FACTORS INFLUENCING HOME-RANGE SIZE OF SWAINSON'S WARBLERS IN EASTERN ARKANSAS

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Abstract. Understanding factors affecting space-use patterns can lead to improved knowledge of the ecology and habitat needs of a species. We radiotracked 37 male Swainson's Warblers (*Limnothlypis swainsonii*) at two sites in eastern Arkansas, White River National Wildlife Refuge, a bottomland site, and St. Francis National Forest, a site with birds in both bottomlands and uplands. We found substantial variation in home-range size and evaluated habitat and nonhabitat predictors of home-range size by information-theoretic techniques. We also evaluated how breeding phase affected home-range size. Several habitat variables were good predictors of home-range size, including understory density, vine-stem density, and other stem-density variables. Overall, vine-stem density and understory density were the best predictors of home-range size, and nonhabitat factors were poor predictors. A three-variable model including density of giant cane (*Arundinaria gigantea*), vine, and shrub stems as separate variables was a much better predictor of home-range size than a model using total stem density, suggesting that Swainson's Warblers respond differently to different stem types. Birds using areas with fewer vines and more cane exploited smaller home ranges, suggesting better habitat quality. Birds that were tracked a greater proportion of time during the incubation and nestling periods used larger home ranges. Though our study found that birds held smaller home ranges in areas of more cane and fewer vines, a combination of stem factors and understory density appears to explain home-range size best. We recommend that management for Swainson's Warbler focus on maintenance of uniformly dense understory vegetation within forests.

Key words: bottomland hardwood forest, *habitat use*, *home-range size*, Limnothlypis swainsonii, *space use*, *Swainson's Warbler*.

Factores que Afectan el Tamaño del Ámbito Hogareño de *Limnothlypis swainsonii* en el Este de Arkansas

Resumen. Entender los factores que afectan los patrones de uso del espacio puede conducir a un mejor conocimiento de la ecología y de los requerimientos de hábitat de las especies. Seguimos a 37 machos de la especie *Limnothlypis swainsonii* mediante radiotelemetría en dos sitios en el este de Arkansas: White River National Wildlife Refuge (un área de tierras bajas) y St. Francis National Forest (un área que alberga aves tanto en tierras bajas como en tierras altas). Encontramos que existe variación sustancial en el tamaño del ámbito hogareño y evaluamos la capacidad de variables relacionadas con el hábitat y de variables no relacionadas con el hábitat para predecir el tamaño del ámbito hogareño mediante técnicas basadas en la teoría de información. También evaluamos cómo la fase de la cría afectó el tamaño del ámbito hogareño. Varias variables del hábitat predijeron adecuadamente el tamaño del ámbito hogareño, incluyendo la densidad del sotobosque, la densidad de tallos y lianas y otras variables relacionadas con la densidad de tallos. En general, la densidad de tallos y lianas y la densidad del sotobosque fueron las variables que mejor predijeron el tamaño del ámbito hogareño, mientras que los factores no basados en el hábitat fueron inadecuados como variables predictivas. Un modelo con tres variables que incluía la densidad de *Arundinaria gigantea*, de lianas y de tallos de arbustos como variables separadas predijo el tamaño del ámbito hogareño mucho mejor que un modelo basado en la densidad total de tallos, lo que sugiere que *L. swainsonii* responde de modo diferencial a los distintos tipos de tallos. Las aves que ocupaban áreas con menos lianas y más *A. gigantea* presentaron ámbitos hogareños más pequeños, lo que sugiere una mejor calidad de hábitat. Las aves que seguimos la mayor parte del tiempo presentaron ámbitos hogareños más grandes durante los períodos de incubación y de cría de pichones. Aunque nuestro estudio encontró que las aves presentaron ámbitos hogareños más pequeños en áreas con más caña y menos lianas, una combinación de factores relacionados con los tallos y con la densidad del sotobosque parece brindar la mejor explicación del tamaño del ámbito hogareño. Recomendamos que el manejo del ambiente para *L. swainsonii* se enfoque en mantener vegetación uniformemente densa en la parte baja del interior de los bosques.

INTRODUCTION

The home range, which is generally defined as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt 1943) is a useful measure of space use and is likely influenced by multiple factors (McLoughlin and Ferguson 2000). Habitat features may be among the most important of these factors, and studies have shown relationships between home-range size and habitat type (e.g., Pejchar et al. 2005), landscape structure (Leonard et al. 2008), distance to landscape features (Leary et al. 1998), and age of habitat (Forsman et al. 2005, Stober and Krementz 2006). Other factors can also influence territory or home-range size, including prey type (Zabel et al. 1995), population density (Morse 1976), body size (Mazerolle and Hobson 2004), age of individual (Wegge and Larsen 1987), year (Marzluff et al. 1997), and phase of the breeding cycle (Derrickson 1978).

