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Mass changes and energetic condition of grassland and shrubland songbirds during autumn stopovers at a reclaimed landfill in the New Jersey meadowlands

Chad L. Seewagen[1]* and Michael Newhouse[2,3]

ABSTRACT—Former landfills have long been recognized as a potential source of early successional habitat for wildlife, but their use by migrating grassland and shrubland songbirds has yet to be studied. We estimated mass change rates of 5 grassland and shrubland songbird species during autumn stopovers at a reclaimed landfill in New Jersey, to assess the quality of a former landfill as a stopover habitat. We also examined minimum length of stay, age ratios, and age differences in body mass and fat scores. Regressions of capture time and body mass were statistically significant and indicated gains of 0.8–1.2% of average body mass per hour in Savannah Sparrows (*Passerculus sandwichensis*), Lincoln's Sparrows (*Melospiza lincolnii*), and Palm Warblers (*Setophaga palmarum*), but coefficients of determination were weak (<0.06). White-crowned Sparrows (*Zonotrichia leucophrys leucophrys*) and Indigo Buntings (*Passerina cyanea*) did not gain significant mass. Minimum length of stay based on recaptures ranged from an average of 4.7 d in Savannah Sparrows to 10.1 d in Indigo Buntings. Adults did not have higher mass gain rates, body mass, or fat scores than immature birds in any species, with the exception of adult Savannah Sparrows being heavier than immatures in 1 year. The age ratio was significantly skewed toward immatures in all species except the Indigo Bunting, in which the opposite pattern occurred. Food availability at our site may have been poor, limiting the ability of birds to gain mass, or possibly time is not as important to these species at this stage of their migration as energy minimization and predator avoidance are. Considering the low temporal pressure and slow pace of autumn migration relative to spring, these autumn migrants might be using the landfill for rest, energy maintenance, and predator avoidance more so than rapid and substantial fuel deposition. The independence of mass change rate and energetic condition from age suggests that any potential age differences in dominance or foraging ability in these species do not affect their ability to refuel during stopover. *Received 3 December 2016. Accepted 18 March 2017.*

Key words: brownfields, early successional habitat, habitat restoration, migration, refueling.

Cambios en la masa y condición energética de aves de pradera y matorral durante paradas migratorias otoñales en vertederos restaurados en New Jersey

RESUMEN (Spanish)—Por mucho tiempo, los sitios usados como vertederos han sido reconocidos como fuente potencial de hábitat sucesional temprano para la vida silvestre, aunque su uso por aves canoras de praderas y matorrales está pendiente de ser estudiado. Para determinar la calidad del antiguo vertedero como hábitat de descanso y abastecimiento, estimamos la tasa de cambio de masa de cinco especies de aves de praderas y matorrales durante paradas migratorias otoñales en un vertedero restaurado en New Jersey, EUA. También examinamos la duración mínima de estadía, proporción de edades y diferencias de edad en masa corporal y categorías de grasa corporal. Las regresiones de hora de captura y masa corporal fueron estadísticamente significativas e indicaron ganancias promedio de masa corporal por hora entre 0.8–1.2% en los gorriones *Passerculus sandwichensis*, *Melospiza lincolnii* y el chipe *Setophaga palmarum*, aunque sus coeficientes de determinación fueron débiles (<0.06). El gorrión *Zonotrichia leucophrys leucophrys* y el colorín *Passerina cyanea* no ganaron masa de manera significativa. Usando como base las recapturas, la duración mínima de estadía varió de un promedio de 4.7 d en *P. sandwichensis* a 10.1 d en *P. cyanea*. Los adultos no tuvieron tasas más altas de ganancia de masa, masa corporal o grasa corporal que las aves juveniles en ninguna de las especies, excepto los adultos de *P. sandwichensis* que en un año fueron más pesados que los juveniles. La proporción de edades estuvo significativamente sesgada hacia los juveniles en todas las especies, excepto en *P. cyanea*, en el cual observamos el patrón opuesto. La disponibilidad de alimento podría haber sido pobre, limitando la capacidad de las aves para ganar masa, o posiblemente el tiempo no es importante para estas especies en esta etapa de su migración, como lo pueden ser la minimización de energía o la evasión de depredadores. Considerando la baja presión temporal y el paso lento de la migración de otoño comparada con la de primavera, estos migrantes otoñales podrían estar usando el vertedero como sitio de descanso, mantenimiento de energía y evasión de depredadores más que como sitio de deposición rápida y sustancial de combustible para la migración. La independencia de la edad respecto a la tasa de cambio de masa y condición energética sugiere que cualquier diferencia potencial entre la edad, y la dominancia o la capacidad de forrajeo en estas especies no afecta su capacidad para reabastecerse durante sus estadías durante la migración. Recibido 3 diciembre 2016. Aceptado 18 marzo 2017.

