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Relationship Between Pedestrian Activity and Avian Body Condition During Fall Migration

Many North American landbirds undergo biannual migrations, which are energetically costly. Quality stopover sites are crucial to avian survival, as they provide opportunities to quickly replenish fat stores, rest, and avoid predation. One component of habitat quality that is often overlooked is the level of pedestrian activity, which birds may interpret as a predatory threat. If intrusion levels are high, birds will flush repeatedly and may not adequately restore energy reserves, which hinders successful migration. We compared body mass index between birds at different intrusion levels, testing the hypothesis that birds near continuous intrusion will be in poorer condition. Results between migratory guilds indicate long-distance migrants were in poorer condition in areas with high pedestrian activity. In contrast, resident species captured in high activity areas were in better condition than those captured in areas with lower activity. Since Neotropical migrants show increased sensitivity to human presence, conservation measures should focus on reducing pedestrian activity for quality stopover habitats.

Keywords

Migratory stopover, Urbanization, Pedestrian activity

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Approximately two-thirds of forest birds that breed in the eastern United States are Neotropical migrants (hereafter referred to as “migrants”): birds that migrate intercontinentally to tropical habitats in Mexico, Central and South America, and the Caribbean during the non-breeding season (Moore 2000). Migration places high energetic demands on migratory species (Moore et al. 1995), and adult mortality is nearly 15 times higher during migration compared to non-migratory periods (Sillett & Holmes 2002). Many birds take this risk because they benefit from: 1) greater survivorship during winter months, 2) the ability to exploit seasonal food abundance, and 3) reduced nest predation in temperate areas during the breeding season (Moore 2000).

Migration consists of a series of flights in which birds must stop to rest, replenish depleted fat stores, avoid predation, and seek shelter from adverse weather conditions (Moore et al. 1995). Depositing fat is regarded as the primary purpose of stopover and is key to successfully completing migration (Alerstam and Lindström 1990). Numerous studies have demonstrated that individual migrants that deposit more fat and that do so in a timelier manner have shorter stopovers, arrive on the breeding or non-breeding ground faster, acquire better territories, and have higher survival rates and reproductive success than individuals who are unable to do so (Smith and Moore 1993, Alerstam and Lindström 1990, Moore et al. 1995, Moore et al. 2005). Both the ability of a bird to regain lost fat stores and the rate of gain mass are metrics used to gauge habitat quality (Carlisle et al. 2012). Theory suggests that migrants should choose a stopover site that will be optimal to maximize food intake while reducing predation and competition, which are considered two of the most important influences for a successful migration (Carlisle et al. 2012). All habitats, however, are not equal, and a migrant is faced with a heterogeneous matrix of habitat during stopover which varies, both temporally and spatially, in food availability, predators, and competitors (Moore & Aborn, 2000). Stopover sites can range in quality and size, from small urbanized parks to large protected forests (Mehlman et al. 2005), and therefore vary widely in their suitability.

Migratory birds are encountering increasingly urbanized habitats. Urbanization is defined as human presence and its effects that are concentrated in residential and industrial settings (Chace & Walsh, 2006). Since a major hindrance during stopover is ability to regain fat stores, a high quality habitat is one in which birds regain mass at a higher rate relative to other available habitats (Moore et al. 1995, Seewagen 2005). The number and quality of stopover sites are likely to decline as human development continues, and this increasing urbanization can force migrants into progressively more unfavorable habitats (Seewagen 2005, Carlisle et al. 2012). When this occurs, there is a potential for increased inter- and intra-specific competition, loss of food resources, and higher predation risk; thus these low quality sites lack the key components for a suitable stopover site (Moore et al. 1995, Carlisle et al. 2012). There are some studies, however, that demonstrate migrants utilize urban areas in similar numbers as non-urban areas, staying for multiple days and successfully replenishing fat stores (Seewagen & Slayton 2008, Seewagen et al. 2010). Thus, even highly urbanized green spaces may be crucial for preservation. It is imperative scientists and managers understand how migrants are affected by urbanization and the further challenges that can bring, namely, the presence of humans. Humans are often associated with disturbances such as deforestation, mining, and forms of recreation, such as boating, biking, or horse riding (Knight & Cole, 1995b). However, even if direct community and/or ecological effects are minimal, the mere presence of humans in an environment can indirectly impact an ecosystem. The impacts of human intrusion (the presence of humans in the environment) are wide-reaching and generally negative (Gutzwiller et al., 1994). Despite the fact that intrusion does not include the habitat alterations or other changes associated with humans, the presence of humans in proximity to wildlife is ubiquitous, pervasive, and can lead to changes in avian behavior (Gutzwiller et al., 1994).

