



THE INFLUENCE OF ENERGETIC CONDITION ON FLIGHT INITIATION AND ORIENTATION OF MIGRATORY SONGBIRDS IN THE GULF OF MAINE REGION

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ABSTRACT.—Energetic condition influences migratory decisions made by songbirds. Over-water or coastal flights are often the shortest routes but may be dangerous for landbirds because they may get caught over water where they are not able to rest and refuel. We investigated how various components of energetic condition were related to the likelihood that a migrant songbird in the Gulf of Maine region would initiate a migratory flight and the direction that it would choose. We used release tests and measurements of energy stores (fat score), plasma triglycerides, and within-day changes in body mass to investigate whether these measures of condition were related to the decisions migrants must make about when to resume migration and which direction they should go. Our results indicated that the amount of fat that a bird had at the time of release influenced the decision to initiate a flight, whereas directional decisions were influenced by both fat and within-day changes in body mass. Plasma triglyceride levels were higher in birds that initiated migratory flights; however, this does not appear to have influenced departure or directional decisions. These results indicate that migrant songbirds on stopover rely on cues about their energetic condition when making departure and orientation decisions and that the amount of fat a bird has may be the most relevant cue for these decisions. *Received 5 November 2009, accepted 28 January 2011.*

Key words: energetics, metabolism, migrant songbirds, migratory behavior, orientation behavior, songbird.

Influencia de la Condición Energética sobre la Iniciación del Vuelo y la Orientación de las Aves Canoras Migratorias en el Golfo de la Región de Maine

RESUMEN.—La condición energética afecta las decisiones que toman las aves canoras migratorias. Las rutas sobre el agua y a lo largo de las costas son usualmente las más cortas, pero pueden ser peligrosas para las aves terrestres pues pueden verse atrapadas sobre el agua donde no son capaces de descansar o reaprovisionarse. Investigamos cómo varios componentes de la condición energética estuvieron relacionados con la probabilidad de que un ave canora migratoria en la región del golfo de Maine pudiera iniciar un vuelo migratorio y la dirección que pudiera elegir. Empleamos evaluaciones de liberación y mediciones de almacenamiento de energía (puntajes de grasa), triglicéridos en el plasma y cambios a lo largo del día en el peso corporal para investigar si estas medidas de la condición estuvieron relacionadas con las decisiones que los migrantes deben hacer sobre cuándo reanudar la migración y en qué dirección ir. Nuestros resultados indicaron que la cantidad de grasa que un ave tuvo al momento de la liberación influyó en la decisión de iniciar el vuelo, mientras que las decisiones sobre la dirección estuvieron influenciadas tanto por la grasa como por los cambios sucedidos a lo largo del día en el peso corporal. Los niveles de triglicéridos en el plasma fueron mayores en las aves que iniciaron los vuelos migratorios; sin embargo, esto no parece haber influenciado la partida o las decisiones de dirección. Estos resultados indican que las aves canoras migratorias en los sitios de parada dependen de señales sobre su condición energética cuando realizan decisiones de partida o de orientación y que la cantidad de grasa que posee un ave puede ser la señal más relevante para tomar estas decisiones.

BIRDS INTEGRATE MULTIPLE environmental factors (e.g., weather, topography, day length, food availability, celestial and magnetic information) with internal cues such as endogenous clocks when making decisions about when and in which direction to initiate a migratory flight (Able 1991, 2000; Dierschke and Delingat 2001; Åkesson and Hedenström 2007; for review, see Berthold 1996). Migrants can integrate these factors with endogenous

physiological cues about energetic condition (energy reserves from fat and skeletal muscle protein, energy-regulating hormones, and plasma levels of lipid and protein metabolites) when making decisions about when and where to migrate (Egeler et al. 2000, Piersma et al. 2000, Löhmus et al. 2003, Lyons et al. 2008). Body mass and scores that indicate fat deposits or flight muscle condition are the available measures of energy reserves. Recent studies

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have found that, as indicators of energy regulation, blood metabolite levels (e.g., plasma triglycerides) and energy-regulating hormones (corticosterone) can provide more information about how an individual is currently using its energy reserves (Williams et al. 1999; Löhmus et al. 2003; Landys et al. 2004, 2005; Guglielmo et al. 2005; Lyons et al. 2008). Plasma triglyceride levels rise during feeding as dietary lipids are absorbed through the gut or are being synthesized *de novo* by the liver from a variety of substrates (Ramenofsky 1990). As a signal of active fat storage, levels of plasma triglycerides can indicate that an individual is experiencing a net gain of lipids, often resulting in an increase of body mass (Jenni-Eiermann and Jenni 1994).