Palabras clave: campos restaurados, hábitat sucesional temprano, migración, recarga de combustible, restauración de hábitat.

Many bird species that inhabit grasslands, shrublands, and other early successional, disturbance-dependent habitats are in steep decline in the northeastern United States, as fire suppression, abandonment of agriculture, and other changing land use patterns over the past century have reduced habitat availability (Norment 2002, Shriver et al. 2005, Sauer and Link 2011). This decline has prompted a strong response from some agencies and conservation organizations to protect and create new breeding habitat for these species to reverse population trends (Vickery and Herkert

[1] Great Hollow Nature Preserve & Ecological Research Center, New Fairfield, CT, USA
[2] New Jersey Sports and Exposition Authority, Lyndhurst, NJ, USA
[3] Current address: Kleinfelder Inc., Fishkill, NY, USA
* Corresponding author: cseewagen@greathollow.org

2001, Norment 2002, Shriver et al. 2005). Much less attention has been paid to meeting the habitat requirements of grassland and shrubland birds during migration, and we know little to nothing about the stopover biology of the majority of these species. Stopover habitats in which birds can rest and refuel are critical for successful migrations (Mehlman et al. 2005, Kirby et al. 2008). As for other groups of migratory birds (Moore et al. 1995, Mehlman et al. 2005, Kirby et al. 2008, Sheehy et al. 2011), successful conservation of migratory grassland and shrubland bird species will partly depend on the conservation of suitable stopover habitat throughout their migration routes and a sound understanding of the biology and habitat requirements of these species during their migrations.

Restored or naturally revegetated landfills have been advocated as a potential source of habitat for grassland, shrubland, and early successional forest wildlife, particularly in urban and industrial areas where large open spaces are often extremely limited (e.g., Davis 1989, Watson and Hack 2000, Tarrant et al. 2013). However, the ability of reclaimed landfills to support productive and diverse communities of birds or other wildlife has not been well studied (Harrison and Davies 2002, Rahman et al. 2011, Tarrant et al. 2013). We are unaware of any research on the use of reclaimed landfills by migrating birds in particular, and it is unknown whether former landfills can provide migrants with suitable stopover habitat. Our objective was to estimate the mass change rates and stopover durations of autumn migrants at a recently closed landfill to gauge the quality of the site as stopover habitat for grassland and shrubland songbirds and add to what little is known about the stopover biology of these species in general. We also examined age ratios and age differences in body mass and fat scores to investigate whether immature birds significantly outnumbered adults and if adults were in better energetic condition, as is sometimes observed among migrating forest songbirds.

Methods

Study site and data collection

We studied birds at the Erie Landfill, a ~17.5 ha former landfill located along the Hackensack River in North Arlington, New Jersey, USA (40°47′24.3″N, 74°06′57.0″W). The landfill was closed to operations in 2005 and capped in 2006. In the years since, it has naturally become vegetated, mostly by nonnative plants. Mugwort (*Artemisia vulgaris*) is overwhelmingly dominant in most areas, and other abundant plant species on the site include eastern cottonwood (*Populus deltoids*), black locust (*Robinia pseudoacacia*), common reed (*Phragmites australis*), foxtail grass (*Alopecurus* sp.), and common sunflower (*Helianthus annuus*).

