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Passerine migrant stopover duration and spatial behaviour at an urban stopover site

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ABSTRACT

Migration routes of many Nearctic–Neotropical landbirds pass through the most urbanized regions of North America. Migrants are known to use urban habitats as stopover sites and often occur in cities at exceptional density; yet knowledge of migrant behaviour and ecology in such places is surprisingly limited. We radio-tracked ovenbirds (*Seiurus aurocapillus*) during stopovers in a New York City park to obtain some of the first detailed information on how landbird migrants utilize an urban habitat as a stopover site. We examined fine-scale movement patterns, home range sizes, stopover durations, and how arrival condition affected each of these metrics. During both seasons, most birds moved widely throughout the site upon presumed arrival and then either continued migration that night or settled into a more defined area on subsequent days. Area usage varied markedly among individuals during both seasons, ranging 1–16 ha. Stopover durations averaged 3.0 days (range = 1–10 days) during spring and 2.9 days (range = 1–14 days) during autumn. Spatial behaviours and stopover durations were not influenced by arrival condition during spring, and during autumn only movement rates and displacement distances were significantly (negatively) condition-related. Our findings do not support previous assumptions that urban stopover habitats are only used by migrants briefly in times of urgency when alternatives are unavailable. At least half of the birds we studied stopped over for multiple days during both seasons, and bird movements were indicative of an ability to search for, locate, and occupy suitable micro-sites. Ovenbird behaviour in our study site was similar in many ways to what has been observed in recent telemetry studies of ovenbirds and other passerine migrants at various non-urban stopover sites.

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1. Introduction

Migration for most landbird species involves long-distance nocturnal flights followed by stopover periods when energy stores are replenished before continuing towards their ultimate destination. More time and energy is spent during stopovers than during flight (Wikelski et al., 2003; Bowlin et al., 2005) and the behaviour of birds in stopover habitats significantly influences the economy, duration, and overall success of their migration. This is particularly so during spring when males face pressure to arrive on their breeding grounds early enough to secure a territory and the energetic condition of both sexes upon arrival can affect reproductive performance (Sandberg and Moore, 1996; Kokko, 1999; Smith and Moore, 2003).

Migrants are expected to select stopover habitats that allow them to refuel with maximum efficiency and remain close to their migratory schedules (Lindström and Alerstam, 1992). Upon landfall birds must familiarize themselves with novel habitat and assess food availability, competition, and predation risk before selecting a particular area to occupy (Chernetsov, 2006). This early phase of stopover is referred to as 'search and settling' and may include behavioural as well as physiological adjustments (Alerstam and Hedenström, 1998; Karasov and Pinshow, 2000). Distribution patterns suggest landbird migrants favor particular habitat characteristics (e.g. Rodewald and Brittingham, 2004, 2007; Strode, 2009) and such preferences usually reflect differences in refueling opportunities (Simons et al., 2000; Buler et al., 2007; Tietz and Johnson, 2007; Ktitorov et al., 2008; Cerasale and Guglielmo, 2010).

Widespread anthropogenic alterations to the North American landscape have degraded and reduced the amount of habitat available for use as stopover sites by Nearctic–Neotropical migrants (McCann et al., 1993; Mehlman et al., 2005; Carlisle et al., 2009). Many species' migration routes follow the Atlantic or Pacific coasts where the largest human population centers of the United States

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are located and urbanization is a predominant land cover type. Migrants encountering metropolitan areas and in need of stopover habitat will usually be limited to small woodlots and forest fragments within city parks. The resulting occurrence of migrants in urban habitats, often at high densities, has been documented and recognized for quite some time (Chapman, 1910; Griscom, 1923; Brawn and Stotz, 2001; Fowle and Kerlinger, 2001). Yet, the potential value of urban habitats to migrants has been largely disregarded until recently (Matthews, 2008; Pennington et al., 2008; Seewagen, 2008a; Seewagen and Slayton, 2008) and knowledge of migratory bird ecology and behaviour in such places remains severely limited.

Radio telemetry studies in non-urban areas have shown migrant songbird behaviour to often consist of exploratory, linear movements upon arrival at a new stopover site, followed by more aggregated movements on subsequent days presumably after a suitable microhabitat has been encountered (Chernetsov, 2005; Buler, 2006; Chernetsov and Mukhin, 2006; Paxton et al., 2008). It is unknown whether the movement patterns of migrants in urban stopover sites fit this trend. If urban habitat quality is marginal and levels of disturbance are great, birds may move widely within the site without ever settling, and depart when the energetic and temporal costs of the stopover begin to exceed the benefits.

We examined the fine-scale movements of a common Neotropical migrant passerine, the ovenbird (*Seiurus aurocapillus*), within an urban stopover site to learn whether birds exhibited the search and settling behaviour characteristic of birds studied in less developed and disturbed, non-urban settings. We additionally measured stopover durations and temporary home range sizes, and how arrival condition and season influenced each of these metrics. Taken together, these investigations provide a more holistic understanding of how landbird migrants are utilizing urban habitats as stopover sites. Detailed knowledge of migrant habitat use and stopover behaviour is needed for effective stopover site conservation and management in rural and urban areas alike (Petit, 2000; Mehlman et al., 2005; Chernetsov, 2006; Rodewald and Brittingham, 2007; Pennington et al., 2008; Carlisle et al., 2009).

