


Effects of habitat, season, and age on winter fat storage by migrant and resident birds in Jamaica

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ABSTRACT. Most small birds wintering in the tropics should show little subcutaneous fat deposition (SFD), except in habitats where food availability may decline in late winter or, for some resident species, to prepare for incubation or brooding fasts. However, these predictions need re-examination in light of a new, precise, cross-validated method to compare SFD among habitats and species. We sampled 170 Nearctic–Neotropical migrant and 279 resident birds during early and late winter in 1993 and 1994 in Jamaica, West Indies. Habitats, from greatest to least expected availability of insect prey, were (1) mangrove forest, (2) montane/foothills forest and cultivation, (3) dry limestone forest, and (4) acacia scrub. Percent lipid, estimated from multiple-regression models using visual fat scoring (0–8 scale), total-body electrical conductivity, and a variety of morphometrics, was categorized by percentile ranks to determine if SFD varied by habitat, season, or age for all species, resident species, migrant species, and several individual species. SFD averaged ~13% total mass for all birds, ranging from 8–24% for well-sampled species. The few bird species in acacia scrub, primarily two facultative long-distance migrants, averaged ~26% lipid content, significantly more than birds in other habitats. Most birds did not vary in SFD in the other three habitats, although Common Yellowthroats (*Geothlypis trichas*) had greater SFD in dry limestone habitat than in montane habitat. Bananaquits (*Coereba flaveola*) and Jamaican Euphonias (*Euphonia jamaica*) in montane habitat, especially in early winter, had higher SFD than other resident species. Contrary to our prediction, adults and juveniles had similar SFD, with the exception of juveniles having more SFD than adults in acacia scrub habitat. Winter fat deposition (or, in some cases, muscle-protein catabolism) in the tropics may be an overlooked strategy, potentially important as a hedge against fasting for floaters, facultative migrants, some territorial migrants in habitats with seasonal declines in food resources, and some resident species prior to breeding.

RESUMEN. Efectos del hábitat, la estación y la edad en el almacenamiento de grasa en invierno por aves migratorias y residentes en Jamaica

La mayoría de las aves pequeñas que pasan el invierno en los trópicos deben mostrar poca deposición de grasa subcutánea (SFD), excepto en los hábitats donde la disponibilidad de alimentos puede disminuir al fin del invierno, o para algunas especies residentes que prepararan para los ayunos durante la incubación. Sin embargo, estas predicciones requieren un nuevo examen a la luz de un método nuevo, preciso y con validación cruzada para comparar el SFD entre hábitats y especies. Tomamos muestras de 170 aves migratorias Neotropicales y 279 aves residentes durante el invierno temprano y tardío en 1993 y 1994 en Jamaica, Indias Occidentales. Los hábitats, de mayor a menor disponibilidad de presas de insectos, fueron (1) bosque de manglar, (2) bosque montano / laderas y campos de cultivo, (3) bosque seco de piedra caliza y (4) matorrales de acacia. El porcentaje de lípidos, estimado a partir de modelos de regresión múltiple que utilizan la puntuación visual de la grasa (escala 0–8), la conductividad eléctrica total del cuerpo y una variedad de morfometría, se clasificó por rangos percentiles para determinar si el SFD varió según el hábitat, la estación o la edad de todas las especies, especies residentes, especies migratorias y varias especies individuales. El SFD promedio fue ~13% de la masa total para todas las aves, con un rango de 8 a 24% para las especies bien muestreadas. Las pocas especies de aves en matorrales de acacia, principalmente dos migrantes facultativos de larga distancia, promediaron un contenido de lípidos de aproximadamente 26%, significativamente más que las aves en otros hábitats. La mayoría de las aves no variaron en SFD en los otros tres hábitats, aunque Mascaritas comunes (*Geothlypis trichas*) tuvieron mayor SFD en el hábitat seco de piedra caliza que en el hábitat montano. Las Reinita-mieleras (*Coereba flaveola*) y las *Euphonia jamaica* en hábitat montano, especialmente al principio del invierno, tuvieron mayor SFD que otras especies residentes. Contrariamente a nuestra predicción, los adultos y los juveniles tenían SFD similar, con la excepción de los juveniles que tienen más SFD que los adultos en el hábitat de matorral de acacia. La deposición de grasa en el invierno (o, en

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algunos casos, el catabolismo de proteínas musculares) en los trópicos puede ser una estrategia pasada por alto, potencialmente importante como una cobertura contra el ayuno para flotadores, migrantes facultativos, algunos migrantes territoriales en hábitats con disminuciones estacionales en los recursos alimenticios, y algunas especies residentes antes de la reproducción.

Key words: energy stores, fasting, Neotropical migrant, winter ecology, total-body electrical conductivity (TOBEC)

Many species of Neotropical migrant warblers (Parulidae) winter in tropical habitats in the West Indies, seasonally augmenting communities occupied by year-round residents. These habitats vary in quality for migrant warblers, most of which are insectivores, due to differences in population densities and availability of arthropod prey (Sherry and Holmes 1996, Johnson et al. 2006, Marra et al. 2015, Sherry et al. 2016a).

To survive over winter in non-breeding habitats, birds must maintain energy reserves sufficient for foraging, self-maintenance, and preparation for timely migration (Blem 1990, Marra et al. 2015). Fat reserves are generally considered the most important energy stores for birds, providing twice the metabolic energy yield as carbohydrates (Hochachka 1973). Therefore, variation in fat deposition among birds in different habitats could provide a measure of habitat quality (Johnson 2007). However, this possibility is complicated by the various costs and benefits of stored fat. Subcutaneous fat deposition (SFD) represents energy that can be used later, provides thermoregulatory insulation (important in some habitats; Rogers and Smith 1993), and is a source of metabolic water that may be important in arid regions (Rutkowska et al. 2016) or during dry periods (Katti and Price 1999). However, SFD may also increase predation risk by reducing maneuverability (Gosler et al. 1995) and may be accomplished by a reduction in protein reserves (Katti and Price 1999). Consequently, models of how migrant birds wintering in the Neotropics adaptively regulate body mass and fat in response to food-limitation and predation risk offer conflicting predictions concerning the mass components (fat vs. lean mass) most responsive to changes in food availability and other components of habitat quality (Rogers 2005, Cooper et al. 2015).

Although SFD is normally associated with birds wintering in cold climates, as fuel for impending long-distance migration or for impending periods of high-energy demand

like reproduction or molt, wintering birds in suboptimal habitats, even in the tropics, may store fat as a hedge against periods of fasting or water shortage. This should be particularly true for migrants overwintering in habitats already occupied by residents and for surplus migrant individuals that must seek resources in less optimal habitats where food availability may periodically be inadequate (Blem 1990). Significant amounts of SFD in birds wintering in the tropics (at least prior to the spring pre-migratory period) can indicate a lower-quality habitat (Cooper et al. 2015) and, possibly, socially subordinate individuals that might use these habitats (e.g., females and first-winter males; Studds and Marra 2005). Birds in the lowest-quality habitats may be the only migratory individuals wintering in the tropics with elevated SFD (Lindström and Piersma 1993, Rogers 2005). This may apply primarily to facultative long-distance migrants, such as Palm Warblers (*Setophaga palmarum*) and Yellow-rumped Warblers (*Setophaga coronata*), that arrive in the Greater Antilles later in the fall than obligate migrants (Dunn and Garrett 1997) and, in many years, not at all (eBird 2018).

