the last two decades (Twedt et al. 2002, Twedt et al. 2010). The authors report that when tracts isolated from surrounding mature forest were planted at low densities with smaller tree species, grassland birds predominate (e.g. red-winged blackbird), and sites are reproductive sinks. In contrast, when large tree species were planted densely in areas adjacent to existing forest, source populations of edge and forest species were established (e.g. yellow-breasted chat). This study has considerable relevance to the Shenandoah Valley because it deals with floodplain forest in an agricultural landscape.

One study on nesting acadian flycatchers is particularly illustrative of the potential of forest restoration for songbirds in an agricultural area, although the cropland under study had not yet been restored (Hoover et al. 2006). In a ridge-and-valley area of Illinois an agricultural corridor caused much of the surrounding forest to suffer "edge effects", in particular increased brown-headed cowbird and predator abundance. Reproductive success was lower for birds nesting within 600 m of the clearing, rendering this habitat a population sink. Elsewhere in the forest, reproduction was high, producing excess young and serving as a population source. It was estimated that reforestation of the 200 ha clearing would improve 1150 ha of surrounding flycatcher habitat, thereby efficiently creating source habitat for 1700 pairs of flycatchers. Overall, the literature reveals that 1) songbird habitat restoration reliably increases and changes the avian community, and 2) while there is no case study of songbird habitat restoration in a mid-Atlantic riparian habitat, much can be gleaned from responses of avian communities to restoration projects elsewhere, including incidental changes after manipulation of agricultural grasslands and regenerating forest.

Overview of this study. The <u>objective</u> of this study was to quantify the densities of breeding birds across a wide variety of habitats in the area surrounding the South River, Virginia. The <u>rationale</u> for this project was to determine how many, and what kinds of, birds would be expected if a particular area of habitat were created, acquired or altered as part of a restoration plan associated with mercury pollution of the South River. The general <u>methodology</u> was to carry out *point counts* (i.e., standing at the center of a circle with 250 m radius) for singing birds between dawn and 10AM during the breeding season (1 June-1 July, 2011). Points were selected randomly, using aerial photographs, within tracts for which access could be obtained. Habitats were classified using GIS, as either *developed* (including recreational parks and wooded suburban residential), *forested* (>40 years of age and classified as either riparian or upland depending on whether it was in the floodplain of the Middle/South Rivers or not), *early successional* (including former severe land disturbance, abandoned agricultural fields and clearcuts <10 years old), *row crop* (mostly soybeans and winter wheat), or *hayfield*, and were ground-truthed during each point count. The only sites classified as *wetlands* were the slough at Cowbane preserve and the created wetland bank site across the river from Cowbane.

Methods. One very experienced observer (Andy McGann, MS Biology, College of William & Mary) did all counts, eliminating the need for any analysis of observer bias, which is one of the largest sources of variability in bird surveys. Andy has over 10 years of experience doing point counts, can identify all species of birds in eastern North America by song, and would earn a rank among the top 1% of birdwatchers in terms of identification skill. I accompanied Andy on many counts during the first week to ensure quality, and after that my role was to locate sites in the field and on aerial photographs, obtain landowner permission, and oversee data analysis. All counts were done in rain-free and low wind situations, eliminating another large source of variability. Finally, all counts were done within the early morning hours, in the same month, after migration and before singing levels are curtailed due to heat and cessation of breeding. Thus, the variation is produced more by the true variation between points rather than other factors. Except for its limited size, this is an extremely rigorous data set.

Andy surveyed 127 points at 42 sites, with each *point* being at the center of an imaginary circle with 250 m radius (at least 500 m from any other point), and each *site* representing single land ownership, but not necessarily a single habitat type or contiguous tract of land. For example, a patch of early successional habitat ("oldfield") behind the DuPont Community Bank site in Stuart's Draft was big enough to accommodate just one survey point, whereas 8 forested points were surveyed on the DuPont-owned ridgetop site immediately across the street from the Invista plant, and 12 points comprising many different habitat types were sampled on multiple discontinuous tracts called the Waynesboro Nursery site. The total number of songbirds detected was over 2101 of 69 species (Fig. 1).

