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RELATIONSHIPS AMONG SURVIVAL, BODY CONDITION, AND HABITAT OF BREEDING SWAINSON'S WARBLERS

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Abstract. For migratory birds, the selection of high-quality breeding and nonbreeding habitats has significant implications for fitness. One potential reflection of habitat quality is body condition. Condition may influence adults' survival, a key demographic variable for population growth. Access to abundant resources should lead to good condition and birds maintaining or improving their condition over time. As many species use multiple habitats, recognizing the relative quality of these alternative environments is important for understanding population dynamics and aiding conservation. One species that uses a range of habitats is Swainson's Warbler (*Limnothlypis swainsonii*), a species of conservation concern that breeds in the southeastern U.S. From 2004 through 2007, we studied survival and body condition of Swainson's Warblers at three sites in eastern Arkansas, two dominated by mature forest, and one in an industrial forest managed for timber production. Birds in better condition at initial capture survived at a higher rate at two of three locations. Moreover, at all sites the birds' body condition improved through the breeding season and varied little by site. Body condition was positively related to dense understory vegetation and negatively related to herbaceous ground cover. Our results suggest that both mature and industrial forests may provide adequate habitat for Swainson's Warbler. Because of the relationship between body condition and survival, the observed habitat-related differences in body condition have implications for habitat quality. To provide high-quality habitat for Swainson's Warbler, management should focus on providing forests with dense understory vegetation and, to facilitate efficient foraging, little herbaceous ground cover.

Key words: *Arkansas*, *body condition*, *bottomland hardwood forest*, *giant cane*, Limnothlypis swainsonii, *Mississippi Alluvial Valley*, *survival*, *Swainson's Warbler.*

Relaciones entre Supervivencia, Condición Corporal y Hábitat de Individuos Reproductivos de *Limnothlypis swainsonii*

Resumen. Para las aves migratorias, la selección de hábitats de alta calidad tiene implicancias significativas para la adecuación biológica de los individuos. Un posible indicador de la calidad del hábitat es la condición corporal. De hecho, ésta puede influenciar la supervivencia de los adultos, una variable demográfica clave para el crecimiento poblacional en todas las especies. El acceso a recursos abundantes debiera resultar en una buena condición corporal y en la habilidad de mantener o aumentar esa condición a lo largo del tiempo. Debido a que muchas especies usan una variedad de hábitats, la cuantificación de las cualidades relativas entre estos diferentes ambientes es importante para entender las dinámicas poblacionales y para ayudar a los programas de conservación. Una especie con estado de conservación preocupante, que se reproduce en el sudeste de Estados Unidos y que utiliza una variedad de hábitats, es *Limnothlypis swainsonii*. Desde 2004 a 2007, estudiamos la supervivencia y condición corporal de esta especie en tres sitios en el este de Arkansas. Dos sitios estaban dominados por bosques maduros y uno por bosques manejados para producción forestal. Los individuos que se encontraban en mejores condiciones al momento de la primera captura sobrevivieron con tasas mayores en dos de los tres sitios de estudio. Además, en todos los sitios la condición corporal de los individuos aumentó a lo largo del periodo reproductivo y varió poco entre los sitios. La condición corporal se correlacionó positivamente con la densidad de la vegetación del sotobosque y negativamente con la cobertura del suelo por herbáceas. Nuestros resultados sugieren que tanto los boques maduros como los explotados pueden proveer hábitats adecuados para *L. swainsonii*. Debido a la relación entre condición corporal y supervivencia, las diferencias en condición corporal observadas con relación a las diferentes características de los hábitats tienen implicancias importantes para la determinación de la calidad del hábitat. Para proveer hábitats de buena calidad para esta especie, las estrategias de manejo debieran enfocarse en el mantenimiento de bosques con un sotobosque denso y con poca cobertura de herbáceas para facilitar las eficiencia de forrajeo de *L. swainsonii*.

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INTRODUCTION

For migratory birds and other organisms, the quality of the habitat in which they settle has important consequences for fitness (Cody 1985, Johnson 2007). By selecting and successfully defending a high-quality habitat, a male bird may influence his probability of successfully pairing, raising offspring, and surviving to reproduce in the future (e.g., Probst and Hayes 1987, Burke and Nol 1998, Marra and Holmes 2001). In addition to affecting survival during a given season, habitat quality may have carry-over effects that influence survival or reproduction during subsequent portions of a bird's life cycle (e.g., Marra et al. 1998, Norris et al. 2004). Indeed, for many birds most mortality likely occurs during migration, and habitat quality during the breeding and wintering periods may affect the probability of surviving the migratory phase of the annual cycle (Marra and Holmes 2001, Sillett and Holmes 2002).

One potentially useful index for assessing habitat quality and its effects on individuals is body condition (Brown 1996, Johnson 2007). Body condition may be a reflection of both access to resources and the ability to defend those resources; individuals with abundant resources that can successfully defend territories are expected to be in better condition than those occupying poor territories. Likewise, individuals in high-quality habitats should maintain or improve their body condition over time (e.g., Strong and Sherry 2000, 2001, Johnson et al. 2006). The relationship between habitat quality and condition is especially important because individuals relegated to poor habitat, as a result of poorer body condition, may have lower chances of survival (Marra and Holmes 2001, Johnson et al. 2006). Given the importance of adults' survival as a driver of avian demography, these potential effects of condition on survival have significant implications for population trends (Sæther and Bakke 2000, Stahl and Oli 2006). With these key linkages involving body condition, adult survival, and population trends, understanding factors influencing condition is especially crucial for species of conservation concern.