We used 9 mist nets (12 × 2.6 m) to passively capture birds at the site 5 d per week, weather permitting, from 30 August to 20 November 2011 to 2013. The nets were opened at sunrise and checked hourly for 8 h unless weather conditions forced earlier closure. All captured birds were banded with a US Geological Survey aluminum leg band, sexed based on plumage characteristics when possible, assigned to an age class of hatching year (immature) or after-hatching year (adult) based on degree of skull pneumatization and/or plumage characteristics when possible (Pyle 1997), measured (unflattened wing length to 1 mm), fat-scored on a 6-point scale (Helms and Drury 1960, Seewagen 2008), weighed to the nearest 0.1 g on a digital balance, and then released.

Statistical analyses

We focused our analyses on 5 songbird species associated with grasslands, shrublands, or other open habitats: Savannah Sparrow (*Passerculus sandwichensis*), Lincoln's Sparrow (*Melospiza lincolnii*), White-crowned Sparrow (*Zonotrichia leucophrys leucophrys*), Palm Warbler (*Setophaga palmarum*), and Indigo Bunting (*Passerina cyanea*). These species were chosen also because they are medium- or long-distance migrants (Ammon 1995, Chilton et al. 1995, Payne 2006, Wheelwright and Rising 2008, Wilson 2013), either uncommonly or never nest or overwinter in the area (Fowle and Kerlinger 2001, McGowan and Corwin 2008, Boyle 2011), and were captured in numbers we considered sufficient for our statistical analyses ($n > 50$).

We estimated mass change rates based on the relationship between body mass and time of capture (expressed as hours since sunrise; Winker et al. 1992, Seewagen et al. 2011, Horton and

Morris 2012, Ware et al. 2015). We tested this relationship in each species by first using general linear models (GLMs), with body mass as the dependent variable, time of capture and age as independent variables, and an interaction term between time of capture and age to identify potential age differences in mass change rates (Jones et al. 2002). When the interaction term was significant, we ran separate linear regressions of body mass and time of capture for the 2 age groups to measure age-specific rates of mass change. Otherwise, or if sample size was small for one or both age groups ($n < 25$), we combined age groups for calculating overall mass change rates. Body mass was adjusted to wing length before all analyses using a scaled mass model (equation 2 in Peig and Green 2009) unless a linear regression of these 2 variables was nonsignificant (Seewagen et al. 2011, Seewagen and Guglielmo 2011, Holzschuh and Deutschlander 2016).

We estimated minimum length of stay among recaptured birds by subtracting the date of first capture from the date of last capture while recognizing that the minority of individuals recaptured may not have been representative of all birds (Winker et al. 1992), and that initial and final captures may not have occurred on the date of arrival and departure, respectively (Cherry 1982, Yong and Finch 2002). We report this information with the intent to provide only a general indication of whether birds were quickly departing the study site, perhaps in search of more natural, less disturbed habitat elsewhere, or remaining onsite for a more extended stopover. We also used time between recaptures to investigate with a Mann-Whitney *U*-test age differences in minimum length of stay in the Savannah Sparrow, which was the only study species with adequate numbers of recaptures ($n = 109$) for comparison.

We used chi-square tests to compare the ratio of immature to adult birds in each species and compared fat scores between age groups using Mann-Whitney *U*-tests (Hailman 1965). Age differences in body mass were determined from the significance of age as an independent variable in the GLM. In the analyses of mass change rates, age ratios, and fat scores, the data were pooled across the 3 study years for each species except for the Savannah Sparrow, which had an exceptionally large total sample size ($n > 1{,}500$). Savannah Sparrow was examined in each year independently to reduce statistical power and inflation of the significance of effects. Analyses were performed using SYSTAT 12, and results were considered significant when $P \leq 0.05$.

Results

The relationship between body mass and capture time was dependent on age in Palm Warblers ($F_{1,486} = 5.62$, $P = 0.018$) but not in Indigo Buntings ($F_{1,120} = 1.29$, $P = 0.26$) or in Savannah Sparrows in 2011 ($F_{1,653} = 2.17$, $P = 0.14$), 2012 ($F_{1,354} = 1.35$, $P = 0.25$), or 2013 ($F_{1,528} = 2.74$, $P = 0.10$). We did not test for age effects on mass change rate in Lincoln's Sparrows or White-crowned Sparrows because of small sample sizes of adults ($n = 21$ and 20, respectively).