Analysis. Because they are not relevant to the question of songbird restoration, I omitted birds of prey and scavengers that are non-territorial and hunt over large areas (3 barred owls, 1 American kestrel, 1 broad-winged hawk, 2 Cooper's hawks, 2 red-shouldered hawks, 4 red-tailed hawks, 1 turkey vulture, 1 black vulture and 1 common raven). In addition, aquatic species were omitted (1 belted kingfisher, 2 green herons), as well as aerial foragers that are not tied to the habitat (3 chimney swifts, 5 cliff swallows, 4 northern rough-winged swallows, 9 barn swallows, 2 purple martins, and 5 tree swallows) and all non-native species (15 European starlings, 5 house sparrows, and 2 rock pigeons). Finally, 65 birds were omitted because they were estimated to be >250 m away, and thus outside of the count circle.

Density of a count circle was calculated as the number of territorial bird families detected within the count circle divided by 19.6 ha ($\pi \times 250\ m^2 = 196349.5\ m^2 = 19.6349$ ha). Because all count circles were the same size, bird density (unadjusted for detectability) is simply the number of birds heard divided by the circle area. For example, at one of the 4 points surveyed in the Ridgeview Park site 13 birds (of 9 species) were seen, for a density of 0.66 birds/ha in developed habitat type. This represents the number of breeding territories, since each bird detected was a member of a separate family (usually a singing male). To determine what density of American crows was found over all of the counts, the total number of crows seen within 250 m of the observer ($n = 60$) is divided by the total area of all point circles (19.6349 ha/point x 127 points = 2493.6 ha) or 0.024 crows per ha.

We assigned each species a conservation value, based on scores assigned by the federal Partners In Flight initiative (http://www.rmbo.org/pif/pifdb.html). These scores range from 8 to 20, with 8 representing an invasive species with an increasing population and large global distribution and 20 being earned only by globally endangered species in decline. The score we used is actually the sum of separate scores given for global population size (bigger population = smaller score), breeding and wintering distribution (bigger distributions = smaller scores), human threats to breeding and non-breeding birds (lowest scores for urban adaptable species), historical population trends (lower score for increasing species) and region-specific scores (lower score if western Virginia is not an essential portion of the species' range). Values ranged from 8 for the 66 mourning doves seen to 19 for the single Kentucky warbler. If desired, these conservation scores could be used as raw scores or normalized on a scale of 0-1, to allow a heavier weighting of birds in greater need of restoration globally.

In total, we detected over 2000 birds using the habitat (i.e. not simply flying over) during the surveys. I analyzed the data only after removing raptors, waterbirds, non-native species, and aerial foragers, as well as those detected outside of the count circle. For each bird, the distance upon first detection was recorded to allow later analysis for differential detection probabilities. The time of each new detection was also recorded, to allow later analysis of whether the 10-minute survey was sufficient (Figure 1). During the second half of the study we resurveyed 12 points (9.5%) that had been surveyed during the first half, to allow later analysis of repeatability or temporal change in detectability. Habitat characteristics were noted in writing during each survey as a method of ground-truthing, and in the few cases where discrepancies existed between the ground-truthing and the aerial imagery, we relied on the ground-truthed classification. One example is the DuPont Community Bank site, which is an abandoned development site that was classified correctly in the aerial imagery as "urban" (open developed land) but has quickly reverted to "early successional" since the aerial imagery was taken. Another type of discrepancy is a shift from winter wheat row crop to hayfield between the time of the photograph and the survey. Finally, several rural sites with a dynamic mix of structures, crops, small woodlots and hayfield were re-classified based on ground-truthing to the majority landcover type (usually hayfield) at the time of survey. Forested sites were divided into "forested-riparian", which were those sites in the floodplain of the South or Middle Rivers and "forested-upland", which were pure forest stands outside of the floodplain. Sites with a majority of mature trees but including residential dwellings were classified as "developed forested" whereas those dominated by impermeable surface and lawns were "developed open".

Results.

Birds detected. After omitting raptors, aerial foragers, waterbirds and non-natives, 69 species remained in the data set:

Table 1. Songbirds detected during counts (including distant and flyover birds) with Partners-in-Flight scores and subjective habitat preference classification.

