

PATTERNS OF FRUGIVORY AND ENERGETIC CONDITION IN NEARCTIC LANDBIRDS DURING AUTUMN MIGRATION¹

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Abstract. Many species of Nearctic landbirds exhibit behavioral plasticity during migration, presumably to compensate for energetic demands of migratory flight. At Block Island, Rhode Island, a northern temperate site, I quantified the extent of one form of behavioral plasticity in Nearctic landbirds: dietary expansion from breeding season insectivory to high levels of frugivory during autumn. I also measured changes in energetic condition of migrants using recapture methods and diurnal regressions of mass change. Based on analyses of 1,568 fecal samples collected from 1993–1995, frugivory during migration was frequent within many species, extensive within individual birds, and widespread among taxa. Migratory species ranged from strict insectivory in the Winter Wren (*Troglodytes troglodytes*) to 96% fruit by volume in the fecal samples of Rose-breasted Grosbeaks (*Pheucticus ludovicianus*). Nine of 17 recaptured species demonstrated mass gains between first and last recapture. Only the Red-eyed Vireo (*Vireo olivaceus*) gained significant mass within a single day, suggesting that the site was suitable for migratory mass gain if a species remained longer than one day. Highly omnivorous species, with greater than one-third of the diet as fruit, gained significantly more mass while on Block Island than did strict insectivores, i.e., species with less than one-third of the diet as fruit. Insectivorous species on average declined in energetic condition during stopover. The extent of frugivory for a species was positively correlated with average change in energetic condition and fat score per day, suggesting that frugivory allowed species to gain mass more efficiently and extensively than exclusive insectivory. I conclude that frugivory in Nearctic landbirds is far more extensive during migration than previously thought, and that dietary plasticity may be an adaptation to energetic demands of migratory flights.

Key words: frugivory, migration, dietary plasticity, stopover ecology, Nearctic-Neotropical migrants.

INTRODUCTION

The extreme physiological demands, energetic pressures and changing resource distribution patterns of migration make it a formative period in the evolution of the morphology (Bairlein 1992), physiology (Bairlein 1987, Jenni-Eiermann and Jenni 1992), and behavior of migratory landbirds (Martin and Karr 1990). Landbirds show extensive behavioral changes during migration, presumably to compensate for these increased energy demands. Much attention has focused on the increase in prey intake rates (Loria and Moore 1990), the selection of highly profitable insect prey (Moore and Simm 1986), and the changes in physiology (Gwinner 1990), social behavior (Rappole and Warner 1976), and habitat selection (Bairlein 1983) that character-

ize migrants responding to energetic demands. Another less studied behavioral shift occurring in many landbirds is expansion from stereotypic insect diets during reproduction (Morse 1989) to dietary plasticity during migration, incorporating non-insect arthropods, seeds, nectar, and fruit (Berthold 1976, Bairlein and Gwinner 1994).

Although it is well known that frugivorous migrants play a role in dispersing seeds of Temperate Zone plants, (Willson 1986), far less is known of the importance of omnivory during migration for the birds themselves. Few studies have comprehensively quantified the extent of frugivory by migrating Nearctic songbirds or examined how frugivory may correlate with birds' abilities to deposit fat stores for migration (Bairlein 1990). Early studies of frugivory in Palearctic migrants by Berthold (1976) defined the paradox of extensive fruit use during migration in some Old World species: fruit is typically lower in lipid and protein nutrients and provides smaller caloric rewards than comparable quantities of insects (Moermond and Denslow 1985,

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Bairlein and Gwinner 1994). In his feeding experiments, birds on fruit diets were consistently incapable of maintaining body mass. Berthold concluded that frugivory during migration was a consequence of concurrent seasonal decline in insect abundance and that fruit functioned solely as a poor supplemental food for songbirds, preferred secondarily to animal matter as a diet for migratory lipogenesis. However, subsequent studies in Palearctic migrants showed that some species are capable of assimilating fruit diets and increasing body mass during migration (Jordano 1988, Bairlein 1990).