Recreational intrusion can no longer be considered neutral to ecosystems, and ecologists are beginning to recognize the consequences of human presence (Flather et al. 1995). In general, intrusion causes displacement of birds, limits access to food and other resources, and reduces reproduction and survival (Gutzwiller et al. 1998, Miller et al. 1998, Fernández-Juricic & Tellería 2000, Smith-Castro & Rodewald 2010). A paper by Boyle and Samson (1985) reviewed published studies of the impact of outdoor recreationists on wildlife and found 81% of those studies found negative effects. Intrusion can lead to increased alertness due to human presence, preventing birds from engaging in normal activities, such as foraging, singing, and territorial displays (Gutzwiller et al. 1994, Gutzwiller et al. 1998, Fernández-Juricic & Tellería 2000). Fernández-Juricic and Tellería (2000) found that Common Blackbird (*Turdus merula*) moved in different patterns, foraged less, and were more vigilant when human visitors were present. As intrusion increased, they also were found further from trails, nearer to cover, and occurred in less density compared to unintruded sites. The mere presence of humans was negatively related to breeding success and altered spatial patterns of bird communities (Fernandez-Juricic, 2000). Miller et al. (1998) also found negative effects of pedestrian trails on bird populations; generalist species were found closer to trails, and nest predation was greater closer to trails.

To date, most research on intrusion has been studied in waterbirds (Burger 1986, Klein et al. 1995, Skagen et al. 2001, Bolduc & Guillemette 2003, Marzano & Dandy 2012) and year-round resident passerines (Gutzwiller et al. 1994, Riffell et al. 1996, Gutzwiller et al. 1998) . Very few studies have investigated the impacts of human presence on migratory passerines (but see Gutzwiller et al. 1998), or compared the relationship between intrusion and breeding migrants (species that breed in an area but migrate during the non-breeding season), passage migrants (species that pass through *en route*), wintering migrants (species that breed elsewhere but spend the winter in an area), and resident species. Furthermore, most forms of nonconsumptive recreation, such as hiking and mountain biking, are expected to increase 63% to 142% by 2040 (Flather et al. 1995), making it increasingly important to understand the potential effects of such activities on migratory species. Burger and Gochfeld (1991) found migratory guild was a significant contributor to a bird's response to human presence: migrant passerines were found to be less tolerant of intrusion. Conversely, resident species tolerated both more people nearby and a closer approach distance. Klein et al. (1995) similarly found that migratory waterbirds were more sensitive to intrusion (both foot and vehicle traffic). A question yet to be addressed in the scientific literature is whether or not individual migrants are able to compensate for energy losses, from decreased foraging and increased flight distances, due to recreational intrusion (Knight & Cole, 1995b). These energetic condition changes are alluded to frequently in the literature (e. g. Frid and Dill 2002), but very few studies have been done to test their relationship. We seek to address this question by examining whether individuals in areas of high pedestrian activity would be in similar body condition as individuals caught in areas of less pedestrian activity.

METHODS

Study Site

Greenway Farm (35° 07’ N, -085° 13’ W) is a 220-ha park along the North Chickamauga Creek in Hixson, TN, with habitat consisting mainly of oak (*Quercus* spp.) –hickory (*Carya* spp.) forest, 12 ha of overgrown field, and 11 ha of regularly mowed turf grass (Figure 1). The average age of most of the trees in the wooded habitat is between 40 and 50 years (Rhonda Seeber, Chattanooga Parks and Recreation Department, personal communication). The overgrown field was an area that was cleared and planted with native warm-season grasses in 1997. No additional management has been done, and the area has since become overgrown predominantly with non-native Chinese privet (*Ligustrum sinese*), Japanese honeysuckle (*Lonicera japonica*), Amur honeysuckle (*Lonicera maackii*), and scattered Bradford pear (*Pyrus calleryana*), as well as native blackberry (*Rubus ursinus*), Eastern red cedar (*Juniperus virginiana*), and sweetgum (*Liquidambar styraciflua*). The park is surrounded on all sides by suburban development; housing density averages 12 houses/ha, and the population density is 550 people/km^2 (City-Data, 2014).

The park is naturally divided into two areas: the Greenway and the Bluff (Figure 1). The Greenway area is framed by North Chickamauga Creek and has an average elevation of 201 m above sea level. This area also contains multiple parking lots, a managed lawn, a dog park, gardens, a storage building, and a small office. In addition, the Greenway serves as the central area where all visitors to the park enter and is the area most used by visitors. The Bluff site is at an elevation of 268 m and a paved trail runs up the bluff and continues to the west end of the park. Exotic vegetation, such as those mentioned in the preceding paragraph, were common but less abundant at this site, the canopy was more closed, and there were more open areas of forest floor with native flora.

Figure 1. Netting sites at Greenway in Hamilton County, Tennessee. The Greenway site is marked in red, and the Bluff site is marked in yellow.

Eight mist nets (12 m x 2.6 m, 30 mm mesh) were set up at each site. Nets at Greenway were located at discrete positions no more than 20 m from the intruded trails. Nets at Bluff were located between 50-100 m from a less-used trail. Mist netting data were collected during the fall migration periods (late August-late October) of 2013 and 2014. Nets were opened within 30 minutes of local sunrise and checked approximately every 30 minutes until 1200 EST. Nets were closed when the ambient temperature exceeded 27° C, wind speed exceeded 10 km/h, or if more than a light drizzle was falling (Ralph et al. 1993). Captured birds were placed in cloth bags and walked back to a processing area; each site had its own banding area. Birds were banded with aluminum US Geological Survey leg bands, had their unflattened wing chords measured using a wing ruler, and weighed using an electronic balance. Visible subcutaneous fat was scored on a 6-point scale based on the one described by Helms and Drury (1960). As fat classes are a subjective measurement, they were assigned by the same observers (LKM at the Bluff site, DAA at the Greenway site) throughout the study to minimize inter-observer variation (Krementz & Pendleton, 1990).