Species	PIF score	# detected	guild
acadian flycatcher	17	11	Interior forest songbird
American crow	11	95	Suburban tolerant
American goldfinch	13	81	Suburban tolerant
American robin	10	60	Suburban tolerant
Baltimore oriole	12	12	Floodplain specialist
black-and-white warbler	16	2	Interior forest songbird
blue-gray gnatcatcher	13	23	Forest edge specialist
brown-headed cowbird	11	40	Forest edge specialist
blue-headed vireo	10	3	Interior forest songbird
blue grosbeak	12	6	Early successional (row crops)

blue jay	12	57	Suburban tolerant
bobolink	11	4	Early successional (grassland)
brown thrasher	14	22	Forest edge specialist
Carolina chickadee	15	60	Suburban tolerant
Carolina wren	11	68	Forest edge specialist
cedar waxwing	11	16	Forest edge specialist
chipping sparrow	12	37	Suburban tolerant
common grackle	12	52	Suburban tolerant
common yellowthroat	12	9	Forest edge specialist
chestnut-sided warbler	12	2	Forest edge specialist
dickcissel	12	2	Early successional (oldfield)
downy woodpecker	14	49	Suburban tolerant
eastern bluebird	11	16	Suburban tolerant
eastern kingbird	13	24	Forest edge specialist
eastern meadowlark	14	38	Early successional (grassland)
eastern phoebe	12	8	Floodplain specialist
eastern towhee	17	72	Early successional (forest)
eastern wood-pewee	15	39	Interior forest songbird
fish crow	12	10	Forest edge specialist
field sparrow	16	55	Early successional (oldfield)
great-crested flycatcher	13	21	Interior forest songbird
gray catbird	12	28	Forest edge specialist
grasshopper sparrow	14	26	Early successional (grassland)
hairy woodpecker	12	12	Interior forest songbird
house finch	8	21	Suburban tolerant
horned lark	11	9	Early successional (bare dirt)
hooded warbler	15	9	Interior forest songbird
house wren	12	14	Forest edge specialist
indigo bunting	14	122	Forest edge specialist
Kentucky warbler	19	1	Interior forest songbird
Louisiana waterthrush	18	8	Floodplain specialist
mourning dove	8	66	Suburban tolerant
northern cardinal	9	79	Suburban tolerant
northern flicker	16	16	Interior forest songbird
northern mockingbird	9	40	Suburban tolerant
orchard oriole	14	14	Forest edge specialist
ovenbird	11	21	Interior forest songbird
pine warbler	11	6	Interior forest songbird
pileated woodpecker	12	23	Interior forest songbird
rose-breasted grosbeak	13	1	Interior forest songbird
red-bellied woodpecker	10	34	Suburban tolerant
red-eyed vireo	12	76	Interior forest songbird
red-headed woodpecker	15	1	Early successional (forest)
ruby-throated hummingbird	11	15	Forest edge specialist
red-winged blackbird	12	66	Early successional (grassland)

Savannah sparrow	12	16	Early successional (grassland)
scarlet tanager	14	42	Interior forest songbird
song sparrow	13	104	Suburban tolerant
tufted titmouse	13	94	Suburban tolerant
vesper sparrow	13	4	Early successional (row crops)
warbling vireo	10	14	Floodplain specialist
white-breasted nuthatch	11	27	Interior forest songbird
worm-eating warbler	18	19	Interior forest songbird
willow flycatcher	11	17	Early successional (oldfield)
wood thrush	16	17	Interior forest songbird
yellow-breasted chat	15	7	Early successional (oldfield)
yellow-billed cuckoo	13	27	Interior forest songbird
yellow-throated vireo	17	2	Floodplain specialist
yellow warbler	11	9	Floodplain specialist

Conservation value of sites. Assessing the “bird value” of a particular tract or habitat type is a subjective matter, because the value of one “American robin year” is not necessarily the same as that of one “Kentucky warbler year”, and assigning relative values depends on the goals of the restoration activity. I have developed one possible method to determine conservation value of sites, though there are many possible approaches:

Site value = total number of individual songbirds x sum of individual PIF scores

This is the most straightforward type of assessment and results in a site with 20 northern mockingbirds (20 x 9 = 180) being equal to a site with 10 worm-eating warbler (10 x 18 = 180). To weight the PIF score more heavily, I used the natural log of the number of birds, so that rarer birds increased the site more than a higher number of birds. Using the example above of two sites with equal unweighted value, the site with 20 mockingbirds would now be assigned a value of approximately 27 (ln20 x 9 = 26.96), whereas the site with rare worm-eating warblers would be assigned approximately 41. Obviously the weighting function can be adjusted to meet the perceived importance of conservation status versus numbers of birds, for example using log$_{10}$ or any other logarithmic function.