Although frugivory is well documented in Nearctic-Neotropical migratory birds during the nonbreeding period in the tropics (Greenberg 1981, Blake and Loiselle 1992), the extent of frugivory and its implications for songbird energetics during autumn migration are relatively unexplored (Willson 1990). In this study I document dietary patterns, stopover behavior, and energetic changes in Nearctic-Neotropical landbirds during migration. I then use these data to test the hypothesis that diet expansion to fruit facilitates improved energetic condition during stopover periods beyond that possible with strict insectivory. For example, if frugivory during migration has evolved in response to the physiological demands of migration, omnivorous migrant species should gain mass more rapidly than stereotypic insectivores, assuming both time and energy are important currencies during migration (Alerstam and Lindstrom 1990).

METHODS

STUDY SITE

I conducted this study on Block Island, Rhode Island (41°12'N, 71°35'W), a 2,900-ha land mass located 19 km off the coast of southern New England, U.S.A. Field work was conducted within Clayhead Preserve, a 70-ha conservation area on the northern tip of the island. During autumn migration, large numbers of individuals consistently use the coastal shrublands of Block Island between migratory flights after being forced offshore by northwest winds associated with regular and frequent autumnal cold fronts. After settling, many individuals concentrate in the coastal habitats at the northern tip of the island to rest and refuel before resumption of southern migratory trajectories or northward re-oriented migrations to the mainland (Able 1977).

Two habitats dominated the study site: a diverse coastal shrubland and shorter-statured bayberry (*Myrica pensylvanica*) and *Rosa* thickets. The dense coastal shrubland habitat ranged from 2–4 m in height and consisted of *Amelanchier* spp., *Viburnum recognitum* (with some *Viburnum dentatum*), *Phytolacca americana*, *Pyrus melanocarpa*, *Rhus radicans*, *Parthenocissus quinquefolia*, and low-density *Myrica pensylvanica*. Bayberry habitats varied in foliage height (0.5–3.5 m) depending on distance from the coastline, where shorter northern bayberry plants were dominant as a result of wind, saltspray, and soil conditions. Several species of *Rosa* and to a lesser extent *Rhus radicans* densely filled interstitial areas between bayberry plants.

DIET ANALYSES

Dietary data were collected from migrant birds between 25 August and 31 October during the autumns of 1993–1995. Birds were captured under permit from the U.S. Fish and Wildlife Service with 12-m mistnets (32 mm mesh) in bayberry and coastal shrubland habitats between 06:00 and 14:00 in 1993, and between 06:00 and 13:00 in 1994 and 1995. Mistnets reached from 0.5–3.0 m in height, thus sampling the majority of the vertical stratum of the low-statured shrubland habitats. Each of 12 (1993–1994) or 16 (1995) mistnets was monitored every 30–45 min throughout the autumn migration period. Upon capture of a bird, the net, time, date, and species were noted, and the bird was placed into a fecal collection bag for transport to a central banding station. After production of a fecal sample and within 10 min, the bird was given a serially numbered U.S. Fish and Wildlife Service band, processed for mass to the nearest 0.01 g, fat score (see below), wing measurement, age and sex determination (according to Pyle et al. 1987), and subsequently released. Although this study focused on Nearctic-Neotropical landbird migrants, data were taken from all species, including some residents and short-distance migrants in order to make dietary comparisons by migratory status.

The advantages and disadvantages of fecal samples in determining diets of birds have been extensively discussed (Rosenberg and Cooper 1990, Blake and Loiselle 1992), and are principally concerned with differential gut passage times and gastro-intestinal processing of differ-

ent food types. However, fecal samples provide an important and useful way of evaluating large numbers of samples (Rosenberg and Cooper 1990), especially from birds that are difficult to observe due to habitat constraints or behavior. This technique also is most appropriate for birds at risk of surviving more invasive methods of diet sampling, as may be the case with landbirds after long-distance nocturnal migrations. Moreover, the larger sample size available through fecal sampling minimizes effects of between-individual variation produced by smaller sample sizes generated from more labor-intensive methods.