One such species of concern, the Swainson's Warbler (*Limnothlypis swainsonii*), is a medium-sized wood warbler that breeds throughout the southeastern United States and winters on islands in the Caribbean basin and on the Yucatán peninsula (Brown and Dickson 1994). Rare over most of its range, yet locally abundant in suitable habitats, Swainson's Warbler typically breeds in infrequently flooded bottomland hardwood forests with a dense understory (e.g., Graves 2001, Brown et al. 2009), although it is also found in other habitats, including mid-seral-stage pine plantations and high-elevation rhododendron and hemlock thickets (Meanley 1971, Henry 2004, Bassett-Touchell and Stouffer 2006, Lanham and Miller 2006). Secretive and poorly understood, the Swainson's Warbler is among the species of greatest conservation concern both regionally and nationally (Hunter et al. 1993, Twedt et al. 1999, Rich et al. 2004).

Many historical accounts of Swainson's Warblers mentioned giant cane (*Arundinaria gigantea*), a bamboo native to the southeastern United States, as a dominant component of occupied habitats (Meanley 1971). Indeed, Brewster (1885) suggested that cane was required for Swainson's Warbler habitat, although rangewide studies have confirmed that Swainson's Warblers are routinely found in habitats without cane (e.g., Meanley 1971, Graves 2002, Bednarz et al. 2005). Likewise, many early accounts mentioned extensive mature forests as a requirement for Swainson's Warblers. However, while Swainson's Warblers are generally associated with extensively forested landscapes (Mitchell et al. 2001), studies in intensively managed and vine-dominated deciduous forests in South Carolina and in pine plantations in Louisiana have established that Swainson's Warblers not only do not require cane, they do not require mature forests (Henry 2004, Peters et al. 2005, Thompson 2005). Swainson's Warblers may prefer cane (Wright 2002, Anich 2008, Benson et al. 2009, Brown et al. 2009), however, and little is known about the relative quality of cane- and non-cane-dominated habitats, or of mature forests versus those in an early seral stage. Understanding these habitat preferences and relative habitat quality is important for Swainson's Warblers given the drastic reductions in the extent of bottomland hardwood forests, especially mature forests and the areas of higher elevation on which cane was formerly abundant (Noss et al. 1995, Platt and Brantley 1997, Twedt and Loesch 1999).

In an effort to better understand factors influencing body condition and survival in Swainson's Warblers as well as to provide information relevant for management for this species of concern, we set out to (1) examine the relationship between body condition and survival in Swainson's Warblers, (2) investigate differences and temporal change in body condition at three locations with different management and habitat composition, and (3) determine the effects of territory-scale habitat differences on body condition at these areas. We predicted that body condition at capture should affect subsequent survival. Furthermore, we expected condition to improve throughout the breeding season in high-quality habitat. Because potentially dominant males may be in better condition, we also expected body condition to be positively associated with the quality of nesting habitat. Given the historic association between cane and Swainson's Warblers, the apparent preference for cane as a nest substrate at our study areas (Benson et al. 2009), and the association of cane with litter arthropods (Brown 2008), we further predicted body condition in cane-dominated areas to be superior to that in areas not dominated by cane. Likewise, although Swainson's Warblers are associated with small-scale disturbances, because they are generally found in extensively forested landscapes (Mitchell et al. 2001), we expected their body condition in mature forest to be superior to that in actively harvested forest. At each location, although we expected cane to be positively associated with body condition, we also predicted areas with a greater density of woody stems of all types to be better-quality habitat (e.g., Graves 2001, Bednarz et al. 2005).

Because areas with a relatively dense understory and well-developed sub-canopy cover may offer more arthropods as food (Brown 2008) and more suitable nest sites, we expected individuals in such habitat to be in relatively good condition. Last, because Swainson's Warblers forage on the ground for arthropods in leaf litter (Graves 1998), we expected the volume of leaf litter to be positively associated with body condition but the cover of forbs and grasses, which may obstruct foraging, to be negatively associated with body condition.

STUDY AREAS

We studied the body condition of Swainson's Warbler at three locations in eastern Arkansas, Big Island (Big I.), Saint Francis National Forest (St. Francis NF), and White River National Wildlife Refuge (White R. NWR). Although similar in some respects, these locations contain different habitats and are managed differently. Big Island was covered with a mix of less mature stands of bottomland hardwood forest of varied ages and is managed primarily for timber production. St. Francis NF, on the edge of Crowley's Ridge, contained a mix of upland and bottomland forest and was managed for multiple uses including timber production and wildlife conservation. White R. NWR is exclusively bottomland and was managed primarily for wildlife.

Big I., located in Desha County of southeastern Arkansas, is surrounded by three rivers, the White to the north, the Arkansas to the west and south, and the Mississippi to the east. Containing over 9000 ha of bottomland forest, Big I. is owned and managed by the Anderson-Tully Company primarily for timber production. Areas Swainson's Warblers used there were dominated by sweetgum (*Liquidambar styraciflua*), oak (*Quercus* spp.), hickory (*Carya* spp.), box elder (*Acer negundo*), green ash (*Fraxinus pennsylvanica*), sugarberry (*Celtis laevigata*), and American sycamore (*Platanus occidentalis*). The dominant understory plant was greenbrier (*Smilax* spp.), accompanied by saplings of the aforementioned trees, grape (*Vitis* spp.), poison ivy (*Toxicodendron radicans*), and Virginia creeper (*Parthenocissus quinquefolia*); cane was present or dominant in some areas but relatively sparsely distributed. In comparison to our other two study locations, areas Swainson's Warblers used at Big I. were dominated by trees of smaller diameter (8–23 cm at breast height [dbh]). In general, they contained a dense midstory but few overstory trees.