Immature Palm Warblers showed significant mass gains over time, whereas adults did not (Table 1). Across age groups, Lincoln's Sparrows gained significant mass while there was no evidence of hourly mass changes in Indigo Buntings and White-crowned Sparrows during the 3-year study period or in Savannah Sparrows in 2011 and 2013 (Table 1). Capture time also explained little variation in body mass in Savannah Sparrows in 2012 ($r^2 = 0.02$), even though the relationship was statistically significant because of the large sample size (Table 1). In groups with a significant relationship between body mass and time of capture, hourly mass change rates ranged from 0.11 to 0.21 g (Table 1) and represented 0.8–1.2% of their average body mass; however, coefficients of determination were low in all cases (Table 1).

Excluding same day recaptures, recapture rates ranged from 3.2% in Palm Warblers to 18.5% in Lincoln's Sparrows. Minimum length of stay averaged highest in Indigo Buntings and lowest in Lincoln's Sparrows and was highly variable among individuals within each species (Table 2). Recaptured immature Savannah Sparrows stayed an average of 0.9 d longer than adults, but the difference was not significant ($U = 1{,}197$, $P = 0.24$).

The age ratio was significantly skewed toward immatures in all species except the Indigo Bunting, in which the opposite pattern occurred (Table 3). Fat scores were generally low, with all

Table 1. Hourly mass change rates (SE) of songbirds during autumn stopovers at a reclaimed landfill in the New Jersey Meadowlands, 2011–2013.

Species	Year	Age	*n*	r^2	*P*	g/h
Palm Warbler	2011–2013	Immature	264	0.050	<0.001	0.11 (0.03)
		Adult	226	0.001	0.73	
Indigo Bunting	2011–2013	All	124	<0.0001	0.83	
Lincoln's Sparrow	2011–2013	All	91	0.048	0.036	0.21 (0.01)
White-crowned Sparrow	2011–2013	All	132	0.020	0.12	
Savannah Sparrow	2011	All	656	0.004	0.10	
	2012	All	357	0.021	0.006	0.14 (0.05)
	2013	All	531	<0.0001	0.95	

species having a median fat score of only 0 or 1, and they did not differ between immatures and adults in any species (Table 4). Body mass also did not differ between age groups in any species with the exception of Savannah Sparrows in 2013, when adult birds were significantly heavier than immatures (Table 4).

Discussion

The stopover biology of grassland and shrubland songbirds is poorly understood relative to that of forest songbirds, and we are unaware of any previous study of grassland and shrubland bird usage of a former landfill as stopover habitat. Here, among 5 species of songbirds associated with grasslands, shrublands, or other open habitats, we found little evidence of diurnal mass gains at our reclaimed landfill study site. We also found no indication that stopover refueling ability or energetic condition was superior in adults, unlike that which is sometimes observed in forest songbirds during autumn migration (Woodrey 2000). Food availability may have been poor at the site and constrained the ability of birds to gain mass, or possibly time is not as important to these species at this stage of their migration as energy minimization and predator avoidance are (sensu Alerstam and Lindström 1990, Hedenström 2008).

Table 2. Recapture rates, length of stay (mean [SD]), and maximum time span between initial and final captures of songbirds stopping over at a reclaimed landfill in the New Jersey Meadowlands, 2011–2013.

Species	Rate (%)	Length of stay (d)	Maximum (d)
Palm Warbler	3.2	4.8 (4.0)	14
Indigo Bunting	12.7	10.1 (9.6)	29
Lincoln's Sparrow	18.5	4.7 (4.3)	16
White-crowned Sparrow	11.4	5.7 (4.9)	14
Savannah Sparrow	7.0	7.3 (5.2)	28

