Long-term Declines of Autumn Fat Scores in Migrating Passerines of Coastal Maine

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Abstract - Long- and short-distance migratory songbirds acquire fat during migratory flights at stopover sites. With phenological shifts mediated by climate change, alterations in food abundance or peak timing could disrupt historical patterns of this fat storage and therefore migration ecology. Furthermore, these potential disruptions may vary by dietary guild and species, affecting birds that rely on plant matter and animal matter differently. Using data collected at a fall-migration stopover in coastal Maine from 2011 to 2024, we investigated patterns of fat acquisition in omnivorous, insectivorous, and frugivorous migratory songbirds. By guild, fat storage declined significantly in insectivores and omnivores, but not frugivores over the 13-year study. Annually, fat storage declined by 44% and 18% in insectivores and omnivores, respectively, over the study period. The overall decrease in acquired fat over time suggests that some species, particularly insectivores, are less able to accumulate fat for migration at this stopover site in southern Maine.

Introduction

Migrating songbirds actively minimize the time they spend on migration and speed up migration along the route (Lindstrom and Alerstam 1992). Instead of maintaining consistent levels of fat throughout the year, long- and short-distance migratory songbirds accumulate fat shortly before migratory flights (Cornelius et al. 2021). As a result, birds with larger fat stores more reliably fly in their seasonally appropriate migration direction (Schmaljohann and Naef-Daenzer 2011) and leave stopover sites quicker (Goymann et al. 2010) than birds with lower fat stores. Of all the body-condition factors tested in migratory songbirds, fat scores may be the most relevant to understanding migratory behavior (Covino et al. 2011).

While fat accumulation is key to migratory success, patterns of fat accumulation may vary based on species diet. Diet affects the rate of mass gain during migratory stopover (Bairlein and Gwinner 1994); the extent of frugivory is positively correlated with fat reserves, which suggests that frugivores may gain mass more efficiently than insectivores (Parrish 1997). However, benefits associated with eating fruit may be tempered by migration strategy, where the stricter body condition requirements of long-distance migrants may benefit from a fruit diet more than short-distance migrants (Carter et al. 2024). Relatedly, Jenni-Eiermann and Jenni (2025) found that frugivores and long-distance nocturnal migrants made the most efficient use of their fat stores, indicating that some birds may use their fat stores more efficiently than others. Birds with different diets may also use their fat reserves in different ways; migrating frugivores catabolized less protein and

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more lipid during migration than insectivores (Gannes 2001). Geography may also influence the relationship between frugivory and fat accumulation. For example, availability of fruit and insects did not impact fat acquisition in western North American in Idaho (Carlisle et al. 2012), whereas diversity and availability of fruit correlated with fat acquisition during fall in eastern North America near Lake Ontario (Smith et al. 2015). Finally, climate change may create phenological mismatches between an individual's arrival at stopover grounds and their preferred food (Kellermann and van Riper 2015), thereby influencing fat accumulation (van Gils et al. 2016). For example, La Sorte and Graham (2021) found that dietary guild predicted which North American birds timed migration with vegetation greenness; however, Wolfe et al. (2014) observed that both omnivores and frugivores were highly synchronized with leaf phenology instead. Only long-distance insectivores showed strong synchronization with vegetation greenness, and insectivores specifically showed little synchronization during fall migration.

Few studies have looked at long-term changes in body fat of songbirds during migration. Ożarowska and Meissner (2023) found increasing body mass and fat reserves of autumn migrating *Sylvia atricapilla* (L.) (Eurasian Blackcap) and hypothesized that this result reflected increasing fruit availability at their study site. We used Ożarowska and Meissner's (2023) approach to assess changes in fat storage among migratory songbirds at a songbird fall-migration stopover site in a coastal forest in southern Maine. We used long-term banding data from a stopover site in Maine using captures of 21 species of short- and long-distance migratory songbirds to assess whether: (1) fat scores, an index of fat storage, exhibited any significant trends from 2011 to 2024 during fall stopovers; and (2) if these trends differed among foraging guilds.