Located in Lee and Phillips counties of east-central Arkansas, St. Francis NF includes over 8500 ha of upland and bottomland forest. It is bordered by the Mississippi and St. Francis rivers on the east and includes upland forests on Crowley's Ridge. Areas used by Swainson's Warblers at St. Francis NF were dominated by elm (*Ulmus* spp.), box elder, sweetgum, maple (*Acer* spp.), oak, hickory, and tulip tree (*Liriodendron tulipifera*). Dominant understory vegetation included greenbrier, poison ivy, Virginia creeper, spicebush (*Lindera benzoin*), and pawpaw (*Asimina triloba*), and cane was not common at this location.

White R. NWR, located in Arkansas, Desha, Phillips, and Monroe counties of east-central Arkansas, is, at over 62 000 ha, among the largest continuous tracts of bottomland hardwood forest in the Mississippi Alluvial Valley (Twedt and Loesch 1999). Swainson's Warbler habitat here was dominated by sugarberry, sweetgum, box elder, elm, oak, American sycamore, and hickory. Dominant understory vegetation included greenbrier, Virginia creeper, peppervine (*Ampelopsis arborea*), grape, spicebush, box elder, and often dense thickets of cane.

METHODS

CAPTURE AND MEASUREMENTS

During the breeding seasons of 2004 through 2007, we located, captured, and color-banded male Swainson's Warblers at our three study locations. Both St. Francis NF and White R. NWR were sampled in all years, whereas Big I. was sampled only from 2005 to 2007. We used only male Swainson's Warblers because of both the fluctuation of females' body mass through the breeding season due to egg production and males being easier to capture than females. We located individuals on the basis of observations from previous years as well as by passive and song-playback surveys in suitable habitat; we captured the birds by targeted mist netting with song playback. Upon capture, we banded each individual with a metal U.S. Geological Survey band as well as a unique combination of three color bands. For each captured Swainson's Warbler, we recorded the length of bill from the anterior edge of the nares to the tip, the left and right tarsi, the left and right unflattened wing chord, and tail, all to the nearest 0.5 mm. We measured mass to the nearest 0.1 g with a spring scale. From 2005 to 2007, in addition to capturing unbanded birds, we returned to all capture and detection sites and identified previously banded individuals by resighting or recapturing those males.

HABITAT MEASUREMENTS

To investigate the relationship between the birds' body condition and habitat features, we used habitat data from three sources. Two were habitat data recorded by a modified BBIRD protocol (Martin et al. 1997) at randomly selected points during a radiotelemetry study of Swainson's Warbler home ranges in 2005 and 2006 (Anich 2008) and randomly selected points sampled in an investigation of the species' nest-site selection from 2005 through 2007 (Benson et al. 2009). On basis of the approximate size of Swainson's Warbler home ranges at St. Francis NF and White R. NWR (Anich et al. 2009), we used data from points sampled within 180 m of capture sites (10.2 ha). For those individuals for which no habitat data were available within 180 m of their capture location, we randomly selected points within this radius for subsequent sampling. At each of these points, we visually estimated the sub-canopy cover, categorizing it as <30% (category 1), 30–60% (2), or >60% (3). Likewise, we estimated density of the understory within 11.3 m of the plot's center as <34% (category 1), 34–65% (2), or >65% (3). From the center of the plot, we recorded percent cover of forbs, grasses, and sedges, and leaf litter, and, at a distance of 5 m in the four cardinal directions, we counted the number of cane, vine, and shrub stems within a 1-m^2 quadrat at a height of 0.3 m and recorded the leaf-litter depth with a ruler. Using our estimates of percent cover of leaf litter and leaf-litter depth, we calculated the estimated volume of leaf litter within each 5-m radius plot as the plot area × percent cover × depth in meters.

DATA ANALYSES

To generate an index of Swainson's Warbler body condition, we first used principal components analysis to generate one variable (PC1) from our six correlated linear measurements, then used residuals from a linear regression between this linear size variable and body mass as an index of condition (Brown 1996, McGarigal et al. 2000). We considered birds relatively heavy for their size (i.e., with positive residuals) to be in good condition, those with negative residuals to be in relatively poor condition.

To examine the influence of body condition on annual survival, we used the residuals from a linear regression between body condition and day of year to remove possible effects of capture date. For birds captured on multiple occasions, we used the data recorded during the initial capture. We estimated apparent survival with Cormack–Jolly–Seber methods in program MARK (Lebreton et al. 1992, White and Burnham 1999). We confirmed goodness of fit, lack of overdispersion, and suitability of models with constant resight/recapture probability in previous analyses (Benson 2008). We considered models with constant survival, survival varying among the three study sites, equal survival at St. Francis NF and White R. NWR, the two mature forest sites, but different at Big I., and with varying additive and interactive effects of body condition at these locations (Table 1).

TABLE 1. Results from models used to investigate the relationship between annual apparent survival (φ) and body condition for male Swainson's Warblers (n = 176) at three locations in Arkansas, 2004 through 2007.

