MOVEMENT PATTERNS AND STOPOVER ECOLOGY OF WILSON'S WARBLERS DURING SPRING MIGRATION ON THE LOWER COLORADO RIVER IN SOUTHWESTERN ARIZONA

Kristina L. Paxton[1,3], Charles Van Riper III[1], and Chris O'brien[2]

[1]*U.S. Geological Survey, Southwest Biological Science Center, Sonoran Desert Research Station, 325 Biological Sciences East, University of Arizona, Tucson, AZ 85721*
[2]*School of Natural Resources, University of Arizona, Tucson, AZ 85721*

Abstract. We used radio-telemetry to examine fine-scale movement patterns of Wilson's Warblers (*Wilsonia pusilla*) at a stopover site on the lower Colorado River during spring migration in 2005 and 2006. The overall movements of Wilson's Warblers were restricted to small, localized areas, with an average linear displacement of only 332 m. Warblers exhibited exploratory behavior characterized by fast, long-distance, directed linear movements during the first and second day after presumed arrival at the stopover site. However, exploration was limited within the overall landscape (<2 km diameter), suggesting a cost to extended exploration. As individuals gained more information about the distribution of resources at the stopover site through exploratory behavior and direct sampling of the habitat, movements became more aggregated within a localized area, suggesting that Wilson's Warblers settled within a microsite at the stopover site to replenish fuel supplies. The overall movement patterns exhibited by warblers during stopover were influenced by the age of the individual and changes in resources, both within a season and between years. Movement patterns of Wilson's Warblers documented during this study provide essential information about the temporal distribution of a warbler's locations within a stopover site, indicating how birds search for and acquire food resources throughout their stopover.

Key words: lower Colorado River, migration, movement, Neotropical migrant, radio-telemetry, riparian woodlands, Wilsonia pusilla.

Patrones de Movimientos y Ecología de las Escalas Migratorias de *Wilsonia pusilla* durante la Migración de Primavera en la Parte Baja del Río Colorado, Suroeste de Arizona

Resumen. Utilizamos radio-telemetría para examinar los patrones de movimiento de *Wilsonia pusilla* a pequeña escala en un sitio de parada migratoria en la parte baja del río Colorado durante la migración de primavera de 2005 y 2006. Los movimientos generales de *W. pusilla* estuvieron restringidos a áreas pequeñas y localizadas, con un desplazamiento lineal de sólo 332 m. Los individuos exhibieron un comportamiento exploratorio caracterizado por movimientos rápidos, de larga distancia y dirigidos, que tuvieron lugar durante el primer y segundo día después del supuesto arribo al sitio de escala. Sin embargo, la exploración se limitó al paisaje general (<2 km de diámetro), lo que sugiere que existe un costo para la exploración extendida. A medida que los individuos adquirieron más información acerca de la distribución de recursos en el sitio de escala, mediante el comportamiento exploratorio y el muestreo directo del ambiente, los movimientos se agruparon más en un área localizada, lo que sugiere que las aves se establecieron en un micrositio dentro del sitio de escala para recuperar sus reservas de energía. Los patrones generales de movimiento exhibidos por las aves durante la época de escala migratoria estuvieron influenciados por la edad de los individuos y por cambios en los recursos, tanto dentro de una estación como entre años. Los patrones de movimiento de *W. pusilla* documentados durante este estudio brindan información esencial sobre la distribución temporal de los lugares en que se ubican los individuos dentro de un sitio de escala, lo que indica cómo las aves buscan y adquieren recursos alimenticios durante las escalas.

INTRODUCTION

Long-distance migration is energetically expensive, and the energy necessary for an entire migration typically exceeds the amount of fuel reserves that small passerines can store and carry (Blem 1990). Therefore, at least 90% of the total migration time of passerines is spent at stopover sites, resting and replenish-ing energy reserves (Hedenström and Alerstam 1997, Lindström 2003). Upon arriving at a stopover site, migratory birds must rapidly acquire food in unfamiliar habitats when energy demands are high (Loria and Moore 1990, Jenni and Schaub 2003). Yet, the time constraints imposed on migrating birds to minimize the time spent en route (Alerstam and Lindström 1990) conflict with the need to explore and become familiar

with the distribution and abundance of available resources at each new stopover site. The amount of exploration at a stopover site is potentially dependent on the energetic condition of a bird upon arrival (Moore and Aborn 2000, Chernetsov 2006), age (Woodrey 2000), and a migrant's time program (Berthold 1990, Gwinner 1986), all of which can be modified by external factors such as competition (Moore et al. 2003), predation risk (Cimprich et al. 2005), and weather conditions (Gauthreaux 1991). How efficiently a migrating bird locates and acquires adequate food resources at a stopover site largely determines the success of migration, and ultimately influences survival (Sillett and Holmes 2002) and reproductive success (Sandberg and Moore 1996, Smith and Moore 2003, Moore et al. 2005).

The hierarchical decision-making process utilized by migrants when selecting stopover habitat (landfall, search and settling within a patch, and acquisition of resources; Hutto 1985a) should act to minimize the time a migrant spends searching for and settling in an area while maximizing refueling rates. Growing evidence suggests that some migrants use visual and acoustic cues to select appropriate habitat just prior to landfall (Herremans 1990, Jenni-Eiermann and Jenni 1999, Bowlin et al. 2005, Buler et al. 2007, Mukhin et al. 2008), potentially minimizing the time and energy expended for exploratory behavior after landfall. Examination of the distribution of migratory birds within and among habitats during migration indicates that birds are not evenly distributed, but are found disproportionately in particular habitats (Barlein 1983, Hutto 1985b, Moore et al. 1990, Finch and Wang 2000, Buler et al. 2007). This relationship is often strongly correlated with differences in food resources across the landscape (Barlein 1983, Hutto 1985b, Buler et al. 2007). However, we are just beginning to understand the process by which migratory birds search for and assess the suitability of habitat at a stopover site, and how they maximize movements within a finite area to replenish fuel reserves (reviewed by Chernetsov 2006). Examination of movement patterns at a stopover site provides critical insight into the temporal distribution of a bird's locations within the site, thus indicating how a bird searches for and acquires food resources throughout its stopover.