Higher-quality habitats characterized by consistently high food availability may reduce the need for winter-long SFD and thus are expected to be saturated with resident and obligate long-distance migrant species, especially more socially dominant adults. In Jamaica, these may include mangrove forests (Sherry et al. 2016a) and montane or foothill forests, particularly where the latter occur within a mosaic of gardens, orchards, and coffee plantations (Sherry et al. 2016b) because these habitats maintain relatively high levels of arthropod abundance throughout winter, especially compared to dry limestone and scrub habitats where arthropod availability declines to a greater degree during the late-winter dry season (Johnson and Sherry 2001, Studds and Marra 2005, Cooper et al. 2015).

For resident birds in the Neotropics during winter, fat storage may be differently constrained

because many of these species have extended breeding seasons and some may breed year-round, e.g., Bananaquits (*Coereba flaveola*) and Jamaican Euphonias (*Euphonia jamaica*). SFD, if it occurs, may signal preparation for incubation or brooding fasts (Milenkaya et al. 2013) and may be particularly pronounced in high-quality habitat with plentiful resources. For resident birds not breeding in the Neotropics in winter (i.e., when Nearctic-breeding migrants are still present), we would expect minimal SFD, although some elevational migrants may store fat to guard against unpredictable food supplies or weather (Lima 1986, Rogers 2005).

Although we hypothesize that habitat quality is negatively correlated with SFD for wintering birds, the distribution of individuals among these habitats could also help explain why habitat quality may correlate with fat storage. Age class affects the distribution of bird species in some habitats. Holmes et al. (1996) reported that more experienced and socially dominant older birds generally preempted first-winter birds from high-quality habitats. Birds in lower-quality habitats with unpredictable food availability may store more fat as a hedge against fasting (Lima 1986), although late-winter (dry season) food reduction has been shown to reduce SFD in migrants wintering in Jamaican mangrove habitat (Brown and Sherry 2006) and other Caribbean forests (McKinnon et al. 2015). Assessing these SFD predictions for environmental and demographic variables requires precise estimates of actual body fat content in wintering birds. We used a multivariate technique, cross-validated with actual laboratory lipid extractions, that provides accurate and precise estimates of percent lipid in small birds (Bergstrom and Sherry 2008).

Our objective was to examine the possible effects of habitat quality, age, residency status, and season (early winter vs. late winter) on fat stores of birds wintering in Jamaica, West Indies. We hypothesized that resident species, with the opportunity to secure optimal habitats through year-round territory defense, would have minimal SFD (except possibly for winter-nesting species) and serve as a null comparison for non-breeding Neotropical migrants wintering in the West Indies. We also hypothesized that, for Nearctic-breeding warblers wintering in Jamaica, greater SFD

would be associated with lower-quality habitat and socially subordinate status (i.e., age) and we tested two predictions: (1) birds in habitats with more reliable winter food supplies would have lower SFD, and (2) first-winter birds would have more SFD than older birds regardless of habitat.

METHODS

Study sites. Four habitats in Jamaica, West Indies, that vary in quality for overwintering songbirds, particularly migrant insectivores, are (1) mangrove forest, (2) montane and foothills forests and cultivated areas, (3) dry limestone forest and scrub, and (4) acacia (*Acacia villosa*) scrub (hereafter, mangrove, mixed montane, dry limestone, and scrub, respectively; Downer and Sutton 1990). Mangrove and dry limestone (three sites at 0–10 m and two sites at 40–130 m elevation, respectively) were largely undisturbed habitats, whereas the three higher-elevation (650–1100 m) sites we sampled in mixed montane habitat (Appendices S1 and S2) were a mosaic of intact montane and foothills forest and cultivated landscapes in the form of agriculture (e.g., coffee farms), orchards, and gardens (Johnson et al. 2006). Our site for scrub (Vernam Fields, elevation 110 m) was an abandoned airfield in Clarendon Parish. Based on relative abundance and reliability of arthropod resources (direct indicators) and a variety of demographic data (indirect indicators), mangrove is considered one of the highest-quality wintering habitats for many migratory warblers (Studds and Marra 2005, Johnson et al. 2006, Sherry et al. 2016a), providing an adequate supply of insects for migrant and resident species (Cooper et al. 2015). Mangrove tends to have more consistent arthropod abundance throughout the winter, possibly due to the buffering effect of regular tidal inundation on declining precipitation (Lefebvre and Poulin 1996). However, mixed montane habitat may provide similarly consistent winter abundance of insect prey attracted to the crops that grow there (Johnson and Sherry 2001, Kellerman et al. 2008, Sherry et al. 2016a), as well as food for fruit- and nectar-consuming birds (most of which also consume insects; see Table 2). Dry limestone and scrub are considered lower-quality habitats than mangrove for

wintering migrants because arthropod abundance decreases during the winter dry season to a greater degree than in mangrove (February–March; Sherry and Holmes 1996, Johnson et al. 2006).

Field methods. Birds were captured with mist-nets, weighed (± 0.1 g), measured, and marked with bands at various locations in mixed montane, dry limestone, and scrub habitats (Appendix S1) in Jamaica during two different time intervals (28 December 1993 to 3 January 1994 = early winter, and 23 March to 5 April 1994 = late winter; Tables 1 and 2). Mangrove forest was sampled only during late winter. Each site was sampled for a period ranging from one to two-and-a-half days consecutively (per season) using 10–12 12-m mist-nets per period per site. This design was intended to minimize recaptures during any one sampling period while providing a representative sample of birds present (sampling was extended beyond 1 day at sites with greater abundance, i.e., higher capture rates). Morphometric measurements included bill length, bill depth, bill width, head length, wing chord, tarsus length, and tail length (Appendix S1; for details, see Bergstrom and Sherry 2008). Visual subcutaneous fat score was assigned using the technique of Kaiser (1993) that, unlike the more typical fat scoring (0–4; Pyle et al. 1987), is based on a 0–8 scale. Birds were also scanned several times (until readings stabilized) in a total-body electrical

conductivity machine (TOBEC using EM-SCAN SA-3000 with 3044 detection chamber, 44-mm diameter; Em-Scan, Inc., Springfield, IL USA; Appendix S2) to obtain a net E-value (minus the E-value of the restraining tube) that correlates positively with lean body mass (Bergstrom and Sherry 2008). All scanning, measuring, weighing, and fat-scoring was done by BJB after practicing these procedures on several hundred birds in the months preceding this study.

Each bird was also aged when possible using plumage, feather condition, and/or visual observation of degree of skull ossification (Pyle et al. 1987). First-year birds were in their hatch year (HY) through 31 December 1993 and were categorized as second-year (SY) birds from 1 January 1994 on. Remaining birds were either ASY (after second year) or AHY (after hatch year) and thus considered adults.