Model	K[a]	ΔAIC_c[b]	w_i
$\varphi_{(\text{Big I.+ condition}) \neq ([\text{St. Francis NF = White R. NWR}] + \text{condition})}p$	5	0	0.41
$\varphi_{(\text{Big I.}) \neq ([\text{St. Francis NF = White R. NWR}] + \text{condition})}p$	4	0.42	0.33
$\varphi_{(\text{Big I. = St. Francis NF = White R. NWR})}p$	2	3.55	0.07
$\varphi_{(\text{Big I.} \neq \text{St. Francis NF = White R. NWR})}p$	3	3.58	0.07
$\varphi_{([\text{Big I.} \neq \text{St. Francis NF} \neq \text{White R. NWR}] \times \text{condition})}p$	7	3.95	0.06
$\varphi_{([\text{Big I.} \neq \text{St. Francis NF = White R. NWR}] + \text{condition})}p$	4	5.09	0.03
$\varphi_{(\text{Big I.} \neq \text{St. Francis NF} \neq \text{White R. NWR})}p$	4	5.59	0.02
$\varphi_{([\text{Big I.} \neq \text{St. Francis NF} \neq \text{White R. NWR}] + \text{condition})}p$	5	7.09	0.01

[a] Number of parameters.
[b] AIC_c for the best-fitting model was 345.94.

TABLE 2. Mean, standard error, and range of values for habitat measurements taken within 180 m of sites of capture of Swainson's Warblers (n = 203) at Big Island, St. Francis National Forest, and White River National Wildlife Refuge, eastern Arkansas, 2005–2007.

Variable	$\bar{x}$	SE	Range
1-m^2 quadrat			
Cane stems (m^{-2})	1.45	0.13	0–8.88
Shrub stems (m^{-2})	0.70	0.04	0–3.13
Vine stems (m^{-2})	3.78	0.21	0.06–18.13
Non-cane stems (m^{-2})	4.52	0.21	0.75–18.38
Total stems (m^{-2})	5.97	0.20	0.75–18.38
Percent cover			
Forbs, grasses, and sedges	13.14	0.68	0–51.30
Litter volume[a] (m^3)	1.44	0.05	0.07–4.52
Subcanopy cover[b]	2.30	0.03	1.25–3.00
Understory density[c]	1.96	0.03	1.00–3.00

[a] Litter volume = plot area × percent leaf litter cover × litter depth in m; units are m^3 per plot.
[b] Subcanopy cover was classified as 1 to 3 for <30%, 30–60%, or >60%, respectively.
[c] Understory density was classified as 1 to 3 for <34%, 34–65%, or >65%, respectively.

We used data recorded from 2005 to 2007, the years in which we had morphometric data from all locations, to compare body condition by location and investigate relationships between condition and habitat variables. We first examined the temporal effects of year and day of year, the effect of location, and additive and interactive combinations of these variables. Although body condition improved through the day at all of our locations, the means and distributions of capture times at all of our locations were similar; because we were less interested in this fine-scale variation, we did not include this effect in subsequent models. After our analysis of temporal and location effects, we assessed 15 a priori models that incorporated habitat variables that may be related to Swainson's Warbler body condition (Table 2); to account for observed temporal effects, we included the most-supported temporal variable in all habitat analyses. Prior to analyses, we evaluated correlations among variables and did not include highly correlated variables ($|r| > 0.70$) in the same model. We fit candidate models by using general linear models (SAS PROC GLM; Littell et al. 2002) and evaluated results from these models with Akaike's information criterion adjusted for small sample size (AIC_c), relative model weights based on AIC_c rankings, and model-averaged estimates (Burnham and Anderson 2002).

RESULTS

For survival analyses, from 2004 to 2006, we captured and recorded complete measurements of 176 male Swainson's Warblers, which we attempted to resight or recapture in subsequent years. Of these, 67 were at Big I. (31 in 2005, 36 in 2006), 37 at St. Francis NF (5, 13, and 19 in 2004, 2005, and