Information inferred from mist-netting or censuses to describe movement patterns of a migratory bird at a stopover site is limited because it typically represents only one point in time, and can often be misleading because it is unknown whether the bird is actually utilizing the area or just moving between areas. However, radio-telemetry coupled with behavioral observations of foraging allows for examination of behavior and movement at finer temporal and spatial scales. This fine-scale information allows us to assess how the locations of a bird are spatially distributed among habitats, both within and among days at a stopover site. In addition, changes in the distribution of locations in a stopover site through time can be examined in relation to seasonal changes in the distribution of resources. Examining a combination of multiple movement variables, such as the rate of movement, directionality of movement, and the total distance encompassed by such movements, allows us to better understand how migratory birds are utilizing a stopover site. For example, upon arrival at a stopover site we would expect migrants to employ exploratory behavior, characterized by quick, directed, long-distance movements through the site (Aborn and Moore 1997), to gain information about the abundance and distribution of predators, competitors, and food resources, and ultimately, habitat quality. In contrast, as birds directly sample habitats through exploration, we would expect movements to become confined to localized, high-quality microsites, where birds can replenish fuel reserves (characterized by fast rates of movement) or rest (characterized by slow rates of movement; Aborn and Moore 1997).

In this study, we used radio-telemetry to examine fine-scale movement patterns of Wilson's Warblers (*Wilsonia pusilla*) during spring migration at a stopover site along the lower Colorado River in southwestern Arizona. The main objective of our study was to characterize movement patterns of warblers throughout their stopover, utilizing multiple movement variables, to determine how warblers were distributed spatially within the site through time. In addition, we examined how factors such as the age, sex, and energetic condition of the bird potentially influenced movement patterns. Finally, research in riparian habitats on the lower Colorado River has indicated that flowering trees have the highest abundance and richness of arthropods and are thus an important cue used by insectivorous warblers to find food during spring migration (McGrath et al. 2008). Therefore, we examined how seasonal changes in the flowering phenology of dominant tree species at the stopover site, a proxy of insect abundance, potentially influenced warbler locations.

METHODS

STUDY SITE AND FIELD METHODS

We conducted our study at Cibola National Wildlife Refuge (NWR; 33°18′N, 114°41′W; elevation 60 m) in La Paz County, Arizona. Cibola NWR is located on the main branch of the lower Colorado River, and is composed of narrow fragmented strips of riparian vegetation adjacent to the river corridor, surrounded by desert upland and agricultural fields (Anderson et al. 2004). We conducted intensive banding efforts during spring migration at a site that was revegetated in 1978 with native riparian tree species, including Fremont cottonwood (*Populus fremontii*), Goodding's willow (*Salix gooddingii*), honey mesquite (*Prosopis glandulosa*), screwbean mesquite (*P. pubescens*), palo verde (*Cercidium floridum*), and nonnative eucalyptus (*Eucalyptus* spp.). Common understory species included seep willow (*Baccharis salicifolia*), arrow weed (*Tessaria sevicea*), and saltbush (*Atriplex* spp.). Vegetation surrounding the 6.5 ha revegetation site was composed primarily of nonnative riparian vegetation (tamarisk [*Tamarix* spp.]),

small mosaics of native and nonnative riparian vegetation, and agriculture.

We used 15 mist nets distributed throughout the site to passively sample warblers beginning 30 min prior to sunrise. We banded all warblers captured with a federal aluminum bird band, and recorded standard morphological measurements. In addition, we fitted 39 Wilson's Warblers captured early in the morning and weighing at least 7.0 g with a 0.35 g radio-transmitter (model LB-2N, Holohil, Carp, Ontario, Canada) attached to the back using a glue-on technique (Johnson et al. 1992, Paxton et al. 2003). The entire processing time for an individual bird, including attachment of a radio-transmitter, was between 15 and 20 min. The radio-transmitters had a battery life expectancy of 8–15 days, and the mass of the transmitters was ≤5% of a warbler's total body mass.

Immediately after radio-transmitter attachment, we released warblers at the capture location and allowed them to recover from handling for 30 min, after which time we located each bird every hour until 20:00 (MST) using a homing-in technique (White and Garrott 1990) with a Telonics (Mesa, Arizona) handheld directional H-antenna and a Communications Specialists, Inc. (Orange, California) R-1000 telemetry receiver. To reduce the chance of disturbing birds, we recorded locations 10–20 m from the bird and determined the bearing to the bird using a compass. We determined point locations with a Global Positioning System (accuracy ±4 m). Warblers were often concealed in the vegetation and visual observations were not always possible, thus we considered bird locations accurate to within 10 m. In addition, we identified the tree species of each warbler location when in monotypic patches; otherwise, warblers were recorded as being in native or nonnative vegetation. Warblers that stayed more than one day at the stopover site were radio-tracked each subsequent day once an hour from sunrise to 20:00 until the night of departure. We determined the night of departure for each bird by another study that continuously monitored the same individual warblers after sunset so that nocturnal departures were directly observed (U.S. Geological Survey, unpubl. data). Departures of all radio-transmittered warblers from the stopover site occurred only after sunset (U.S. Geological Survey, unpubl. data).

We continuously observed a subset of individuals ($n = 10$) for 20 min every hour to determine their level of activity. We quantified activity based on signal direction and fluctuation (Aborn and Moore 2004). Birds were categorized as 'active' when signal strength fluctuated but stayed within a confined area, 'inactive' when there was no variation in signal strength, and 'long flight' when the signal continuously faded in one particular direction, indicating that the bird was steadily moving away from the observer. Direct observations of warblers (3% of total observations) verified that signal strength and direction correctly quantified activity, and indicated that 'active' individuals were primarily foraging while 'inactive' individuals were perched.

STATISTICAL ANALYSES

We characterized movements of warblers using three measures that were calculated on a daily basis for each bird ($n = 102$ days). Movement rate (m hr^{-1}) was calculated as the total distance moved (sum of the distances of all movements) divided by the number of hours radio-tracked to standardize the distance moved in a day. Linear displacement was calculated as the straight-line distance between the first location of the day and the roosting site of the warbler at 20:00. The linearity index was defined as the linear displacement of the bird divided by the total distance moved. This index ranged from 0 (indicating meandering movements) to 1 (indicating linear movements). We analyzed each measurement of movement separately as they each described a unique aspect of behavior, while the combination of information from all three measures provided a holistic understanding of warbler movement behavior. We log-transformed movement data to normalize distributions.

We analyzed factors potentially influencing movement patterns of Wilson's Warblers during stopover using a generalized estimating equations model in SPSS version 15.0 (SPSS 2006). Generalized estimating equations are extensions of generalized linear models that account for correlation (i.e., nonindependence) among observations from the same individual (Hardin and Hilbe 2003). We specified an identity link function and a normal distribution for our response variable, and used an exchangeable working correlation structure, with an individual warbler identifier as the clustering variable. By estimating the exchangeable correlation in measurements of movement for an individual warbler sampled across multiple days, estimates of standard errors are robust to any lack of independence (Hardin and Hilbe 2003).