Methods

Field-site description

We conducted fieldwork at the University of New England's 147-ha forest in Biddeford, Maine (43.27277°N, 70.24498°W). We captured birds using 3 mist net arrays, with each array including five 9 m x 12 m nets. Two arrays were located in wetland sites largely composed of *Acer rubrum* L. (Red Maple), *Vaccinium corymbosum* L. (Highbush Blueberry) and *Ilex verticillata* (L.) A. Gray (Common Winterberry). The third array was in an upland site largely composed of *Quercus rubra* L. (Northern Red Oak), *Vaccinium angustifolium* Aiton (Lowbush Blueberry), and *Pinus strobus* L. (White Pine). We banded songbirds 2 days a week from 0630 h to 0930 h from 1 September to 31 October during 2011–2024 but excluded 2015 and 2021. We sampled this 3-h period to minimize time-of-day bias. Fat scores were determined by 1 observer (N.G. Perlut) throughout the study. The observer blew on the birds' furcula to visually assess fat storage on a scale from 0, no fat, to 5, overflowing or maximum fat (Helms and Drury 1960). We excluded captures of resident species and included all short- and long-distance migratory songbirds. For each year, we excluded weeks with only 1 capture of an individual within each

guild to ensure that a small number of birds did not overly represent the sample for that period. In cases where we recaptured an individual (3.7% of captures), both the initial capture and subsequent captures were included in the dataset because the same bird could have acquired or depleted fat between captures. Due to the repeated measurement of a small number of individual birds, we included band number as a nested random effect in our models.

Statistical analysis

We used information from Billerman et al. (2022) to assign each species to 3 diet categories (frugivores, insectivores, and omnivores); we placed birds in categories that most accurately reflected their diet during fall migration. We also used Parrish (2000) to determine which typically insectivorous birds shift to omnivory during fall migration. We categorized birds that consumed seeds, buds, and flowers as frugivores and species that consumed arachnids, eggs, and vertebrates as omnivores (Table 1).

We ran models in R (v. 4.5.1; R Core Team 2025). We built zero-inflated gamma general linear mixed models (GLMM) to test if year, foraging guild, and the year * foraging guild interaction terms explained fat storage in songbirds during fall migration, including band number as a nested random effect in our models. We used zero-inflated gamma models because of the large number of individuals that had fat scores of 0. We first tested the effects of sample size and species composition on the full dataset. Of the 56 species we captured (n = 1297 individuals), 35 species

Table 1. Bird species that had ≥10 captures across the study, with dietary guild assignment and sample size, caught in Maine during 2011–2024.

Species	Common name	Foraging guild	Sample size
Catharus guttatus (Pallas)	Hermit Thrush	Omnivore	273
Catharus ustulatus (Nuttall)	Swainson's Thrush	Frugivore	20
Certhia americana Bonaparte	Brown Creeper	Insectivore	16
Corthylio calendula (L.)	Ruby-crowned Kinglet	Insectivore	144
Dumetella carolinensis (L.)	Gray Catbird	Omnivore	45
Geothlypis trichas (L.)	Common Yellowthroat	Omnivore	60
Junco hyemalis (L.)	Dark-eyed Junco	Omnivore	24
Melospiza georgiana (Latham)	Swamp Sparrow	Omnivore	55
Mniotilta varia (L.)	Black-and-white Warbler	Insectivore	10
Sayornis phoebe (Latham)	Eastern Phoebe	Omnivore	21
Seiurus aurocapilla (L.)	Ovenbird	Insectivore	28
Setophaga coronata (L.)	Myrtle Warbler	Omnivore	34
Setophaga magnolia (Wilson)	Magnolia Warbler	Omnivore	13
Setophaga palmarum (Gmelin)	Palm Warbler	Omnivore	17
Setophaga ruticilla (L.)	American Redstart	Omnivore	18
Setophaga striata (Forster)	Blackpoll Warbler	Omnivore	171
Setophaga virens (Gmelin)	Black-throated Green Warbler	Omnivore	15
Sitta canadensis L.	Red-breasted Nuthatch	Omnivore	13
Vireo olivaceus (L.)	Red-eyed Vireo	Omnivore	86
Vireo solitarius (Wilson)	Blue-headed Vireo	Insectivore	23
Zonotrichia albicollis (Gmelin)	White-throated Sparrow	Frugivore	108