Relationships involving habitat quality can be complex, and investigators have used many techniques to attempt to quantify it (Johnson 2007), including measuring home-range size (e.g., Glenn et al. 2004). If home-range size is determined primarily by resource abundance, dense resources should result in small home ranges and widely spaced resources should result in large home ranges (e.g., Village 1982, Rothstein et al. 1984). Small home ranges and territories are likely also associated with lower costs of foraging movements and territory defense, and they may reduce exposure to predators (Schoener 1971, Wolf and Hainsworth 1971, Thompson and Fritzell 1989). For these reasons, in this paper we assume that smaller home ranges reflect better-quality and more efficiently exploited habitat than do larger home ranges.

In some instances, however, home-range size may not be a good indicator of habitat quality (sensu Van Horne 1983). Small territories (presumably associated with small home ranges) could be more costly to defend if the defended area is extremely desirable, though at extremely high levels of intrusion birds may simply stop defending a territory (Gill and Wolf 1975). If numbers are high and habitat is limited, birds may be densely packed into existing habitat and hold small home ranges but lack the resources necessary for successful reproduction. Home-range size and habitat quality may also be decoupled if birds are occupying an ecological trap.

While small-scale variability in habitat quality may not be reflected in the variation of home-range size, in marginal habitat, birds may use especially large home ranges. In our research on Swainson's Warbler (*Limnothlypis swainsonii*), we found individuals using a surprisingly large range of home-range sizes (1.55 to 30.75 ha; mean = 9.38, SE = 1.2 ha, *n* = 37; Anich et al. 2009b), including 11 birds with home ranges >10 ha. This variation in home-range size provided us the opportunity to examine factors responsible for Swainson's Warblers using large home ranges, which may be related to habitat quality.

Swainson's Warbler is a medium-sized wood-warbler that breeds in the southeastern United States and winters on Caribbean islands and the Yucatán Peninsula (Brown and Dickson 1994). It is secretive and feeds primarily on invertebrates obtained by flipping leaf litter. Pairs are usually socially monogamous, and males are territorial (Brown and Dickson 1994). Uncommon and local throughout its breeding range, Swainson's Warbler is a species of critical conservation concern because of widespread loss of suitable habitat and small estimated global population (Brown and Dickson 1994, Partners in Flight 2007). Though multiple studies have examined characteristics of Swainson's Warbler habitat (Eddleman et al. 1980, Graves 2001, 2002, Somershoe et al. 2003, Peters et al. 2005), the species' secretive nature has made examination of habitat quality at the home-range scale difficult.

Early accounts reported that giant cane (*Arundinaria gigantea*), a native bamboo, is an essential component of Swainson's Warbler habitat (Brewster 1885, Meanley 1945). Cane has declined by >98% in the Southeast, and canebrake ecosystems are now critically endangered (Noss et al. 1995, Platt et al. 2001). However, Swainson's Warbler is not restricted to the bottomlands where cane occurs; it also occurs in thickets of rhododendron (*Rhododendron* spp.) and eastern hemlock (*Tsuga canadensis*) in the Appalachian Mountains (Brooks and Legg 1942, Lanham and Miller 2006) and in young, second-growth stands of loblolly pine (*Pinus taeda*; Carrie 1996, Bassett-Touchell and Stouffer 2006) on the Gulf Coastal Plain. Also, Graves (2002) found little to no cane at five bottomland locations across the Southeast that Swainson's Warblers inhabited. Consequently, the importance of cane stands for Swainson's Warblers is unclear. Although Swainson's Warblers do not require cane, the quality of cane relative to other habitats is not well understood and has been debated (Graves 2002, Somershoe et al. 2003, Peters et al. 2005). Given floristic variation throughout the range of Swainson's Warbler, it is unknown whether the birds respond similarly to similar structural cues in different areas and whether similar habitat and nonhabitat features are important in the variety of vegetation associations Swainson's Warblers use.

Here, we used radiotelemetry to estimate home-range size and relate home-range size to variables hypothesized to be important for Swainson's Warblers. We used regression and information-theoretic techniques to evaluate two sets of a priori models as predictors of home-range size: (1) habitat models and (2) nonhabitat aspects of Swainson's Warbler ecology. We also, in a separate analysis due to limited sample size, examined (3) the effect of breeding phase on home-range size.