Six dependant variables were selected a priori for model inclusion, as all of these variables are thought to be important factors influencing stopover ecology (Moore 2000). The variables were: the year that the warbler was radio-tracked, categorized as 2005 or 2006 (Year); the day of stopover with the day of capture equal to day 1 (Day), ranging from day 1 to day 5 (days 5–8 were combined because only three birds stayed more than five days); the day of the year (converted to ordinal date) corresponding to the date of stopover (Season); age of the warbler categorized as second year, SY, or after-second-year, ASY (Age); sex of the warbler (Sex); and the warbler fat score assessed at initial capture (Fat) , ranging from 0 to 5 as described by Helms and Drury (1960). Because weather conditions remained fairly consistent during the period of the study, proximate effects of daily weather were not assessed. Candidate model sets ($n = 101$) for all three measurements of movement included a fully specified global model with all main effects, a null model, and reduced forms of the general model including all possible combinations of each factor. We incorporated biologically meaningful second-order interactions in both the full general model and reduced forms.

We used the quasi-likelihood criterion (QIC_u) to rank, compare, and evaluate all candidate models. The QIC_u is a modified version of Akaike's information criterion (AIC) in which the likelihood has been replaced by the quasi-likelihood, which is appropriate to assess model fit for nonlikelihood-based methods such as generalized estimating equations (Pan 2001). We present all models with $\Delta QIC_u \leq 2$ as possible competing models for each measurement of movement (considered the subset of best models; Burnham and Anderson 2002), and also present the null model for assessing the relative explanatory power of the models under consideration. For each measure of movement, parameter estimates were averaged across models containing each explanatory variable (only for variables in greater than one model) and standard errors were calculated from unconditional variances due to model selection uncertainty (Burnham and Anderson 2002). We also estimated the relative importance of each variable (j) by calculating $w_+(j)$, where $w_+(j)$ is the sum of w_i (Akaike weights) across all models in the set in which variable j occurred (Burnham and Anderson 2002). Variables with strong support have cumulative Akaike weights near 1. Because measurements of movement were modeled based on log-transformed data, antilogarithms of parameter estimates and standard errors were taken. Thus, parameter estimates are multiplicative, and values equal to 1 indicate no effect, values >1 indicate a positive effect, and values <1 show a negative effect (Sokal and Rohlf 1995).

At Cibola NWR, the flowering phenology of tree species changes throughout the migration season. The native Goodding's willow, palo verde, and honey mesquite begin flowering at the beginning of spring migration, in the given order, and are the primary tree species flowering until 23 April. There is then a period of overlap in flowering between native and nonnative tree species, until at the end of spring migration (beginning 10 May), nonnative tamarisk is the only tree flowering (McGrath et al. 2008). We observed the flowering phenology of dominant tree species to verify that the date ranges indicated by McGrath et al. (2008) were accurate for both years of our study. We used a binomial logistic regression within a generalized estimating equations framework to determine if the probability of warbler locations in native vegetation (or conversely, nonnative vegetation) changed throughout the season. We specified a logit link function and a binomial distribution for our response variable, and used an exchangeable working correlation structure, with an individual warbler identifier as the clustering variable.

To examine how movement varied within a stopover day, we determined the relationship between individual activity level and movement rate for a subset of warblers observed for continuous 20 min periods each hour throughout the day. We used a Spearman's rho correlation to determine if there was a correlation between hourly observed activity level (proportion of active observations) and the linear distance moved that hour. This analysis included observations from 10 warblers examined from 08:00 to 20:00 during the first two days of stopover. Subsequent stopover days were excluded from the

TABLE 1.   Generalized estimating equations examining the variation in three measurements of movement for Wilson's Warblers during spring migration at Cibola National Wildlife Refuge, Arizona, in 2005 and 2006. Measurements of movement include: movement rate (m hr^{-1}), which equals the total distance moved divided by the number of hours radio-tracked; linear displacement, calculated as the straight-line distance between the first location of the day and the warbler's location at sunset; and the linearity index, ranging from 0 (indicating meandering movements) to 1 (indicating linear movements). All top competing models ($\Delta QIC_u \leq 2$) and the null model are shown for each of the three measurements of movement. The QIC_u is a modified version of Akaike's information criterion (AIC) in which the likelihood has been substituted by the quasi-likelihood. The number of parameters (K), differences in QIC_u values (ΔQIC_u), and Akaike weights (w_i) are shown for each model. See Table 2 for an explanation of model variables.

Model description	K	ΔQIC_u[a]	w_i
Movement rate			
Year, Age	4	0.00	0.15
Year, Age, Sex	5	1.11	0.09
Year, Season	4	1.18	0.08
Year, Age, Day	5	1.39	0.08
Year, Age, Season	5	1.58	0.07
Null	2	5.86	0.00
Linear displacement			
Day, Season	4	0.00	0.23
Day, Season, Year	5	0.10	0.21
Day, Season, Age	5	1.37	0.11
Null	2	29.28	0.00
Linearity index			
Day, Season, Year	5	0.00	0.20
Day, Season	4	0.05	0.19
Day, Year	4	1.73	0.08
Day, Season, Year, Age	6	1.80	0.08
Day, Season, Age	5	1.93	0.08
Null	2	27.79	0.00

[a] The QIC_u of the top models was: movement rate = 52.46, linear displacement = 148.24, and linearity index = 106.35.

analysis due to decreased sample sizes. All reported values are means ± SE and significance was accepted at $P < 0.05$.

RESULTS

Twenty-two warblers were radio-tracked in 2005 for a total of 540 hr, and 17 warblers were radio-tracked in 2006 for a total of 641 hr. The average minimum stopover duration (elapsed time between capture and departure) was 2.4 ± 2.0 days in 2005 and 4.2 ± 2.1 days in 2006.