The need for a bird to accurately assess its energetic state is especially important during migration. In an autumn study along the southern New England coast, Able (1977) showed that fatter birds were more likely to display oriented behavior than lean birds. Further, in the Gulf of Mexico region, Sandberg and Moore (1996) and Sandberg et al. (2002) demonstrated that lean Neotropical migrants in autumn oriented in directions that would take them farther inland or along the western Gulf coast, such that they avoided an over-water flight. By contrast, fat birds oriented in a southerly direction, which would take them across the Gulf of Mexico. Although it is clear from studies like these that measures of current energy reserves, such as mass and fat deposits, have important effects on migratory behavior, few studies have investigated how more energetically dynamic measures, such as plasma triglycerides, can influence migratory decisions in songbirds.

Many bird species migrate across the eastern United States to reach breeding grounds to the north in spring and wintering areas throughout the southeastern United States, the Caribbean, and Central and South America in autumn. Geographic and topographic features of the northeastern region provide natural flyways, including mountain ranges that run parallel to the Gulf of Maine coastline, which extend from the Bay of Fundy to Cape Cod, Massachusetts (see Baird and Nisbet 1960, Drury and Keith 1962, Murray 1966, Richardson 1978).

During fall migration, many songbirds have been observed migrating off the southern New England coastline at night, generally in a south or southwest direction (Drury and Keith 1962). Many landbirds appear to take a shortcut across the Gulf of Maine from New Brunswick or Nova Scotia (Davis 2001, Fitzgerald and Taylor 2008) to minimize total migration time (time minimizers or risk-prone; Alerstam and Lindström 1990), presumably with sufficient energy stores for meeting unexpected contingencies that might put them at risk during an extended over-water flight. By contrast, many migrants opt to go around large ecological barriers (bodies of water or deserts) in spite of the potentially longer and more time-consuming flight. Although the longer and indirect route may incur lower risk, it may require more extensive energy stores or more stopovers along the route (energy maximizers or risk-averse; Alerstam and Lindström 1990).

The topography along the northern coast of the Gulf of Maine provides an ideal setting to study intensively the basis of the decisions made by migrating songbirds en route (see Fig. 1). The coastline runs in a northeast–southwest line, whereas the majority of peninsulas, often separated by extensive inlets and bays, follow a north–south orientation. Because the topography of our study site, Schoodic Peninsula, is such that crossing open water is inevitable

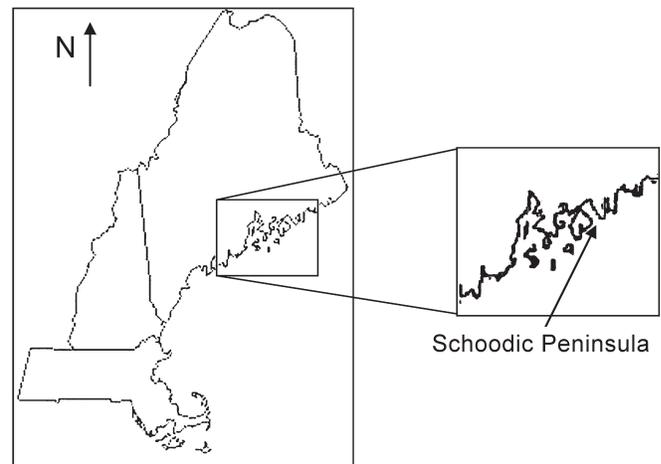


FIG. 1. Map of the Gulf of Maine region, indicating the study site, Schoodic Peninsula ($44^{\circ}20'N$, $68^{\circ}03'W$; elevation 19 m) in Acadia National Park, Hancock County, Maine.

unless flights are oriented strongly toward the north, it is an ideal site from which to examine differences in migratory behavior in relation to variation in energetic condition. Birds at Schoodic Peninsula that have sufficient energy reserves to minimize migration distance, and to incur the risk of doing so, must be prepared to undertake flights near or across open water, and they are expected to follow the coastline during autumn migration (e.g., southwest heading). However, migrants with low energy reserves at Schoodic may try to minimize the risks over or near open water and would be expected to either remain on stopover until sufficient reserves have been gained or to fly in a more northerly direction to get farther inland. In the present study, we specifically predicted that birds that were in better condition or experiencing net energy gain (greater fat, body mass, plasma triglyceride levels) would be more likely to initiate migratory flights after their release and to orient in a seasonally appropriate direction that would minimize migration time and distance. Conversely, we predicted that birds in poorer condition would be less likely to initiate flights upon release but, should they do so, would fly in a direction that would take them farther inland so as to avoid an over-water flight.