METHODS

STUDY AREAS

Because Swainson's Warblers are found in both bottomland forest and upland forest ecosystems, we studied them at two sites in Arkansas with different elevations and vegetation types: St. Francis National Forest (NF), and the Alligator Lake area of White River National Wildlife Refuge (White R. NWR). St. Francis NF is a 9150-ha forest reserve located on the

southernmost tip of Crowley's Ridge, which rises 80 m above the Mississippi River floodplain, providing some areas of the forest with topographic relief. It is bordered by the Mississippi River on the east, and we found Swainson's Warblers in ravines and along streams in upland areas as well as along swamps in bottomland forest. Trees dominating Swainson's Warbler habitat at St. Francis NF included elm (*Ulmus* spp.), box elder (*Acer negundo*), sweetgum (*Liquidambar styraciflua*), maple (*Acer* spp.), oak (*Quercus* spp.), hickory (*Carya* spp.), and tuliptree (*Liriodendron tulipifera*). Dominant vines in this area were greenbrier (*Smilax* spp.), poison ivy (*Toxicodendron radicans*), and Virginia creeper (*Parthenocissus quinquefolia*). The understory shrub layer was dominated by spicebush (*Lindera benzoin*) and pawpaw (*Asimina triloba*), and this study area contained few stands of cane.

White R. NWR is among the largest tracts of contiguous bottomland hardwood forest remaining in the Mississippi Alluvial Valley (approximately 65 000 ha; Gardiner and Oliver 2005). Elevations at this bottomland study site varied by only 7 m, but the Alligator Lake area where we worked is slightly higher than most of the refuge and is not flooded regularly. Dominant trees in habitats occupied by Swainson's Warblers in White R. NWR included sugarberry (*Celtis laevigata*), sweetgum, box elder, elm, American sycamore (*Platanus occidentalis*), and hickory. Dominant vines in these areas included Virginia creeper, greenbrier, peppervine (*Ampelopsis arborea*), and grape (*Vitis* spp.). This site contained relatively few shrubs, primarily spicebush and box elder, and some dense patches of cane.

RADIOTELEMETRY

To determine locations the birds used, we captured and fitted male Swainson's Warblers with radiotransmitters. We surveyed both sites extensively for Swainson's Warblers, and territorial males were located, banded, and monitored. We captured Swainson's Warblers by using targeted mist netting with song playbacks and banded captured birds with an aluminum U.S. Geological Survey band as well as a unique combination of three color bands. We affixed a 0.42-g transmitter, (LB-2N, Holohil Systems, Ltd., Carp, Ontario) to the interscapular region of each bird with cyanoacrylate glue (Sykes et al. 1990, Johnson et al. 1991, Anich et al. 2009a).

The transmitters' limited life and retention time, as well as the brevity of the period in which birds could be easily captured by target netting, necessitated the accumulation of sufficient location points in a short time. To accomplish this, we captured four birds in the same general area over 1 or 2 days, then rotated tracking them until we obtained at least 50 location points on each bird. Though selection of birds was not random, this procedure ensured home-range boundaries of adjacent birds were determined concurrently, and tracking nearby birds also facilitated the efficient recording of 50 location points per bird. We tracked each bird for 5 to 13 days,

from 06:00 to 19:00 hr CDT, and between 27 April and 3 July in 2005 and 2006. For each bird, we obtained at least one observation for every hour of the day. Location points were taken ≥20 min apart to provide biologically independent locations (e.g., Barg et. al. 2005). Birds could traverse the entire home range in this time and rarely stayed in the same location for >20 min. We tracked birds in every section of our study areas where Swainson's Warblers occurred, and at St. Francis NF almost all known males were tracked. No individuals were tracked twice, and no birds tracked in 2006 used any areas that were used by birds tracked in 2005.

Radio-marked birds were tracked by homing with H-antennas (Telonics, Inc., Mesa, AZ) and radio receivers (Communications Specialists, Inc., Orange, CA). We homed slowly toward each bird, making an effort not to disturb it, and when we detected it visually or aurally, we recorded the location with a hand-held Global Positioning System receiver (GPS 12, Garmin Intl., Olathe, KS) and marked it with flagging. When birds did not sing or were not visible (often in extremely thick vegetation), the strength of the telemetry signal allowed us to determine the bird's approximate location, and we often approached the thicket with the antenna from several angles to confirm the bird's presence.

ESTIMATION OF HOME-RANGE SIZE

We estimated home ranges by the fixed-kernel technique, which generates utilization distributions with probability contours around point locations and has little bias (Van Winkle 1975, Worton 1989, Seaman and Powell 1996). We used the Animal Movement extension (Hooge and Eichenlaub 2000) in ArcView 3.3 (Environmental Systems Research Institute, Redlands, CA) to calculate 95% fixed-kernel home ranges for each radiotracked Swainson's Warbler. We used least-squares cross-validation (LSCV) to calculate kernel smoothing parameters as recommended by Kernohan et al. (2001). On the recommendation of Seaman et al. (1999) to use a minimum of 30 location points, preferably 50 or more, for kernel analyses of home range, we attempted to record 50 points for each bird. Bootstrap analysis (e.g., Barg et al. 2005) suggested this number of points was more than adequate for a sufficient estimate of our birds' home ranges (Anich et al. 2009b).