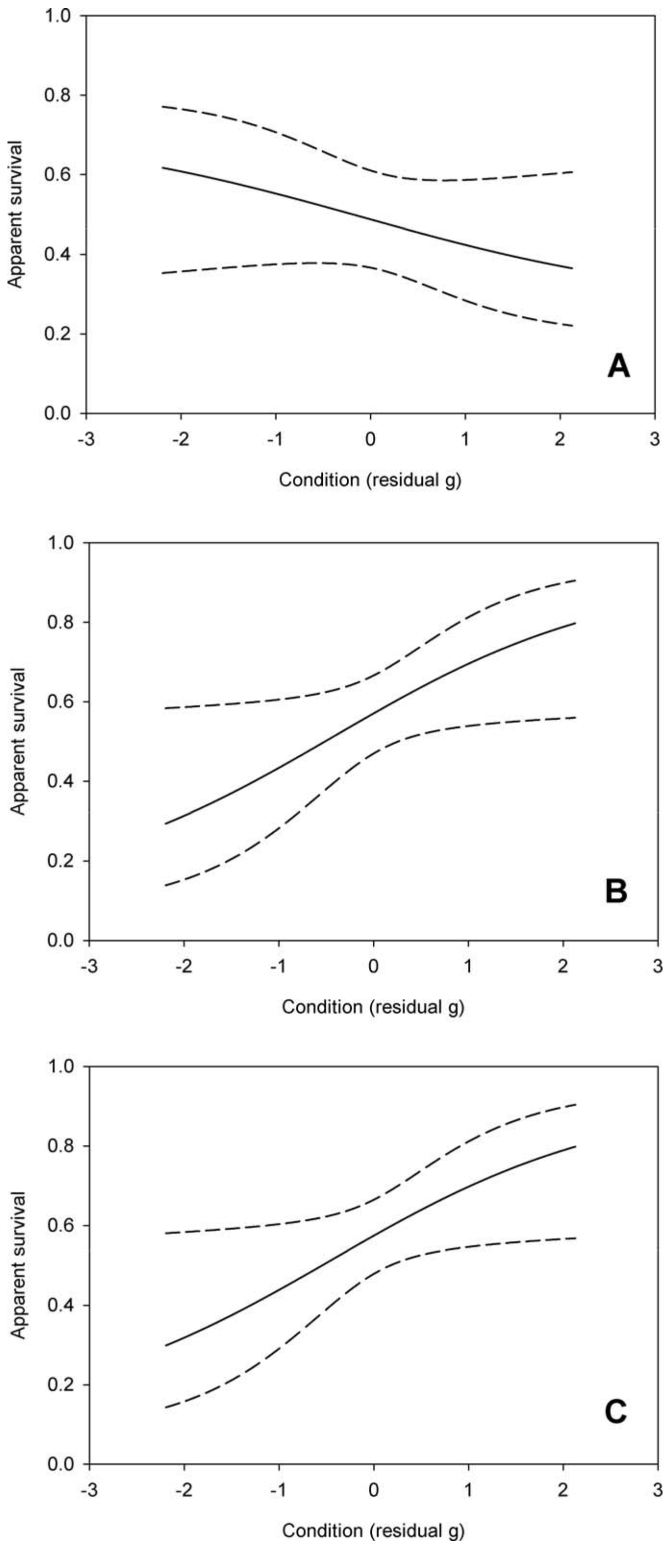

FIGURE 1. Model-averaged relationship (±95% confidence intervals) between body condition and apparent survival (φ) of Swainson's Warblers at (A) Big Island, (B) St. Francis National Forest, and (C) White River National Wildlife Refuge, 2004–2007.

2006, respectively), and 72 at White R. NWR (21, 29, and 22 in 2004, 2005, and 2006, respectively). For these 176 males, the first principal component (PC1) explained 38% of the variation (eigenvalue = 2.26) in linear measurements and all variables loaded positively, suggesting that PC1 represented overall size. As expected, there was a positive relationship between PC1 and mass (mass = 0.33 × PC1 + 15.52; $r^2 = 0.18$). Similarly, there was a positive relationship between condition (residual mass) and day of year (condition = 0.013 × day – 1.97; $r^2 = 0.10$), so we used the residuals of this relationship to control for the effect of capture date on estimates of body condition in survival analyses.

There was strong evidence that survival at St. Francis NF and White R. NWR was similar ($\Sigma w_i = 0.84$) but differed from that at Big I. ($\Sigma w_i = 0.93$; Table 1). Moreover, the top two survival models incorporated effects of body condition on survival, with the relationship varying between the two mature forest sites and Big I.; the annual survival probabilities of birds in better condition at initial capture were higher at St. Francis NF and White R. NWR but not at Big I. (Fig. 1). Model-averaged 95% confidence intervals for the body-condition parameter incorporated zero for Big I. but not for St. Francis NF or White R. NWR.

For body-condition analyses, from 22 April to 16 July, 2005–2007, we captured and recorded measurements of 211 male Swainson's Warblers, 84 at Big I. (31, 36, and 17 in 2005, 2006, and 2007, respectively), 48 at St. Francis NF (13, 19, and 16 in 2005, 2006, and 2007, respectively), and 79 at White R. NWR (35, 25, and 19 in 2005, 2006, and 2007, respectively; Table 3). The first principal component (PC1) explained 41% of the variation (eigenvalue = 2.48) in linear measurements, and all variables loaded positively (Table 3). There was a positive relationship between PC1 and mass (mass = 0.35 × PC1 + 15.39; $r^2 = 0.19$), and PC1 was a better predictor of mass than was any single measurement ($w_i = 0.80$).

There was strong evidence for an effect of day of year on condition ($\Sigma w_i = 0.99$) but limited evidence for effects of year ($\Sigma w_i = 0.50$) and location ($\Sigma w_i = 0.44$; Table 4). Models with year or location but not day of year received no support. The

TABLE 3. Mean, standard error, range of values, and principal component loadings for measurements of male Swainson's Warblers (n = 211) captured at Big Island, St. Francis National Forest, and White River National Wildlife Refuge, eastern Arkansas, 2005–2007.

Variable	$\bar{x}$	SE	Range	PC1	PC2
Bill (mm)	11.42	0.04	9.5–12.8	0.41	0.28
Left tarsus (mm)	17.80	0.04	15.9–19.3	0.68	0.61
Right tarsus (mm)	17.80	0.04	16.1–19.4	0.66	0.64
Left wing (mm)	69.83	0.13	57.5–75.0	0.74	−0.48
Right wing (mm)	69.86	0.11	66.5–75.0	0.77	−0.49
Tail (mm)	48.21	0.13	41.5–53.0	0.51	−0.41
Mass (g)	15.39	0.06	12.9–17.4		

TABLE 4. Results from best-fitting temporal and location models used to predict body condition of Swainson's Warblers ($n = 211$) at Big Island, St. Francis National Forest, and White River National Wildlife Refuge, eastern Arkansas, 2005–2007.

Model	K^a	ΔAIC_c [b]	w_i
Year × day of year	4	0	0.20
Day of year	2	0.09	0.19
Year + day of year	4	0.20	0.18
Location × day of year	4	0.29	0.17
Location + day of year	4	0.64	0.14
Location + year + day of year	10	1.72	0.08
Null (intercept only)	1	28.06	<0.01

[a] Number of parameters.
[b] AIC_c for the best-ranked model was −159.17.