METHODS

We conducted this study at Schoodic Peninsula ($44^{\circ}20'N$, $68^{\circ}03'W$; elevation 19 m) in Acadia National Park, Hancock County, Maine (Fig. 1), during the autumn migration period from mid-August until late October, 2006 and 2007. We captured birds, weather permitting, from sunrise until early afternoon using 5 to 10 mist nets (12×2.6 m and 6×2.6 m, 30-mm mesh) that were checked every 20 min. After capture, birds were banded and measured for wing chord, tarsus and tail lengths (all to nearest 0.1 mm), and body mass (to nearest 0.5 g). We also assigned a furcular fat score as follows: 0 = no fat visible; 0.5 = trace of fat; 1 = fat lining but not filling the furcular region; 2 = fat filling the furcular region but not mounded; 3 = fat filling the furcular region and mounded; and 4 = fat heavily mounded and spilling out of the furcular region (Helms and Drury 1960, Cherry 1982).

Bird handling and sampling.—After banding and measuring each bird, we placed it in an individual cage (30 × 30 × 30 cm) and provided ad libitum access to water and food (mealworms [*Tenebrio* spp. larvae] for warblers, vireos, and thrushes; mealworms and seed for sparrows). We kept the cages indoors in a separate room that was not disturbed by human activity and that maintained natural photoperiod through windows and artificial lighting. Only birds that appeared to have adjusted to captivity as indicated by their use of perches and signs of food ingestion were kept and used in release tests. Approximately 1–2 h prior to the evening release tests (see below), we removed each bird from its cage and took final measurements of mass and fat score. We also obtained a small blood sample (no more than 80 µL) by puncturing the brachial vein with a 26-gauge needle and collecting the blood directly into an 80-µL heparinized capillary tube. We kept blood samples on ice until they were centrifuged 2 to 3 h later at 6,000 rpm for 10 min. Plasma was then collected with a 50-µL Hamilton syringe and kept frozen (–5°C) in microcentrifuge tubes until analyzed. We measured plasma triglyceride levels with a colorimetric enzymatic endpoint assay (GPO-Trinder, kit 337; B Sigma-Aldrich, St. Louis, Missouri) modified for 5-µL sample volume, run in duplicate, in a 96-well plate read on a SpectraCount reader (Packard, Palo Alto, California).

Release tests.—After blood samples were obtained, we followed methods described by Able and Terrill (1987) and Sandberg and Moore (1996) to glue (3M Super Strength Adhesive) a small gelatin capsule (Electron Microscopy Sciences, Hatfield, Pennsylvania; dimensions = 5.0 × 1.5 mm, mass of filled capsule and glue ≈ 0.2 g) containing chemiluminescent liquid from commercial light sticks (Northern Products, Leominster, Massachusetts) to the birds' upper tail coverts so that we could determine flight direction upon release of the bird. We placed the birds in individual cloth bags and transferred them ~150 m to the release site (the maximum time in a bag for each bird was 30 min). The release site was a nearby sports field, ~100 m in diameter, with a surrounding tree line ~30 m tall.

Following Able and Terrill (1987) and Sandberg and Moore (1996), we conducted release tests to investigate departure and orientation decisions of migrants approximately 45 to 75 min after local civil twilight. We tested birds on as many nights as possible, excluding nights with >75% cloud cover, precipitation, or high winds. We released each bird (individually) without biasing its flight direction by holding it in an open palm directly over the release person's head until the bird left their hand. The releaser also rotated the direction they were facing (and thus the potential direction each bird was facing) 90° between each bird's release. Each bird was observed with 8 × 42 binoculars after it left the releaser's hands. If the bird flew higher than, and remained above, the tree line for at least 45–60 s (~600 m away), we considered it to have initiated a migratory flight. We also recorded the direction in which the bird was last visible, to the nearest whole degree in relation to geographic north using a digital compass. If a bird landed in a tree or did not fly high enough to clear the tree line, thus making it difficult to rule out landing, we recorded it as not initiating a migratory flight. We used songbird species considered to be nocturnal migrants and only those individuals robust enough to yield blood samples and that had adapted to the short period in captivity (see Table 1).