I collected fecal samples into plastic storage bags, labeled them with the species, date, time, and netting location, and then froze them until time of analysis. Before analysis, I thawed and rinsed samples into petri dishes with 70% ethyl alcohol solution. Samples were loosened with forceps to allow equal dissipation of all solid matter within the dish. I noted the presence of fruit and insect matter, and the presence and number of seeds in all samples. Thereafter, binocular microscopes were used to approximate volume of fruit matter versus insect matter in the sample (Herrera 1987). Because the volume of each fecal sample varied, the amount of fruit and insect material in the sample was estimated as a volumetric proportion of the total fecal sample material to the nearest 10%. Volume is probably not related to the energetic content of fruit and insect resources, because fruit is higher in the amount of gut volume it occupies than most insect resources, yet lower in provided energy. Thus, these volumetric estimates should be viewed as a means of diet classification, not relative energy contribution of resources, per se. In general, seeds were not abundant in fecal samples, with the exception of *Phytolacca* and *Viburnum* seeds in larger landbird species, and *Myrica* seeds in *Dendroica coronata*. Nonetheless, seeds were excluded in estimations of the fruit-insect volumetric ratio of the diet.

Fruit species consumed by the sampled bird were determined by identification of seeds, passed pulp, or passed fruit skin fragments in the feces. To assist in identification of fruit species consumed, I collected representative fruits of all available fruiting plants in the study site for determination of the cell structure of fruit skin, consistency of the pulp, and shape and size

of the seeds. The total number of fruit species in each sample also was recorded.

I attempted to identify insect orders in feces through identification of passed insect parts (Ralph et al. 1985). Because of the degree of mechanical digestion that had occurred in many of the samples, not all insect orders consumed could be identified in the feces, which is one drawback of diet analysis by fecal samples (Rosenberg and Cooper 1990). The list of consumed insect orders and fruit species presented here should therefore be viewed as a minimal representation of the diet of sampled landbird species.

STOPOVER ENERGETIC CONDITION

Changes in energetic status of migrants were primarily examined through analyses of recaptured individuals. To insure large sample sizes, recapture data included birds recaptured within a season at my study site during 1993–1995 and birds recaptured during the autumns of 1969–1989 at a long-term banding station operated by E. Lapham, which was located < 1 km away from the author's site within the same contiguous coastal shrubland habitat. Methodology for age, sex, morphological, and energetic data at both sites were identical. As in other studies (Moore and Kerlinger 1987, Winker et al. 1992), recaptures represented a small percentage of the total number of individuals captured in mistnets (mean of banded individuals recaptured between 1993–1995 = 6.5%, $n = 4,596$ banded birds), in part due to constraints of a necessarily limited netting effort sampling a 60-ha study area. This technique, however, allows an accurate assessment of energetic status changes during staging periods that is comparable across studies (*sensu* Moore and Kerlinger 1987, Kuenzi et al. 1991). By recapturing an individual bird at least once during its stay on Block Island, I was able to determine a conservative estimate of its stopover length and of changes in fat and energetic status.

Energetic condition estimates for small landbirds are problematic during migration because of the difficulty of determining if changes in body mass are due to increases in subcutaneous fat (the principal fuel for migratory flight) or increases in muscle mass accrued early in migration (Lindstrom and Piersma 1993). I therefore used a series of energetic-condition estimation techniques in both recaptured and single-captured migrants. I used changes in mass to assess within-species energy dynamics during

stopover periods. However, body mass is influenced by body size and precludes reliable across-species comparisons of energetic strategies. I therefore visually estimated the fat score of individuals from 0 (no fat in furcular and abdominal regions) to 5 (continual covering of fat from furcula to abdomen) according to Helms and Drury (1960). This categorical estimate of fat condition is a sliding-scale estimate of lipid content that is expressed somewhat independent of the overall dimensions or non-lipid mass of a bird, and is a reliable indicator of total body fat composition (Conway et al. 1994). I also determined the energetic condition (EC) for all banded birds by dividing body mass (to the nearest 0.01 g) by the unflattened wing length cubed and then multiplying by 100,000 for calculations (Winker et al. 1992). This measure allows comparison of energetic condition across birds of a range of body sizes and equates the volumetric measure of mass to the linear wing measurement. It does, however, assume that changes in mass are due to fat deposition rather than significant increases in muscle mass (Lindstrom and Piersma 1993). I determined stopover length by subtracting the last date from the first date of capture.