VEGETATION SAMPLING

Using a modified BBIRD protocol (Martin et al. 1997, Bednarz et al. 2005), we recorded vegetation data in plots of radius 5 m at five points randomly selected within the home range of each bird. Within each plot, we used a ruler to measure leaf-litter depth 5 m from the center of the plot in the four cardinal directions. We estimated percent cover of forbs, leaf litter, and bare ground within four quadrants of a 5-m circle and later averaged these four values to produce one estimate of percent ground cover for each variable. We counted the number of shrub, cane, and vine stems at ≥0.3 m height in four 1-m^2 quadrats 5 m from

the center point and measured the mean height of the canopy with a clinometer. We counted the number of medium (diameter at breast height [dbh] 23–38 cm) and large (dbh >38 cm) trees. We used a coverboard to estimate vegetation density in 0.5-m increments from 0 to 2.5 m above the ground (Nudds 1977). The coverboard was set at the center of the plot, and estimates were made from 11.3 m in the four cardinal directions. Coverboard measurements from the five height increments were highly correlated, so we averaged these values into one measurement of understory vegetation density. Because heterogeneity of variables may be an important factor, we also calculated the standard deviation among the plots within each bird's home range for measurements of total stem density, leaf litter cover, and understory density. We present a summary of vegetation measurements at each site in Appendix A.

STATISTICAL ANALYSES

Habitat predictors of home-range size. To determine important habitat factors influencing home-range size in Swainson's

Warblers, we first removed highly correlated variables ($|r| > 0.7$). On the basis of the existing literature and our own field observations, we formulated 22 a priori models including habitat variables that we thought would be good predictors of home-range sizes (Table 1). We then used SAS to perform linear regressions (SAS Institute 2003) and evaluated those models with Akaike's information criterion for small sample sizes (AIC_c; Burnham and Anderson 2002). We calculated AIC_c weights (w_i), which are the AIC_c values standardized across models to sum to 1.0, allowing us to compute the relative likelihood that a model is the best model in the set (Burnham and Anderson 2002). Home-range sizes were log-transformed prior to analyses to better meet assumptions for statistical analysis. Because of the two study sites' differences in vegetation structure and topography, we thought that Swainson's Warblers might respond to habitat in St. Francis NF and White R. NWR differently and therefore included terms for an interaction with study site in 7 of 22 candidate habitat models (see Anich [2008] for results of all models by

TABLE 1.   A priori candidate models of habitat factors used to predict size of home ranges of Swainson's Warblers at two sites in eastern Arkansas in 2005 and 2006, St. Francis National Forest (SFNF) and White River National Wildlife Refuge (WRNWR).

Candidate model	Variables
Cane	Cane-stem density[a]
Shrub	Shrub-stem density[a]
Vine	Vine-stem density[a]
Total stem	Total stem density[b]
Total stem variability	SD[c] total stem density
Understory density	Understory density[d]
Litter volume	Litter volume[e]
Cane and litter	Cane-stem density, percent leaf litter[f]
Understory distribution	Understory density, SD understory density
Understory density and litter cover	Understory density, percent leaf litter
Understory density and litter variation	Understory density, SD percent leaf litter
Mature forest	Canopy height[g], medium and large trees[h]
Vine and understory distribution	Vine-stem density, SD understory density
Cane by site	Cane-stem density SFNF, cane-stem density WRNWR
Shrub by site	Shrub-stem density SFNF, shrub-stem density WRNWR
Vine by site	Vine-stem density SFNF, vine-stem density WRNWR
Total stem by site	Total stem density SFNF, total stem density WRNWR
Understory density by site	Understory density SFNF, understory density WRNWR
Stem type	Cane-stem, vine-stem, shrub-stem densities
Foraging substrates	Percent forbs[f], percent bare ground[f], percent leaf litter
Cane and understory density by site	Cane-stem density SFNF, cane-stem density WRNWR, understory density SFNF, understory density WRNWR
Vine and understory density by site	Vine-stem density SFNF, vine-stem density WRNWR, understory density SFNF, understory density WRNWR

[a] Stems per m², measured within four 1-m² quadrats.
[b] Sum of the cane, vine, and shrub stems per m².
[c] Standard deviation among points in a home range.
[d] Percent vegetation cover, measured with a 2.5-m coverboard (Nudds 1977).
[e] Calculated as mean leaf-litter depth (mm) × estimated percent litter coverage × plot area.
[f] Estimated percent cover within 5-m-radius circle.
[g] Mean height of the canopy (m) measured with a clinometer.
[h] Number of trees >23 cm dbh in 5-m-radius circle.

site). To account for model-selection uncertainty, we also summed the AIC_c weights for each habitat variable across all models in which that variable occurred; large values for summed weights indicate greater support for the influence of that variable. To estimate the magnitude of these effects given uncertainty, we also summed AIC_c weights for the 90% confidence set of models (i.e., models that accounted for 90% of the total AIC_c weight) and used these values to generate model-averaged parameter estimates (Burnham and Anderson 2002:149–171).