TABLE 1. Species composition of birds tested during fall migration of 2006 and 2007 at Schoodic Peninsula, Maine.

Species	2006	2007	Total
Blue-headed Vireo (<i>Vireo solitarius</i>)	1	5	6
Red-eyed Vireo (<i>V. olivaceus</i>)	3	15	18
Veery (<i>Catharus fuscescens</i>)	2	0	2
Swainson's Thrush (<i>C. ustulatus</i>)	3	4	7
Hermit Thrush (<i>C. guttatus</i>)	14	7	21
Magnolia Warbler (<i>Dendroica magnolia</i>)	2	2	4
Black-throated Blue Warbler (<i>D. caerulescens</i>)	0	2	2
Yellow-rumped Warbler (<i>D. coronata coronata</i>)	2	3	5
Black-throated Green Warbler (<i>D. virens</i>)	2	3	5
Yellow Palm Warbler (<i>D. palmarum hypochrysea</i>)	2	5	7
Blackpoll Warbler (<i>D. striata</i>)	2	1	3
Black-and-white Warbler (<i>Mniotilta varia</i>)	3	3	6
American Redstart (<i>Setophaga ruticilla</i>)	1	0	1
Ovenbird (<i>Seiurus aurocapilla</i>)	2	1	3
Northern Waterthrush (<i>Parkesia noveboracensis</i>)	0	9	9
Chipping Sparrow (<i>Spizella passerina</i>)	0	2	2
Song Sparrow (<i>Melospiza melodia</i>)	4	4	8
Lincoln's Sparrow (<i>M. lincolni</i>)	0	1	1
Swamp Sparrow (<i>M. georgiana</i>)	1	4	5
White-throated Sparrow (<i>Zonotrichia albicollis</i>)	8	30	38
Totals	52	101	153

Statistical analyses.—For some analyses, birds were grouped on the basis of their fat score at the time of testing; “lean” birds had a fat score of 0 or 0.5, whereas “non-lean” birds had a fat score ≥1. Percent mass change for each individual was calculated as the difference between final and initial mass divided by initial mass and time to the nearest number of hours spent in captivity (i.e., [final mass – initial mass]/initial mass/number of hours). Individuals whose mass change was within the measurement error of the scale were excluded from use in further analyses of percent mass change. Plasma triglyceride levels, as indicators of energetic trajectory through lipid use, were also included in analyses for all individuals.

We used nonparametric statistics because the data were not distributed normally and standard transformations did not correct the distribution sufficiently. To compare the proportion of birds that initiated a migratory flight by fat grouping, we used Pearson's chi-square test. We used the asymptotic Wilcoxon ranked-sum test to look for differences in the percent mass changes and in plasma triglyceride levels between birds that did or did not initiate flight. The asymptotic Wilcoxon ranked-sum test was also used as a paired test when analyzing the relationship between plasma triglyceride level and mass change. We used stepwise logistic regression with backwards elimination to investigate whether our three condition variables had independent effects on flight initiation.

Mean directions and resultant vector lengths (a measure of variance around the mean and how well the mean represents the

directions of sample group overall) were calculated to determine whether the mean direction of each sample group differed significantly from the uniform alternative (null hypothesis) using the Rayleigh test of uniformity (Batschelet 1981, Jammalamadaka and SenGupta 2001). Watson's U^2 test for circular data (Mardia 1972, Batschelet 1981, Jammalamadaka and SenGupta 2001) was used to compare the direction between our two study years as well as between fat categories. Spherically projected linear models (Presnell et al. 1998) were used to model the dependence of direction on fat score, percent mass change, and plasma triglycerides (for a similar application, see Marchetti and Scapini 2003). The marginal effect of each variable on direction was calculated by subtracting the -2 log likelihood value of the model including just the variable from the null model (constant only). The adjusted effect of each variable on direction was calculated by subtracting the -2 log likelihood value of the full model including all three condition variables against the model with the variable excluded. Thus, for example, to evaluate how within-day changes in body mass influenced direction, we compared the full model with the model including fat and plasma triglycerides. This measured the effect of a variable above and beyond that of the others. The likelihood ratio test was then based on the difference in twice the log likelihoods of the two chosen models, and the associated significance or P value was calculated using its chi-squared distribution with degrees of freedom equal to the difference in degrees of freedom of the two models that were compared. We evaluated the effect of fat score on orientation direction using both Watson's U^2 test and the spherically projected linear models. We felt that although the latter provides a more widely applicable analysis of these types of data, the comparison of the fat categories in the Watson's U^2 test is more relevant for researchers in a field setting. All analyses were run using R, version 2.10.1 (R Foundation for Statistical Computing, Vienna).