MOVEMENT RATE

The top candidate models describing the movement rate of Wilson's Warblers indicated considerable annual variation and that the age of the warbler strongly influenced the rate of movement (Table 1). However, none of our top models supported an interaction between year and other variables of interest (Table 1). The mean rate of movement was 61 ± 6 m hr^{-1} (range: 11–173 m hr^{-1}) in 2005 compared to 102 ± 14 m hr^{-1}
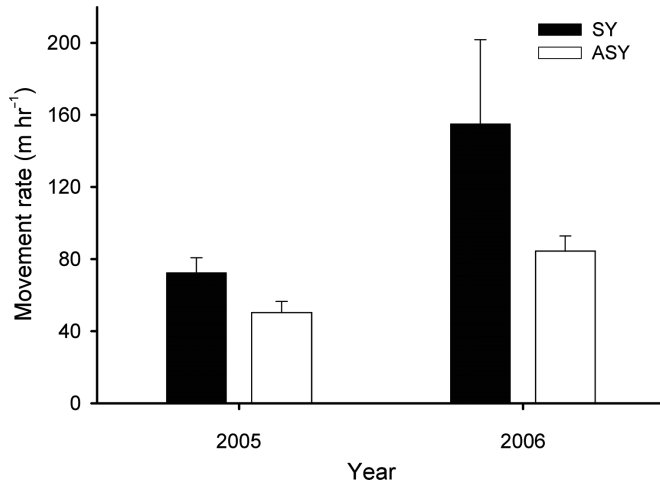
FIGURE 1.   Mean movement rate (± SE) of second-year (SY) and after-second-year (ASY) Wilson's Warblers during spring migration in 2005 and 2006 at a site on the lower Colorado River in Arizona. SY warblers had higher rates of movement in both years.

(range: 11–720 m hr^{-1}) in 2006. Model-averaged parameter estimates and unconditional 95% confidence intervals indicated that the rate of movement of SY warblers was 55% more than that of ASY warblers (Fig. 1, Table 2). There was moderate support for changes in movement rates across the migration season, suggesting that the movement rate of warblers positively increased per ordinal date as the migration season progressed (Table 2). There was little support for a difference in movement rate between the sexes or on successive days at the stopover site (Table 2).

LINEAR DISPLACEMENT

In contrast to movement rate, model selection for the linear displacement of warblers indicated that the day of stopover and the
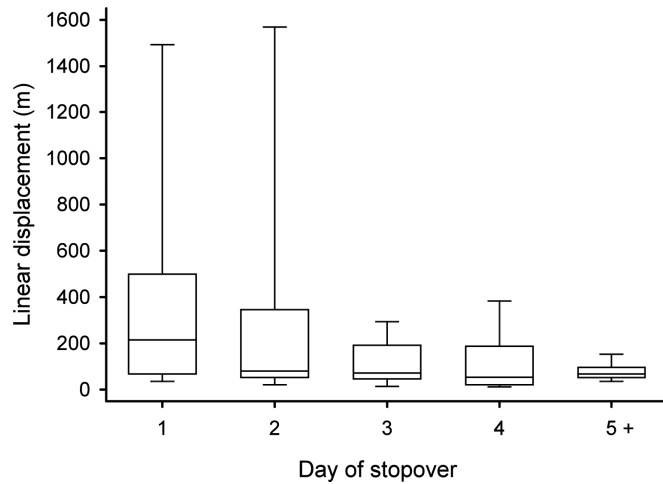

FIGURE 2.   Changes in the average linear displacement of Wilson's Warblers from sunrise to sunset at a site in southwestern Arizona for each day of stopover during spring migration. Box plot whiskers depict the 10th and 90th percentiles and boxes show the 25th and 75th percentiles with the mean value indicated; outliers are not shown. Days 5–8 (5+) were combined because only three birds remained at the site more than five days. The linear displacement of warblers decreased with each day spent at the stopover site, suggesting that warblers stayed in more localized areas the longer they were at the stopover site.

time of season were the most influential variables (Table 1). On average, warblers moved 332 ± 75 m (range: 0–6341 m) from their location at sunrise (or release point) to their roosting location. For every successive day a warbler stayed at the stopover site, there was a 22% decrease in linear displacement (Fig. 2, Table 2). While the time of season positively affected linear displacement by only 3% each day (Fig. 3, Table 2), this accounted for considerable differences in the distance moved from

TABLE 2.   Relative importance, model-averaged parameter estimates, and unconditional 95% confidence intervals (CI) for variables modeled relative to three measurements of movement (see Table 1 for explanations) for Wilson's Warblers during spring migration at Cibola National Wildlife Refuge, Arizona, in 2005 and 2006. The value in parentheses following categorical variables indicates the category modeled. Continuous variables included in the model were: the day of stopover, with the day of capture equal to day 1 (Day); the day of the year corresponding to the date of stopover (Season); and the warbler fat score assessed at initial capture (Fat). Relative importance was calculated as the summation of Akaike weights across all models containing the variable. Movement variables were log-transformed, and the antilogarithms of parameter estimates and standard errors were taken to calculate weighted averages of parameter estimates and unconditional 95% CI. Thus, parameter estimates are multiplicative, and values equal to 1 indicate no effect, values >1 indicate a positive effect, and values <1 show a negative effect.

|	Movement rate			Linear displacement			Linearity index		
Variable	Relative importance	Parameter estimate	95% CI	Relative importance	Parameter estimate	95% CI	Relative importance	Parameter estimate	95% CI
Year (2005)	1.00	0.55	0.53 to 0.57	0.39	—	—	0.57	1.43	1.27 to 1.58
Day	0.16	—	—	1.00	0.80	0.79 to 0.81	1.00	0.76	0.75 to 0.78
Season	0.33	1.02	1.01 to 1.03	1.00	1.03	1.02 to 1.04	0.87	1.02	1.01 to 1.02
Age (SY)	0.82	1.55	1.47 to 1.63	0.21	—	—	0.25	0.89	0.84 to 0.94
Sex (M)	0.19	—	—	—	—	—	—	—	—
Fat	—	—	—	—	—	—	—	—	—
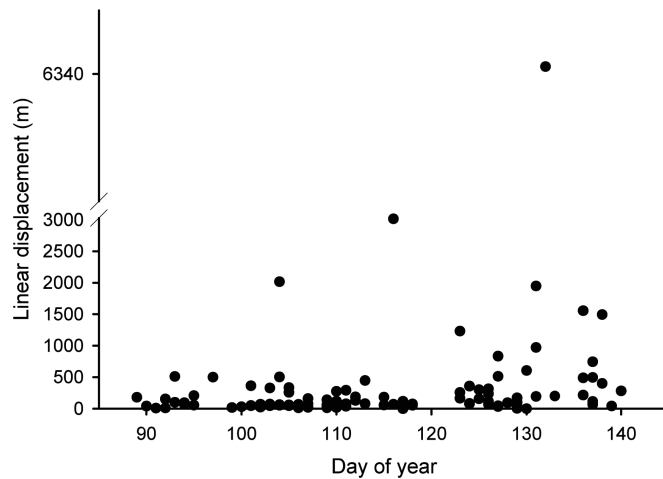
FIGURE 3.   The linear displacement of individual Wilson's Warblers during spring migration at a site in southwestern Arizona as a function of the day of the year. On the y axis, a break in linear displacement occurs between 3030 m and 6330 m. Day 90 corresponds to 31 March and day 140 corresponds to 20 May. Increases in linear displacement indicate longer-distance exploratory movements away from the capture site as the migration season progressed.