We classified birds into one of three migratory guilds based on their relation to our study site: Resident species, Short-Distance Migrants, and Long-Distance Migrants. Resident species are those that stay in the study area year-round. Short-Distance Migrants are species that live in the area in winter only, migrating from further north in the fall and leaving in the spring before breeding season (Moore et al. 1995). Long-Distance Migrants are species that breed in North America and migrate to Central and South America and the Caribbean during the non-breeding season (Moore et al., 1995). Whether we categorized them as short-distance or long-distance, all migrants were considered to be in the migratory phase of their life cycle, based on when our sampling took place.

Pedestrian Intrusion Rates

Pedestrian intrusion rate was determined by two methods: Stationary observation and passive walking observation. For the stationary observations, an observer counted the number of pedestrians that passed from a stationary location on 11 random days when netting was occurring. The observer sat in a single spot and documented any person or group of persons that passed them on the trail. If there was a group of people, the number of people was recorded and used in the analyses. Since the nets at both locations were located on trails that formed a loop, any passerby would have disturbed all nets in the area. In addition, since the trails were in a loop, pedestrians would necessarily have to pass by the observer, ensuring that no pedestrians were missed. The density of the off-trail vegetation combined with the responsible behavior of the pedestrians using the park ensured that no pedestrians ventured off trail and would be missed by the observer. There were three different observers during the study, which may result in inconsistencies due to inter-observer errors; however, counting the number of people that pass is a discrete task, and is therefore unlikely that inter-observer error plays a significant role in this study. We used a Mann-Whitney test to compare averages at an alpha (α) level of 0.05.

To supplement the stationary observations, we also collected data on the amount of intrusion by recording the number of people encountered during net checks. This was documented for as many days as possible ($n = 47$; on days when lots of birds were being captured, the focus was on extracting and processing the birds and not on recording pedestrians) and recorded by the primary bander. We compared average number of people passing per hour between the Greenway and Bluff sites using a Mann-Whitney test where $\alpha = 0.05$.

Food Sampling and Vegetation Structure

Since body mass indices are impacted by the amount of food availability in an area, we conducted fruit sampling. Many passerine species switch diets seasonally from arthropods in spring to fruits in fall (Fristoe, 2014). A standard method to sample fruit is via fruit count: randomly selecting fruiting branches in the fall and counting the number of berries present (Lashley et al., 2014). We walked the netting trails, stopping every 50 m (at Greenway site) and 75 m (at Bluff site, since the trail was longer) and haphazardly selected three branches (one branch along the trail and two branches ~5 m off the trail to both the right and the left) near the trail to count berries. This was performed at ten stops per site in 2013 and 2014, resulting in 30 sampling points per site per year.

Because of time and manpower constraints, we were unable to sample arthropods in the fall. Arthropods were, however, sampled during spring migration. To accomplish this, ten points were sampled along the walking trials in each area. Sampling points were located 50-75 m apart. Three branches were haphazardly selected; one along the edge of the trail and two branches 5 m off the trail to both the right and the left, resulting in 30 samples per site per year. The height of branches selected was within the average height of mist nets to directly compare arthropod availability in the layer of forest in which we were most commonly mist-netting birds. Branches were covered with a 50-liter plastic trash bag, household insecticide was sprayed into the bag, and then the bag was tied closed with a drawstring. After 1 hour, the branch was shaken to dislodge the arthropods, and then the bag was carefully removed to ensure arthropods stayed inside. Bags were placed in a freezer until arthropod sorting and counting could be performed. Arthropods were sorted and classified down to order, and abundance was counted.

The amount of vegetation present can also have an influence on bird body mass by blocking visual contact with pedestrians. If avifauna cannot see pedestrians, they may pose less of a threat, and thus do not hinder foraging and fat acquisition (Fernández-Juricic et al., 2009). Vegetation characteristics can also alter bird numbers and behavior (Marshall & Cooper, 2004; Robinson & Holmes, 1984). To compare habitat differences between the sites, we measured foliage density, canopy cover, and community similarity. A total of 10 points were evaluated at each site and the results of the foliage density and canopy cover were averaged to give the mean percentages at each site.

To examine differences in foliage density, we used a vegetation profile board similar to that described by Nudds (1977). The profile board consisted of a 0.30 m X 1.22 m board painted in five alternating segments of black and white (35 cm each) with a total height of 1.75 m. A stake was attached to the bottom so that the board could be inserted into the ground and samples could be completed by one person. Four samples were taken every 50 m; one at either edge of the trail, and one 20 m away from the edge on either side of the trail. Foliage was visually estimated by the percent of each board segment covered by vegetation to the nearest 5%. Readings were taken with eye level at a height of one meter starting with the bottom segment and moving to the top (see Mitchell & Hughes, 1995).