Nonhabitat predictors of home-range size. Because factors unrelated to habitat can influence home-range size, we also used AIC_c to evaluate the effects of seven other potentially important factors. We performed this analysis separately from that of habitat variables because of limited sample sizes. We investigated whether home-range size was related to body size (wing length), study site, or year. We also examined whether home-range size was related to number of neighboring Swainson's Warblers or the SD of elevation measurements across a home range. We used a 30-m digital elevation model (U. S. Geological Survey 1999, GeoStor 2007) to calculate elevations for every point. Because the timing of our radiotracking could have influenced estimates of home-range size, we checked for relationships with the number of days and with the mean day of the year on which a bird was radiotracked.

Breeding-phase predictors of home-range size. Because renesting by Swainson's Warblers at our study sites was common (Benson 2008), the phase of the breeding cycle of birds tracked concurrently was often asynchronous, which means that the relationship between day of year and home-range size is likely confounded by renesting. For this reason, we also investigated whether the phase of breeding cycle was related to home-range size. We calculated the proportion of days that each bird spent in three phases of the breeding cycle (nest building/egg laying, incubation/nestling, fledgling) during the period in which it was tracked to ascertain any relationship between breeding phase and home-range size. These phase divisions were defined by the behavior of males during the breeding cycle. During the nest-building and egg-laying stages the male typically stays close to the female, while during the incubation and nestling stages the male typically spends time apart from the female and visits the nest only briefly (Meanley 1969; TJB, unpubl. data). During the fledgling-care period, the male may move shorter distances and more slowly, as he is often traveling with and feeding the young. Because of frequent renesting, dense vegetation, and often cryptic nests, we were unable to obtain reliable information on the breeding phase of our entire sample of birds and thus cannot factor breeding phase into our habitat or nonhabitat models. Therefore, we used linear regression to examine possible breeding-phase effects on the subset ($n = 20$) of our birds for which we had breeding-phase information.

RESULTS

HOME-RANGE SIZE

In 2005, we recorded 805 location points on 16 male Swainson's Warblers, seven at St. Francis NF and nine at White R. NWR. In 2006, we recorded 1046 location points on 21 male Swainson's Warblers, 10 at St. Francis NF and 11 at White R. NWR. The mean number of locations per bird was 50.03 (range 44–52), and at least 50 points were obtained on 35 of the 37 birds in the sample. We visually sighted radio-marked birds at 23% of location points and detected them by ear at 55% of locations. In total, 63% of all points were confirmed through either visual or auditory means. We used triangulation to estimate locations for 3% of points, often when a body of water prevented us from reaching the bird before it moved. We found that 95% fixed-kernel home-range estimates ranged from 1.55 to 30.75 ha (mean = 9.38 ha, SE = 1.2, $n = 37$; Anich et al. 2009b). Estimates at the two sites were similar, ranging from 2.23 to 28.37 ha at St. Francis NF (mean = 10.24 ha, SE = 1.8, $n = 17$) and 1.55 to 30.75 ha at White R. NWR (mean = 8.65 ha, SE = 1.7, $n = 20$).

HABITAT PREDICTORS OF HOME-RANGE SIZE

The model with the highest AIC_c weight (0.33) included vine-stem density and understory density affecting home-range size, but the relationships varied by site (Table 2). The second most likely model ($w_i = 0.23$) included the effect of vine-stem density varying by site, and the third most likely ($w_i = 0.13$) included density of cane stems, vine stems, and shrub stems. The top four models included a variable for vine-stem density. Models containing SD total stems, SD understory density, understory density, and SD leaf-litter cover were also better predictors of home-range size than the intercept-only model (Table 2). Sums of the AIC_c weights showed vine-stem density, understory density, and other stem variables to be the best predictors of home-range size (Table 3).

NONHABITAT PREDICTORS OF HOME-RANGE SIZE

Of the nonhabitat models we examined, only number of neighbors was a better predictor of home-range size than the intercept-only model, and all models had low r^2 values (<0.1), indicating that none of the nonhabitat predictors were effective at explaining variation in home-range size (Table 4).

INFLUENCE OF BREEDING PHASE ON HOME-RANGE SIZE

For our analysis of the effect of breeding phase on home-range size, we had reliable information on nesting of only a subset of our birds ($n = 20$), but there was a significant

TABLE 2.   Habitat models used as predictors of size of home ranges (log-transformed) of Swainson's Warblers at St. Francis National Forest (SFNF; $n = 17$) and White River National Wildlife Refuge (WRNWR; $n = 20$) in eastern Arkansas. Models with the lowest AIC_c and highest weight (w_i) are the best-supported models. Only models better than the intercept-only model are shown (weights are based on the full model set shown in Table 1).