sunrise to sunset when applied across the 2½ month migration time period. There was low support for linear displacement being greater in 2005 than in 2006, and the weighted average suggested no difference between age classes (Table 2).
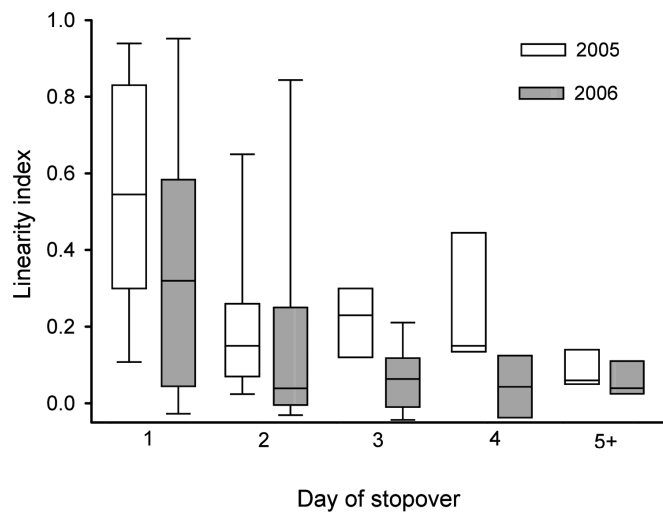

FIGURE 4.   Average linearity index of Wilson's Warblers, by year, during spring migration at a site in southwestern Arizona, as a function of the day of stopover. Linearity index values range from 0 (indicating meandering movements) to 1 (indicating linear movements). Box plot whiskers depict the 10th and 90th percentiles and boxes show the 25th and 75th percentiles with the mean value indicated; outliers are not shown. Small samples for certain days prevented estimates of the 10th and 90th percentiles. Days 5–8 (5+) were combined because only three birds remained at the site more than five days. The linearity index decreased with each successive day a warbler remained at the stopover site.
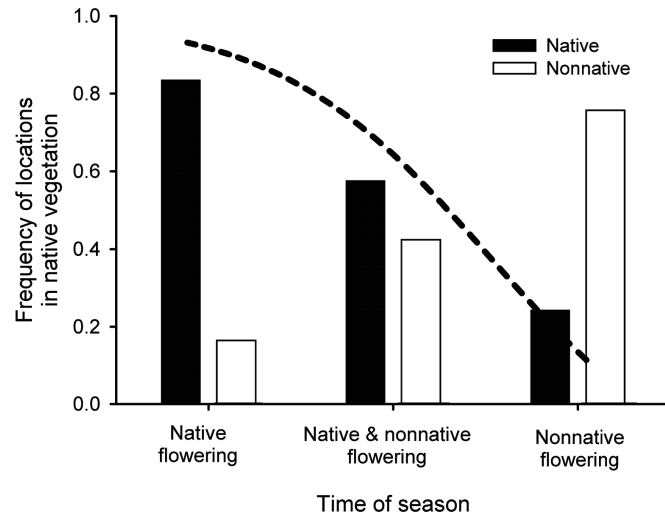

FIGURE 5.   The frequency with which Wilson's Warblers were located in native and nonnative vegetation as a function of time of season. The spring migration season was divided a priori into three time periods based on flowering phenology of vegetation at Cibola National Wildlife Refuge, Arizona. Native vegetation flowered predominantly at the beginning of migration (30 March–23 April); conversely, only nonnative vegetation was flowering at the end of the migration season (10 May–20 May). The dotted line represents the predicted frequency of locations in native tree species as a function of time of season, based on a binomial logistic regression of observed locations. The frequency of warbler locations in native vegetation decreased throughout the season, corresponding to changes in the flowering phenology of native vegetation.

LINEARITY INDEX

Top candidate models for the linearity index were similar to those for linear displacement, suggesting that the day of stopover and the time of season were the most influential variables (Table 1). However, there was also substantial support for annual variation (Table 2). In 2005 the average linearity index was 0.36 ± 0.04 (range: 0.20–0.96), compared to 0.23 ± 0.26 (range: 0.00–0.97) in 2006. There was a decrease of 32% in the linearity index for each successive day a warbler stayed at the stopover site, suggesting that movements became more aggregated within localized areas of use with each successive day of stopover (Fig. 4). Model-averaged parameter estimates and unconditional 95% confidence intervals also showed a positive influence of the time of season on the linearity index (Table 2), such that warbler movements increased in linearity as the migration season progressed. There was low support for a difference in the linearity index between SY warblers and ASY warblers.

SEASONAL CHANGES IN LOCATIONS

The frequency of warbler locations in native vegetation decreased throughout the migration season ($\beta = -0.07$, range = -0.11 to -0.04; Wald $\chi^2_2 = 14.9$, $P < 0.001$; Fig. 5). For each successive ordinal date, the odds of a warbler being in native
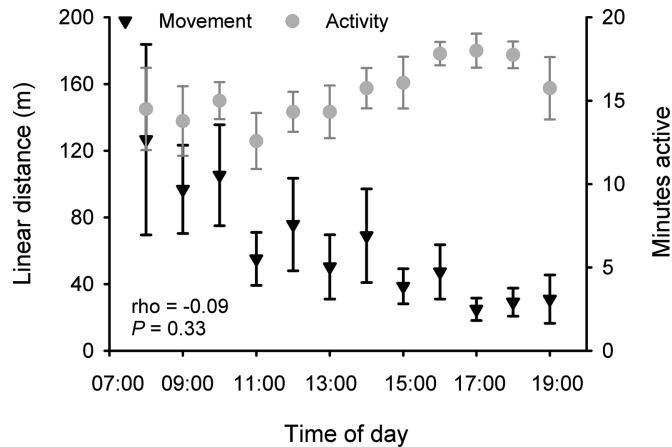
FIGURE 6.   Average linear distance (± SE) moved by Wilson's Warblers each hour and the corresponding average number of minutes (± SE) a warbler was active for a 20 min period during that time interval at a stopover site in southwestern Arizona during spring migration. The daily level of activity was not significantly correlated with the distanced moved, suggesting that warblers consistently foraged throughout the day, during both exploratory and localized movements.

vegetation were only 0.93 that of the previous date, such that by the end of the migration season the majority of locations were in nonnative tamarisk vegetation. The change in frequency of warbler locations in native versus nonnative vegetation corresponded to shifts in the flowering phenology of vegetation: 84% of locations were in native vegetation when primarily native vegetation was flowering (30 March to 23 April), compared to only 24% of locations when primarily nonnative vegetation was flowering (10 May to 20 May).