had <10 captures across the study. Due to this broad variation in sample size across species, our initial GLMM showed strong random effects of species on fat deposits ($P < 0.001$). To minimize species effects, we used the same models but limited our analysis to the 21 species that had ≥10 captures across the study because the GLMM no longer showed random effects of species (frugivores: 2 species and 128 captures; insectivores: 5 species and 221 captures; omnivores: 14 species and 845 captures; Table 1), where species no longer explained patterns in fat deposition. Nonetheless, we included species as a fixed effect in our models. We first tested if fat storage shifted over the 13-year study period in all birds (fat = year). Second, again with species as a fixed effect, we tested if fat storage changed across the study period within the 3 foraging guilds (fat = year + foraging guild + year * foraging guild).

Results

Fat deposits declined significantly across years ($n = 1194$, $t = -2.509$, $P = 0.012$). Neither foraging guild alone ($t = 1.72$, $P = 0.863$) or the year * guild interaction ($t = 1.48$, $P = 0.138$) explained trends in fat stores over the study. However, fat storage in insectivores and omnivores, but not frugivores, declined significantly between 2011 and 2024 (Table 2). Annually, fat storage declined by 43.8% and 17.6% in insectivores and omnivores, respectively (Fig. 1); Fat scores declined from 2.4 to 1.35 for insectivores and from 1.7 to 1.4 for omnivores.

Discussion

Our results show an alarming long-term decline in the autumn fat scores of migratory songbirds at a forested stopover site in coastal Maine (Fig. 1). Specifically, fat storage in insectivores and omnivores, but not frugivores, declined significantly over the 13-year study period. One explanation for the decreased levels of fat is that birds were increasingly unable to store fat due to a decline in food availability at or near our study site. Global insect populations have plummeted by 45% in the last 40 years (Dirzo et al. 2014). A meta-analysis of 1676 study sites around the world showed a 9% decrease in terrestrial insects per decade, with even higher declines in North America (van Klink et al. 2020). Habitat loss due to development, invasive plants, and non-native lumber, agriculture, lawn, and garden species are not only destructive to plant food sources, but a major source of declines in insect abundance.

Table 2. Output for GLMM model including year, foraging guild, and the year * foraging guild interaction terms, testing if fat storage changed over time for songbirds in 3 foraging guilds caught in coastal Maine during fall migration in 2011–2024 ($n = 1194$ individuals; frugivore: 2 species and 128 captures; insectivore: 5 species and 221 captures; omnivore: 14 species and 845 captures). The estimate represents the amount of change per year.

Guild	Estimate	SE	*t*	*P*.value
Frugivore	-0.083	0.065	-1.268	0.21
Insectivore	-0.322	0.047	-6.856	<0.001
Omnivore	-0.092	0.029	-3.155	0.002

While our results were clear, we do not know if there are fitness and population consequences to decreasing fat storage at our stopover site. Other studies have identified related population effects. For example, in Galapagos, invasive *Rubus niveus* Thunb. (Mysore Raspberry) in unmanaged areas led to a greater abundance of lower-quality insects, contributing to the decline of non-migratory *Certhidea olivacea* Gould (Green Warbler-Finch; Hood-Nowotny et al. 2023). Likewise, McKinnon et al. (2015) found a decrease in abundance of insects and fruit correlated with a decrease in abundance in migratory songbirds during their wintering period. Insectivores in our study exhibited the largest rate of decline over the study period. We suspect that this decline might reflect local insect declines; however, we did not simultaneously assess insect populations, and our study site remained relatively stable over the study period (e.g. no habitat loss, little change in the plant community). Therefore, the long-term decrease in fat storage that we observed may be an indication of decreased food availability, food quality, or increased competition at our study site. Stopover-specific decreases in food are especially concerning for species who need to accumulate fat to migrate because fat stores may predict how long a bird stays at a stopover location; songbirds with less fat are known to stay longer at stopover locations (Seewagen and Guglielmo 2009). However, there is some contrary evidence, as in Salewski and Schaub (2007), that birds who arrived at fall stopover sites with less fat did not necessarily stay longer at the stopover. The implications of changes in stopover ecology can profoundly affect other stages in the annual cycle. For example, carry-over effects from stopover sites can have stronger influence on breeding phenology than breeding climate (Finch et al. 2014).