2. Methods

2.1. Study species

The ovenbird is a common forest-dwelling passerine that breeds across much of Canada and the eastern United States, and over-winters throughout Central America and the Caribbean islands. Ovenbirds are most often found on the forest floor where they forage for insects in the leaf litter (Van Horn and Donovan, 1994). We selected ovenbirds as our focal species because they are long-distance migrants that do not nest or over-winter in New York City (Van Horn and Donovan, 1994; DeCandido and Allen, 2005), they are common enough during migration to provide adequate sample sizes, and their body mass is sufficient for carrying radio transmitters (Bayne and Hobson, 2001; Brown, 2006; Buler, 2006). In addition, ovenbird movement patterns in a non-urban stopover site have been described (Buler, 2006) which provides useful context in which to interpret our findings.

2.2. Study site

We studied ovenbird stopover behaviour in New York City's Prospect Park (Fig. 1). New York City is the United States' largest city (US Census Bureau, 2010) and is located at the nexus of four major migration routes (southeastern U.S. route, circum-Gulf route, trans-Gulf route, and Caribbean island-western North Atlantic route) that over 100 species of birds follow each year (Rappole et al., 2000).

Prospect Park is a 213 ha public park in the center of the borough of Brooklyn (Kings County). Brooklyn has a human population of approximately 2.6 million and a total land area of 183 km^2, equaling a population density of 13,970 people/km^2 (US Census Bureau, 2010). More than 6 million people visit Prospect Park each year (Wells, 1998). The park is a highly isolated habitat island surrounded by heavy urbanization and contains the last remaining eastern deciduous woodland in Brooklyn. Aside from neighboring Greenwood Cemetery, the nearest significant greenspace (>100 ha) is approximately 7 km northeast in the borough of Queens. Exceptional concentrations of landbird migrants routinely occur in Prospect Park due to its geographic position and expansive inhospitable surroundings (Wells, 1998; Fowle and Kerlinger, 2001).

Prospect Park is a mosaic of landscaped meadows and lawns, athletic fields, manmade water-bodies, and remaining natural forests and wetlands. Approximately half of the park is mature deciduous forest (Wells, 1998). We captured birds in 'The Ravine' section (40° 39′ 49″ N, −73° −58′ −12″ W) of the ∼100 ha forest in the center of the park that represents the majority of the park's wooded area (Mittelbach and Crewdson, 1998). Its northern and southern edges are bordered by a two-lane road (closed to public vehicular traffic at most times of day) and the eastern and western edges are bordered by a long recreational field and a lake, respectively. The forest is heavily fragmented by meandering, paved walking trails ∼5 m wide. The tree community is dominated by black cherry (*Prunus serotina*), red oak (*Quercus rubra*), tulip poplar (*Liriodendron tulipifera*), and willows (*Salix* spp.), and the woody understory is primarily composed of arrowwood viburnum (*Viburnum dentatum*) and shadbush (*Amelanchier humilis*). The area is actively managed to control the spread of exotic invasive plants and promote the growth of native flora.

2.3. Capture and radio-tagging

Spring and autumn migrants were passively captured in 8–10 mist nets daily during 5–18 May and 9 September–1 October, 2009. These dates correspond with the peak spring and autumn passage periods of ovenbirds through NYC. Nets were opened at sunrise and checked for birds every 20 min for approximately 3 h. Captured ovenbirds were banded with USGS aluminum leg bands, weighed to 0.1 g on a digital balance, measured (unflattened wing length to 1 mm), assigned to age and sex when possible, and fat-scored on a 6-point scale (Moore and Kerlinger, 1987; Seewagen, 2008b). We attempted to increase the likelihood radio-tracking began on a bird's first stopover day by radio-tagging birds on mornings when it appeared a new wave of migrants had arrived, following one or two previous mornings when relatively few migrants were present in the park (Chernetsov and Mukhin, 2006; Seewagen and Guglielmo, 2010). Nevertheless, we could not be certain birds were tagged on the morning of arrival. Measures of stopover duration may be conservative and we hereafter use the term "minimum stopover duration" (MSD) because of the uncertainty.