Statistical analyses. Before statistical analysis, equations for predicting body composition were applied to the mass, morphometric, and visual categorical (e.g., fat score) variables recorded in the field. Lipid mass was estimated using the most appropriate best-multiple regression equation for the species, group, or size of bird; all lipid mass-prediction equations included body mass and visual fat score as predictors, all included some combination of the above-mentioned morphometric variables, and some also included TOBEC (Bergstrom and Sherry

Table 1. Number of first-year and adult birds captured in each of the four Jamaican habitats during early winter and late winter combined (numbers included in the analysis are lower, due to partial missing data or poor fit of multiple-regression models for certain species; see Methods).

Habitat	Number of first year	Number of adult	Age unknown	Total
A. Non-resident species (Nearctic-Neotropical migrants)				
Mangrove forest	17	20	7	44
Blue Mountains and foothills	13	12	8	33
Dry limestone forest	35	37	3	75
Acacia scrub	5	12	0	17
Total	71	80	19	170
B. Resident species ^a				
Mangrove forest	2	13	18	33
Blue Mountains and foothills	60	97	4	161
Dry limestone forest	18	45	19	82
Acacia scrub	1	1	0	2
Total	81	157	41	279

^aIncludes 12 Yellow Warblers of the resident race, *Setophaga petechia gundlachi*.

Table 2. Number of birds captured by species in four habitats in Jamaica in early and late winter, with their residency status, diet, and earliest typical nesting month for each resident species.

No. indiv.	Common name	Scientific name	Habitat	Season	Status	Diet	Nest
40	Bananaquit	<i>Actitis macularius</i>	1, 2, 3	1, 2	R	N, I, F	Any
39	Ovenbird	<i>Seiurus aurocapilla</i>	1, 2, 3	1, 2	M	I	—
38	Orangequit	<i>Euneornis campestris</i>	1, 2	1, 2	R	F, N, I	Apr
36	Black-faced Grassquit	<i>Tiaris bicolor</i>	2 (one 3)	1, 2	R	S, I	Any
29	American Redstart	<i>Setophaga ruticilla</i>	1, 2, 3	1, 2	M	I	—
28	Greater Antillean Bullfinch	<i>Loxigilla violacea ruficollis</i>	1, 2, 3	1, 2	R	S, F, I	Mar
16	Common Yellowthroat	<i>Geothlypis trichas</i>	2, 3	1, 2	M	I	—
14	Northern Waterthrush	<i>Parkesia noveboracensis</i>	1, 2	1, 2	M	I	—
13	Black-and-white Warbler	<i>Mniotilta varia</i>	1, 2, 3	1, 2	M	I	—
12	Western Palm Warbler	<i>Setophaga p. palmarum</i>	4	1, 2	M	I	—
12	Yellow Warbler	<i>Setophaga petechia gundlachi</i>	1, 3	1, 2	R	I	Apr
11	Jamaican Tody	<i>Todus todus</i>	1, 2, 3	1, 2	R	I	Dec
11	Yellow-shouldered Grassquit	<i>Loxipasser anoxanthus</i>	1, 2, 3	1, 2	R	S, I	Mar
10	Jamaican Euphonia	<i>Euphonia jamaica</i>	2, 3	1, 2	R	F, I	Feb
10	Sad Flycatcher	<i>Myiarchus barbirostris</i>	2, 3	1, 2	R	I	?
9	White-eyed Thrush	<i>Turdus jamaicensis</i>	2	1, 2	R	I, F	Apr
9	Worm-eating Warbler	<i>Helminthos vermivorus</i>	1, 2, 3	1, 2	M	I	—
8	White-chinned Thrush	<i>Turdus auranus</i>	1, 2, 3	1, 2	R	I, F	May
8	Black-throated Blue Warbler	<i>Setophaga caerulescens</i>	1, 2	1, 2	M	I	—
8	Jamaican (White-eyed) Vireo	<i>Vireo modestus</i>	1, 2, 3	1, 2	R	I, F	Apr
8	Prairie Warbler	<i>Setophaga discolor</i>	2, 3	1, 2	M	I	—
7	Black-whiskered Vireo	<i>Vireo altiloquus</i>	1, 3	2	M	I, F	—
7	Loggerhead Kingbird	<i>Tyrannus caudifasciatus jamaicensis</i>	1, 2, 3	1, 2	R	I	Feb
5	Common Ground-Dove	<i>Columbina passerina</i>	2, 3	1, 2	R	S, F, I	?
5	Magnolia Warbler	<i>Setophaga magnolia</i>	1, 3	2	M	I	—
5	Yellow-rumped Warbler	<i>Setophaga coronata</i>	4	1	M	I	—
5	Jamaican Oriole	<i>Icterus l. leucoperyx</i>	2, 3	1, 2	R	I, F, N	Mar
4	Rufous-tailed Flycatcher	<i>Myiarchus validus</i>	2, 3	1, 2	R	I	Apr
4	Stolid Flycatcher	<i>Myiarchus s. stolidus</i>	1, 2, 3	1, 2	R	I, F, N	Apr
4	Jamaican Spindalis	<i>Spindalis nigricephala</i>	2	1, 2	R	I	Mar
3	Arrow-headed Warbler	<i>Setophaga phaeetra</i>	1, 2	1	R	I	Mar
3	Jamaican Elaenia	<i>Myiopagis cotta</i>	2, 3	1, 2	R	I	Mar
3	Rufous-throated Solitaire	<i>Myadestes genibarbis</i>	2	1	R	I, F	?

Table 2. Continued

No. indiv.	Common name	Scientific name	Habitat	Season	Status	Diet	Nest
3	Swainson's Warbler	<i>Limnothlypis swainsonii</i>	1, 3	2	M	I	—
2	Blue-winged Warbler	<i>Vermivora cyanoptera</i>	1	2	M	I	—
2	Caribbean Dove	<i>Leptotila jamaicensis</i>	3	2	R	S, F, I	Mar
2	Jamaican Pewee	<i>Contopus pallidus</i>	2	1	R	I	Apr
2	Northern Mockingbird	<i>Mimus polyglottus</i>	2, 3	1, 2	R	F, I, V	Apr
2	Northern Parula	<i>Setophaga americana</i>	2, 3	1, 2	M	I	—
2	Spotted Sandpiper	<i>Actitis macularius</i>	1	2	M	I	—
2	Yellow-faced Grassquit	<i>Tiaria olivacea</i>	3, 4	2	R	S, I	Apr
2	Jamaican Woodpecker	<i>Melanerpes radiolatus</i>	2, 3	2	R	I	Dec
1	Blue Mountain Vireo	<i>Turdus aurantius</i>	2	1	R	I, F	Mar
1	Jamaican Mango	<i>Anthracoceros mango</i>	3	2	R	N, I	Apr
1	Mangrove Cuckoo	<i>Coccyzus minor</i>	4	2	R	I, V, F	Mar
1	Red-billed Streamertail	<i>Trochilus p. polytmus</i>	2	1	R	N, I	Apr

Habitats = mangrove (1), montane (2), dry limestone (3), and scrub (4); Seasons = early winter (1) and late winter (2); Status = resident (R) and migrant (M); Diet = insects and/or other arthropods (I), fruit (F), nectar (N), seeds (S), and vertebrates (V); Nest = typical month of earliest nesting (? = poorly known, Any = year-round, and — = non-breeding in Jamaica). Diet and nesting data from Downer and Surton (1990) and HBW (2018).