To measure canopy cover, we used a densiometer. At each of the foliage density sampling points, we looked through the densiometer and estimated the percentage of view that was obscured by canopy.

At each sampling point, we also identified tree species within a 10 m radius at the two off-trail points. The species compositions were then compared using a Sørenson’s Index of Similarity, which is the ratio of shared species between two communities and the total number of species in both communities. Thus, values closer to 1 indicate greater similarity.

Body Condition

Wing length and mass were used to calculate the Scaled Mass Index (SMI) (Peig & Green, 2009) to compare measure of body condition. SMI scales individuals being compared to produce a better indicator of body condition based on relative size and the strength of the relationship between wing length and mass.

Data for recaptured birds were disregarded if the bird was caught in the same year; if, however, the same bird was caught the next year, we considered it to be an independent data point. Though we acknowledge that this does not eliminate pseudoreplication, it is minimized, and such instances were rare (*n*=13).

Because avifauna families differ substantially in terms of body size, foraging behavior, etc., we partitioned our analyses into all species and Family. All Species included every individual captured, whereas Family included all members of a taxonomic family for which we had sufficient sample sizes at each site ($n \geq 30$) to see if trends in body condition appeared for a more taxonomically focused group of birds. SMI was recalculated depending on which group we were analyzing. For example, when all species were analyzed, we calculated SMI for all species for both the Greenway and Bluff site. When we analyzed SMI by certain families, we recalculated the SMI for those groups, thus rescaling the body mass and wing-length relationship necessary for the SMI calculations.

Statistical Analysis

To examine the relationship between location and SMI across migratory guilds and years, we used a three-way mixed-factor ANOVA. Location (Bluff and Greenway) and Migratory Guild (long-distance migrants, short-distance migrants, and residents) were treated as fixed effects. Year was treated as a random effect because year was not a treatment of interest, but instead a sample of two specific years meant to be representative of a larger subset of all possible years (Gotelli & Ellison, 2004). We included all two-way interactions (i.e. the interactions between location and migratory guild, location and year, and migratory guild and year) in the model. Because there was no *a priori* biological reason to hypothesize that a three-way interaction (location x migratory guild x year) would exist, and because including additional terms in the model can reduce statistical power to detect other significant relationships, we did not include the three-way interaction in the model (Gotelli & Ellison, 2004). For all our analyses, the assumption of homogeneity of variance was violated, so we rank transformed the data and re-ran the analyses. We used Tukey post-hoc tests to determine differences between migratory guilds in order to isolate which means were significantly different.

To determine if there was a difference in the fruit biomass between sites, we averaged the number of berries and performed an ANOVA, with site being treated as a fixed factor and the average number of berries was treated as the response variable. To quantify arthropod abundance between sites, we used a chi-square test to compare the proportion of arthropods between sites. Average canopy cover and foliage density between sites were compared using a Student’s t test.

All statistical analyses were run using either SPSS™ (v. 22) or Sigma Stat™ (v. 2.0), and non-parametric tests were substituted where appropriate.

RESULTS

Overall Results

Sampling effort was equal between sites, with a total effort of 4,320 total net-hours (1 net-hour = 1 net open for 1 hour; 2,145 net-hours at Greenway, 2,175 net-hours at Bluff). A total of 791 birds were captured; 400 birds were caught at the more intruded Greenway site, whereas 391 birds were caught at the less intruded Bluff site (Table 1).

Table 1. Sample sizes of species captured at each site during this study. For Guild, L = Long-distance migrant, S = Short-distance migrant, R = Resident.

Species	Bluff	Greenway	Guild
Acadian Flycatcher *Empidonax virescens*	2	0	L
American Redstart *Setophaga ruticilla*	3	24	L
American Robin *Turdus migratorius*	14	3	R
Black-and-white Warbler *Mniotilta varia*	3	6	L
Black-throated-blue Warbler *Setophaga caerulescens*	1	0	L
Black-throated-green Warbler *Setophaga virens*	0	1	L
Blue Jay *Cyanocitta chrystata*	4	9	R
Blue-winged Warbler *Vermivora cyanoptera*	0	3	L
Brown Thrasher *Toxostoma rufum*	8	22	R
Canada Warbler *Cardellina canadensis*	4	15	L
Carolina Chickadee *Poecile carolinensis*	6	9	R
Carolina Wren *Thryothorus ludovicianus*	20	25	R
Chestnut-sided Warbler *Setophaga pensyvanica*	1	4	L
Common Yellowthroat *Geothlypis tricas*	0	4	L
Downy Woodpecker *Picoides pubescens*	0	1	R
Eastern Towhee *Pipilo erythrophthalmus*	1	9	R
Eastern Wood-Pewee *Cantopus virens*	1	6	L
Field Sparrow *Spizella pusilla*	0	1	R
Gray Catbird *Dumatella carolinensis*	4	17	L
Gray-cheeked Thrush *Catharus minimus*	31	3	L
Hermit Thrush *Catharus guttatus*	12	11	S
Hooded Warbler *Setophaga citrina*	42	39	L
House Wren *Troglodytes aedon*	1	2	L
Indgo Bunting *Passerina cyanea*	0	6	L
Kentucky Warbler *Geothlypis formosa*	5	3	L
Least Flycatcher *Empidonax minimus*	1	0	L
Magnolia Warbler *Setophaga magnolia*	18	58	L
Northern Cardinal *Cardinalis cardinalis*	29	30	R
Northern Flicker *Colaptes auratus*	0	2	R
Northern Mockingbird *Mimus polyglottis*	0	2	R
Northern Waterthrush *Parkesia noveboracencis*	0	5	L
Golden-crowned Kinglet *Regulus satrapa*	2	2	S
Ovenbird *Seiurus aurocapilla*	16	12	L
Red-bellied Woodpecker *Melanerpes carolinus*	1	0	R
Ruby-crowned Kinglet *Regulus calendula*	1	2	S
Scarlet Tanager *Piranga olivacia*	1	0	L
Song Sparrow *Melospiza melodia*	0	1	R
Swainson's Thrush *Catharus ustulatus*	32	11	L