Birds were radio-tagged by trimming a few feathers in the interscapular region and affixing the transmitter (model A2426, Advanced telemetry Systems, MN, USA) with eyelash adhesive (American International Industries, CA, USA) directly to the exposed skin (adapted from Raim, 1978). Birds were wrapped in a cotton bag for ∼10 min while the adhesive dried and then released at their capture location. Transmitters had a battery life of 21 d and a measured range of ∼100 m in the forested study area. Transmitters weighed <3% of each bird's body mass (Gaunt et al., 1997) and we assumed they did not adversely affect the birds' condition or mobility (Brigham, 1989; Sykes et al., 1990; Naef-Daenzer, 1994; Rae et al., 2009). Direct observations of radio-tagged birds throughout stopovers provided no indication the
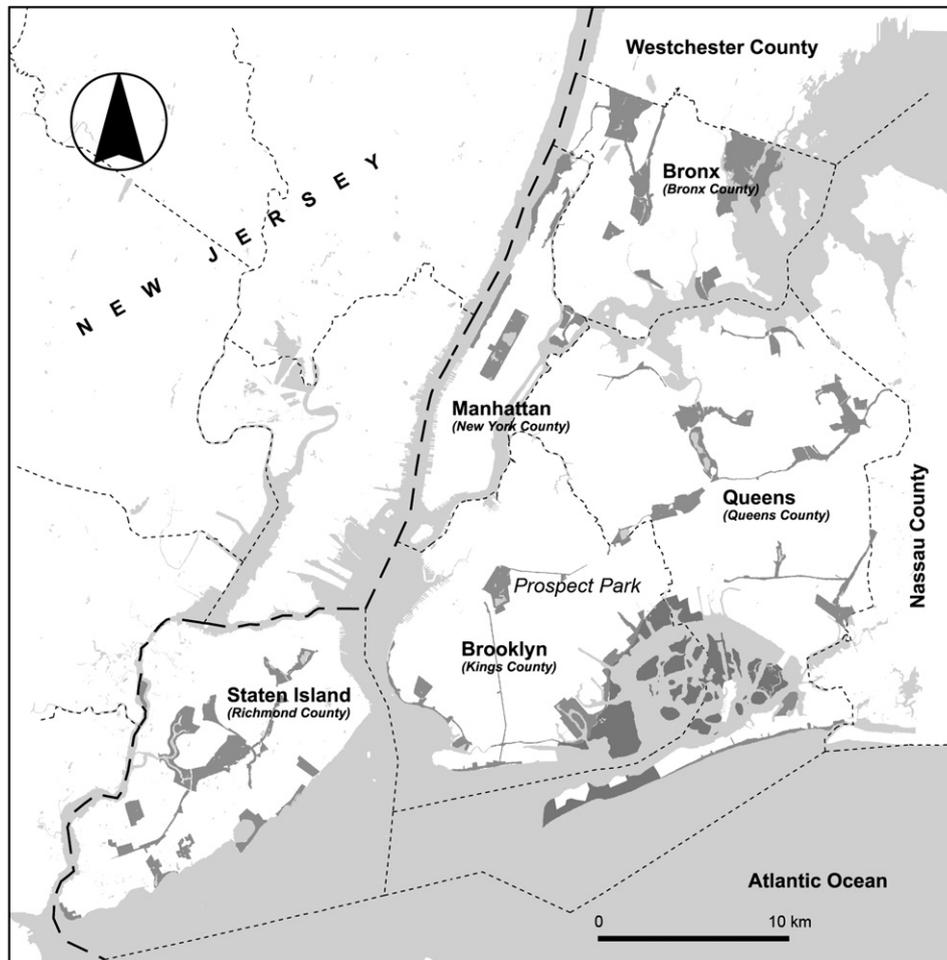
Fig. 1. Natural areas (>100 ha) remaining within New York City, USA (indicated in dark gray). New York City includes Brooklyn, Bronx, Manhattan, Queens, and Staten Island. Ovenbird stopover behavior was studied in Prospect Park, Brooklyn. Reproduced with permission from DeCandido et al. (2004).

transmitters were altering their behaviour. Radio-tagged birds were commonly observed foraging normally and no birds were seen attempting to pull off their transmitter. Other telemetry studies have also reported no noticeable adverse reactions of ovenbirds to radio transmitters (Brown, 2006; Buler, 2006).

2.4. Radio-tracking

Birds were located every 45–60 min following release until twilight using a Yagi antenna connected to an R-1000 (Communications Specialists, CA, USA) or R4500S (Advanced Telemetry Systems, MN, USA) receiver. Birds that were still present on subsequent days were located every 45–60 min between sunrise and twilight. This sampling rate was chosen to allow birds ample time to move from one end of their home range to another and increase the independence of observations (White and Garrott, 1990; Chernetsov and Mukhin, 2006).

Bird positions were determined by homing (White and Garrott, 1990; Bayne and Hobson, 2001; Paxton et al., 2008) and birds were approached to within an estimated 10 m to avoid disturbance from the observer (Paxton et al., 2008). It was determined a bird was ~10 m away based on visual observation or signal strength. When a signal could not be detected from a bird's last known position, observers expanded outward at approximately 50 m intervals on foot or by bicycle until either the bird was found or it could be concluded the bird was no longer present anywhere in the park.

Birds were assumed to have resumed migration if they were undetected for at least two consecutive days after last contact. No birds ever reappeared following a day of no detection.

Bird locations were recorded with a handheld Global Positioning System (model GPS 12, Garmin, KS, USA) at an average accuracy of ± 9 m during spring and ± 10 m during autumn. During spring, coordinates were recorded as degrees, minutes, and seconds. It was later decided higher resolution coordinates would be more appropriate for the small-scale movements of ovenbirds observed during spring, and coordinates during autumn were therefore recorded in UTM format.