ACTIVITY LEVELS AND MOVEMENT RATES

We found no relationship between hourly activity levels of individual warblers and movement rate, so that while the distance moved decreased throughout the day, warblers were consistently active the entire day ($r_s = -0.09$, $P = 0.33$; Fig. 6). This result suggests that even when movements were confined to localized areas, birds still exhibited high levels of foraging.

DISCUSSION

Movement patterns from this study provide insight into the temporal and spatial distribution of Wilson's Warblers at a stopover site, thus elucidating how birds search for and assess the distribution and abundance of resources. The overall movements of warblers at the stopover site were restricted to localized areas close to capture locations, with linear displacement from sunrise to sunset averaging only 332 m. Exploratory behavior characterized by long-distance linear movements was exhibited primarily during the first or second day of stopover. Moreover, all exploration was restricted to relatively small

areas (primarily <2 km in diameter) within the overall landscape, never leaving riparian habitat. Movement restricted to relatively localized areas is consistent with the few other studies that have examined movement patterns of passerines at stopover sites. For example, Summer Tanagers (*Piranga rubra*) and Ovenbirds (*Seiurus aurocapilla*) at stopover sites along the Gulf of Mexico moved on average only 500 m and 365 m from their release sites, respectively (Aborn and Moore 1997, Buler 2006). *Catharus* thrushes, followed for multiple days after initial capture in the eastern United States, moved less than 100 m from their landing location (Cochran and Wikelski 2005), while European Robins (*Erithacus rubecula*) and Sedge Warblers (*Acrocephalus schoenobaenus*) stopping over on the Courish Spit on the southeastern Baltic coast remained within 350–400 m of their landing locations (Chernetsov 2005). The consistency of movements restricted to localized areas during stopover among these studies suggests that the general location where a bird lands is critical in determining the resources that will ultimately be available to a migrant at a stopover site. Extended exploration at each new stopover site may be too costly or time-consuming if food resources are not adequate, thus the bird may choose departure from the site over extended exploration (Jenni and Schaub 2003). In addition, increased exploration at a stopover site may expose birds to a greater risk of predation (Cimprich et al. 2005).

The integration of information from the three different measures of movement in our study illustrates changes in how warblers were utilizing habitat throughout their stopover. While the rate of movement remained consistent throughout stopover, both linear displacement and the linearity index decreased with each successive day. Thus, fewer long-distance linear movements, which are characteristic of exploratory behavior, were exhibited by warblers as the duration of stopover increased, resulting in movements that became more aggregated within localized areas. In addition, activity levels consistent with foraging behavior indicated that warblers were directly sampling the habitat during the first two days of stopover. These results indicate that, as birds gained more information about the distribution of resources at the stopover site through exploratory behavior and direct sampling of habitats, warblers settled within a presumably high-quality microsite to replenish fuel supplies.

Exploratory movements, characterized by directed long-distance movements, were primarily exhibited during the first two days of stopover. However, the first two days also had the most variability in the linear displacement and linearity index of warblers. Two explanations may account for this variability. First, there is likely individual variation in the amount of time needed to explore the stopover site before locating a habitat microsite within which to settle. Second, while we believe that most birds were captured on their day of arrival at the stopover site, this may not always have been true, resulting in some individuals already having settled within a microsite on

the day of capture. However, given the direction and strength of our observed pattern, we would only expect the pattern to be strengthened had all individuals been captured on the day of arrival. In addition, the extent and distance of exploratory movements during the presumed day of arrival in our study is consistent with findings by Buler (2006), who experimentally simulated landfall by releasing birds into novel habitats at dawn.

FACTORS INFLUENCING OVERALL
MOVEMENT PATTERNS

Time of season. As the migration season progressed, all three of our measurements of movement changed. Movements made by warblers migrating later in the season were characterized by faster rates, longer distances, and more linearity in direction, suggesting an increased intensity of exploratory movements. Increased exploration as the migration season progressed corresponded with likely changes in resources within the stopover site, measured by seasonal changes in the flowering phenology of dominant tree species (McGrath et al. 2008). Likewise, the location of warblers in the stopover site paralleled changes in the flowering phenology of native and nonnative tree species, suggesting that birds were assessing changes in the distribution of resources at the site. Our results highlight the fact that flowering phenology strongly influenced the location of warblers, and that as the migration season progressed, extended exploration was potentially required to locate adequate food resources within areas surrounding the capture site dominated by nonnative vegetation. The use of simple proximate cues such as flowers in unfamiliar habitats at each new stopover site may aid quick assessment of available food resources and reduce searching time. Structural features that correlate with food availability have also been shown to influence the dispersion of birds during other periods of the annual cycle (Greenburg 1985, Parrish 1995, Whelan 2001).

Annual differences. The linear displacement of warblers from sunrise to sunset remained consistent throughout our study, indicating that birds stayed within small localized areas each year. However, in 2006, increased rates of movement and decreased linearity index values indicated that warblers exhibited faster, more meandering movements within the localized areas of use compared to 2005. In addition, the minimum stopover duration for Wilson's Warblers was twice as long in 2006. During the two-year period of our study, mean monthly winter precipitation (November–March) varied dramatically from 30 ± 30 mm in 2004–2005 to only 1 ± 3 mm in 2005–2006 (data from the Blythe weather station at California Airport; Western Region Climate Center, <http://www.wrcc.dri.edu>). In arid ecosystems of the Southwest, water is a key limiting resource, and the amount and timing of precipitation strongly influences primary productivity, which is an important determinant of the abundance of primary consumers (i.e., arthropods; Noy-Meir

1973, Whitford 2002). Reduced winter precipitation preceding spring migration in 2006, compared to the 50-year average of 30 ± 40 mm, could have affected the abundance and distribution of arthropod communities at our study site (Noy-Meir 1973, Durst et al. 2008), and thus the movement patterns of warblers. Differences in movement patterns between the two years of our study suggest that while warblers consistently remain within relatively localized areas at a stopover site, more movement within the site and longer stopover durations may be required to locate adequate food resources during dry years.