Using the weighting scheme described here, the relative value of each landcover type was:

Table 2. Relative bird value for each type of habitat surveyed (with ranks).

Habitat type	**# points**	**Birds/Km^2**	**#Birds x PIF**	**ln#Birds x PIF**
Developed	17	78 (4th)	186 (5th)	408 (5th)
Wetland	6	84 (2nd)	210 (2nd)	480 (1st)
Early Successional	15	80 (3rd)	196 (3rd)	415 (3rd)
Forest-riparian	16	77 (5th)	189 (4th)	412 (4th)
Forest-upland	39	66 (7th)	162 (6th)	345 (6th)
Pasture-Hay	23	90 (1st)	216 (1st)	453 (2nd)
Row Crops	11	67 (6th)	162 (7th)	322 (7th)

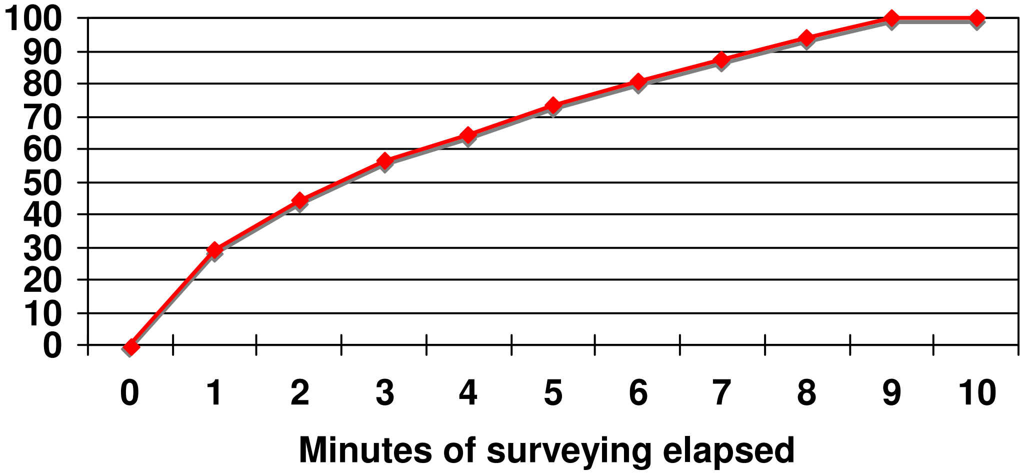
Two results are notable here. One is that the early successional habitats (hayfields, recovering clearcuts and emergent wetlands) had the most individual birds and the highest conservation values. Much attention has been paid to the value of forested habitats for songbirds, but on our study site, upland forests have little undergrowth due to excessive deer browsing, and riparian forests occur in small tracts between residential or agricultural areas, so the existing bird value is not much higher than that found in wooded suburbs or cropfields. Many species require undergrowth for nesting and disappear from smaller islands of habitat due to edge effects. Hayfields, emergent wetlands and recovering clearcuts, on the other hand, have very dense vegetation in which many species of birds can nest and forage, and the sites sampled here were within large tracts of similar habitat (wetland bank, Cowbane preserve, most hayfields). These results are very specific to the historical landscape development of the South and Middle River area and differ from what I expected based on literature. Most experts would predict that large upland forest tracts would have a greater bird conservation value than a suburban habitat, but that presumes that the upland forests are in good condition with a healthy understory and mixed ages of trees. Much of what we sampled was even-aged stands of mid-aged forest (>50 years since logging) with abundant evidence of deer-damage and numerous edge effects.

The second point is that the actual value of hayfields is dependent on the schedule of mowing, and this is not reflected in the numbers shown here. We counted territorial birds, but if the field is mowed while young are in the nest or shortly thereafter (which we observed during our counts), the habitat has no value to the avian residents. In fact, by luring them in and then preventing them from breeding successfully, rapidly rotated hayfields could have a negative conservation value, despite their high scores in Table 2. Thus, the scores shown here would only be realized if farmers agreed to forego an early hay crop, switch to cool season grasses, or otherwise manage their property with songbird reproductive success in mind. Other habitats likely do not have the same problem, because they do not undergo a massive disturbance during the nesting season (even row crops are harvested later, and birds typically nest along the cropfield edges in trees and shrubs).