2.5. Movement characteristics and home range estimation

We calculated three movement parameters to characterize daily spatial behaviour: movement rate, displacement distance, and a linearity index (Chernetsov, 2005; Buler, 2006; Chernetsov and Mukhin, 2006; Paxton et al., 2008). Movement rate (m h^{-1}) was calculated as the sum of the distances between each successive location in a day divided by total tracking time. Displacement (m) was calculated as the linear distance between a bird's locations at sunrise (or release) and twilight. The linearity index was calculated as displacement distance divided by the sum of all distances between successive locations within a day. The linearity index is a measure of aggregation, with values ranging from 0 (indicating clustered movements) to 1 (indicating linear movements).

Distances between points were measured using the Hawth's Tools extension in ArcMap v. 9.2 (Beyer, 2004; ESRI, Redlands, CA, USA).

We used Hawth's Tools to measure fixed kernel home range sizes of birds tracked for at least two days (and with ≥18 known locations), with least squares cross validation smoothing parameters (Seaman et al., 1999; Borger et al., 2006) calculated with Animal Movement 2.0 in ArcView 3.2 (Hooge and Eichenlaub, 2000; ESRI, Redlands, CA, USA). Home range estimates for birds with more sampling locations were not inflated, as we found no significant effect of location sample size on home range area among birds that stayed two or more days. We report fixed kernel home ranges measured with 50, 90, and 95% isopleths because the 95% isopleth is most commonly used, but it may overestimate home range size and more conservative isopleths of 50–90% have been recommended (Borger et al., 2006). Lastly, we used the site fidelity test in Animal Movement 2.0 to determine whether birds (tracked at least two days) occupied defined areas or moved at random. The site fidelity test uses a Monte Carlo simulation to compare the parameters of a bird's actual movements to 1000 randomly generated paths, starting from the bird's first location.

2.6. Statistical analyses

Non-normal data were $log_{10} + 1$ transformed to achieve normality and non-parametric tests were used when transformations failed to normalize data. We used SPSS 17 (SPSS Inc., Chicago, IL, USA) for all analyses and accepted significance at $p \leq 0.05$. Age and sex were not considered because total sample sizes were small, spring birds could not be sexed with sufficient confidence, and exploratory analyses revealed no significant differences during autumn between juvenile and adult movement parameters, MSD, or home range sizes. All data are reported as means ± SE.

We used multivariate analysis of variance (MANOVA) to examine daily changes in movement parameters, with days since radio-tagging (stopover day) as the independent variable and movement rate, displacement distance, and the linearity index as response variables. When overall differences among days were significant, we ran a univariate analysis of variance (ANOVA) with Tukey's HSD post-hoc tests for each individual movement parameter. Movement data collected after the fourth day of a stopover were combined into the category 5+ because few birds stayed at the site more than five days in either season. First-day movement parameters of birds that stayed at the stopover site for only one day were compared to those that stayed multiple days with MANOVA, with stopover length (i.e., one day or more than one day) as the grouping variable and first-day movement rate, displacement distance, and linearity index as dependent variables.

Spring and autumn MSDs were non-normal and compared with a Mann–Whitney U-test. MSD was measured as days elapsed between the morning of initial capture and the evening of last contact. Spring and autumn 95% fixed kernel home range sizes were compared with a Student's t-test. Fat mass upon capture was estimated with a predictive model (Seewagen, 2008b) and compared between spring and autumn birds with a Welch-corrected t-test. Differences in GPS format resolution during spring and autumn precluded direct seasonal comparisons of the more fine-scale movement parameters.

We used simple linear regression or Spearman rank correlation to individually examine the relationship between arrival fat mass and first-day movement parameters, total home range size (95%), and MSD. Adjusted r^2 and standardised regression slopes (β) are presented to indicate effect sizes and directions of effects (Nakagawa and Cuthill, 2007; Ferguson, 2009).

3. Results

3.1. Spring

We radio-tagged thirty three ovenbirds during spring. The first bird was tagged 5 May and the last tagged bird left the site 21 May. Transmitters fell off six birds before departure, resulting in incomplete movement data and indeterminate stopover durations for these individuals. In addition, first-day movement data from two birds were omitted due to poor GPS accuracy, providing a final sample size of 25 individuals for the first-day movement parameter analyses.

MSD averaged 3.0 ± 0.5 d and ranged 1–10 d. ($n = 27$). Thirteen birds (48%) departed the first night following their capture. Most birds remained close to where they were captured and released throughout their stopover. Maximum linear distances birds traveled from their release point averaged 236 ± 30 m (range = 47–715 m). Ovenbirds did not spend time in non-forested areas, but birds that moved far from their release location usually crossed park roads or the large recreational field bordering the study site in doing so.

Overall differences in movement parameters among days were significant (Wilk's $\lambda = 0.62$, $F_{12, 156} = 2.63$, $p = 0.003$; Fig. 2). There were no daily differences in movement rate ($F_{4, 61} = 0.67$, $p = 0.62$), whereas there were significant daily differences in linearity ($F_{4, 61} = 2.97$, $p = 0.026$), and daily differences in displacement distance that approached significance ($F_{4, 61} = 2.35$, $p = 0.06$). Displacement distances and linearity indices beyond the fourth stopover day were significantly lower than on previous days (Tukey's HSD post-hoc tests; displacement: $p = 0.038$; linearity index: $p = 0.024$; Fig. 2). During the first stopover day, the movement parameters of birds that departed that night were not significantly different from those of birds that stayed additional days (Wilk's $\lambda = 0.77$, $F_{3, 21} = 2.05$, $p = 0.14$).