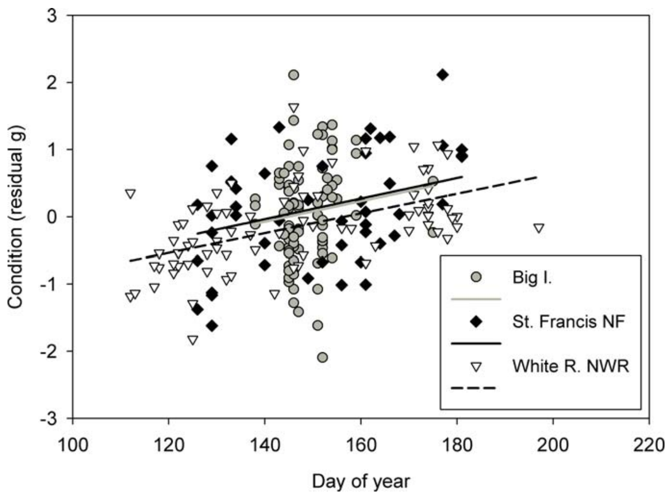

FIGURE 2. Model-averaged relationship between body condition of male Swainson's Warblers and day of year through the breeding season at Big Island, St. Francis National Forest, and White River National Wildlife Refuge, eastern Arkansas. Condition was derived as the residuals from a linear regression of the first principal component of linear measurements on body mass.

body condition of Swainson's Warblers improved through the breeding season in all three years and at all three locations but was somewhat lower in 2007 than in 2005 and 2006. It was slightly lower at White R. NWR than at the other two locations (Fig. 2). However, the 95% confidence intervals for all year or location parameters overlapped considerably.

The 180-m buffer around the capture location of 203 of 211 birds included at least one point of habitat sampling, and most included multiple points ($\bar{x} = 6.45$, SE = 0.36; Table 2). Seven models fit better than the day-of-year model, and the best-fitting habitat models incorporated effects of forb, grass, and sedge cover, litter volume, and understory density in addition to day of year; there were several closely competing models (Table 5). Forb and grass cover occurred in the top two models and accounted for 38% of the Akaike weight; understory density occurred in five of the top seven models and accounted for 46% of the weight. The 95% confidence intervals for the parameters associated with forb and grass cover, understory density, and day of year did not include zero, indicating that these effects were likely important; however, confidence intervals for the parameters associated with all other variables did include zero, indicating that these variables were likely less important. Forb and grass cover were associated with poorer body condition, whereas understory density was associated with better body condition (Fig. 3).

DISCUSSION

At two of our three study areas the relationship between body condition at initial capture and subsequent survival of male Swainson's Warblers was strong (Fig. 1). Although appearing negative, the model-averaged 95% confidence interval for the body-condition parameter at Big I. overlapped zero, suggesting no relationship between condition and survival at this location. The reason for this difference between Big I. and the other two sites is likely related to the differences in their

TABLE 5. Results from best-fitting a priori habitat models used to predict body condition of Swainson's Warblers ($n = 203$) at Big Island, St. Francis National Forest, and White River National Wildlife Refuge, eastern Arkansas, 2005–2007.

Model[a]	K^b	ΔAIC_c [c]	w_i	R^2
Percent forb/grass + litter volume + day of year	4	0	0.21	0.17
Percent forb/grass + day of year	3	0.41	0.17	0.16
Understory density + day of year	3	0.73	0.15	0.15
Understory density + sub-canopy cover + day of year	4	1.05	0.13	0.16
Understory density + litter volume + day of year	4	1.89	0.08	0.16
Day of year	2	3.46	0.04	0.13
Null (intercept only)	1	30.74	0.00	

[a] All habitat models included the best-fitting single temporal variable.
[b] Number of parameters.
[c] AIC_c for the best-ranked model was −155.73.