Tennessee Warbler *Oreothlypis peregrina*	2	7	L
Trail's Flycatcher *Empidonax trailii*	2	0	L
Tufted Titmouse *Baeolophus bicolor*	25	12	R
Veery *Catharus fuscesens*	13	3	L
White-eyed Vireo *Vireo griseus*	4	10	L
White-throated Sparrow *Zonotrichia albicollis*	1	7	S
Winter Wren *Troglodytes hiemalis*	1	3	S
Wood Thrush *Hylocychla mustelina*	68	1	L
Worm-eating Warbler *Helmitheros vermivorum*	7	2	L
Yellow-bellied Flycatcher *Empidonax flaviventris*	1	2	L
Yellow-bellied Sapsucker *Sphyrapicus varius*	2	0	S
Yellow-breasted Chat *Ictera virens*	0	2	L
Yellow-rumped Warbler *Setophaga coronata*	1	3	S
Total	391	400	

Intrusion Level

Stationary Observations: The mean number of people passing/hour was significantly different between sites (Z= -2.485, *p*=0.006). Greenway and Bluff trails had a mean +/- SE of 3.55 ± 0.44 and of 0.57 ± 0.48 people passing per hour, respectively. Thus, Greenway site had approximately 6 times more people passing per hour than the less intruded Bluff site.

Passive Observations: Greenway and Bluff trails had a mean +/- SE of 1.63 ± 0.20 and of 0.45 ± 0.06 people passing per hour, respectively. Again, Greenway trails had a significantly greater amount of pedestrian activity than Bluff trails (Z= -3.775, *p*<0.001).

Food Availability

Greenway and Bluff trails contained a mean +/- SE of 30.3 ± 5.2 berries per branch and 17.2 ± 3.8 berries per branch, respectively. The difference, however, was not significant ($F_{1,1}$=5.011, *p*=0.267).

We found there to be unequal proportions of arthropods between locations; Bluff had a higher percentage of total arthropods, 55.7%, compared to Greenway, which had 44.3% of total arthropods which was significantly different (x^2=6.553, df=1, *p*=0.0127; Table 1). While these samples were taken during spring migration, the proportions of arthropods would be expected to be consistent between the two sites, even if the absolute abundance is likely to be lower in the fall.

Vegetation Structure

The Greenway had a mean +/- SE of 36.8 ± 2.3% foliage density, while Bluff had 39.8 ±2.4%, which was not significantly different (U=711.00, Z=-0.877, *p*=0.380). There was, however, a difference in canopy cover, with Bluff having a more closed canopy (Bluff: 70.2 ± 13.3%, Greenway: 53.6 ± 17.0%, t=2.486, *p*=0.023). Out of a combined total of 17 tree species found, 11 of them were shared at both sites, giving a Sørenson's Index value of 0.78, indicating a high degree of similarity in species composition between sites.

Body Condition

There was no significant relationship between location and ranked SMI ($F_{1,1.278}$=1.566, *p*=0.393) or between year and ranked SMI ($F_{1,1.654}$=0.219, *p*=0.694) for all species combined. However, there was a significant relationship between migratory guild and ranked SMI ($F_{2,1.989}$=48.279, *p*=0.021), implying the guild to which a bird belongs to may be the primary determinant of its SMI. Specifically, the SMI for long-distance and short-distance migrants was not significantly different (Tukey HSD, mean difference=60.057, *p*=0.083), but residents' SMI was significantly greater than both short-distance (mean difference=172.549, *p*<0.0001) and long-distance migrants (mean difference=232.606, p<0.0001).

There was a significant interaction between location and migratory guild ($F_{2,781}$=35.204, *p*<0.0001, Fig. 2). Specifically, SMI was higher in long-distance migrants at the less intruded site compared with the more intruded site. Short-distance migrants' SMI also differed with respect to location, with SMI being greater at the less intruded site, although the difference was less pronounced (Fig. 2). Resident species were in higher body condition at the more intruded site than at the less intruded site, which is in contrast to the pattern observed in migratory species (Fig. 2).