Other studies both support and contradict our study results showing differences in fat storage trends among foraging guilds. At a site in southeastern South Dakota, insectivores were able to successfully refuel at both a riparian woodland and an anthropogenic woodlot (Liu et al. 2022). However, in other areas overtaken by invasive plants and other anthropogenic modifications, frugivores increasingly struggled to gain fat needed for migration (Campo-Celada et al. 2022). These 2

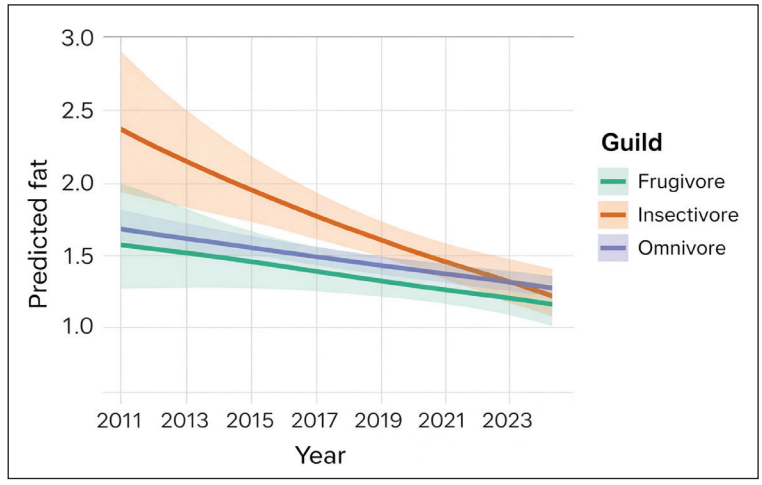


Figure. 1. Predicted fat stores from zero-inflated gamma general linear mixed models (GLMM) decreased significantly from 2011 to 2024 in omnivores and insectivores but not frugivores. The shaded areas represent 95% confidence bands.

contrasting studies could be a result of the macronutrient composition of insects vs. fruits—insects generally have more protein content, while many, but not all, fruits are rich in fat. Because of these differences, frugivores can potentially use their fat stores more efficiently during migration (Jenni-Eiermann and Jenni 2025).

Many species switch their diets to eat more fruit during fall migration (Parrish 2020); since frugivores have maintained fat levels at our study site, potential diet switching that affords the flexibility to eat more fruit may help mediate losses in fat storage. Birds select diets that have higher proportions of certain fatty acids that are beneficial for long periods of exercise (Alan et al. 2013, Pierce and McWilliams 2005). During fall migration, when these same resources are being consumed by more species of birds, there may be higher competition for already diminished food availability among insectivores and omnivores but not frugivores or species with elastic diets that can increase fruit consumption in fall.

Fat acquisition during fall migration is clearly a complex and nuanced phenomenon that is shifting in different guilds by varying degrees. Decreasing fat storage in migratory songbirds could be an ecological problem if birds rely on large accumulations to complete migration. Habitat loss can decrease food availability, leading to decreased annual survival (Campo-Celada et al. 2022, Hood-Nowotny et al. 2023, Martay et al. 2023, Wolfe et al. 2014). If fat acquisition continues to decrease, birds may increasingly fail to survive their long, strenuous migrations, or they may have to adapt their migration strategies entirely. High fat levels are especially important for birds while crossing barrier habitats; therefore, decreased fat levels may lead to birds taking slower routes with more stopovers rather than long, barrier-crossing flights over oceans and deserts (Bairlein and Gwinner 1994).

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