Despite the extensive use of recapture data in studies of energetic condition during migratory stopover (Moore and Kerlinger 1987, Jordano 1988), some have suggested that recapture data may not represent energetic changes of the migrant population as a whole (Winker et al. 1992). This may be true if the majority of individuals are not recaptured because they use fat stores gained during that single day to depart soon after arrival at a stopover site, or if recaptured individuals were less capable of rapid mass gain at that location. Therefore, to confirm energetic trends generated for Block Island from recaptured individuals, I performed linear regression analyses between the daily Energetic Condition index and capture time of all single-capture individuals to determine if birds were gaining within one day, sufficient mass to depart from Block Island. Because almost all birds arrive more or less synchronously at the site in the pre-dawn to early morning hours (pers. observ.), I did not standardize the energetic condition of each capture to a specific time of day for analyses. A significant positive linear relationship between energetic condition and time of capture would suggest that birds gained mass within one

day (Winker et al. 1992). Energetic condition changes using the regression technique were then compared with recapture data to determine their concordance. If species that show no gain using recapture data demonstrate positive diurnal mass changes by the regression technique, then recapture data may not be illustrative of the entire population. Agreement of the two methods would suggest that both adequately depict landbird behavior at the site.

DATA TREATMENT AND STATISTICAL ANALYSES

Because the volume and species composition of landbirds differed between years and sample sizes among the three years were uneven for many species, I present dietary data for each species as the average over 1993–1995. To investigate patterns of frugivory in relation to energetic status during stopover periods, migrant species were assigned a migratory and dietary classification. Migratory status of each captured species (long-distance migrant, short-distance migrant, or resident) was based on classifications in Rappole et al. (1983) and Hussell et al. (1992). I then decided *a priori* that species whose diet-by-volume consisted of one-third or more fruit as judged by fecal samples would be considered omnivores, and those birds with less than one-third fruit in fecal samples would be classified as insectivores (Foster 1987). Given that many of these species are departing from a strictly insectivorous diet during the breeding season, I consider this quantitative threshold of omnivory to be conservative.

Percentage estimates of fruit volume in fecal samples and of frequency of fruit in the diet were arcsine transformed before all analyses, so that the data met parametric test assumptions. For clarity, untransformed data were used to generate figures. I used nonparametric tests (Mann-Whitney *U*-tests) for variables that still failed to reach normality or homogeneity of variance after transformation (e. g., percent of individuals recaptured, percent of recaptures gaining mass, and stopover length).

Although I report diet characteristics for non-migratory species (such as Carolina Wrens and Song Sparrows, scientific names are presented in Table 1) and breeding birds that could not be reliably separated from migrating individuals (including Gray Catbirds, Common Yellowthroats, White-eyed Vireos), these were not in-

cluded in stopover analyses due to absence or uncertainty of migratory status. Changes in energetic status indices between first and last capture were compared conservatively in recaptured individuals using two-tailed paired *t*-tests in order to determine whether the species gained or lost significant mass on Block Island during stopover periods. Recaptured individuals were classified as omnivores or insectivores according to dietary analyses presented here. Subsequently, I compared the rate of change per day of stopover and percent change of original score at first capture between insectivorous species and omnivorous species by unpaired two-tailed *t*-tests. I was unable to perform analyses of energetic change between omnivores and insectivores within a species due to limitations of fecal sample collection methodology. Because diet was measured using the continuous variable of mean percent fruit volume per fecal sample, I investigated the relationship between change in energetic status of a species with diet by linear regression.

RESULTS

PATTERNS OF FRUGIVORY

A total of 1,568 fecal samples was analyzed from 69 species of landbirds during autumn migration (Table 1). Sample sizes for individual species varied between only one in rarely captured individuals to 357 for the Yellow-rumped Warbler; however, only species with four or more samples are treated in diet analyses. The presence of fruit in fecal samples was widespread: the average occurrence of fruit in samples of any one species was 85.7%. Seventeen (36.2%) of 47 species with sufficient sample sizes had fruit in all fecal samples collected. Among migratory species, only the Winter Wren never contained fruit in its feces. Although no species was entirely frugivorous, several species showed very low frequencies of fecal samples with insects: nearly half of the samples of American Robin, Cedar Waxwing, and Dark-eyed Junco completely lacked arthropod prey (Table 1).