Model[a]	K[b]	ΔAIC_c	w_i	R^2
Vine stems[c] SFNF, vine stems WRNWR, understory density[d] SFNF, understory density WRNWR	6	0.00	0.33	0.40
Vine stems SFNF, vine stems WRNWR	4	0.74	0.23	0.29
Cane stems[c], vine stems, shrub stems[c]	4	1.91	0.13	0.27
Vine stems	2	3.21	0.07	0.14
Total stems[e] SD[f]	2	3.72	0.05	0.13
Vine stems, understory density SD	3	4.27	0.04	0.17
Cane stems	2	4.40	0.04	0.11
Understory density	2	4.74	0.03	0.10
Understory density, litter[g] SD	3	6.33	0.01	0.12
Intercept only	1	6.43	0.01	

[a] AIC_c of best model = −27.01.
[b] Number of model parameters.
[c] Stems per m^2, measured within four 1-m^2 quadrats.
[d] Percent vegetation cover, measured with a 2.5-m coverboard (Nudds 1977).
[e] Sum of the cane, vine, and shrub stems per m^2.
[f] Standard deviation among points in a home range.
[g] Estimated percent cover within 5-m-radius circle.

positive relationship between the proportion of days that a bird was in the incubation/nestling period and home-range size ($F_{1,18} = 10.8$, $P = 0.005$, $r^2 = 0.38$, $\beta = 1.16$). In the nest building/egg laying period, there was no significant relationship between home-range size and proportion of days tracked ($F_{1,18} = 0.2$, $P = 0.23$), and the number of birds tracked during the fledgling-care period was inadequate for analysis ($n = 2$).

TABLE 3.   Sums of AIC_c weights (w_i) and model-averaged coefficients (with 95% confidence intervals) for each habitat variable used to predict size of home ranges (log-transformed) of Swainson's Warblers at two sites in Arkansas, White River National Wildlife Refuge (WRNWR) and St. Francis National Forest (SFNF). Coefficients are reported only for variables that are in the 90% confidence set (Burnham and Anderson 2002).

Variable	β[a]	95% CI	Σw_i
Vine stems[b] SFNF	0.176	−0.007, 0.358	0.56
Vine stems WRNWR	0.302	0.056, 0.548	0.56
Understory density[c] SFNF	−0.026	−0.051, −0.001	0.33
Understory density WRNWR	0.010	−0.016, 0.036	0.33
Cane stems[b]	−0.068	−0.192, 0.056	0.16
Shrub stems[b]	0.269	−0.186, 0.725	0.13
SD[d] Total stems[e]	0.156	0.019, 0.292	0.05
SD Understory density	−0.020	−0.054, 0.015	0.04

[a] Model-averaged parameter based on 90% confidence set of models (Burnham and Anderson 2002).
[b] Stems per m^2, measured within four 1-m^2 quadrats.
[c] Measured with a 2.5-m coverboard (Nudds 1977).
[d] Standard deviation among points in a home range.
[e] Sum of the cane, vine, and shrub stems per m^2.

TABLE 4.   Nonhabitat models used as predictors of size of home ranges of Swainson's Warblers ($n = 36$), at two sites in eastern Arkansas, St. Francis National Forest (SFNF) and White River National Wildlife Refuge (WRNWR). Models with the lowest AIC_c and highest weight (w_i) are the best-supported models.

Model[a]	K[b]	ΔAIC_c	w_i	r^2
−0.176 Number of neighbors + 2.400	2	0.00	0.22	0.09
Intercept only (intercept = 1.965)	1	0.15	0.21	
0.097 SD elevation[c] + 1.799	2	0.70	0.16	0.07
0.109 Wing length (mm) − 5.660	2	0.79	0.15	0.07
0.107 Number of days radiotracked + 1.075	2	2.06	0.08	0.04
−0.271 Study site[d] + 2.108	2	2.24	0.07	0.03
−0.007 Mean day of year radiotracked + 3.008	2	2.43	0.07	0.03
−0.159 Year[e] + 2.058	2	3.05	0.05	0.01

[a] AIC_c of best model = −20.17.
[b] Number of model parameters.
[c] Standard deviation in elevation among all points in a home range.
[d] Where SFNF was coded 0 and WRNWR was coded 1.
[e] Where 2005 was coded 0 and 2006 was coded 1.

DISCUSSION

NONHABITAT PREDICTORS OF HOME-RANGE SIZE

Our nonhabitat models were generally poor predictors of home-range size. However, the best of these models showed a weak negative relationship between the number of neighbors and home-range size, indicating that home ranges were smaller in areas with more competing males. Other authors have found similar relationships between territory or home-range size and population density (Morse 1976, Hooper et al. 1982, Smith and Shugart 1987), possibly because of more birds being attracted to the best habitats. There was little support for models including site, year, number of telemetry points, or mean day of year that we tracked a bird, indicating that these factors had little effect on our estimates of Swainson's Warblers' home ranges.