Fifteen birds provided enough locations for home range estimates. Home range size differed greatly depending on the isopleth (Table 1) and individual variation was high (range = 1.0–13.3 ha at 95%). On average, ovenbirds occupied 4.8 ± 1.1 ha when measured with the commonly used 95% isopleth. Site fidelity tests suggested 53% of these birds exhibited non-random, area-restricted movements (all $p < 0.02$).

Few ovenbirds ($n = 2$) were considered lean (<10% fat) upon capture. Estimated fat stores averaged 3.1 ± 0.1 g and most birds' fat stores represented 14–20% (mean = 14.8 ± 0.5%) of their total body mass. There was no significant relationship between fat mass and first-day movement rate (adjusted $r^2 = 0.07$, $F_{1, 23} = 3.14$, $p = 0.09$), displacement distance (adjusted $r^2 = -0.04$, $F_{1, 23} = 0.05$, $p = 0.82$) or linearity (adjusted $r^2 = -0.04$, $F_{1, 23} = 0.05$, $p = 0.83$) on the day of arrival, total home range size (adjusted $r^2 = -0.08$, $F_{1, 13} = 0.00$, $p = 0.97$), or MSD ($r_S = -0.01$, $p = 0.96$).

3.2. Autumn

Twenty four ovenbirds were radio-tagged during autumn and transmitters fell off two birds before their departure. The first ovenbird was tagged 10 September and the final tagged ovenbird left the site 4 October. Birds stopped over for an average of 2.9 ± 0.7 d ($n = 22$). Eleven (50%) birds departed the first night after their capture and the longest stopover lasted 14 d. Durations of spring and autumn stopovers did not differ (Table 1).

Autumn migrants also remained close to their capture/release location. The farthest birds moved from their release point at any time during the stopover averaged 238 ± 35 m (range = 54–778 m). As in spring, birds were not found in non-forested areas but some individuals crossed park roads or open fields to reach other wooded sections of the park.
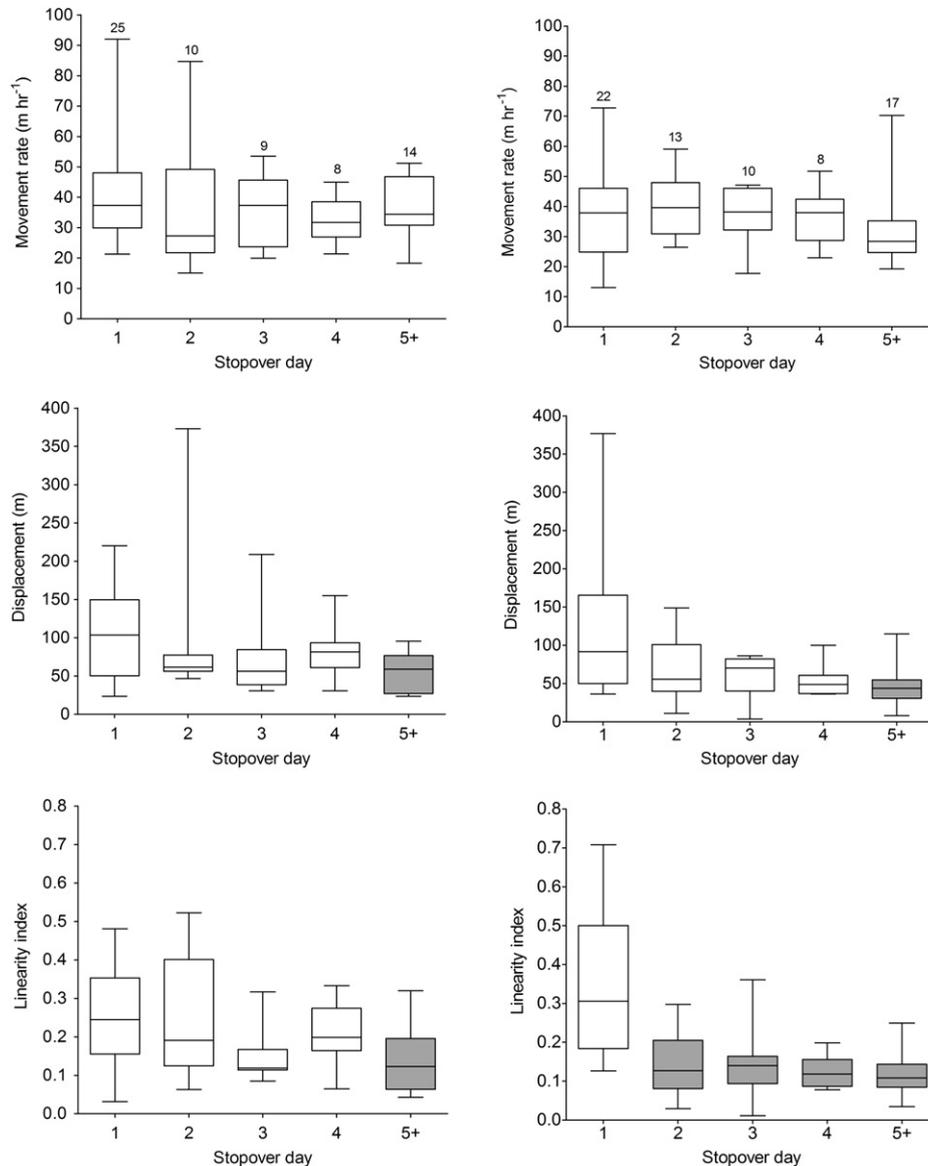
Fig. 2. Daily changes in three movement parameters of ovenbirds during spring (left) and autumn (right) 2009 stopovers in Prospect Park, Brooklyn, New York. Box plot whiskers show value ranges and boxes show median values and the 25th and 75th percentiles. Sample sizes are shown above bars. Individual days that differed significantly from the first day are indicated by shading; days represented by the same type of box (i.e., open, shaded) did not differ from each other (Tukey's HSD post-hoc tests).