I averaged the mean percentage of fruit in a fecal sample over all three sampling years to derive an overall estimate of the degree of frugivory for each species (Table 1). The mean proportional fruit volume per sample varied from 0.0% in the wren species (above) to 96.0% fruit

in the diets of Rose-breasted Grosbeaks. Even species with morphology generally associated with specialized insectivory contained measurable amounts of fruit within their fecal samples (e. g., Brown Creepers with 21.7% fruit/fecal sample and Black and White Warblers with 9.0% fruit/fecal sample). The two measures of the degree of frugivory (frequency of fruit occurrence in fecal samples, and the mean proportion by volume of fruit per fecal sample) were highly correlated ($r = 0.95$, $P < 0.001$). I therefore used only the average percent fruit volume per fecal sample in subsequent analyses.

Percent fruit volume per fecal sample varied among taxa (Fig. 1). Cuckoos, nuthatches and wrens showed conspicuously low proportions of fruit in average samples, whereas samples from flycatchers, thrushes, waxwings, vireos, warblers, and sparrows contained greater than half of the average fecal volume as fruit material (Fig. 1). In general, larger species (measured as seasonal body mass, from Clench and Leberman 1978) were more omnivorous ($F_{2,44} = 28.2$, $r^2 = 0.56$, $P < 0.001$, Fig. 2), but there was great variation in the extent of frugivory among birds weighing between 7–15 g. Birds over 15 g typically had greater than 50% average fruit volume per sample (Fig. 2). Frugivory also differed among birds according to migratory status: residents in the two years for which there were sufficient data (1994–1995) displayed lower levels of frugivory than did migrants ($F_{2,1269} = 10.3$, $P < 0.001$, Fig. 3). In 1994, however, a Bonferroni post hoc test showed differences in frugivory between resident and short distance migratory birds ($P < 0.01$), and between short and long-distance migrants ($P < 0.001$), and a strong but non-significant difference between residents and long-distance migrants ($P = 0.053$, Fig. 3).

Six species of fruit were commonly used by birds during autumn on Block Island, but only three fruit species were found in 20% or more of fecal samples (northern arrowwood *Viburnum recognitum*, northern bayberry *Myrica pensylvanica*, and pokeweed *Phytolacca americana*). Virginia creeper (*Parthenocissus quinquefolia*) and various *Rosa* spp. were relatively uncommon in bird diets. In contrast, *Viburnum recognitum* was found in 66.5% of all fecal samples analyzed for diet taxa composition and was found in all fecal samples of 31 species (50.8% of the 61 bird species sampled for fruit taxa

TABLE 1. Dietary observations from fecal samples collected from mist-netted birds on Block Island, Rhode Island during autumn migration, 1993–1995. Species with sample sizes of $n < 4$ are summarized at end of table, but are not included in table totals below.