2008). Estimated lipid mass was divided by live body mass recorded in the field and expressed as percent body fat. Fat category constituted an ordinal variable from 1 to 10 (in our case) representing increasing 5% intervals in regression-estimated percentage body fat (0–4.9%, 5.0–9.9%, and so on) and was used as the primary dependent variable (Appendix S1). We attempted to use the most specific prediction equation to estimate body fat mass for each bird, some species-specific, others group-specific (e.g., warblers), still others body-size specific (large, medium, and small; all lipid-prediction equations are shown in Appendix 1 in Bergstrom and Sherry 2008). However, some equations designed for certain bird species or groups did not work on our dataset either because of missing measurements or consistently negative estimated percent body fat. As a result, all estimates of lipid for large birds were determined using the “all-birds” equation instead of the “large-bird” equation (Bergstrom and Sherry 2008). Lipid indices for Orangequits (*Euneornis campestris*), Black-faced Grassquits (*Tiaris bicolor*), Jamaican Euphonias (*Euphonia jamaica*), and Yellow-shouldered Grassquits (*Loxipasser anoxanthus*) were also estimated using the all-birds equation. For similar reasons, instead of the warbler equation, larger warblers, including Worm-eating Warblers (*Helmitheros vermivorum*) and Common Yellowthroats (*Geothlypis trichas*), were modeled with the medium-bird equation, and the smaller Magnolia Warblers (*Setophaga magnolia*), Prairie Warblers (*S. discolor*), and Blue-winged Warblers (*Vermivora cyanoptera*) with the small-bird equation. Lipid mass for other warbler species was modeled with the warbler equation (Bergstrom and Sherry 2008). Jamaican Todies (*Todus todus*) were excluded from analysis because of their negative estimated percent body fat (resulting from unusual body measurements, i.e., very long bills for their small body size). Habitat type, season (early vs. late winter), residency status (year-round breeding resident vs. non-breeding winter resident or migrant), and age were potential predictors of body condition for further analysis (see Methods; Appendix S1, Table 2).

For one set of analyses, fat category served as the response or dependent variable, and habitat, residency status (resident vs. migrant),

age (first-year vs. adult), and season (early vs. late winter) served as independent variables. For another set of analyses, habitat served as the dependent variable, with age and residency status serving as independent variables. Minitab 17.3.1 (Minitab 2016) was used to perform general linear models (GLM) when covariates were declared (i.e., ANCOVA, yielding *F* statistics), linear regression, and, for two- or multi-group comparisons when covariates were not used, two-sample *t*-tests with the unequal variances option (when sample sizes were large; *F* and *t*-tests are robust to deviations from normality or homoscedasticity when sample sizes are large and/or when groups are of approximately equal size; Glass et al. 1972), and the non-parametric Mann–Whitney (*W*) or Kruskal–Wallis (*H*) tests for two- or multi-sample comparisons when sample sizes were smaller, or greatly unequal between groups, and/or when covariates were not declared. Values are provided as means \pm 1 SD.

RESULTS

Sample sizes by habitat, residency status, season, and age. Of 447 birds sampled, 62% were residents representing 30 species, and the remaining 38% were migrants representing 16 species, mostly warblers (Table 1). The latter were predominantly insectivorous, but insects also form either a primary or an important part of the diet for the resident species we sampled (Table 2). Of the total sample of birds, 194 (43%) were captured in mixed montane habitat, of which 83% were resident species, 19 birds were captured in scrub, 77 in mangrove, and 157 in dry limestone (Table 1). Contrary to our prediction, 68% of birds captured in scrub, the lowest-quality habitat, were adults, slightly more than the overall composition of 61% adults in all habitats combined, and an older age structure than the 53% adult in the subsample of migrant birds in all habitats. However, overall age structure did not differ among the four habitats ($H_3 = 0.7$, $P = 0.90$, $N = 384$). Across all habitats, migrant species comprised a more equal mix of age classes than did resident species (Table 1). Birds were captured during both seasons in three habitats, but mangrove was sampled only in late winter. We captured 162 birds in early

winter and 285 in late winter (Appendix S1). No species was captured in all four habitats (Table 2). There were no recaptures within either season. Twelve birds banded in early winter were recaptured in late winter (4% of late-winter captures), including one each of White-eyed Thrush, Orangequit, Black-faced Grassquit, Common Yellowthroat, and Ovenbird, and two Bananquits at Green Hills (montane habitat); and one Worm-eating Warbler and two each of American Redstarts and Ovenbirds at Alligator Hole (dry limestone habitat; see Table 2 for scientific names).

Fat storage by habitat, residency status, season, and age. The modal fat category for all 362 birds with estimable lipid was 1 (regression-estimated, 0–4.9% lipid), the mean was 2.7 ± 1.8 , which is equivalent to 13% lipid, and the maximum per individual was a Black-faced Grassquit in mixed montane habitat with a fat category of 10 (~47% lipid). SFD varied significantly among the four habitats (GLM, $F_{3, 358} = 13.3$; $P < 0.001$), primarily because birds captured in scrub had a mean fat category of 5.2, whereas birds in the other three habitats had similarly low amounts of SFD (all means between 2.5–2.7, Fig. 1;

Kruskal–Wallis test of fat category among the three habitats excluding scrub: $H_2 = 3.4$, $P = 0.18$). In the above GLM, residency status was a non-significant covariate ($F_{1, 357} = 0.01$, $P = 0.91$). There was no difference in SFD between resident and migrant birds ($t_{327} = 1.5$, $P = 0.14$). SFD among all birds did not differ between early winter and late winter ($F_{1, 314} = 0.43$, $P = 0.51$; with age as a non-significant covariate: $F_{1, 314} = 2.4$, $P = 0.12$). For all birds in all habitats, SFD of adults and first-year birds did not differ significantly ($F_{1, 358} = 3.2$, $P = 0.076$; mean fat category = 2.9 ± 1.7 for 190 adults, vs. 2.6 ± 1.9 for 127 first-year birds), with residency as a non-significant covariate ($F_{1, 358} = 2.5$, $P = 0.12$). However, for birds in scrub only, five first-year birds had a significantly higher mean fat category (7.2 ± 1.9) than 12 adults (4.4 ± 2.0 ; $H_1 = 4.8$, $P = 0.03$). All but one bird in this sample with estimable percent body fat were migrants representing just two species, Western Palm Warblers (*S. p. palmarum*) and Yellow-rumped Warblers ($N = 4$, mean fat category = 6.2), and neither species was captured in any other habitat. The remaining bird in scrub was an adult male Yellow-faced Grassquit with a fat category of 7.