Table 1

Fat mass, minimum stopover duration (MSD), and fixed kernel home range size (measured at three isopleth levels) of ovenbirds radio-tracked during spring and autumn 2009 stopovers in Prospect Park, Brooklyn, New York do not differ between seasons. Seasonal differences in fat mass and MSD tested with a Welch-corrected t-test and Mann–Whitney U-test, respectively. Spring and autumn 95% home range sizes compared with a Student's t-test. Values are means ± SE.

	Spring	Autumn	df	p
Fat (g)	3.1 ± 0.1	3.0 ± 0.4	27	0.70
n	33	22		
MSD (d)	2.8 ± 0.5	2.9 ± 0.7	1	0.92
n	27	22		
95% home range (ha)	4.8 ± 1.1	3.7 ± 1.2	26	0.48
n	15	13		
90% home range (ha)	3.6 ± 0.8	2.8 ± 0.9		
50% home range (ha)	0.9 ± 0.2	0.7 ± 0.2		

Overall, ovenbird movement behaviour significantly differed from day to day (Wilk's $\lambda = 0.28$, $F_{12, 166} = 8.47$, $p < 0.001$; Fig. 2). In independent analyses, differences in movement rate among days were not significant ($F_{4, 65} = 0.93$, $p = 0.45$), whereas there were significant daily differences in displacement distance ($F_{4, 65} = 4.8$, $p = 0.002$) and linearity ($F_{4,65} = 10.5$, $p < 0.001$). Displacement distances beyond the fourth stopover day were significantly lower than on previous days (Fig. 2). Linearity declined more rapidly than during spring stopovers, with index values from day two onwards being significantly lower than on the first day (Fig. 2). Ovenbirds moved more broadly and in a straighter direction on day one than on any other day. Movement parameters on the first stopover day did not differ between birds that departed that night and those that remained additional days (Wilk's $\lambda = 0.87$, $F_{3, 18} = 0.94$, $p = 0.44$). Most birds moved widely throughout the site on their arrival day and then either resumed migration or settled into a more defined area for the remainder of their stopover.

Thirteen birds were tracked long enough to quantify area usage. Individual variation was high, with estimates ranging 0.7–15.8 ha (at 95%). Seven birds (54%) showed significant site fidelity and moved non-randomly (all $p < 0.04$). Home ranges during autumn averaged 23% smaller than during spring, but the size difference was non-significant (Table 1).

More ovenbirds (10 of 24) were considered lean and there was more individual variation in fat mass during autumn, but overall, average autumn fat mass ($13.3 \pm 1.2\%$ of total body mass) was not significantly different from spring (Table 1). In contrast to spring, some first-day movement behaviours during autumn were associated with fat stores. Fat negatively influenced first-day movement rate (adjusted $r^2 = 0.21$, $\beta = -0.50$, $F_{1, 20} = 6.5$, $p = 0.019$) and displacement distance (adjusted $r^2 = 0.20$, $\beta = -0.49$, $F_{1, 20} = 6.2$, $p = 0.022$); fatter birds moved more slowly and remained closer to their capture location than leaner birds. As in spring, fat content during autumn was unrelated to first-day linearity index (adjusted $r^2 = 0.04$, $F_{1, 20} = 1.24$, $p = 0.28$), total home range size (adjusted $r^2 = 0.02$, $F_{1,11} = 1.28$, $p = 0.28$), and MSD ($r_S = -0.06$, $p = 0.79$).