RESULTS

We tested a total of 153 migratory songbirds comprising 20 species (52 individuals in 2006, 101 individuals in 2007; Table 1) during the two fall migration periods. Time in captivity (capture to release) averaged 9.5 h (years pooled). There were no year effects for comparisons of fat score, percent change in body mass per hour, and plasma triglyceride values ($P > 0.05$ for all variables). Twelve birds were recaptured within 1–7 days after release; all of these had been recorded as not initiating flight, thus supporting our criterion for categorizing departure decisions. Four of these birds were recaptured the morning after they were used in release tests, and none of them had the glow capsule still attached, which suggests that the time that the capsule remained on the birds was <12 h.

Flight initiation.—Although 39% of the 62 lean birds initiated migratory flight, nearly twice as many (73%) of the 91 non-lean birds did so ($\chi^2 = 18.84$, $df = 1$, $P < 0.0001$). Additionally, birds that initiated migratory flight ($n = 90$) were more likely to have gained mass during the captive period, whereas birds that did not initiate flight ($n = 63$) usually lost mass. This difference in the change of body mass between groups was significant ($W = 4574$, $P < 0.0001$; Fig. 2A; note that statistical analyses were done using percent mass change corrected for time in captivity, but overall percent mass change is illustrated in Fig. 2A). Plasma triglyceride levels were also greater in birds that initiated migratory flight than in birds that did not ($W = 566$, $P < 0.001$; Fig. 2B). Further, there was a significant positive relationship between plasma triglyceride levels and percent mass change per hour ($W = 9316$, $P < 0.0001$; Fig. 3; note that statistical analyses were done using percent mass change corrected for time in captivity, but overall percent mass change is illustrated in Fig. 3). The stepwise logistic regression