It should be noted that while the different types of scoring systems changed the absolute differences in ratings of each habitat type (Table 2), the relative rankings varied little. For example, upland forests (heavily degraded by deer in this area) had very similar densities and unweighted conservation values to row crops. When conservation value was weighted, the upland forests improved their scores, mainly due to the presence of a few warbler and thrush species with high PIF scores. Relative ranks reversed in this case, but both were still the worst-ranked sites under either scoring scheme. This suggests that the weighting of conservation scores is effective in differentiating sites, and so the exact weighting scheme must be agreed upon, but may not make a huge difference in relative ranks.

Quality assurance. One question that must be asked about the surveys is if visiting each site once for 10 minutes provided a meaningful picture of the birds present. To check whether 10 minutes was a long enough sampling period, I calculated the number of new detections that occurred during each minute, summed across all surveys. It is clear that most birds were detected within the first three minutes, with a very gradual increase during the subsequent 7 minutes, indicating that even longer surveys would have changed the results little (Figure 1). Over 90% of the birds were detected before the start of the 8th minute of a typical survey. It appears that the duration of the surveys was sufficient to detect most of the birds that were detectable.

Figure 1. Cumulative percent of birds detected during each minute of surveys.



The next question is whether visiting each site once was sufficient and whether singing diminished from the beginning to the end of our survey period. To answer this we resurveyed 12 plots on June 28-30 that had been surveyed from June 1 - June 15. The average number of birds detected was similar on the two counts (first count = 16.4, recount = 16.8) and the averaged summed PIF scores were similar as well (first count = 206.9, recount = 210). Thus, there was no tendency to find fewer or less valuable birds on the later counts and we can assume that all counts were done during the active nesting period when detection probability is highest. Repeatability is harder to examine, and the relatively small sample size necessitates a non-parametric correlation analysis. The Spearman rank correlation (i.e., a measure of whether a point count had the same relative rank, in terms of number of birds detected, both times it was counted) generated a test statistic of 0.6048, which indicates a significant correlation ($P < 0.05$) with a 2-tailed test. This indicates that had we surveyed each point twice, the results would have been similar to what we found from a single survey in terms of which points had the most birds and which had the fewest. A more sophisticated analysis using a similarity index, actually comparing *which* species were seen (as opposed to how many), would require a larger sample size of recounts.

Accuracy of uncorrected density estimates. To illustrate the process of adjusting for detectability, I will first work through an example. As calculated above in Methods, we found American crow density to be 0.024/ha. The crow is a large, loud species that is very easy to detect. If a crow is present, an observer is very likely to notice it within 10 minutes because they call a lot and move around noisily. Thus, we would expect our estimate to be accurate whether we corrected for detectability or not, because nearly all crows are going to be detected. Using the program DISTANCE (http://www.ruwpa.st-and.ac.uk/distance/) we calculated the distance-corrected density estimate for American crow and it was 0.026 crows/ha with a 95% confidence interval of 0.012-0.055. Our uncorrected estimate is very similar. The crow had a detection probability of 0.52, by far the highest of any species we analyzed with program DISTANCE (see Table 3). DISTANCE essentially uses the recorded detection distances for each bird to calculate detection probabilities that are then used to adjust the estimated densities, so quiet birds that are rarely detected at long distances (i.e. low detection probability) will gain in density after adjustment. Densities of loud, obvious birds like the American crow will change little after adjustment.

Unfortunately, DISTANCE can only be used reliably with species for which there are >50 detections, so I was only able to use it for 15 species to compare our estimates with the distance-corrected estimates.