The rate at which birds recover body mass has been used as an indicator of absolute stopover habitat quality (e.g., Seewagen and Slayton 2008, Craves et al. 2009), but this indicator generally assumes that migrants are operating under a time minimization strategy that favors refueling at or near the maximum rate allowed by the conditions at the site. Optimal migration theory posits that birds may use alternate strategies in which the minimization of energy expenditure and predation risk are prioritized over the minimization of time taken to reach their destination (Hedenström 2008). These alternate strategies are likely common during autumn when selection pressure for, and the benefits of, early arrival at the destination is lower than that experienced by migrants during spring (Schmaljohann et al. 2012, Nilsson et al. 2013). The lower pressure for time minimization during autumn manifests in a slower pace of migration than during spring (McKinnon et al. 2013), including less rapid and extensive refueling (Seewagen et al. 2013). We therefore cannot conclude that because we did not detect mass gains in most cases the reclaimed landfill offers poor conditions for refueling. It is equally possible that the birds we studied are using the landfill site during autumn for rest, energy maintenance, and predator avoidance more than for rapid and substantial fuel deposition.

In cases where we did find a relationship between body mass and time of day, the rates of mass gain were comparable to, and often higher than, the few reports of spring or autumn mass

Table 3. Age distribution of songbirds captured during autumn stopovers at a reclaimed landfill in the New Jersey Meadowlands, 2011–2013.

Species	Year	Immature	Adult	% Immature	χ^2	*P*
Palm Warbler	2011–2013	273	229	54.4	3.9	0.050
Indigo Bunting	2011–2013	31	94	24.8	31.8	<0.0001
Lincoln's Sparrow	2011–2013	71	21	77.2	27.2	<0.0001
White-crowned Sparrow	2011–2013	112	20	84.5	64.1	<0.0001
Savannah Sparrow	2011	453	204	69.0	94.4	<0.0001
	2012	190	168	53.1	1.4	0.25
	2013	360	172	67.7	66.4	<0.0001

changes by these species in more natural habitats. For example, the 1.1% of average total body mass per hour gained among immature Palm Warblers at the Erie Landfill is similar to the 0.6–1.3% of average lean body mass gained per hour during autumn stopovers at 3 sites along Long Point, Ontario, Canada (Dunn 2001), and to the 0.99% of average lean body mass gained per hour during spring stopovers along Braddock Bay, New York (Bonter et al. 2007). Lincoln's Sparrows, which gained 1.2% of average total body mass per hour at the Erie Landfill, gained 0.3–1.1% of average lean body mass per hour during autumn stopovers at multiple sites across Canada (Dunn 2002) while showing no significant hourly changes in mass along Braddock Bay, New York, during spring (Bonter et al. 2007) or in central New Mexico during spring or autumn (Yong and Finch 2002). Savannah Sparrows, which gained 0.8% of average total body mass per hour at the Erie Landfill in 2012 also showed no significant hourly changes in mass during spring or autumn stopovers in central New Mexico (Yong and Finch 2002).

More than 10% of Indigo Buntings, Lincoln's Sparrows, and White-crowned Sparrows were recaptured during their stopovers at the Erie Landfill, often multiple days after their initial capture. Minimum length of stay also averaged several days in Palm Warblers and Savannah Sparrows, although the lower recapture rates in these species question the extent to which the behavior of the recaptured individuals was representative of behavior of the many more birds captured only once. Nevertheless, we documented many birds using the landfill for extended stopovers, possibly indicating that the site was meeting their resource requirements. The minimum length of stay of White-crowned Sparrows averaged higher at the Erie Landfill than at a site in rural Maine during spring and autumn (Cherry 1982) but much lower than along the Rio Grande in central New Mexico (spring and autumn combined; Yong and Finch 2002). Minimum length of stay in Savannah Sparrows and Lincoln's Sparrows was also much shorter at the Erie Landfill than in central New Mexico (Yong and Finch 2002), but comparisons may not be appropriate because of the distinctiveness of, and

Table 4. Mean body mass (SD) and median fat scores of immature and adult songbirds during autumn stopovers at a reclaimed landfill in the New Jersey Meadowlands, 2011–2013.