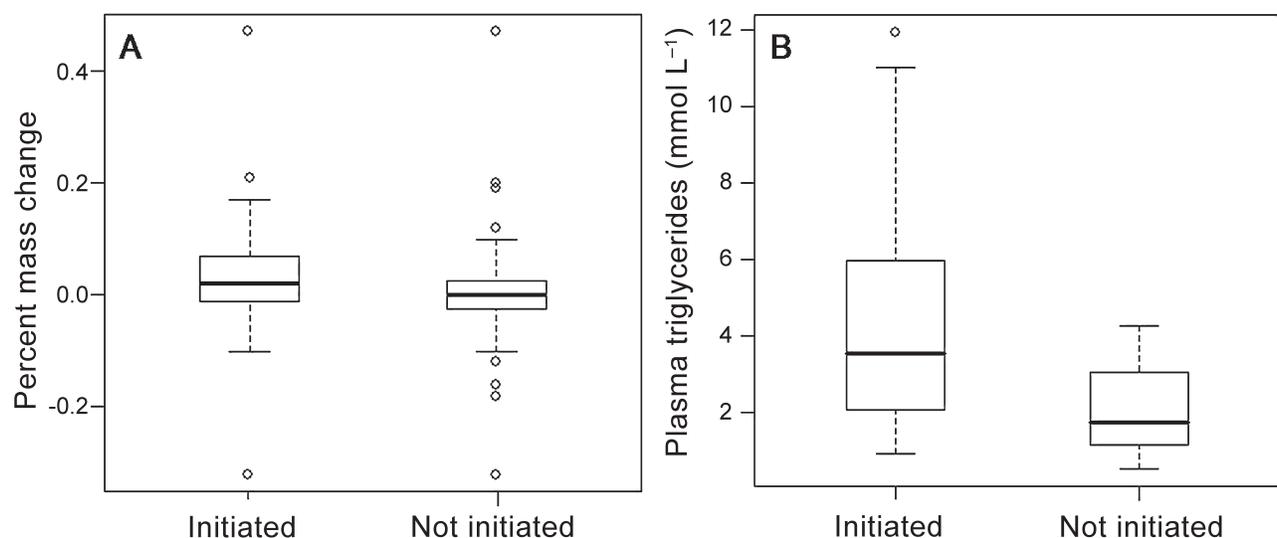


FIG. 2. Box-plot showing (A) percent mass change and (B) plasma triglyceride levels in relation to flight initiation during fall migration, 2006 and 2007, at Schoodic Peninsula, Maine. The bold solid line represents median values. Also shown are outliers (small circles), the upper and lower quartiles (boxed areas), and the range ("whiskers"). Birds that initiated a migratory flight ($n = 90$) exhibited higher increases in body mass ($P < 0.0001$) and higher levels of plasma triglycerides ($P < 0.001$) than birds that did not initiate flight ($n = 63$). Note that percent mass change per hour was used in analyses, whereas percent mass change is presented here.

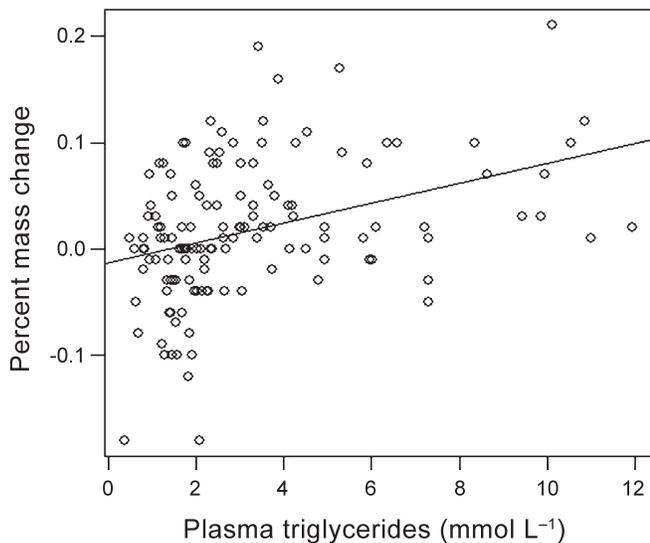


FIG. 3. Percent mass change in relation to plasma triglyceride levels for migrant passerines at Schoodic Peninsula, Maine, in 2006 and 2007. As plasma triglyceride levels increased, percent mass change (corrected for time in captivity) also increased ($n = 153$, $P < 0.001$). Note that percent mass change per hour was used in analyses, whereas percent mass change is presented here.

resulted in a final model that included both fat score and triglycerides ($Z = 3.7$, $P < 0.001$); however, fat score was the only individual variable that had a significant effect on initiation using these models ($Z = 4.2$, $P < 0.001$). To investigate whether plasma triglycerides

significantly strengthened the model once fat score had been taken into account, we compared the model that included only fat score with the model that contained both fat score and plasma triglycerides. The fact that there was no significant difference between the two models ($P > 0.10$) indicated that the final model maintained significance because the effect of fat score on flight initiation was so strong.

Orientation.—The mean direction of flight in 2006 (294°) did not differ from that in 2007 (279° ; Watson's U^2 , $P > 0.10$), and the mean direction of flight for the pooled data was 284° ($r = 0.64$, $P < 0.001$, $n = 86$). Lean birds oriented toward the north–northwest (326° , $r = 0.80$, $P < 0.001$, $n = 24$), whereas non-lean birds significantly shifted orientation to the west–southwest (255° , $r = 0.77$, $P < 0.001$, $n = 62$; Watson's U^2 , $P < 0.001$; Fig. 4).

After fitting the spherically projected linear models using a backward selection strategy, the marginal and adjusted effects of both fat and percent mass change per hour on orientation direction were significant ($P < 0.01$; Table 2), but plasma triglyceride levels were not ($P > 0.10$). The model that best fit the data incorporated both fat and percent mass change per hour; we could not reduce it further because of the significant differences between models fat + percent mass change and fat (likelihood ratio test 13.4, $df = 2$) and between models fat + percent mass change and percent mass change (likelihood ratio test 12.14, $df = 2$).