Table 3. Comparison of observed densities and distance-corrected densities

Species	Density uncorrected	Density corrected	Relative % difference, RPD	Detection probability
American crow	0.024	0.026	7.46	0.52
American goldfinch	0.017	0.267	93.69	0.10
American robin	0.021	0.132	83.90	0.11
blue jay	0.021	0.051	59.11	0.21
Carolina chickadee	0.024	0.171	85.93	0.24
Carolina wren	0.027	0.183	85.32	0.19
eastern towhee	0.028	0.146	80.77	0.12
field sparrow	0.020	0.051	59.90	0.34
indigo bunting	0.048	0.223	78.42	0.15
mourning dove	0.024	0.092	73.85	0.20
Northern cardinal	0.030	0.272	88.79	0.15
red-eyed vireo	0.031	0.341	90.83	0.06
red-winged blackbird	0.024	0.290	91.70	0.07
song sparrow	0.040	0.339	88.17	0.15
tufted titmouse	0.038	0.245	84.61	0.18

The important results in this table are that, whereas the observed and distance-corrected density estimates are very close for the noisy, easy to detect American crow (RPD < 10%), the same is not true for any of the other 14 species. In all other cases, correcting the estimate to take into account the species' probability of detection dramatically increases the estimated density. For example, the red-eyed vireo estimate of 0.03/ha increases by almost an order of magnitude to 0.34/ha when the low detection probability of the vireo is taken into account. Vireos are cryptically colored, quiet singers that take long breaks from vocalizing and remain hidden in the treetops of their small territories. Thus, an observer standing in the middle of a 19 ha count circle is likely to miss many of the vireos present. In fact, the discrepancy between the observed and distance-corrected estimates is very closely tied to detection probability (calculated by DISTANCE based on proportion of birds detected at various distances from the observer). A regression analysis of how well detection probability predicted RPD revealed a very strong negative relationship ($r^2 = 0.82$, $F = 62.7$, $P < 0.0001$), indicating that the harder a bird is to detect, the greater the discrepancy between the corrected and uncorrected estimates.

Incidental observations during this study. As with most research projects, the unexpected findings were the most interesting.

The first surprise for me was that the difference in bird conservation value between the most pristine habitats and the most degraded were not as big as expected. For example row crops and upland forest shared similar low densities of birds and had the lowest conservation values of all habitats. Even the best habitats, for example wetlands, did not have twice the density or conservation value of the worst (row crop and upland forest). Native birds with relatively high PIF scores manage to colonize and breed on even the most degraded habitats, for example Carolina chickadees have the same PIF score as rare hooded warblers, but are common in suburban neighborhoods and near rural residences. In the absence of reproductive success data showing that these degraded habitats are population sinks with very little reproduction, the presence of songbirds already existing in these habitats limits the number of bird years that could be gained through habitat conversion. This suggests that if one were to acquire abandoned cropland and restore it to emergent wetland or riparian forest it would require an enormous amount of acreage to directly offset the bird years lost over a half-century due to mercury pollution of the South River. However, if planning is done carefully so that restored sites are located next to, and reduce edge effects in, existing habitat (as in the case study of the acadian flycatcher in Illinois discussed above), then each hectare of restoration through habitat conversion could produce a much greater number of bird years.

The second surprise was the low bird conservation value of the upland forests. Almost all sites were embedded in very large contiguous forested habitat on public land, including Shenandoah National Park. While it is well known that mature forest can contain lower densities of birds due to lower productivity of the vegetation or reduced structural complexity, I expected to detect many more hooded, Kentucky and worm-eating warblers. This would have considerably increased the relative conservation values of this habitat due to their high PIF scores, especially with the logarithmically weighted index that I used. Because we casually observed very consistent evidence of deer overabundance, my hypothesis is that deer have degraded these public lands, especially in the National Park where hunting is forbidden. There is an emerging literature on the devastating effect of deer overabundance on forest ecosystems, particularly songbird populations (e.g., an up-to-date summary can be found in the introduction of Holt et al. 2011). Two experimental deer exclusion studies have been done in eastern deciduous upland forest (deCalesta 1994 in Pennsylvania, McShea & Rappole 2000 in the Shenandoah Valley of Virginia), and these showed dramatic responses of songbirds to release from deer browse. If one could establish that deer are indeed overabundant in the upland forests we surveyed, it would be possible to confidently predict, without further study, that deer exclusion would affect songbird populations in these areas.