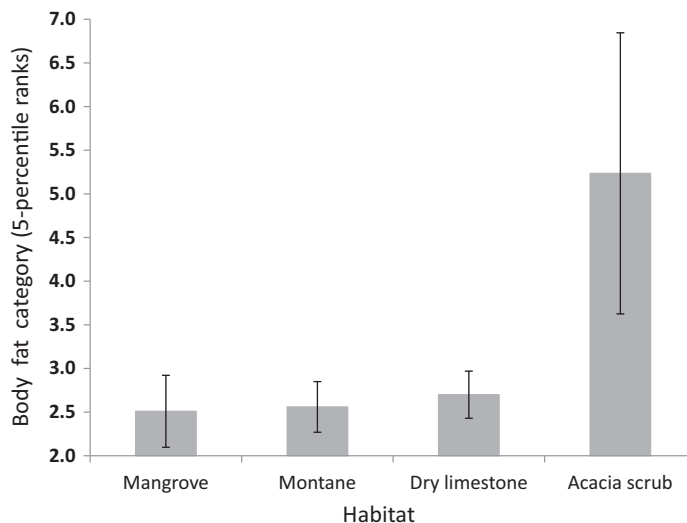


Fig. 1. Multiple-regression estimated percentage body fat (categorized by 5-percentile ranks) among the whole sample of wintering birds in four Jamaica habitats. Error bars represent 95% confidence intervals based on pooled standard deviation. See Methods for further descriptions of variables and fat estimation techniques. Numbers of birds with estimable percentage body fat per habitat were as follows: mangrove (65), montane (132), dry limestone (148), and scrub (17).

Patterns of SFD among species. Of species with at least eight individuals where we were able to estimate percent lipid, only two migrant species (Prairie Warblers and Palm Warblers) and two resident species (Jamaican Euphonias and Bananaquits) had mean regression-estimated fat categories > 3 , with Palm Warblers having the highest at 4.8 (Fig. 2). Jamaican Euphonias and Bananaquits had significantly greater SFDs than the other seven resident species combined ($W = 799.5$, $P = 0.002$ and $W = 2506$, $P < 0.001$, respectively). Palm Warblers had

significantly greater SFD than the seven lowest-mean migrant species combined ($W = 1219.5$, $P = 0.0008$), and Prairie Warblers did not differ from these species (Fig. 2, $P = 0.8$).

Single-species comparisons. Seven species had sufficient sample sizes ($N > 15$) to test for the same predictor variables as above with fat category as the response variable. Four of these species occurred in mangrove, mixed montane, and dry limestone habitats, including two migrants (Ovenbirds, $N = 39$; American Redstarts, $N = 28$) and two

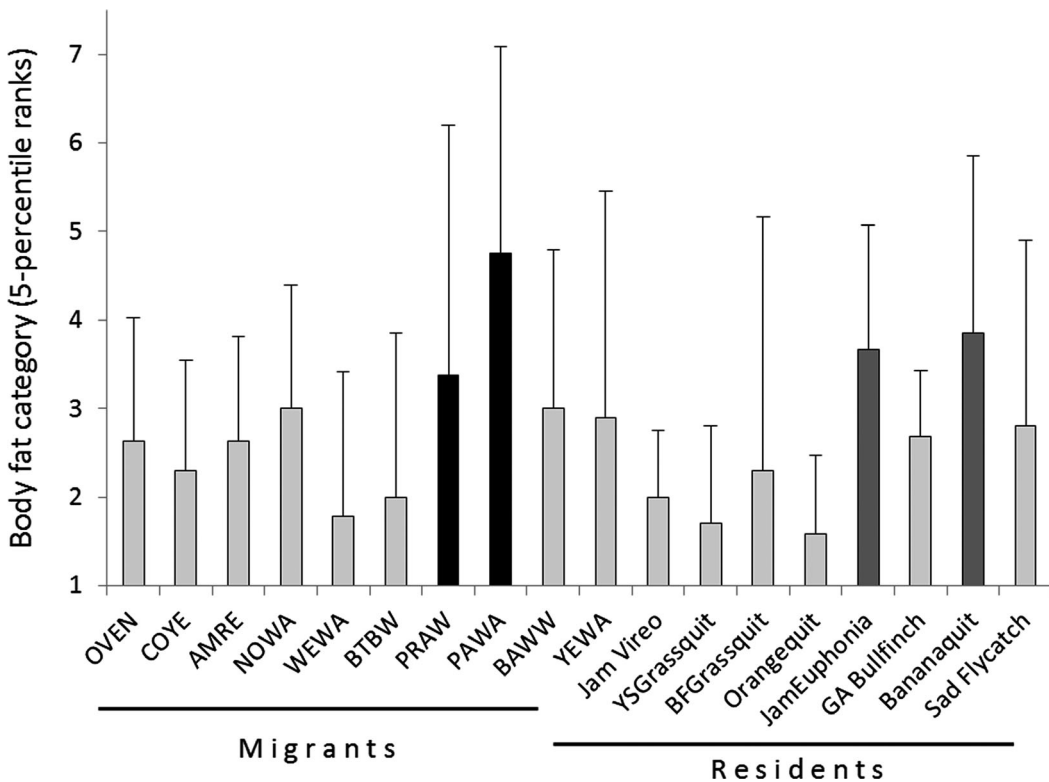


Fig. 2. Mean (\pm SD) body fat category for each of nine migrant and nine resident species of Jamaica birds where estimates of percentage lipid were obtained by multiple-regression estimation for ≥ 8 birds (see Methods). Of these, only two migrant species (black bars: Prairie Warbler and Palm Warbler) and two resident species (medium gray bars: Jamaican Euphonia and Bananaquit) had mean estimated fat categories > 3 . Not shown here because $N = 5$, Yellow-rumped Warblers had a mean fat category of 6.2 ($\sim 31\%$ body fat). Banders codes as follows: Ovenbird (OVEN), Common Yellowthroat (COYE), American Redstart (AMRE), Northern Waterthrush (NOWA), Worm-eating Warbler (WEWA), Black-throated Blue Warbler (BTBW), Prairie Warbler (PRAW), Palm Warbler (PAWA), Black-and-white Warbler (BAWW), and Yellow Warbler (YEWA). Abbreviations for resident species are as follows: Jam Vireo, Jamaican Vireo; YS Grassquit, Yellow-shouldered Grassquit; BF Grassquit, Black-faced Grassquit; JamEuphonia, Jamaican Euphonia; GA Bullfinch, Greater Antillean Bullfinch; and Sad Flycatcher, Sad Flycatcher. For these and other species, scientific names and additional information are found in Table 2.

residents (Bananaquits, $N = 40$; Greater Antillean Bullfinches, $N = 28$). Orangequits (residents, $N = 37$) were captured only in mangrove and mixed montane habitats, and Common Yellowthroats (migrants, $N = 16$) were captured only in mixed montane and dry limestone habitats. Orangequits stored little fat (mean fat category = 1.6, or $\sim 8\%$), and SFD of Orangequits did not differ either between mangrove and mixed montane habitats ($H_2 = 0.1$, $P = 0.77$) or between seasons ($H_1 = 0.1$, $P = 0.73$). Eight Common Yellowthroat individuals in dry limestone habitat had significantly more SFD (3.3 ± 1.0) than eight individuals in montane habitat (1.4 ± 0.5 ; GLM, $F_{1,13} = 14$, $P = 0.002$, with season a non-significant covariate, $F_{1,13} = 0.01$, $P = 0.93$). For Ovenbirds, American Redstarts, and Greater Antillean Bullfinches, we found no differences in estimated fat category among mangrove, mixed montane, and dry limestone habitats (H_s , all $P > 0.20$). For American Redstarts, season was a significant covariate ($F_{1,23} = 5.4$, $P = 0.03$) of habitat (with habitat a non-significant main effect, $F_{2,23} = 1.6$, $P = 0.22$) in a two-factor GLM predicting fat because eight individuals in dry limestone habitat in late winter had mean fat scores of 3.6, whereas 18 individuals in other combinations of season and habitat had mean fat scores of 2.1.