4. Discussion

4.1. Movement patterns

Radio-tracking ovenbirds in the United States' largest city provided some of the first detailed information on how landbird migrants utilize stopover habitats within heavily urbanized landscapes (see also Matthews and Rodewald, 2010a,b). Our study site was a highly isolated habitat fragment located in one of the most densely populated, urban areas of North America. Yet the spatial behaviour of ovenbirds in Prospect Park was in many ways similar to what has been consistently observed in passerine migrants at non-urban stopover sites. Specifically, bird movements upon arrival were characteristic of exploration and searching, and then became more localized within defined areas later in the stopover period. Ovenbirds showed this same pattern during spring stopovers in non-urban forests of coastal Mississippi, USA (Buler, 2006). There, ovenbirds exhibited exploratory, linear movements on the first day of a stopover, followed by relatively area-restricted movements the next day. Migrant summer tanagers (Piranga rubra) on a barrier island off the Mississippi coast behaved similarly (Aborn and Moore, 1997). Paxton et al. (2008) documented increasingly aggregated movements of Wilson's warblers (Wilsonia pusilla) during the course of spring stopovers in southwestern Arizona, USA and Chernetsov (2005) and Chernetsov and Mukhin (2006) found this trend among European robins (Erithacus rubecula) on the Baltic Coast of Russia. We are aware of only one previous investigation of migrant songbird spatial behaviour in an urban area (Matthews and Rodewald, 2010a). Matthews and Rodewald (2010a) measured movement rates of radio-tagged Swainson's thrushes (Catharus ustulatus) in Columbus, Ohio, USA during spring migration but did not examine daily displacement or linearity. Movement rates on the first two days of stopover did not differ from each other, but it cannot be determined from this information alone whether or not birds ever settled into defined areas.

Differences in GPS format resolution prevented legitimate statistical comparisons of movement parameters between seasons, but generally, ovenbird settling in Prospect Park occurred more slowly during spring than autumn. During spring, movement linearity did not significantly decrease until the fifth stopover day, whereas during autumn, exploratory behaviour appeared to cease by the second day. Chernetsov (2005) and Chernetsov and Mukhin (2006) found an opposite pattern, where European robins settled slightly faster during spring than autumn. Why search and settling times would differ between seasons is unclear. In our study, one

interpretation is that autumn migrants more quickly encountered areas with suitable refueling conditions because food resources were more abundant during autumn than spring. Food availability influenced movements of ovenbirds during spring stopovers in Mississippi (Buler, 2006) and northern wheatears (Oenanthe oenanthe) on an island in the North Sea (Delingat and Dierschke, 2000); birds moved more when food was less abundant. Conversely, food abundance in Prospect Park may have been similar between seasons but the energetic needs of spring and autumn migrants differed. Greater temporal constraints and the faster pace of spring migration (Berthold, 2001; Stutchbury et al., 2008) may have required spring ovenbirds to forage more widely throughout the site to meet energy demands. Plasma triglyceride levels of ovenbirds we sampled in Prospect Park 2007–2008 indicated more rapid refueling during spring than autumn stopovers (Seewagen and Guglielmo, unpublished data) but it is unknown whether this reflected seasonal differences in food availability or foraging effort. A third explanation is that the greater density of migrants in the park during spring than autumn (based on capture rates) increased competition and it took ovenbirds longer to find unoccupied areas. Stopover territory defense by landbird species, including ovenbirds, has been observed (Rappole and Warner, 1976; Bibby and Green, 1980; Dierschke et al., 2005; Buler, 2006; but see Chernetsov and Mukhin, 2006) and it is possible newly arrived individuals were being displaced by established birds. Lastly, the more distinct patterns found in autumn may have simply resulted from the higher resolution GPS coordinate format used to record bird locations. The resolution in spring may have been too coarse to detect true differences in fine-scale movements between the first few stopover days.

4.2. Stopover duration

There was a wide range of MSD during both seasons, with many birds departing within one day and some others remaining for nearly a week. High intraspecific variation in stopover duration at a given site is common among passerine migrants (e.g. Morris et al., 1996; Tsvey et al., 2007; Hays, 2008). The stopover durations of ovenbirds in Prospect Park were comparable to those of ovenbirds elsewhere in New York City (Seewagen and Guglielmo, 2010) and Swainson's thrushes in urban forests of Ohio, USA (Matthews and Rodewald, 2010b). Stopover durations were also similar to those of spring migrant ovenbirds in non-urban habitats along the Gulf of Mexico (Moore and Kerlinger, 1987; Buler, 2006) and the coast of Maine (Morris et al., 1996).

Stopover periods of ovenbirds in Prospect Park did not differ between seasons. Autumn stopovers are usually longer than spring stopovers in passerine migrants (e.g. Rguibi-Idrissi et al., 2003; Stutchbury et al., 2008) for several suspected reasons (Berthold, 2001; Bauchinger and Klaassen, 2005), but the pattern is only general and not always found (Morris and Glasgow, 2001; Chernetsov and Mukhin, 2006).