Bird species	<i>n</i>	No. (%) samples with fruit	No. (%) samples with insects	No. (%) samples with fruit and insects	Percentage ($\bar{x} \pm SD$) fruit in sample	Diet ^a
Eastern Phoebe <i>Sayornis phoebe</i>	35	34 (97.1)	28 (80.0)	28 (80.0)	70.9 \pm 27.1	Omnivore
Least Flycatcher <i>Empidonax minimus</i>	7	6 (85.7)	7 (100)	6 (85.7)	52.9 \pm 37.7	Omnivore
Yellow-bellied Flycatcher <i>Empidonax flaviventris</i>	6	6 (100)	5 (83.3)	5 (83.3)	58.3 \pm 35.5	Omnivore
Traill's Flycatcher <i>Empidonax traillii</i>	6	6 (100)	5 (83.3)	5 (83.3)	60.0 \pm 29.7	Omnivore
<i>Empidonax</i> spp.	7	7 (100)	7 (100)	7 (100)	57.1 \pm 22.9	Omnivore
Black-capped Chickadee <i>Parus atricapillus</i>	14	10 (71.4)	13 (92.9)	9 (64.3)	47.9 \pm 39.9	Omnivore
Brown Creeper <i>Certhia familiaris</i>	6	3 (50.0)	6 (100)	3 (50.0)	21.7 \pm 34.9	Insectivore
Carolina Wren <i>Thryothorus ludovicianus</i>	6	0 (0.0)	6 (100)	0 (0.0)	0.0 \pm 0.0	Insectivore
House Wren <i>Troglodytes aedon</i>	5	3 (60.0)	5 (100)	3 (60.0)	34.0 \pm 35.8	Omnivore
Winter Wren <i>Troglodytes troglodytes</i>	6	0 (0.0)	6 (100)	0 (0.0)	0.0 \pm 0.0	Insectivore
Ruby-crowned Kinglet <i>Regulus calendula</i>	28	5 (17.9)	28 (100)	5 (17.9)	6.1 \pm 14.7	Insectivore
Golden-crowned Kinglet <i>Regulus satrapa</i>	42	9 (21.4)	41 (97.6)	8 (19.1)	9.5 \pm 21.9	Insectivore
American Robin <i>Turdus migratorius</i>	11	11 (100)	6 (54.5)	6 (54.5)	91.8 \pm 8.7	Omnivore
Gray-cheeked Thrush <i>Catharus minimus</i>	8	8 (100)	5 (62.5)	5 (62.5)	85.0 \pm 30.7	Omnivore
Swainson's Thrush <i>Catharus ustulatus</i>	23	22 (95.7)	16 (69.6)	15 (65.2)	80.0 \pm 26.1	Omnivore
Hermit Thrush <i>Catharus guttatus</i>	94	94 (100)	67 (71.3)	67 (71.3)	83.6 \pm 18.9	Omnivore
Veery <i>Catharus fuscescens</i>	15	15 (100)	9 (60.0)	9 (60.0)	82.7 \pm 25.8	Omnivore
Gray Catbird <i>Dumetella carolinensis</i>	209	208 (99.5)	123 (58.9)	122 (58.4)	83.9 \pm 19.6	Omnivore
Cedar Waxwing <i>Bombycilla cedrorum</i>	9	9 (100)	4 (44.4)	4 (44.4)	91.1 \pm 16.2	Omnivore
Red-eyed Vireo <i>Vireo olivaceus</i>	194	194 (100)	185 (95.4)	185 (95.4)	73.9 \pm 19.5	Omnivore
Warbling Vireo <i>Vireo gilvus</i>	4	4 (100)	3 (75.0)	3 (75.0)	72.5 \pm 30.9	Omnivore
Philadelphia Vireo <i>Vireo philadelphicus</i>	7	7 (100)	6 (85.7)	6 (85.7)	72.9 \pm 24.9	Omnivore
White-eyed Vireo <i>Vireo griseus</i>	13	13 (100)	11 (84.6)	11 (84.6)	66.2 \pm 27.3	Omnivore
Solitary Vireo <i>Vireo solitarius</i>	22	19 (86.4)	20 (90.9)	17 (77.3)	48.6 \pm 33.4	Omnivore
Nashville Warbler <i>Vermivora ruficapilla</i>	5	3 (60.0)	5 (100)	3 (60.0)	52.0 \pm 47.6	Omnivore
Northern Parula <i>Parula americana</i>	7	7 (100)	6 (85.7)	6 (85.7)	47.1 \pm 32.5	Omnivore
Black and White Warbler <i>Mniotilta varia</i>	20	4 (20.0)	20 (100)	4 (20.0)	9.0 \pm 21.0	Insectivore
Black-throated Blue Warbler <i>Dendroica caerulescens</i>	42	27 (64.3)	39 (92.9)	22 (52.4)	35.9 \pm 37.5	Omnivore
Magnolia Warbler <i>Dendroica magnolia</i>	8	6 (75.0)	5 (62.5)	3 (37.5)	68.8 \pm 43.2	Omnivore

TABLE 1. Continued.