Bananaquits had more fat in mixed montane (mean fat category 4.9, or 24.5%) than mangrove (2.0, or 10%) habitat, with intermediate levels in dry limestone habitat (3.7, or 18.5%; $H_2 = 10.5$, $P = 0.005$). However, this may have been confounded by our lack of early winter sampling of mangrove habitat, and we note there was also significantly greater fat storage by Bananaquits in early winter (5.2, or 26%) than late winter (2.7, or 13.5%; $H_1 = 10.6$, $P < 0.001$). However, in a GLM ANCOVA, after removing the nearly significant effect of season as a covariate ($F_{1,25} = 3.8$, $P = 0.06$), habitat was not significant as a main effect on estimated fat category ($F_{2,25} = 1.6$, $P = 0.23$).

Body mass: relationships to SFD, season, and habitat for some species. As an *a posteriori* test, we found a significant positive relationship between total body mass and estimated fat category for Bananaquits (linear regression, $F_{1,27} = 6.1$, $P = 0.02$; for the

entire sample of Jamaica birds, we found no relationship between total body mass and estimated fat category; linear regression, $F_{1,361} = 3.1$, $P = 0.08$). Ovenbirds had the same significant positive regression of estimated fat category on body mass ($F_{1,37} = 8.0$, $P = 0.008$) as Bananaquits. In contrast, lower-mass American Redstarts had higher estimated fat categories ($F_{1,25} = 5.9$, $P = 0.02$) and, although they did not vary among all three habitats in SFD, American Redstarts were significantly heavier in montane habitat (7.9 g) than in mangrove and dry limestone habitats combined (~ 6.9 g; $H_1 = 5.4$, $P = 0.02$). American Redstarts were significantly heavier in early winter (7.4 g) than in late winter (6.8 g; $H_1 = 8.8$, $P = 0.003$), but there was no age effect on body mass ($H_1 = 0.1$, $P = 0.72$). The body mass of Bananaquits and Greater Antillean Bullfinches did not differ by habitat, season, or age (non-parametric, or GLM, with or without covariates). The body mass of Ovenbirds did not differ either among habitats ($H_2 = 2.5$, $P = 0.29$) or between seasons ($H_1 = 0.54$, $P = 0.46$), but 12 adult Ovenbirds (20.6 ± 2.2 g) were heavier than 18 first-year birds (19.3 ± 1.7 g; $H_1 = 4.4$, $P = 0.04$).

DISCUSSION

Effect of winter habitat quality on subcutaneous fat deposition (SFD). We expected SFD to be greater in migrant than resident species of birds and to increase gradually from reputedly highest-quality (mangrove) to lowest-quality (scrub) habitats, with birds wintering in the other two habitats having intermediate levels of SFD. However, we found that habitat quality was associated with SFD only when comparing one reputedly poor habitat, i.e., acacia scrub, where birds stored significantly more fat, to all other habitats where SFD generally averaged 5–15% of body mass (except for Bananaquits and Jamaican Euphonias in mixed montane habitat and Prairie Warblers found mostly in dry limestone habitat that averaged 17–24% body fat). This result provides little insight concerning resource availability or conditions in acacia scrub habitat (or dry limestone), but we can infer that maintaining greater SFD is a survival strategy in a habitat with low or

inconsistent food or water availability, and allows birds to either cope with periods of fasting or have the fuel needed to leave the habitat if necessary (Lima 1986). Coping may be associated with larger territories or home ranges facilitated by lower densities of competitors (Fretwell and Lucas 1968), and maintaining sufficient fuel to leave a habitat may help explain the frequency of transients in many warbler species (Peele et al. 2015).

An alternative explanation for elevated SFD in acacia scrub habitat is that most of the birds captured there were Western Palm Warblers and Yellow-rumped Warblers, species known to use different non-breeding habitats than the other warbler species in our study, and tending to be nomadic flocking species even in their annual winter range in the southern United States (Dunn and Garrett 1997). In Jamaica, these two species are facultative rather than regular migrants, tending to arrive late, if they arrive at all in any given winter, and to select and move among habitats already occupied by other small insectivorous songbirds (Downer and Sutton 1990, eBird 2018). This suggests that the wintering strategies of these species are transience rather than territory defense. Because of this and their occurrence in acacia scrub habitat allotopically from other Neotropical migrants, we were unable to make direct comparisons of SFD among habitats (Sherry and Holmes 1996). However, no obligate wintering migrant species and only one resident species of songbird (which had ~ 33% estimated body fat) were captured in acacia scrub, suggesting its unsuitability as habitat for obligate winter songbirds. Our sampling year was not meteorologically aberrant; actual rainfall in Jamaica from October 1993 through April 1994 was 1382 mm, which was typical based on the 24-year mean for that seven-month period from 1991 through 2015 of 1190 ± 78 (SE) mm (range = 630–2357 mm; World Bank 2018).

Whether as transients (including inter-habitat migrants; Loiselle and Blake 1991) or longer-term winter residents in poor, low-density wintering habitats such as acacia scrub, birds found there would be expected to maintain higher SFD during the pre-migration late-winter period. The 17 migrant and two resident birds in acacia scrub were all captured at a single site (Vernam Fields), and the habitat at that location may have been

atypical for acacia scrub in bird species composition or diversity. However, acacia scrub is particularly inhospitable compared to several other types of Jamaican scrub habitats that host a greater abundance and diversity of birds (e.g., xeric logwood scrub; Peele et al. 2015). The dry limestone ecosystem includes a more species-diverse (plants as well as birds) scrub habitat interspersed with dry forests (Downer and Sutton 1990; Fig. 3e in Appendix S2).

Among the other three habitats, insect abundance in dry limestone has been reported to decline more during the winter months, due to less rainfall, than in mangrove and mixed montane habitats (Sherry and Holmes 1996, Johnson and Sherry 2001, Kellerman et al. 2008). Although we found that the SFD of birds overwintering in dry limestone was similar to that of birds in mixed montane and mangrove habitats, our sample of migrant, insectivorous Common Yellowthroats (split evenly between two habitats) had significantly greater SFD in dry limestone than in montane, providing single-species support for the above-cited studies, and for our initial hypothesis that SFD would be higher in the lower-quality habitat.