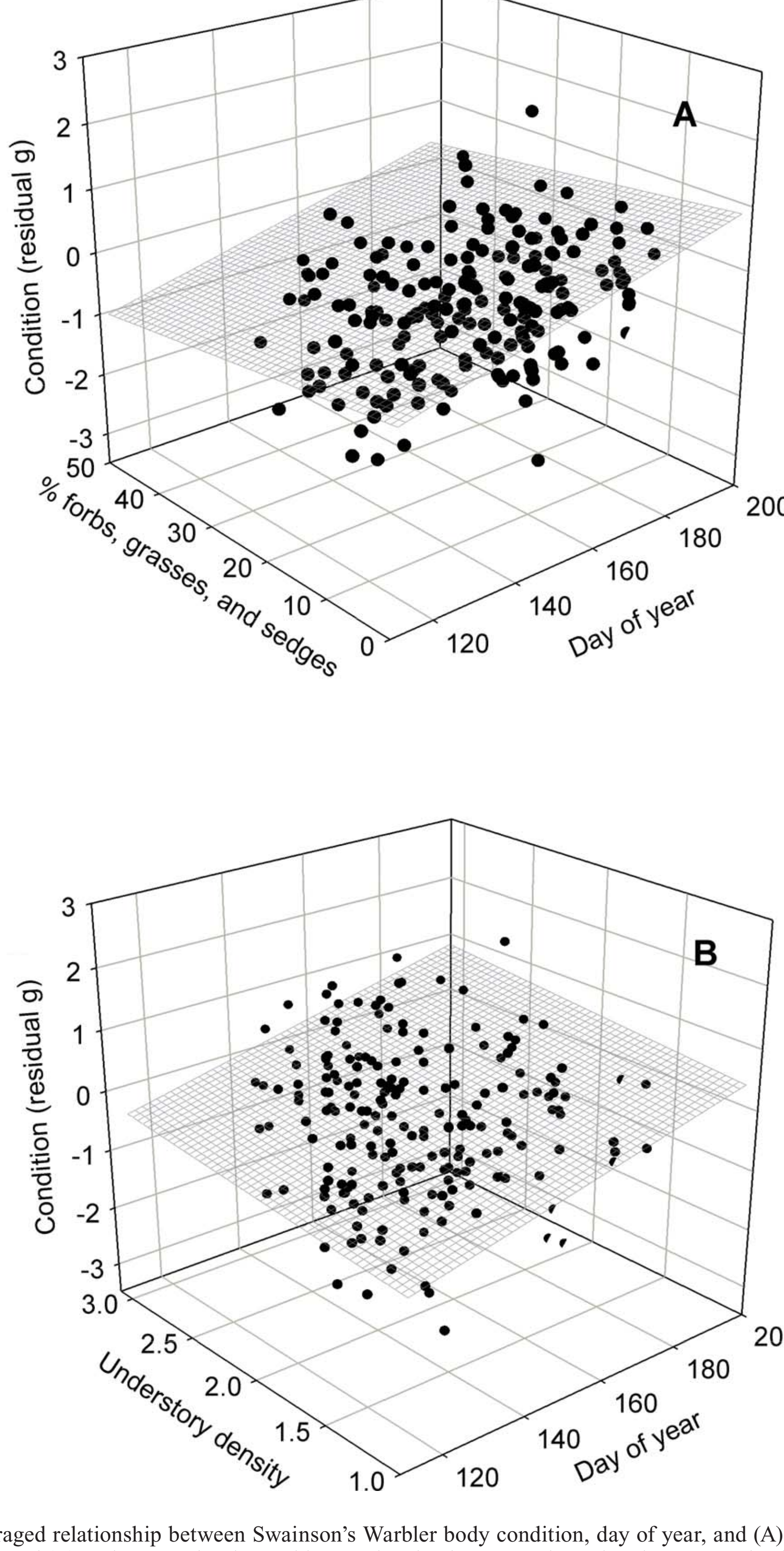

FIGURE 3. Model-averaged relationship between Swainson's Warbler body condition, day of year, and (A) estimated percent cover of forbs, grasses, and sedges and (B) understory-density ranking at Big Island, St. Francis National Forest, and White River National Wildlife Refuge, eastern Arkansas, 2005–2007. Condition was derived as the residuals from a linear regression of the first principal component of linear measurements on body mass.

management and resulting habitat structure. Big I. is privately owned and actively harvested, so the suitability of forest stands there changes rapidly. At Big I., harvesting of stands with suitable Swainson's Warbler habitat is associated with high rates of emigration (Benson 2008). At the two mature-forest sites the warblers' site fidelity was relatively high, and suitable habitat at these sites changed little over the course of our study. Consequently, the relationship between body condition and survival at St. Francis NF and White R. NWR likely indicates that birds in good condition survive at a higher rate or are less likely to emigrate, whereas the lack of this pattern at Big I. may be largely a result of timber harvest.

At all three study locations, Swainson's Warblers improved their body condition through the breeding season despite the stress of reproduction, suggesting the quality of all three is adequate. Counter to our expectations, there was no evidence that the condition of birds at the cane-dominated White R. NWR was superior to the condition of those at the other two locations, which have little cane. Likewise, the two mature-forest locations, St. Francis NF and White R. NWR, did not have birds that were in better condition than those at Big I., the actively harvested site. In fact, at White R. NWR the birds' condition appeared to be slightly poorer than at the other two sites, although 95% confidence intervals for the parameter estimates for each site overlapped considerably and this observed difference was likely caused by sampling at White R. NWR earlier in the season, when birds were in poorer condition than on the later dates when Big I. and St. Francis NF were sampled. This similarity suggests that, despite differences in habitat structure and composition, these three disparate areas on average provided habitat of similar quality in which birds were able to improve body condition prior to fall migration. Although we perceived these habitats as noticeably different, the resources available to the birds as indicated by body condition seemed, on average, to be similar.

Contrary to our expectations, cane density was not among the best predictors of body condition (Table 5), and birds banded in habitat with more cane were not in better condition than those in non-cane-dominated sites. Several recent studies have found that cane density is greater in occupied than in unoccupied areas (Brown et al. 2009), in used areas than in random areas within home ranges (Anich 2008), and at nest sites than at paired random sites (Benson et al. 2009). However, Anich (2008) found fewer cane stems at locations where Swainson's Warbler forage than at locations where they perch and sing, presumably trying to attract females, suggesting that cane may be preferred more because of its suitability as a nest substrate than because of its quality as foraging habitat (Benson et al. 2009). Despite this difference in habitat used for foraging versus displaying, increased density of cane may be associated with increased abundance of arthropods in litter (Brown 2008).

On the other hand, we did find poorer body condition in birds with greater cover of forbs and grasses in their territories (Fig. 3A). Henry (2004) and Anich (2008) also found Swainson's Warbler presence or habitat use to be negatively associated with forb cover, and we hypothesized that this relationship may be related to decreased foraging success in forb- or grass-dominated areas. Because Swainson's Warblers often move rapidly along the forest floor, actively lifting leaves in search of prey, ground-level vegetation may reduce foraging efficiency; the birds often forage in areas of low forb and grass-stem density (Graves 1998). Leaf litter is also important to Swainson's Warblers, and increased cover and depth is associated with habitat use (e.g., Bednarz et al. 2005, Anich 2008, Brown et al. 2009). Although litter volume appeared in several of our top models for body condition, in all of these models the 95% confidence interval for this variable's parameter estimate included zero. However, even though evidence for this effect was weak, the direction of this relationship was opposite of our predictions. Although Swainson's Warblers, with their specialized foraging behavior, require litter (Graves 1998), too much may also decrease their foraging efficiency, and an intermediate volume of leaf litter may be optimal. For example, if the abundance of arthropods does not increase with litter volume, or if the relationship between arthropod abundance and litter is nonlinear, the presence of additional litter may obstruct the warblers' searching behavior and decrease their foraging success per unit time.