Bird species	<i>n</i>	No. (%) samples with fruit	No. (%) samples with insects	No. (%) samples with fruit and insects	Percentage ($\bar{x} \pm \text{SD}$) fruit in sample	Diet ^a
Yellow-rumped Warbler <i>Dendroica coronata</i>	357	356 (99.7)	312 (87.4)	311 (87.1)	81.9 \pm 17.0	Omnivore
Black-throated Green Warbler <i>Dendroica virens</i>	6	3 (50)	5 (83.3)	2 (33.3)	45.0 \pm 49.7	Omnivore
Blackpoll Warbler <i>Dendroica striata</i>	18	13 (72.2)	18 (100)	13 (72.2)	41.1 \pm 36.3	Omnivore
Mourning Warbler <i>Oporornis philadelphia</i>	6	5 (83.3)	4 (66.7)	3 (50.0)	76.7 \pm 38.3	Omnivore
Canada Warbler <i>Wilsonia canadensis</i>	5	2 (40.0)	5 (100)	2 (40.0)	24.0 \pm 39.1	Insectivore
Wilson's Warbler <i>Wilsonia pusilla</i>	4	3 (75.0)	4 (100)	3 (75.0)	20.0 \pm 21.6	Insectivore
Ovenbird <i>Seiurus aurocapillus</i>	28	20 (71.4)	25 (89.3)	14 (50.0)	49.1 \pm 41.5	Omnivore
Northern Waterthrush <i>Seiurus noveboracensis</i>	46	38 (82.6)	36 (78.3)	28 (60.9)	65.2 \pm 36.3	Omnivore
Common Yellowthroat <i>Geothlypis trichas</i>	18	16 (88.9)	17 (94.4)	15 (83.3)	62.2 \pm 29.4	Omnivore
Yellow-breasted Chat <i>Icteria virens</i>	5	5 (100)	3 (60.0)	3 (60.0)	92.0 \pm 8.4	Omnivore
American Redstart <i>Setophaga ruticilla</i>	68	13 (19.1)	68 (100)	13 (19.1)	4.3 \pm 12.1	Insectivore
Rose-breasted Grosbeak <i>Pheucticus ludovicianus</i>	5	5 (100)	2 (40.0)	2 (40.0)	96.0 \pm 5.5	Omnivore
Rufous-sided Towhee <i>Pipilo erythrophthalmus</i>	21	21 (100)	15 (71.4)	15 (71.4)	81.4 \pm 17.4	Omnivore
Song Sparrow <i>Melospiza melodia</i>	14	11 (78.6)	12 (85.7)	9 (64.3)	49.3 \pm 40.3	Omnivore
Dark-eyed Junco <i>Junco hyemalis</i>	14	10 (71.4)	7 (50.0)	3 (21.4)	62.1 \pm 45.9	Omnivore
White-throated Sparrow <i>Zonotrichia albicollis</i>	38	35 (92.1)	32 (84.2)	30 (78.9)	62.1 \pm 31.7	Omnivore
Lincoln's Sparrow <i>Melospiza lincolnii</i>	4	3 (75.0)	3 (75.0)	2 (50.0)	65.0 \pm 45.1	Omnivore
Swamp Sparrow <i>Melospiza georgiana</i>	11	9 (81.8)	8 (72.7)	6 (54.5)	51.8 \pm 40.9	Omnivore
Purple Finch <i>Carpodacus purpureus</i>	5	5 (100)	1 (20.0)	1 (20.0)	94.0 \pm 13.4	Omnivore
Total 47 Species	1,532	1,313 (85.7)	1,264 (82.5)	1,042 (68.0)		

^a Diet classifications: Omnivores = mean percent fruit/fecal sample greater than 33%; Insectivores = Mean percent fruit/sample less than or equal to 33%.

Species with small samples given below in the following format: Species: *n*, mean % fruit/sample averaged over all observations (1993–1995). Yellow-billed Cuckoo, *Coccyzus americanus*: 1, 10%; Black-billed Cuckoo, *C. erythrophthalmus*: 3, 6.7%; Great-crested Flycatcher, *Myiarchus crinitus*: 2, 65.0%; Acadian Flycatcher, *Empidonax virescens*: 1, 60%; White-breasted Nuthatch, *Sitta carolinensis*: 2, 45.0%; Red-breasted Nuthatch, *Sitta canadensis*: 3, 0.0%; Brown Thrasher, *Toxostoma rufum*: 2, 75.0%; Tennessee Warbler, *Vermivora peregrina*: 2, 0.0%; Blackburnian Warbler, *Dendroica fusca*: 1, 100%; Chestnut-sided Warbler, *D. pensylvanica*: 2, 90.0%; Cape May Warbler, *D. nigra*: 1, 0%; Bay-breasted Warbler, *D. castanea*: 1, 0%; Palm Warbler, *D. palmarum*: 2, 55.0%; Yellow Warbler, *D. petechia*: 1, 60%; Connecticut Warbler, *Oporornis agilis*: 1, 10%; Hooded Warbler, *Wilsonia citrina*: 3, 13.3%; Field Sparrow, *Spizella pusilla*: 3, 3.3%; Chipping Sparrow, *S. passerina*: 1, 10%; White-crowned Sparrow, *Zonotrichia leucophrys*: 2, 75.0%; Scarlet Tanager, *Piranga olivacea*: 1, 50%; American Goldfinch, *Carduelis tristis*: 1, 0%.