For two resident species, Bananaquits and Jamaican Euphonias, we found significantly greater fat storage than for other resident species (as well as for many migrants) in our study; SFD was significantly higher for Bananaquits in mixed montane habitat and in early winter (nine of 10 Jamaican Euphonias were captured in montane habitat and eight of those in early winter so that no similar comparisons could be made). Bananaquits in locations with greater access to fruit in Dominica had significantly greater SFD than in other localities, especially in January, with levels declining dramatically by April (a similar seasonal pattern to our data; Douglas et al. 2013). Bananaquits breed by February or earlier in the West Indies (Diamond 1973, Wunderle 1982). Bananaquits and Jamaican Euphonias breed earlier than most other resident birds in Jamaica, and have previously been documented to have significantly more SFD during December and January than other resident species (Diamond 1973). This suggests that Bananaquits and Jamaican Euphonias may have had elevated SFD at our montane sites because of the availability of

ample fruit and insect food sources, and in preparation for early winter breeding.

Our higher-elevation sites included gardens, orchards, and coffee plantations that provided abundant fruit and nectar sources and insects attracted to both (Johnson and Sherry 2001, Sherry et al. 2016b). In fact, the abundance of arthropods has been found to increase toward late winter in Jamaican coffee plantations (Johnson and Sherry 2001), allowing better maintenance of over-winter body mass by American Redstarts in this habitat than in dry limestone and scrub habitats (Johnson and Sherry 2001). Because of this, a significant positive relationship between elevation and body size previously reported for Bananaquits in Jamaica (Diamond 1973) may also explain our finding of a positive relationship between body size and SFD in this species. In our study, American Redstarts overall lost significant mass over the winter period (but no difference in SFD) and were also heavier at the higher-elevation sites, which may reflect size-based habitat selection. Diamond (1973) found the same elevational pattern for migrant Black-and-white Warblers in winter and attributed it to Bergmann's Rule. Body-mass changes decoupled from changes in SFD have been reported in Palearctic-breeding migrants during winter in the tropics, and this has been attributed to higher SFD in poor habitats or during lean periods being offset by loss of muscle mass (Riddington and Gosler 1995, Katti and Price 1999). Because we did not find elevated SFD in American Redstarts in any habitat or season, we conclude that winter SFD is not a bet-hedging strategy the species employs, so over-winter mass loss may represent loss of muscle mass in response to late-winter food shortage and/or the gradual reduction in the pectoralis muscle hypertrophy that occurred prior to southward fall migration, i.e., birds not needing to power long-distance flight could increase maneuverability and reduce energy demands by reducing pectoralis muscle mass (Dietz et al. 2007).

Age differences in SFD. Overall, adults and first-year birds had similar amounts of SFD. First-year birds might be expected to store more fat than adults because they usually occupy lower-quality habitats due to their subordinate status and lack of experience in finding and defending high-quality winter territories (Sherry and Holmes 1996, Peele et al.

2015), a pattern not observed in our data (Table 1). In some cases, however, juveniles might occupy high-quality habitats by relying on cues from adults. Because adults tend to have more experience in choosing winter habitats, they could reliably indicate high-quality habitats to later-arriving naive juveniles trying to secure habitat (Sherry and Holmes 1996) by occupying vacancies in unsaturated habitats, competing for territories, or surviving as floaters among territorial birds (Peele et al. 2015). However, in the one habitat where SFD was pronounced in our study (acacia scrub), juveniles had significantly more fat than adults, as hypothesized. Contrary to our predictions, less than a third of the migrant birds captured in scrub habitat were first-year birds, proportionately less than any of the other three habitats that we predicted would provide greater and more reliable over-winter arthropod availability.

With the above exceptions noted, and some arguably complex interactions among variables, season (early or late winter) and residency status (resident or migrant) did not affect the amount of fat stored by birds in the habitats we sampled. These results contradict the findings of Holmes et al. (1996) and Johnson et al. (2006). The less-than-expected variation in fat storage among the three habitats in our study, other than the harshest (scrub), parallels the results of a recent study of Wood Thrushes (*Hylocichla mustelina*) overwintering in Belize (McKinnon et al. 2015) where birds were found to be in equally poor body condition in each of three habitats due to late-winter drying and reduced abundance of arthropods and fruits. Another possible source of variation in SFD that may have obscured patterns, and which our study was not designed to detect, is subtle within-habitat variation in wintering strategy, particularly by species of wintering migrants, especially transient versus territorial behavior. Up to 50% of individuals occupying some habitats in Jamaica are transient individuals that can be difficult to detect without intensive survey methods such as territory mapping (Peele et al. 2015). Fat levels might be expected to be greater in transient individuals as a bet-hedging strategy (references in Introduction), particularly if they tend to be socially subordinate, which could obscure patterns among habitats.

We conclude with several observations. First, the mean percentage body fat among tropical wintering birds in our study ($\sim 13 \pm 1.8\%$) was slightly greater (although much less variable) than that reported in a previous study using the same estimation techniques on Nearctic-Neotropical birds sampled largely at spring and fall migration stopover sites in the southeastern United States ($12 \pm 9.6\%$; Bergstrom and Sherry 2008), where birds often have considerable SFD related to migration (but may sometimes have depleted fat stores following a long migration bout, especially in the spring). Thus, fat stores in these tropical wintering birds were far from negligible. Second, a few species of resident and migrant birds in our study, and in different habitats, had significantly greater winter SFD than other species, reinforcing the idea that birds store fat for different ecological reasons and that no one hypothesis is likely to explain all the patterns. Third, lean-mass loss during the winter may be a survival strategy for some species that do not have winter SFD. Fourth, more research is needed in a variety of habitats and seasons to better understand factors that influence fat deposition and changes in lean mass, ideally in conjunction with estimates of food availability and predictability, and with information on the status of individuals as either territorial or transient. Finally, experiments (Cooper et al. 2015) will be valuable for testing specific hypotheses. Studies like ours, that are comparative and can identify patterns, are important in helping to determine where experimentation will be most productive. For example, in conjunction with assessment of body condition over winter in different habitats, territory mapping of individual birds and experimental food supplementation are two possible experimental approaches for examining what drives SFD.