We then looked at how the fitted direction of those models changed with different values of percent mass change per hour. We found that if the value of percent mass change per hour was increased (i.e., birds showed a more rapid mass gain), the predicted direction shifted more to the south. Conversely, if the value of percent mass change per hour was decreased, the direction shifted more to the north.

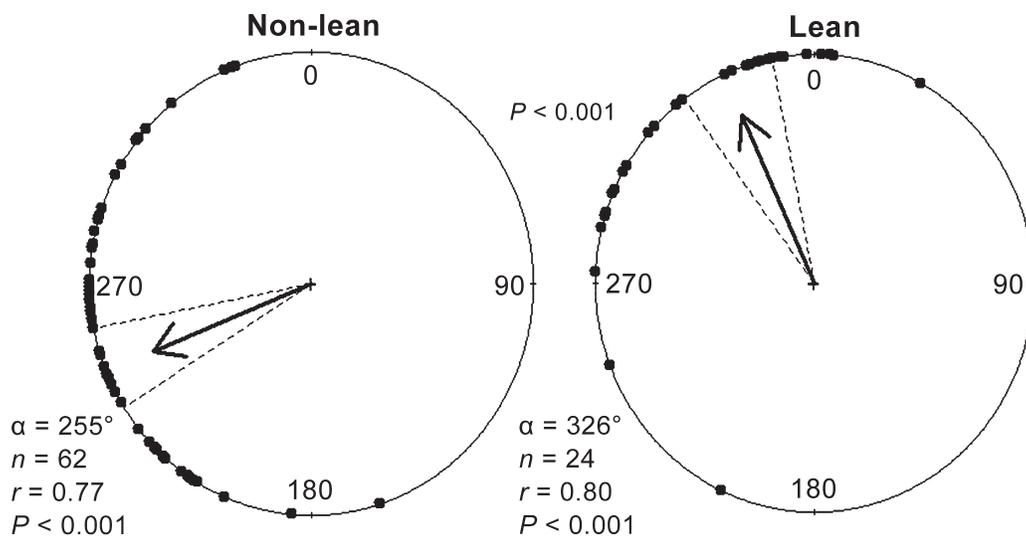


FIG. 4. Chosen directions (solid dots, in relation to geographic north) of songbirds that initiated a migratory flight after being released at Schoodic Peninsula, Maine, during fall migration of 2006 and 2007. Birds were grouped by the amount of fat they had at the time of testing. The mean direction (α) is represented by the solid arrow (mean resultant vector), which is of length r , as calculated using the Rayleigh test, and is proportional to the strength in which the mean represents the sample (Batchelet 1981). Broken lines represent bootstrapped 95% confidence intervals for the mean. Also shown are sample size (n) and the P value obtained from the Rayleigh test. P value between the two plots indicates the result from Watson's U^2 test for two groups of circular data.

TABLE 2. Results of spherically projected models used to investigate the effects of energetic condition on orientation of migrating passerines at Schoodic Peninsula, Maine, in 2006 and 2007. Degrees of freedom and $-2 \log$ likelihood values are given for each model that was fitted and used in testing variable effects. Both marginal and adjusted effects of fat score, percent mass change per hour, and plasma triglycerides were calculated. The influences of fat and of percent mass change per hour on orientation direction were significant. Plasma triglycerides did not have a significant effect on orientation.

Model	$-2 \log$ likelihood		
Null model	235.13		
Fat	221.96		
Percent mass change per hour	220.70		
Plasma triglycerides	231.47		
Fat + percent mass change per hour	209.56		
Percent mass change per hour + plasma triglycerides	219.58		
Fat + plasma triglycerides	218.15		
Fat + percent mass change per hour + plasma triglycerides	208.63		
Effects	$\Delta -2 \log$ likelihood ^a	df	<i>P</i> value
Marginal effects			
Fat	13.17	2	0.001
Percent mass change per hour	14.43	2	<0.001
Plasma triglycerides	3.66	2	0.16
Adjusted effects			
Fat	10.97	2	0.004
Percent mass change per hour	9.52	2	0.009
Plasma triglycerides	0.93	2	0.63

^a $\Delta -2 \log$ likelihood values were calculated for marginal effects by subtracting the $-2 \log$ likelihood value of the model including just the variable from the null model. This was done for the adjusted effects by subtracting the $-2 \log$ likelihood value of the full model including all three condition variables from the model with the variable excluded.