INFLUENCE OF BREEDING PHASE ON HOME-RANGE SIZE

We did find a significant positive relationship between home-range size and the proportion of days that we tracked a bird during the incubation/nestling period. Although territories and home ranges are not always equivalent, there was a strong positive relationship between territory and home-range sizes among the Swainson's Warblers we studied (Anich et al. 2009b), and common factors likely affect the size of both. Using territory size, Stenger and Falls (1959) observed an increase in the space Ovenbirds (*Seiurus aurocapilla*) use during the incubation period. In male Hooded Warblers (*Wilsonia citrina*) however, Pitcher and Stutchbury (2000) found no difference by phase of the breeding cycle in the number of extraterritorial forays. In our birds, the largest movements from the center of the home range tended to occur while the female was incubating and caring for nestlings. During this period, male Swainson's Warblers periodically feed the nestlings but overall spend little time at the nest (TJB, unpubl. data). As polygyny and extra-pair copulations in Swainson's Warblers are likely (Graves 1992; J. Gerwin, pers. comm.; TJB, unpubl. data), we suggest that males use the incubation/nestling phase to search for other females and explore areas adjacent to their territory. Meanley (1971) reported that Swainson's Warbler territories are smallest during the mating and nest-building periods, but we did not find a significant relationship between home-range size and proportion of time tracked in the mating/nest-building period. The males stayed close to the females during this phase; however, the area they used was not smaller than in other phases of the breeding cycle, possibly because the male and female travel throughout the territory to search for and select a nest site (Meanley 1971).

HABITAT PREDICTORS OF HOME-RANGE SIZE

The best predictors of the size of Swainson's Warblers' home ranges included understory and vine-stem density, although the effects of these variables differed by site, with the effect of vine stems being more pronounced at White R. NWR and that of understory density being stronger at St. Francis NF. These differences were likely related to site-level differences in vegetation structure and composition (Appendix A). Not only were vines more abundant at White R. NWR, the context in which they were abundant differed: vine stems were negatively associated with cane-stem density ($r = -0.50$, $P = 0.023$) and positively associated with patchiness of understory density ($r = 0.56$, $P = 0.010$) at White R. NWR, but not at St. Francis NF ($r = 0.15$ and 0.18, $P = 0.56$ and 0.48, respectively). Moreover, at St. Francis NF Swainson's Warblers may respond more strongly to understory density because the understory at this site was generally less dense than at White R. NWR and the relationship with home-range size may reach an asymptote at high densities.

At both sites, the model-averaged coefficients indicated a positive relationship between vine density and home-range size, suggesting that areas with fewer vines were of higher quality for Swainson's Warblers. Indeed, the two home ranges with the greatest estimated vine density (6.9 and 6.1 vine stems m^{-2}) were the two largest (28.37 and 30.75 ha, respectively); these home ranges were relatively linear with patchily distributed vine cover. Because kernel estimators can cause boundaries to be inflated, and this effect is magnified in linear home ranges, we ran models using minimum-convex-polygon estimates of home range to test whether this was affecting our results, but the results were qualitatively the same. Large home ranges in vine-dominated habitats suggest birds in those areas may be forced to range widely to find sufficient foraging habitat. In South Carolina, however, Peters et al. (2005) noted the importance of vines to Swainson's Warblers and found vine abundance to be a good predictor of occupancy. Peters et al. (2005) studied two sites, one where vine habitat seemed to be thick and uniform with a dense population of Swainson's Warblers, the other consisting of patchily distributed cane with fewer Swainson's Warblers. Conversely, at our sites, we saw a general pattern where cane-dominated areas were dense and uniform with abundant Swainson's Warblers, while our vine-dominated habitats were patchily distributed and Swainson's Warblers were more widely distributed in them. Collectively, these results suggest that uniformity of dense understory is more important for Swainson's Warbler habitat quality than any particular vegetation type. However, a three-variable model including cane-, vine-, and shrub-stem density as separate variables was ranked higher than a model in which cane, vine, and shrub counts were pooled into one variable, suggesting that at our study sites Swainson's Warblers view different stem types differently.