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LITERATURE CITED

- BERGSTROM, B. J., AND T. W. SHERRY. 2008. Estimating lipid and lean body mass in small passerine birds using TOBEC, external morphology and subcutaneous fat-scoring. *Journal of Avian Biology* 39: 507–513.
- BLEM, C. R. 1990. Avian energy storage. *Current Ornithology* 7: 59–113.
- BROWN, D. R., AND T. W. SHERRY. 2006. Food supply controls the body condition of a migrant bird wintering in the tropics. *Oecologia* 149: 22–32.
- COOPER, N. W., T. W. SHERRY, AND P. P. MARRA. 2015. Experimental reduction of winter food decreases body condition and delays migration in a long-distance migratory bird. *Ecology* 96: 1933–1942.
- DIAMOND, A. W. 1973. Altitudinal variation in a resident and a migrant passerine on Jamaica. *Auk* 90: 610–618.
- . 1974. Annual cycles in Jamaican forest birds. *Journal of Zoology* 173: 277–301.
- DIETZ, M. W., T. A. PIERSMA, A. HEDENSTRÖM, AND M. BRUGGE. 2007. Intraspecific variation in avian pectoral muscle mass: constraints on maintaining manoeuvrability with increasing body mass. *Functional Ecology* 21: 317–326.
- DOUGLAS, L. R., G. WINKEL, AND T. W. SHERRY. 2013. Does the Bananaquit benefit commensally from parrot frugivory? An assessment using habitat quality. *Biotropica* 45: 457–464.
- DOWNER, A., AND R. L. SUTTON. 1990. *Birds of Jamaica: a photographic field guide*. Cambridge University Press, Cambridge, UK.
- DUNN, J., AND K. GARRETT. 1997. *A field guide to warblers of North America*. Houghton Mifflin, New York, NY.
- EBIRD [online]. 2018. Species maps. Cornell Lab of Ornithology. <<https://ebird.org/map>> (Accessed 30 November 2018).
- FRETWELL, S. D., AND H. L. LUCAS, JR. 1968. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19: 16–32.
- GLASS, G. V., P. D. PECKHAM, AND J. R. SANDERS. 1972. Consequences of failure to meet assumptions underlying the fixed effects analyses of variance and covariance. *Review of Educational Research* 42: 237–288.
- GOSLER, A. G., J. J. GREENWOOD, AND C. PERRINS. 1995. Predation risk and the cost of being fat. *Nature* 377: 621–623.
- [HBW] HANDBOOK OF BIRDS OF THE WORLD ALIVE [online]. 2018. Species accounts. <<https://www.hbw.com/species>> (Accessed 30 November 2018).
- HOCHACHKA, P. W. 1973. Comparative intermediary metabolism. In: *Comparative animal physiology* (C. L. Prosser, ed.), pp. 212–278. Saunders, Philadelphia, PA.
- HOLMES, R. T., P. P. MARRA, AND T. W. SHERRY. 1996. Habitat-specific demography of breeding Black-throated Blue Warblers (*Dendroica caerulescens*): implications for population dynamics. *Journal of Animal Ecology* 65: 183–195.
- JOHNSON, M. D. 2007. Measuring habitat quality: a review. *Condor* 109: 489–504.

- , AND T. W. SHERRY. 2001. Effects of food availability on the distribution of migratory warblers among habitats in Jamaica. *Journal of Animal Ecology* 70: 546–560.
- , ———, R. T. HOLMES, AND P. P. MARRA. 2006. Assessing habitat quality for a migratory songbird wintering in natural and agricultural habitats. *Conservation Biology* 20: 1433–1444.
- KAISER, A. 1993. A new multi-category classification of subcutaneous fat deposits of songbirds. *Journal of Field Ornithology* 64: 246–255.
- KATTI, M., AND T. PRICE. 1999. Annual variation in fat storage by a migrant warbler overwintering in the Indian tropics. *Journal of Animal Ecology* 68: 815–823.
- KELLERMAN, J. L., M. D. JOHNSON, A. M. STERCHO, AND S. C. HACKETT. 2008. Ecological and economic services provided by birds on Jamaican Blue Mountain coffee farms. *Conservation Biology* 22: 1177–1185.
- LEFEBVRE, G., AND B. POULIN. 1996. Seasonal abundance of migrant birds and food resources in Panamanian mangrove forests. *Wilson Bulletin* 108: 748–759.
- LIMA, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* 67: 377–385.
- LINDSTRÖM, A., AND T. PIERSMA. 1993. Mass changes in migrating birds: the evidence for fat and protein storage re-examined. *Ibis* 135: 70–78.
- LOISELLE, B. A., AND J. G. BLAKE. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology* 72: 180–193.
- MARRA, P. P., E. B. COHEN, S. R. LOSS, J. E. RUTTER, AND C. M. TONRA. 2015. A call for full annual cycle research in animal ecology. *Biology Letters* 11: 20150552.
- MCKINNON, E. A., J. A. ROTENBURG, AND B. J. M. STUTCHBURY. 2015. Seasonal change in tropical habitat quality and body condition for a declining migratory songbird. *Oecologia* 179: 363–375.
- MILENKAYA, O., N. WEINSTEIN, S. LEGGE, AND J. R. WALTERS. 2013. Variation in body condition indices of Crimson Finches by sex, breeding stage, age, time of day, and year. *Conservation Physiology* 1: cot020.
- MINITAB. 2016. Minitab statistical software, ver. 17.3.1. Minitab, Inc., State College, PA.
- PEELE, A. M., P. P. MARRA, T. S. SILLETT, AND T. W. SHERRY. 2015. Combining survey methods to estimate abundance and transience of birds among tropical non-breeding habitats. *Auk* 132: 926–937.
- PYLE, P., S. N. G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, CA.
- RIDDINGTON, R., AND A. G. GOSLER. 1995. Differences in reproductive success and parental qualities between habitats in the Great Tits *Parus major*. *Ibis* 137: 371–378.
- ROGERS, C. M. 2005. Food limitation among wintering birds: a view from adaptive body mass models. In: *Birds of two worlds: the ecology and evolution of migration* (R. Greenberg and P. P. Marra, eds.), pp. 106–113. Johns Hopkins University Press, Baltimore, MD.
- , AND J. N. M. SMITH. 1993. Life history in the non-breeding period: tradeoffs in avian fat reserves. *Ecology* 74: 419–426.
- RUTKOWSKA, J., E. T. SADOWSKA, M. CICHON, AND U. BAUCHINGER. 2016. Increased fat catabolism sustains water balance during fasting in Zebra Finches. *Journal of Experimental Biology* 219: 2623–2628.
- SHERRY, T. W., AND R. T. HOLMES. 1996. Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. *Ecology* 77: 36–48.
- , ———, P. PYLE, AND M. A. PATTEN. 2016a. American Redstart (*Setophaga ruticilla*). In: *The Birds of North America* (P. G. Rodewald, ed.). Cornell Lab of Ornithology, Ithaca, NY.
- , M. D. JOHNSON, K. A. WILLIAMS, J. D. KABAN, C. K. MCAVOY, A. M. HALLAUER, S. RAINEY, AND S. XU. 2016b. Dietary opportunism, resource partitioning, and consumption of coffee berry borers by five species of migratory wood warblers (Parulidae) wintering in Jamaican shade coffee plantations. *Journal of Field Ornithology* 87: 273–292.
- STUDDS, C. E., AND P. P. MARRA. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory songbird. *Ecology* 86: 2380–2385.
- WORLD BANK [online]. 2018. Climate change knowledge portal. The World Bank Group. <http://sdwebx.worldbank.org/climateportal/index.cfm?page=downscaled_data_download&menu=historical> (Accessed 30 November 2018).
- WUNDERLE, J. M., Jr. 1982. The timing of the breeding season in the Bananaquit (*Coereba flaveola*) on the island of Grenada, W. I. *Biotropica* 14: 124–131.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Appendix S1. Raw data spreadsheet for birds sampled in Jamaica 1993–1994.

Appendix S2. Photographs of habitats and field sites, and TOBEC equipment.