DISCUSSION

The results of our study illustrate that a bird's energy reserves can influence not only the decision to initiate a migratory flight, but also the direction of that flight. Our results for migrants negotiating ecological barriers are congruent with the results of previous studies (Sandberg et al. 1991, 2002; Åkesson et al. 1996; Sandberg and Moore 1996; Deutschlander and Muheim 2009; Fusani et al. 2009) and further illustrate that songbirds on migration adjust their behavior on the basis of their en route energetic condition.

In general, actively refueling birds (elevated triglycerides, positive mass change) that were also in better condition (higher fat scores) at the time of testing were more likely to initiate a migratory flight than birds that had few (if any) fat reserves and showed no evidence of being in the process of refueling. Among these variables, however, fat score was the strongest predictor of an individual's decision to initiate a migratory flight. The statistical relationship between flight initiation and fat score was so strong that it may have driven those seen between flight initiation and plasma triglycerides and between flight initiation and percent mass change. Birds with higher fat scores tended to orient toward the west-southwest, whereas those with lower fat scores oriented in a northerly direction. The mechanism by which fat tissue can provide information to the brain regions where migratory decisions are made is unknown, but both corticosterone and leptin have been implicated as "readiness cues" that may provide information

about peripheral energy stores (Boswell et al. 1995, Piersma et al. 2000, Holberton and Dufty 2004, Kochan et al. 2006, Sharp et al. 2008). Collectively, it appears that existing fat reserves play the ultimate role in decisions of whether to migrate and also of whether to fly around or go across an ecological barrier.

In the present study, we also found that birds were more likely to take a more direct route (orient in a more southerly direction), even if it took them out over water, if they had shown a faster rate of mass gain (greater percent mass change per hour). Orientation direction was influenced by within-day mass change, but this decision did not appear to be influenced by plasma triglycerides. Although the use of plasma triglycerides as a cue may be secondary to those from fat, the majority of birds that initiated flight in this study also had elevated triglycerides ($>2 \text{ mmol L}^{-1}$), which suggests that this metabolite may also provide important information on when to resume migration during stopover. Furthermore, higher plasma triglyceride levels were associated with greater within-day changes in body mass, a pattern also found by Williams et al. (1999) for shorebirds on stopover. To fully understand the relationship between levels of circulating triglycerides and migratory behavior, it would have been ideal to have had a wider range of triglyceride values than we observed. However, all of the birds that we used had the same opportunity to feed ad libitum on the day of measurement and, thus, all birds were essentially exposed to a good stopover site. Therefore, our study did not mimic the wide range of situations that a bird might encounter on a daily basis during migration, and for this reason we cannot rule

out the possibility that triglycerides may play a role in modifying migratory decisions.

Although migrants can catabolize muscle protein as an energy source (Jenni et al. 2000, Lindström et al. 2000), fat is considered the primary source of fuel for migratory flights (Berthold 1996). The duration and distance of individual flights are therefore functions of the amount of fat an individual carries. Using the Yellow Warbler (*Dendroica petechia*) as a model, Roberts et al. (2005) calculated that lean birds with, at most, only a trace of fat had an estimated maximum flight distance of ~150 km (0 km for no fat and a range of 146–165 km for trace fat). They estimated the maximum flight distance for birds with greater amounts of fat (at minimum, covering the bottom of the furculum; categorized as “non-lean” in this study) to be at least ~300 km (range = 292 km to > 900 km). Using these estimates, non-lean (fat score ≥ 1) songbirds departing from Schoodic Peninsula would be able to fly ≥ 300 km, enabling them to reach southern New England in a single flight, a destination that is consistent with their departure direction. Given the westerly departure direction of lean birds (zero or trace of fat), at maximum they would be able to fly 150 km toward inland Maine. This behavior would take them away from the coast, which would decrease the risks associated with coastal flights during which they may get caught over water without enough fuel to make it back to land.

To ensure survival, migratory landbirds must consider energetic condition when negotiating topographic features, especially ecological barriers like the Gulf of Maine. Additionally, decisions made by migrants will ultimately affect stopover length and total migration time, and thus will affect the timing of arrival and potential competitive ability (for territories or food) on the wintering grounds. Because the majority of annual mortalities of migrant songbirds occur during migration (Sillert and Holmes 2002, Newton 2006), understanding the relationship between energetic condition and decisions made by migrating birds is crucial for conservation of stopover areas.

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