In addition to variables that may affect foraging success, we also found understory vegetation density to be positively associated with the warblers' body condition (Fig. 3B). A dense understory with abundant woody stems of small diameter is a common component of Swainson's Warbler habitat throughout the species' range (Meanley 1971, Graves 2002, Henry 2004, Bednarz et al. 2005, Peters et al. 2005), and both understory density and density of stems are good predictors of Swainson's Warbler nest sites (Peters et al. 2005, Benson et al. 2009). However, these variables are likely related to the availability of nest sites rather than to the quality of foraging habitat, and the association of body condition with understory density may have reflected that better-quality males were more likely to gain better-quality territories with a higher probability of attracting females. Higher-quality males, in turn, may have an increased survival rate or a lower probability of emigrating. These possible relationships among body condition, habitat selection, dominance, territory defense, and apparent survival warrant further study.

Most previous studies of habitat-related patterns of body condition or relationships between condition and survival in migratory passerines have focused on the nonbreeding period (e.g., Marra and Holberton 1998, Strong and Sherry 2000, 2001, Latta and Faaborg 2002, Johnson et al. 2006, but see Bayne and Hobson 2002). Likewise, breeding-season studies have often investigated the effects of factors not related to habitat, such as breeding effort or weather, on body condition (Brown 1996, Chastel and Kersten 2002, Carbonell et al. 2003). One of the reasons for this greater focus on body condition during the nonbreeding period is the view that populations may be limited during this time (e.g., Rappole and McDonald 1994, Sherry and Holmes 1996) and that during the breeding season resources for many migratory species may be superabundant (e.g., Wiens 1974, 1977, Martin 1986). However, despite the trend for body condition to improve through the breeding season, we found considerable individual variation in condition that may have consequences for fitness. Even if resources, on average, are not limiting, spatial and temporal variability in resources and variation among individuals in intrinsic quality will lead to differences among individuals in condition, and it is these differences that ultimately shape decisions at the level of the individual (Martin 1986). Indeed, at St. Francis NF and White R. NWR the relationship between body condition and the warblers' apparent survival was strong, indicating that fine-scale decisions about habitat selection have significant implications for fitness.

Although some (e.g., Green 2001) have criticized the use of mass/size residuals as indicators of body condition, Schulte-Hostedde et al. (2005) demonstrated this method for estimating body condition to be reliable, and, for birds, this index has been corroborated as a reliable metric with several other types of data. For example, Marra and Holberton (1998) found size-corrected mass to be related to mass loss and concentrations of stress hormones, and other studies have found hypothesized habitat-related differences in body condition (e.g., Latta and Faaborg 2002, Bearhop et al. 2004). More importantly, Marra and Holmes (2001) found habitat-related differences in size-corrected mass to mirror patterns in survival, Johnson et al. (2006) found changes in size-corrected mass to be a very strong predictor of survival, and we found a >2-fold difference in predicted survival between birds in the poorest and those in the best condition.

Overall, our estimates of body condition based on size-corrected mass appear to provide an accurate index of body condition in Swainson's Warbler. At our study areas, we found that, on average, the birds' condition improved through the breeding season but that relative condition at any point in time was related to habitat features, specifically, a positive relationship with understory density and a negative relationship with the cover of forbs and grasses. Given the relationship between condition and survival in Swainson's Warbler, the variation among occupied areas in understory density or cover of forbs and grasses could result in differences of 5% to 10% in individuals' apparent survival.

Despite these discernable patterns, a large proportion of the variation in Swainson's Warbler body condition remained unexplained. Similarly, even though several habitat models improved upon the day-of-year model, these variables resulted in only modest increases in predictive ability (increased R^2 by 0.02–0.04). Some of these differences may have been related to unmeasured attributes such as age, which we were unable to consider because of the unreliability of plumage-based indicators for this species, genetically based differences in individuals' quality, and possibly carry-over effects from habitat quality during the nonbreeding period. Likewise, although possibly correlated with some of our habitat measurements, one potentially important predictor of body condition that we did not consider was food abundance. Indeed, Strong and Sherry (2000) found the abundance of primary food resources for another ground-foraging species, the Ovenbird (*Seiurus aurocapilla*), to be a major determinant of body condition during the nonbreeding period. Similarly, the abundance and spatial distribution of food resources for Swainson's Warblers are likely important, and more study is needed both on the species' preferred foods (but see Savage 2009) and on the effects of variability in these resources on body condition.

The influence of breeding-season body condition on apparent survival has significant conservation and management implications. Whether driven primarily by true survival or permanent emigration, apparent survival disproportionately affects the local population dynamics of many bird species (Sæther and Bakke 2000, Stahl and Oli 2006). Given this influence, the link between breeding-season habitat quality and body condition suggests that, by manipulating habitat quality, managers can promote stable populations of this and other species of conservation concern. For Swainson's Warbler, this management includes providing infrequently flooded bottomland forest areas (Benson and Bednarz 2010) with dense understories and little herbaceous ground cover, conditions that can likely be achieved through low-intensity timber harvesting (e.g., Twedt and Somershoe 2009).

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