4.3. Home range

Individual variation in home range size was high during both seasons. Average area usage of ovenbirds in Prospect Park during both seasons was generally greater than what has been reported for passerine migrants elsewhere; although, inconsistent sampling and home range estimation methodologies, which can produce dramatically different results, hinder comparisons between telemetry studies (Kernohan et al., 2001; Borger et al., 2006). Buler (2006) measured area usage of spring migrant ovenbirds in Mississippi on their first stopover day and subsequent days separately; 95% fixed kernel home range size averaged 1.5 ha during the first day and 0.6 ha on following days. European robins on the Baltic

Coast had mean 95% fixed kernel home ranges of 0.4 ha during spring and autumn (Chernetsov and Mukhin, 2006). Minimum convex polygon home ranges of Swainson's thrushes during autumn stopovers in northern California averaged 1.9 ha (Tietz and Johnson, 2007). Mean 50% fixed kernel home ranges of Swainson's thrushes in various urban forest fragments of Columbus, Ohio ranged approximately 0.4–3.0 ha during spring (calculated from Fig. 4 in Matthews and Rodewald, 2010a) and in some cases appeared constrained by patch size. In this study, even the largest 95% fixed kernel home ranges of ovenbirds during spring and autumn represented only 16% and 13% of the 100 ha forest area, respectively, suggesting forest size in Prospect Park exceeds the area requirements of individual migrant ovenbirds.

4.4. Influence of arrival condition

Stopover behaviour is expected to be largely condition-dependent. A scenario in which lean birds must forage widely and intensively at the expense of increased predation risk while fatter birds with little need to refuel can remain sedentary and less exposed to predators as they await departure (Chernetsov, 2006) has intuitive appeal. Indeed, lean ovenbirds and other passerine migrants moved faster, more frequently, and/or covered greater distances than fatter conspecifics during spring stopovers along the Gulf of Mexico (Loria and Moore, 1990; Aborn and Moore, 1997; Buler, 2006). Similarly, lean Swainson's thrushes during spring stopovers in Ohio, USA had higher movement rates than fatter thrushes (Matthews and Rodewald, 2010a). However, an alternative and converse scenario is also plausible. In this scenario, lean birds cannot afford temporal and energetic costs of prolonged exploration and choose to acquire resources from a small area encountered early, while fatter birds invest time and energy in extended searching for the most optimal habitat (Chernetsov, 2006). First-day movement patterns of ovenbirds in Prospect Park were not influenced by their condition (i.e., fat mass) during spring, but during fall, fatter birds moved at a slower rate and were closer to their capture location at the end of the day than leaner birds. Chernetsov and Mukhin (2006) found European robin spatial behaviour was not associated with fat stores during spring or autumn stopovers on the Baltic Coast. Wilson's warblers also showed no relationship between their arrival condition and movement patterns during spring stopovers in Arizona, USA (Paxton et al., 2008). Inconsistencies between studies may be due to the possible occurrence of both scenarios (Chernetsov, 2006) or differing influences on bird movements from other factors (e.g. predation risk, weather, resource distribution).

Many studies have shown passerine migrant stopover durations to be mediated by energetic condition upon arrival; lean birds tend to remain at stopover sites longer than fat birds (Cherry, 1982; Loria and Moore, 1990; Yong and Moore, 1997; Matthews and Rodewald, 2010b; Seewagen and Guglielmo, 2010; but see Salewski and Schaub, 2007). Ovenbirds previously studied in a different New York City park clearly fit this trend (Seewagen and Guglielmo, 2010). Arrival condition of ovenbirds in Prospect Park, however, did not significantly influence their departure decisions during either season. On the Gulf of Mexico, it was weather and prey availability, and not energetic condition that most significantly affected ovenbird stopover duration (Buler, 2006). Refueling rate, distance from final destination, time of season, and predation risk can also influence the length of time passerine migrants spend at a stopover site (Yong and Moore, 1997; Åkesson and Hedenström, 2000; Danhardt and Lindström, 2001; Dierschke and Delingat, 2001; Hays, 2008; Schaub et al., 2008). Other such factors likely contributed to ovenbird departures from Prospect Park more so than arrival condition.

5. Conclusion

Decreasing daily exploration by ovenbirds in Prospect Park suggests they eventually encountered and occupied suitable stopover habitat. More broadly, the similarity of their spatial behaviour to that of passerine migrants studied at other stopover sites implies they are utilizing this urban stopover habitat in a similar fashion as less-disturbed, larger forest tracts elsewhere. Our findings do not support the speculation that urban stopover habitats likely offer poor conditions for landbird migrants and are only used abruptly in times of urgency when alternatives are unavailable (e.g. Mehlman et al., 2005). Indeed, at least half of the birds we studied stopped over for multiple days during spring and autumn, and bird movements during both seasons were indicative of an ability to search for, locate, and occupy adequate habitat patches. Our results add to a growing body of evidence that habitats remaining within human-dominated landscapes can in fact represent suitable stopover sites for migrating landbirds (Seewagen and Slayton, 2008; Matthews, 2008; Craves, 2009).

It is now widely recognized that meeting the habitat requirements of migration is integral to successful migratory landbird conservation strategies which at one time focused only on issues concerning breeding and over-wintering areas (McCann et al., 1993; Mehlman et al., 2005). However, identifying important stopover sites and setting conservation priorities have been slowed by an incomplete understanding of migrant stopover habitat selection processes and migrant ecology and behaviour at stopover sites (Petit, 2000; Mehlman et al., 2005; Carlisle et al., 2009). Much progress has been made in recent years towards filling these knowledge gaps, but even the most basic information on migrant use of urban stopover habitats is still lacking. Further study is needed to allow land managers in metropolitan areas who strive to provide quality stopover habitats for landbird migrants to make more science-based decisions.

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