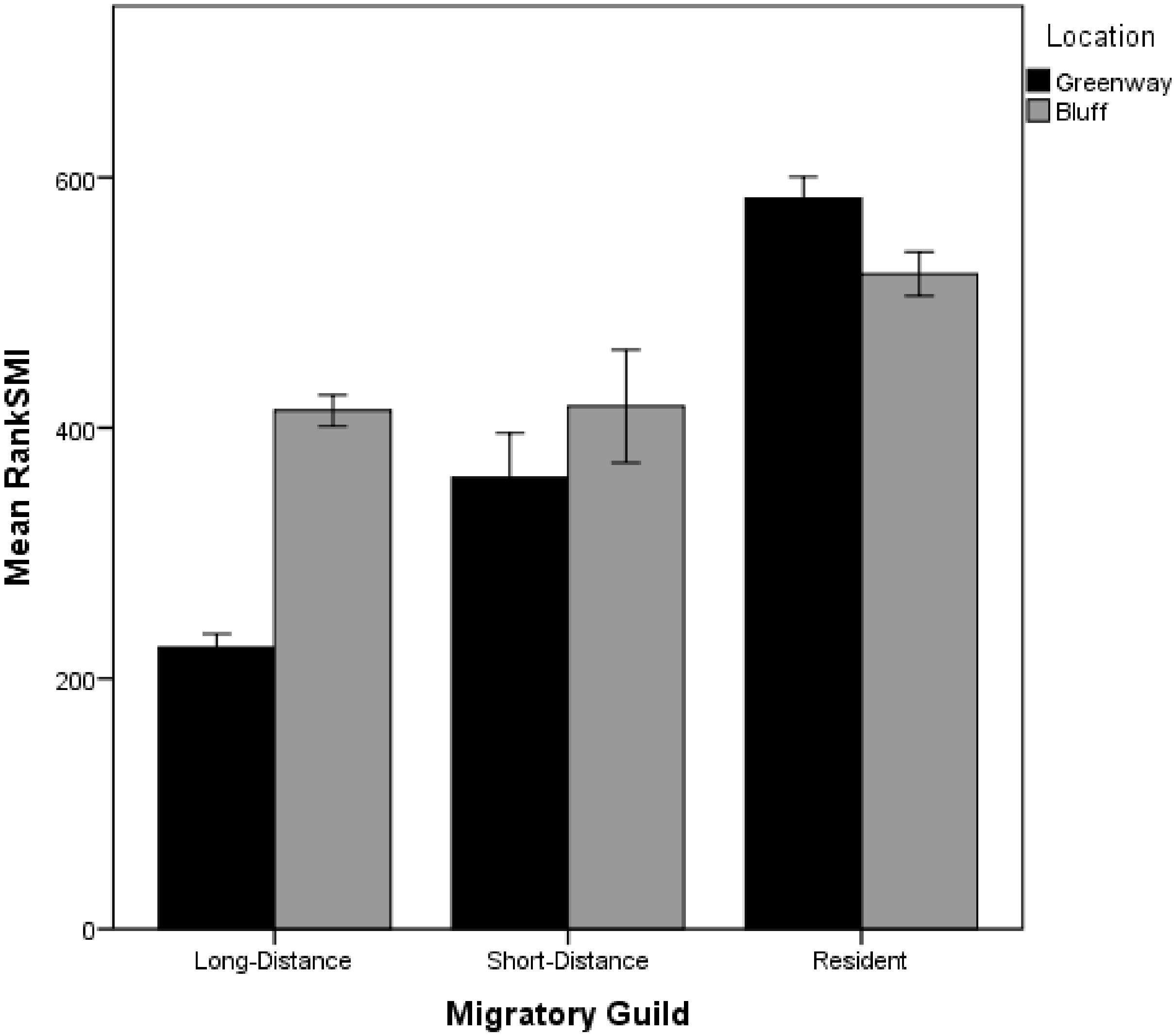

Figure 2. Mean Ranked SMI for Migratory Guild between Greenway and Bluff sites observed during the fall migration, 2013 and 2014. Whiskers indicate +/- 1 standard error.

Family Differences

Turdidae – Thrushes. Thrushes were the only family with sufficient samples sizes for analyses. Resident thrushes (e. g. American Robin, *Turdus migratorius*) were left out of the analysis because their sample size was not sufficient (*n*=3 at Greenway, *n*=14 at Bluff), so only the two migratory guilds were analyzed. There was no significant relationship between year and ranked SMI ($F_{1,0.176}$=1.275, *p*=0.748) or between migratory guild and ranked SMI ($F_{1,0.931}$=1.321, *p*=0.467). However, there was a significant relationship between location and ranked SMI ($F_{1,88.634}$ =14.133, *p*<0.0001, Fig. 3); specifically, the less intruded site contained birds of higher ranked SMI than the more intruded site. Therefore, for thrushes, both long and short-distance migrants had a better body condition near areas of lower pedestrian activity.