		Fat score				Body mass (g)			
Species	Year	Immature	Adult	*U*	*P*	Immature	Adult	*F*	*P*
Palm Warbler	2011–2013	1	1	30,730	0.85	10.2 (0.8)	10.1 (0.7)	1.4	0.25
Indigo Bunting	2011–2013	1	0	1,208	0.24	15.8 (2.0)	15.5 (2.4)	1.8	0.18
Lincoln's Sparrow	2011–2013	1	1	729	0.88	17.2 (1.3)	18.0 (2.0)	0.3	0.57
White-crowned Sparrow	2011–2013	1	1	909	0.18	26.7 (2.0)	27.1 (2.2)	0.4	0.52
Savannah Sparrow	2011	0	1	45,183	0.58	17.9 (1.4)	18.1 (1.5)	1.0	0.32
	2012	0	0	15,948	0.89	17.3 (3.6)	17.7 (2.1)	0.1	0.76
	2013	0	0	30,108	0.67	17.6 (1.4)	18.0 (1.6)	9.0	0.003

differences between, eastern and western North American migration systems (Kelly and Hutto 2005). We are not aware of any other reports of autumn stopover durations of our study species in eastern North America.

Among forest songbirds, immature birds can be socially subordinate to adults and sometimes show poorer foraging ability, poorer food selection, and less efficient nutrient assimilation (Hume and Biebach 1996, Woodrey 2000, Moore et al. 2003). Immatures of these species are consequently found to sometimes have smaller fuel loads and longer stopovers during migration (Woodrey 2000, Morris et al. 1996, Moore et al. 2003, Mackenzie 2010), yet it is rarely demonstrated that adults actually refuel at a faster rate (see Seewagen et al. 2013 for discussion). Here, too, among 5 species of birds associated with grassland and shrubland habitats, we found no evidence of greater refueling performance by adults than immatures. We also found no difference between adults and immatures in the size of their fat stores or their body mass (with the exception of Savannah Sparrows in 1 of the 3 study years), and we found no age difference in minimum stopover duration in the one species we were able to investigate. This finding might mean that by the start of their autumn migration, age differences no longer exist in dominance or foraging ability in our study species that would affect their ability to refuel during stopover. Indeed, Wheelwright and Templeton (2003) found that immature Savannah Sparrows are less efficient foragers than adults during the post-fledging period but are able to forage as well as adults by the time they depart on autumn migration.

The immature-skewed age ratio we observed in 4 of our 5 study species is consistent with that often found among forest songbird migrants at autumn stopover sites (Robbins et al. 1959, Murray 1966, Ralph 1981, Morris et al. 1996). In coastal areas (such as our site) this skewed ratio has been suggested to be the result of immatures migrating closer to coasts than adults (Ralph 1981); however, age ratios among migrating forest songbirds can be just as heavily skewed toward immatures in inland areas (Dunn and Nol 1980, Rimmer and McFarland 2000, Mills 2016). Based on known fecundity and survival rates of migratory forest songbirds, Mills (2016) found the proportion of immature birds captured at autumn migration banding stations was too implausibly high to be an indication of true population age structure and suggested instead it was an artifact of sampling biases. This sampling bias may also hold true for shrubland and grassland songbirds; at our study site, longer stopovers or other attributes of immature birds may have made them more likely to be captured than adults (Mills 2016) and partly accounted for the skewed age ratios among our study species.

In conclusion, we found a recently reclaimed landfill being used by an abundance of grassland and shrubland songbirds in a heavily urbanized and industrialized region where alternative stopover habitat for these species is limited. Although we did not observe strong trends of increasing body mass during the morning hours, there was no evidence to suggest that the landfill we studied is an energy sink where birds lose mass. Former landfills, mining fields, and other such areas that have been reclaimed following human disturbances have the potential to provide an important source of habitat for rest and energy maintenance for these species during migration as other sources of open, early successional habitats continue to decline. However, additional research on the stopover biology of grassland and shrubland bird species at a variety of reclamation sites and in multiple geographic regions will be needed to comprehensively understand the value of reclaimed landfills as stopover habitat for these declining groups of birds. In addition, a commitment by landowners to maintain such sites in an early successional stage is required for the sites to provide appropriate habitat for these species over long time periods.

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