Condition. We found no relationship between the condition of a bird upon arrival and our measurements of movement. This pattern is consistent with movement data of European Robins during both spring and fall migration on the southeastern Baltic coast (Chernetsov and Mukhin 2006). However, we would predict that movement patterns would vary with the energetic condition of a bird, reflecting different priorities: replenishment of depleted fat stores in energetically constrained, or lean, birds versus conservation of remaining fat stores and predator avoidance in fat birds (Moore et al. 1995). Consistent with this prediction, lean Summer Tanagers and Ovenbirds radio-tracked during stopover on the Gulf of Mexico exhibited longer-distance movements at faster rates than did fatter birds (Moore and Aborn 2000, Buler 2006). However, a fat-depleted individual may not have enough energy reserves to extensively explore a site and thus may be more willing to accept the first area encountered at a stopover site that provides a positive refueling rate (Guglielmo et al. 2002, Chernetsov 2006). The inconsistency among studies highlights the complexity of the relationship between fat reserves upon arrival and stopover behavior, and that contrasting factors likely play a role in determining movement patterns.

Age. Movement patterns at the stopover site were strongly influenced by warbler age. We found similar linear displacement patterns for both age classes; however, second-year warblers exhibited faster rates of movement and more meandering movements within localized areas of use compared to after-second-year warblers, suggesting different foraging efficiencies between age classes. This pattern was consistent over the two years of our study, although a greater difference in movement rates between the age classes was exhibited in 2006. The inexperience or subordinate status of second-year birds often places them at a competitive disadvantage, potentially affecting their access to resources (Sherry and Holmes 1989, Wunderle 1991, Woodrey 2000), and could seriously handicap their ability to find enough food to satisfy energetic requirements when food resources are scarce (Terrill 1987).

In conclusion, this study and others (reviewed by Chernetsov 2006) provide growing evidence that movements of migrating passerines are restricted to relatively small areas at stopover sites. Given the large-scale loss and degradation of riparian habitats in the southwestern U.S. and their critical importance as stopover sites (Rich et al. 2004), this study

emphasizes the importance of preserving patches of high-quality habitat along migration routes.

LITERATURE CITED

ABORN, D. A., AND F. R. MOORE. 1997. Pattern of movement by Summer Tanagers (*Piranga rubra*) during migratory stopover: a telemetry study. Behaviour 134:1077–1100.

Aborn, D. A., and F. R. Moore. 2004. Activity budgets of Summer Tanagers during spring migratory stopover. Wilson Bulletin 116:64–68.

ALERSTAM, T., AND A. LINDSTRÖM. 1990. Optimal bird migration: the relative importance of time, energy, and safety, p. 331–351. *In* E. Gwinner [ED.], Bird migration: physiology and ecophysiology. Springer-Verlag, Berlin.

ANDERSON, B. W., P. E. RUSSELL, AND R. D. OHMART. 2004. Riparian revegetation: an account of two decades of experience in the arid southwest. Avvar Books, Blythe, CA.

BAIRLEIN, F. 1983. Habitat selection and associations of species in European passerine birds during southward, post-breeding migrations. Ornis Scandinavica 14:239–245.

BERTHOLD, P. 1990. Genetics of migration, p. 269–280. *In* E. Gwinner [ED.], Bird migration: physiology and ecophysiology. Springer-Verlag, Berlin.

BLEM, C. R. 1990. Avian energy storage. Current Ornithology 7:59–113.

BOWLIN, M. S., W. W. COCHRAN, AND M. C. WIKELSKI. 2005. Biotelemetry of New World thrushes during migration: physiology, energetics and orientation in the wild. Integrative and Comparative Biology 45:295–304.

BULER, J. J. 2006. Understanding habitat use by landbirds during migration along the Mississippi Gulf Coast using a scale-dependent approach. Ph.D. dissertation, University of Southern Mississippi, Hattiesburg, MS.

BULER, J. J., F. R. MOORE, AND S. WOLTMANN. 2007. A multi-scale examination of stopover habitat use by birds. Ecology 88:1789–1802.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd Ed. Springer-Verlag, New York.

CHERNETSOV, N. 2005. Spatial behavior of medium and long-distance migrants at stopovers studied by radio tracking. Annals of the New York Academy of Sciences 1046:242–252.

CHERNETSOV, N. 2006. Habitat selection by nocturnal passerine migrants en route: mechanisms and results. Journal of Ornithology 147:185–191.

CHERNETSOV, N., AND A. MUKHIN. 2006. Spatial behavior of European Robins during migratory stopovers: a telemetry study. Wilson Journal of Ornithology 118:364–373.

CIMPRICH, D., M. WOODREY, AND F. MOORE. 2005. Passerine migrants respond to variation in predation risk during stopover. Animal Behaviour 69:1173–1179.

COCHRAN, W. W., AND M. WIKELSKI. 2005. Individual migratory tactics of New World *Catharus* thrushes, p. 274–289. *In* R. Greenberg and P. P. Marra [EDS.], Birds of two worlds. Johns Hopkins University Press, Baltimore, MD.

DURST, S. L., T. C. THEIMER, E. H. PAXTON, AND M. K. SOGGE. 2008. Temporal variation in the arthropod community of desert riparian habitats with varying amounts of saltcedar (*Tamarix ramosissima*). Journal of Arid Environments 72:1644–1653.

FINCH, D. M., AND Y. WANG. 2000. Landbird migration in riparian habitats of the middle Rio Grande: a case study. Studies in Avian Biology 20:88–98.

GAUTHREAUX, S. A., JR. 1991. The flight behavior of migrating birds in changing wind fields: radar and visual analyses. American Zoologist 31:187–204.

GREENBERG, R. 1985. A comparison of foliage discrimination learning in a specialist and a generalist species of migrant wood warbler (Aves: Parulidae). Canadian Journal of Zoology 63:773–776.

GUGLIELMO, C. G., P. D. O'HARA, AND T. D. WILLIAMS. 2002. Extrinsic and intrinsic sources of variation in plasma lipid metabolites of free-living Western Sandpipers. Auk 119:437–445.

GWINNER, E. 1986. Circannual rhythms in the control of avian migrations. Advances in the Study of Behavior 16:191–228.

HARDIN, J. W., AND J. M. HILBE. 2003. Generalized estimating equations. Chapman and Hall/CRC Press, London, UK.