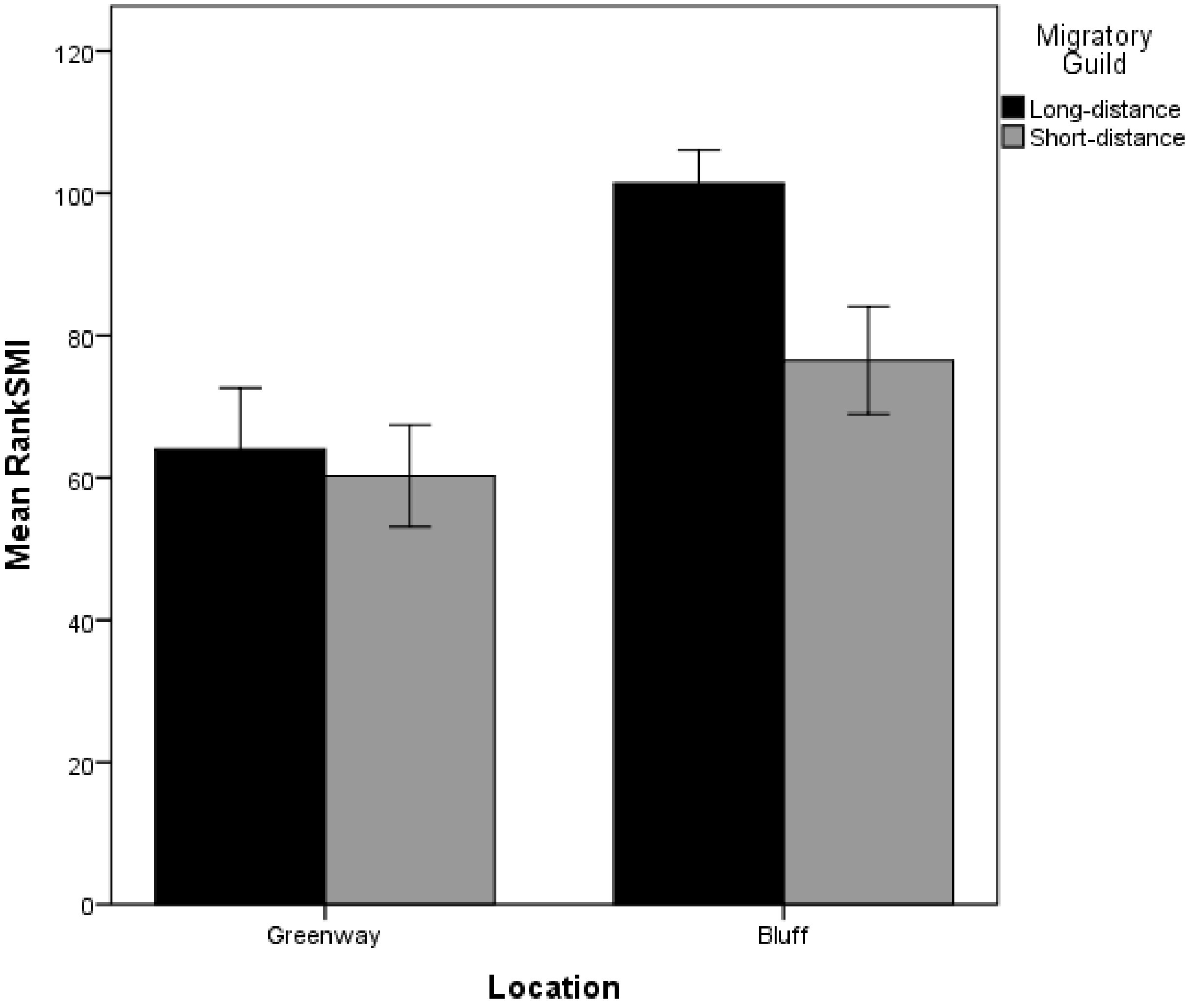

Figure 3. Mean Ranked SMI for Migratory Guild (long-distance and short-distance) of Thrushes (family Turdidae) between Greenway and Bluff sites observed during the fall migration for 2013 and 2014. Whiskers indicate +/- 1 standard error.

DISCUSSION

While there was no significant difference in fruit availability between sites, there was a greater proportion of arthropods at the Bluff site, at least during spring migration. Since birds were in better condition at the Bluff site, it is possible that the difference in arthropod abundance accounts for the difference in body condition. However, some studies indicate that food availability differences do not deter migrating birds from accumulating sufficient mass during stopover (e.g. Cimprich et al., 2005). This suggests that the differences in bird body condition we observed are more strongly correlated with pedestrian activity, where there was a much greater disparity between sites. In addition, there was little difference in vegetation structure and composition between sites, which further supports any differences in body condition being attributable to differences in pedestrian activity. Moore and Aborn (2000) found that Summer Tanagers (*Piranga rubra*) with greater fat reserves spent most of their time during stopover in pine forest, which had greater canopy cover than scrub habitat, which is where lean tanagers spent their stopover. Scrub habitat, however, had greater food availability. Similarly, Cohen et al. (2012) found that Red-eyed Vireos (*Vireo olivaceous*) selected stopover habitats with greater food availability, and those sites also had greater canopy cover. In contrast to these studies, however, food availability at our sites was similar, even though canopy cover was greater at the Bluff site, so it is still likely that pedestrian activity was the major contributor to the observed differences in body condition, rather than differences associated with canopy cover.