The final observation made during the study that impressed me was the intensity of the hay harvest at the sites we surveyed. On more than one occasion we observed grasshopper sparrows or eastern meadowlarks carrying food to a nest in a hayfield during a point count, only to see the entire field mowed down in the time it took us to walk to the next point and back to the car. The nests were certainly destroyed and the babies killed. In other words, the high avian conservation value I calculated for hayfield sites is likely an illusion. There are no unmowed buffers in these fields and they are often fertilized, allowing multiple crops during a single breeding season, at intervals shorter than one nesting cycle. Nesting birds may be wasting their lives trying to reproduce in typical Shenandoah Valley hayfields. But this unfortunate circumstance presents a relatively low-cost alternative for songbird restoration. By slowing the rotation, leaving unmowed strips or buffers, or switching to cool-season grasses, avian productivity could be greatly increased without acquisition and reforestation. Because grassland birds are among the highest conservation priority among all songbirds nationally, the conservation value of such an alternative is fundamentally sound. There is a very large literature on grassland management and bird productivity, but the ideal solution depends heavily on what farmers are willing to do at this location. One drawback is that agreements with farmers might require more intense monitoring and administration than reforestation or deer exclusion projects, as each farm would require one or more inspections during each nesting season and annual payments would likely be required.

Proposed follow-up study. My results thus far can reliably predict the species of birds occurring in all habitats of the SRW, and provide a comparison of the relative avian density and conservation value of each of the major habitat types. As in the 2005 surveys, approximately 70 species occur, most of which are native forest songbirds. The highest densities and conservation values occur on the few wetlands present, hayfields, and early successional habitats (oldfields, clearcuts, CRP riparian forest buffers). With the results of this study in hand, I proposed one technique that could help decide which of two properties or restoration plans would provide greater *relative* avian conservation value. The suggested approach is to simply calculate the proportions of each habitat type, multiply the area by the avian conservation value of each habitat type, and then sum the resulting products (assuming equal reproductive success). The property or plan with the higher score would be the preferred option.

However, due to the limited size of the data set, more data are needed before any reliable calculation of bird years or other *absolute* measure of avian conservation value can be calculated. There is no way to use the present data to determine, for example, how many acres of a particular habitat or restoration activity it would take to offset a given amount of bird injury. This is because I did not detect enough individuals (~50-60) to calculate distance-corrected density estimates for the majority of species. For those species in which detection probabilities could be calculated, the distance-corrected densities were approximately 10x greater than uncorrected densities. In other words, we missed most of the birds on the plots during the surveys, but don't know how many we missed. One might think that the uncorrected density estimates could be corrected en masse, based on the results from the few species with sufficient data for distance correction. However, because detectability estimates vary by habitat type (e.g., much greater in hayfields than in forest), and different species are present in the different habitat types, the density estimate for each species must be corrected using detectability data from that species and this study site.

I propose one additional round of surveys, this time with three observers working for 45 consecutive days to survey 225 points each, for a total of 675 more counts from May 20 -July 10, 2012. Based on this summer's data, that would generate >50 detections for 81% of the species encountered in 2011, leaving only the rarest 13 species with unreliable density estimates. Two of these, Louisiana waterthrush and eastern phoebe, will have more detections if we target more riparian areas. Rare species such as Kentucky warbler and red-headed woodpecker can not surpass this threshold with any reasonable amount of effort, so other techniques will be required to develop expectations for this and a few other species of high conservation value.

The methods used would be as in 2011, with the addition of quality assurance measures for inter-observer reliability, transects for deer droppings in each site and habitat type (2 per site, 8 per habitat type), and follow-up species distribution models for the most important species. The final report would provide:

1) Distance-corrected density estimates for all songbird species on each site *surveyed.*
2) Maps of the entire study region predicting the probability of occurrence of critical species at *any* location, not just those surveyed (based on species distribution models).
3) A start to addressing the question of whether the relatively low avian conservation value of the upland forested sites was related to degradation by overabundant deer.
4) Specific recommendations, based on literature and distance-corrected density estimates from 2011-2012 data, of a range of hypothetical deer management and hayfield rotation scenarios that may serve as inexpensive alternatives to more traditional land acquisition and reforestation projects.
5) An analysis of the value of alternative restoration scenarios based on whether the site was adjacent to existing habitat or isolated. It is predicted that by placing a restoration project adjacent to existing habitat, the existing habitat will also be improved through elimination of edge effects, with a concomitant increase in bird years produced overall. However, this is conjecture in need of a modeling experiment using my data.

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Figure 2. Survey points – 2011