Because many studies have associated Swainson's Warblers with cane, many of our a priori models included cane as a variable. At our study sites, cane is an oft-used nest substrate and is the best predictor of occupancy (Brown et al. 2009, Benson et al. 2009). At both of our sites, smaller home ranges (with presumably higher-quality habitat) tended to be composed of more cane and fewer vines, as cane-stem density had an inverse relationship and vine-stem density had a positive relationship with home-range size. Indeed, the birds whose home ranges had the two highest mean cane stem counts (9.1 and 8.2 cane stems m^{-2}) held among the smallest home ranges (3.36 and 3.18 ha),

suggesting that cane thickets can provide the birds much more concentrated habitat. However, cane was apparently not the only cause of small home ranges, as some birds using areas with few cane stems also held small home ranges, and cane density alone was not among the most highly ranked predictors of home-range size. It therefore appears that a combination of stem variables and understory density may be the most important indicators of home-range size, and equating habitat quality directly with cane-stem density does not account for other factors.

The relatively high ranking of understory-density models was consistent with other studies citing the importance of dense understory thickets for Swainson's Warblers (Eddleman 1978, Graves 2002), and in our study areas this variable was the best predictor of nest sites (Benson et al. 2009). Although over their range Swainson's Warblers inhabit multiple vegetation types, the need for a dense understory seems to be common throughout. Graves (2001, 2002) and Bednarz et al. (2005) also recognized that floristic differences seem to be less important than overall vegetative structure in determining habitat suitable for Swainson's Warblers. At our sites, sparse and patchy understory structure was also associated with increased nest predation and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Benson et al. 2010a, b), supporting our conclusion that spare and patchy understories represent poor-quality habitat.

On the basis of these results, we suggest that management for Swainson's Warblers focus on maintenance of forests with dense understory vegetation. Though we found that home ranges were smaller in areas of more cane and fewer vines, studies across the range suggest that overall vegetation density is the most important attribute. We suggest increasing and maintaining patches of giant cane where feasible, as at our study sites, cane provides a suitably thick understory for Swainson's Warblers. However, opening gaps in the canopy to allow for dense growth of the understory, whether of cane or not, will likely provide high-quality habitat (Twedt and Somershoe 2009). There is a need for manipulative experiments to study the effect of forest management on Swainson's Warblers, and both timber harvest and controlled burns may help maintain a dense forest understory. Additionally, managers should keep in mind that the quality of the understory is likely to be influenced by successional changes, and long-term monitoring is critical to understanding use of sites over time.

ACKNOWLEDGMENTS

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APPENDIX A.   Mean, 95% confidence interval, and range of habitat data recorded at randomly selected vegetation plots sampled within the home ranges of Swainson's Warblers at two study sites in Arkansas, St. Francis National Forest and White River National Wildlife Refuge.

	St. Francis NF ($n = 17$)			White R. NWR ($n = 20$)		
	Mean	95% CI	Range	Mean	95% CI	Range
Cane stems[a]	0.5	0.1, 0.8	0.0–2.2	3.1	1.9, 4.3	0.4–10.1
Shrub stems[a]	1.4	1.1, 1.6	0.5–2.4	0.3	0.1, 0.4	0.0–1.3
Vine stems[a]	1.3	0.4, 2.2	0.0–7.5	2.6	1.9, 3.3	0.5–5.3
Total stems[b]	3.1	2.2, 4.1	1.2–8.0	6.0	5.0, 7.0	2.6–10.6
SD[c] total stems	1.8	1.2, 2.5	0.4–4.7	2.9	2.0, 3.8	0.7–8.7
SD understory density[d]	16.9	13.5, 20.3	3.8–28.4	19.1	15.1, 23.0	8.4–33.6
Understory density	45.0	38.1, 51.8	21.6–69.5	58.4	51.3, 65.4	31.6–89.0
Litter volume[e]	1.3	0.8, 1.7	0.2–3.3	2.1	1.7, 2.4	0.7–3.5
Leaf litter[f]	59.3	51.8, 66.7	29.3–81.3	77.1	68.7, 85.6	35.2–98.3
SD leaf litter	28.1	22.4, 33.7	7.7–44.7	13.6	8.3, 18.8	0.5–44.6
Canopy height[g]	28.7	26.3, 31.1	20.2–38.2	32.4	28.9, 35.9	5.1–41.0
Medium and large trees[h]	1.1	0.9, 1.4	0.4–1.8	1.1	0.9, 1.3	0.4–2.4
Forbs[f]	18.8	14.5, 23.1	6.2–40.5	5.0	3.6, 6.3	1.4–10.4
Bare ground[f]	23.2	15.0, 31.4	1.9–66.5	5.4	3.4, 7.4	0.3–17.7

[a] Stems per m^2, measured within four 1-m^2 quadrats.

[b] Sum of the cane, vine, and shrub stems per m^2.

[c] Standard deviation among points in a home range.

[d] Percent vegetation cover, measured with a 2.5-m coverboard (Nudds 1977).

[e] Calculated as mean leaf-litter depth (mm) × estimated percent litter coverage × plot area.

[f] Estimated percent cover within 5-m-radius circle.

[g] Mean height of the canopy (m) measured with a clinometer.

[h] Number of trees >23 cm dbh in 5-m-radius circle.