HEDENSTRÖM, A., AND T. ALERSTAM. 1997. Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. Journal of Theoretical Biology 189:227–234.

HELMS, C. W., AND W. H. DRURY JR. 1960. Winter and migratory weight and fat field studies on some North American buntings. Bird-Banding 31:1–40.

HERREMANS, M. 1990. Can night migrants use interspecific song recognition to assess habitat? Gerfaut 80:141–148.

HUTTO, R. L. 1985a. Habitat selection by nonbreeding, migratory land birds, p. 455–476. *In* M. L. Cody [ED.], Habitat selection in birds. Academic Press, San Diego, CA.

HUTTO, R. L. 1985b. Seasonal changes in the habitat distribution of transient insectivorous birds in southeastern Arizona: competition mediated? Auk 102:120–132.

JENNI, L., AND M. SCHAUB. 2003. Behavioural and physiological reactions to environmental variation in bird migration, p. 155–171. *In* P. Berthold, E. Gwinner, and E. Sonnenschein [EDS.], Avian migration. Springer-Verlag, Berlin.

JENNI-EIERMANN, S. J., AND L. JENNI. 1999. Habitat utilisation and energy storage in passerine birds during migratory stopover. Proceedings of the International Ornithological Congress 22:803–818.

JOHNSON, G. D., J. L. PEBWORTH, AND H. O. KRUEGER. 1992. Retention of transmitters attached to passerines using a glue-on technique. Journal of Field Ornithology 62:486–491.

LINDSTRÖM, A. 2003. Fuel deposition rates in migrating birds: causes, constraints, and consequences, p. 307–320. *In* P. Berthold, E. Gwinner, and E. Sonnenschein [EDS.], Avian migration. Springer-Verlag, Berlin.

LORIA, D. E., AND F. R. MOORE. 1990. Energy demands of migration on Red-eyed Vireos, *Vireo olivaceus*. Behavioral Ecology 1:24–35.

McGRATH, L. J., C. VAN RIPER III, AND J. J. FONTAINE [ONLINE]. 2008. Flower power: tree flowering phenology as a settlement cue for migrating birds. Journal of Animal Ecology. doi: 10.1111/j.1365-2656.2008.01464.x

MOORE, F. R. [ED.]. 2000. Stopover ecology of Neartic-Neotropical landbird migrants: habitat relations and conservation implications. Studies in Avian Biology 20.

MOORE, F. R., AND D. A. ABORN. 2000. Mechanisms of en route habitat selection: how do migrants make habitat decisions during stopover? Studies in Avian Biology 20:34–42.

MOORE, F. R., S. A. GAUTHREAUX JR., P. KERLINGER, AND T. R. SIMONS. 1995. Habitat requirements during migration: important link in conservation, p. 121–144. *In* T. E. Martin and D. M. Finch [EDS.], Ecology and management of Neotropical migratory birds. Oxford University Press, New York.

MOORE, F. R., P. KERLINGER, AND T. R. SIMONS. 1990. Stopover on a Gulf Coast barrier island by spring trans-Gulf migrants. Wilson Bulletin 102:487–500.

MOORE, F. R., S. MABEY, AND M. WOODREY. 2003. Priority access to food in migratory birds: age, sex and motivational asymmetries, p. 281–292. *In* P. Berthold, E. Gwinner, and E. Sonnenschein [EDS.], Avian migration. Springer-Verlag, Berlin.

MOORE, F. R., R. J. SMITH, AND R. SANDBERG. 2005. Stopover ecology of intercontinental migrants; en route problems and consequences for reproductive performance, p. 251–261. *In* R. Greenberg and P. P. Marra [EDS.], Birds of two worlds. Johns Hopkins University Press, Baltimore, MD.

MUKHIN, A., N. CHERNETSOV, AND D. KISHKINEV. 2008. Acoustic information as a distant cue for habitat recognition by nocturnally migrating passerines during landfall. Behavioral Ecology 19:716–723.

NOY-MEIR, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4:25–51.

PAN, W. 2001. Akaike's information criterion in generalized estimating equations. Biometrics 57:120–125.

PARRISH, J. D. 1995. Effects of needle architecture on warbler habitat selection in a coastal spruce forest. Ecology 76:1813–1820.

PAXTON, E. H., S. N. CARDINAL, AND T. J. KORONKIEWICZ. 2003. Using radiotelemetry to determine home range size, habitat use, and movement patterns of Willow Flycatchers. Studies in Avian Biology 26:185–189.

RICH, T. D., C. J. BEARDMORE, H. BERLANGA, P. J. BLANCHER, M. S. W. BRADSTREET, G. S. BUTCHER, D. W. DEMAREST, E. DUNN, W. C. HUNTER, E. E. INIGO-ELIAS, J. A. KENNEDY, A. M. MARTELL, A. O. PANJABI, D. N. PASHLEY, K. V. ROSENBERG, C. M. RUSTAY, J. S. WENDT, AND T. C. WILL. 2004. Partners in Flight North American landbird conservation plan. Cornell Lab of Ornithology, Ithaca, NY.

SANDBERG, R., AND F. R. MOORE. 1996. Fat stores and arrival on the breeding grounds: reproductive consequences for passerine migrants. Oikos 77:577–581.

SHERRY, T. W., AND R. T. HOLMES. 1989. Age-specific social dominance affects habitat use by breeding American Redstarts (*Setophaga ruticilla*): a removal experiment. Behavioral Ecology and Sociobiology 25:327–333.

SILLETT, T. S., AND R. T. HOLMES. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

SMITH, R., AND F. R. MOORE. 2003. Arrival fat and reproductive performance in a long-distance passerine migrant. Oecologia 134:325–331.

SOKAL, R. R., AND J. F. ROHLF. 1995. Biometry. 3rd Ed. W. H. Freeman and Company, New York.

SPSS. 2006. Statistical software version 15.0. SPSS, Inc., Chicago.

TERRILL, S. B. 1987. Social dominance and migratory restlessness in the Dark-eyed Junco (*Junco hyemalis*). Behavioral Ecology and Sociobiology 21:1–11.

WHELAN, C. J. 2001. Foliage structure influences foraging of insectivorous forest birds: an experimental study. Ecology 82:219–231.

WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, CA.

WHITFORD, W. G. 2002. Ecology of desert ecosystems. Academic Press, New York.

WOODREY, M. 2000. Age-dependent aspects of stopover biology of passerine migrants. Studies in Avian Biology 20:43–52.

WUNDERLE, J. M., JR. 1991. Age-specific foraging proficiency in birds. Current Ornithology 8:273–324.