When all species were considered together, there was no relationship between SMI and location, which does not support our broad hypothesis that bird body condition will be lower in more intruded areas. However, when we separated our data into migratory guilds, significant trends emerged. Migrants, specifically long-distance migrants, tended to have increased SMI away from intrusion. This supports our hypothesis that migrants have an increased sensitivity to human presence, which displays itself through reduced body fat. Since migration is an energetically costly and challenging time in the life cycle of a bird (Moore, 2000, Sillett & Holmes, 2002), it is understandable that they require stopover habitat which has minimal human presence in order to have the best chance of a successful migration. Our results contrast with McCabe and Olsen (2015), who found that during fall stopover, long-distance migrants selected patches with higher fruit availability, despite some of those patches having higher predation risk. They concluded that during stopover, long-distance migrants are willing to accept more risk in order to meet their energetic demands and resume migration as quickly as possible. One explanation for the difference between their results and ours might be the level of predation. In the McCabe and Olsen study, raptor abundance might have been low enough or variable enough that migrants did not perceive predation risk to be sufficient to outweigh mass gain. At our more intruded Greenway site, pedestrian activity was very frequent, and might have been high enough that migrants opted for safety over food availability. Our findings for short-distance migrants are consistent with McCabe and Olsen (2015), who found that migrants flying shorter distances did not select habitats on the basis of fruit availability. The reasoning is that because migrants that do not have as far to travel do not have to fatten to the same degree as migrants flying longer distances, and therefore can better balance the trade-off between foraging and predation risk. Short-distance migrants at our study area were still in better condition away from intrusion, but the difference was not as pronounced compared with species migrating longer distances. Thus, short-distance migrants were still sensitive to potential predation risk, but may not have needed to accumulate as much mass. Resident species consistently had higher SMI than migratory species, and gained more mass overall, even nearer to human activity. This implies year-round avifauna may have either benefitted from or habituated to the continuous presence of intruders. Substantial evidence in the literature suggests resident birds may become acclimated to human intrusion (Miller et al., 1998; Fernández-Juricic et al., 2003; Fernández-Juricic et al., 2009). This tolerance could give residents an advantage to exploit food resources that may otherwise be inaccessible to migrants. In fact, Fernández-Juricic et al. (2003) suggested a “resource-use-disturbance trade-off hypothesis” to explain why some species may benefit near human presence. House Sparrows (*Passer domesticus*) benefited at intermediate rates of pedestrian intrusion for both breeding success and food consumption. These birds may be attracted to human presence since they see humans as a cue to finding food, but high levels of intrusion also discouraged foraging rates. Similarly, the resident species in our study may associate humans with unexploited food resources and are thus attracted to those areas with pedestrians and their associated alterations yet avoid high quantities of intrusion.

Thrushes gained significantly more body mass away from intrusion. Since all thrushes analyzed were migratory, our results show that regardless of migratory distance, thrushes as a whole obtain higher body mass away from intrusion, and that long-distance migrants were more sensitive to intrusion than short-distance migratory thrushes.

Since our data propose Neotropical migrants show reduced body mass in relationship to intrusion, consideration must be given to ensure these species are protected from the associations of human activity during stopover. For wildlife and land managers, we recommend that, if possible, their sites have large plots of unintruded native forested areas for migrants to rest, replenish fat stores, and avoid predators. These plots should be away from residential housing, roads, and trails, and restrict access by visitors. Trail design is also an important factor: a bird community is more affected as trail length increases and it intersects with a larger number of habitats (McKinney, 2005). A simple trail design, compared with a lengthier, more complex trail system, reduces intrusion for birds and benefits forest communities (Rodríguez-Prieto et al., 2014). Where trails are already in place, we recommend incorporating buffer zones that prevent pedestrians from close approaches to wildlife and taking measures to discourage recreationists from straying off of trails.

Vegetation structure is an area for future research. Despite finding few differences in vegetation measures between locations, it could still be a valuable mechanism that provides a visual obstruction and cover from predators for forest birds (Fernández-Juricic et al., 2009). Birds may affiliate human pedestrians as a potential threat (Frid and Dill 2002), and any vegetation blocking this visual detection could suppress the relationship of avifauna to intrusion. Blumstein (2006) hypothesized the opposite: that vegetation density may compromise visibility, and thus species in denser habitats react more warily to intrusion. However, no correlation between habitat structure and flightiness was detected in his analysis. Vertical height of vegetation can also reduce the potentially negative impacts of intrusion as well (Marzano & Dandy, 2012). Correlations between forest structure and human presence have been suggested in the literature (Gutzwiller et al., 1998, Fernández-Juricic et al., 2004, Fernández-Juricic et al., 2009,Marzano & Dandy, 2012), but to our knowledge, is still largely untested. Even though vegetation structure was not found to play a significant role in the bird SMI differences in our study, it could still be beneficial to integrate dense shrubbery along the trails, preferably native berry or nectar producers, such as American holly (*Ilex opaca*) or Sweetbay magnolia (*Magnolia virginiana*) as a physical barrier than could block the visual cue warning birds of an oncoming predator.

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