composition). *Viburnum* also was the most frequently used fruit type in 31 of 39 (79.5%) bird species that used two or more fruit species during autumn migration periods. Although thrushes, vireos, emberizine sparrows, and most warblers showed greatest use of *Viburnum*, Yellow-rumped Warblers used *Myrica pensylvanica*

most heavily (identified in 97.5% of all samples). Species-specific descriptions of the relative occurrence of fruit taxa in bird diets are available from the author.

I analyzed a subset of the fecal samples ($n = 912$) from 55 bird species for determination of insect taxa consumption. Hymenoptera (58.4%

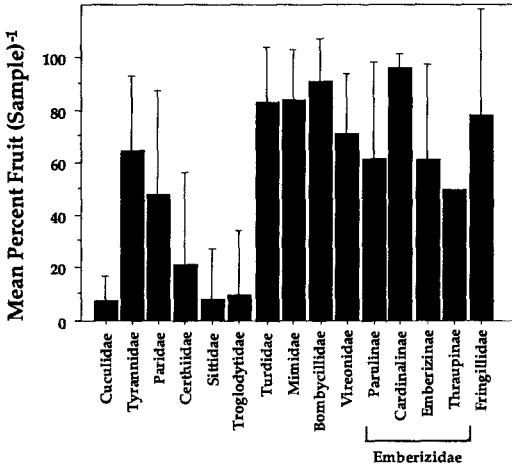


FIGURE 1. Degree of frugivory in Neotropical migrant landbird taxa on Block Island during autumn, 1993–1995, expressed as the mean percent of fruit volume per fecal sample for each taxon. Error bars represent one standard deviation. The family Emberizidae is broken down into the component subfamilies that were sampled.

of all samples), Coleoptera (27.2%), and Diptera (25.0%) most frequently occurred in bird diets. Species-specific descriptions of the relative occurrence of insect taxa in bird diets also are available from the author.

ENERGETIC CONDITION

A total of 1,078 individuals of 18 Nearctic migrant species was recaptured on Block Island between 1969 and 1995, which allowed determination of stopover length and energetic status changes over that period. Numbers of recaptures per species ranged from 4 (the minimum sample size accepted in these analyses) in Blackpoll Warblers and Northern Orioles to 307 in Red-eyed Vireos. Stopover length in recaptured species ranged from a mean (± SD) of 2.57 ± 2.51 days in Golden-crowned Kinglets to 7.17 ± 6.42 days in Ovenbirds. To determine a conservative estimate of the proportion of the transient population sampled through recaptures, I calculated the mean proportion of birds that were recaptured in the same season. Recapture rates ranged from less than 0.1% of the banded population in four species (Table 2) to 28.3% of banded birds for Northern Waterthrushes, with a mean recapture rate of 6.5% across species. Ruby-crowned Kinglets showed the lowest percent of recaptures gaining mass (30.8%), whereas more than

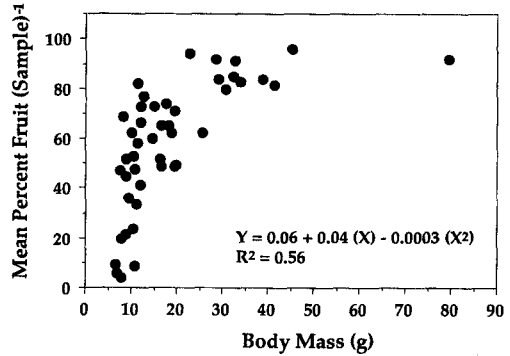


FIGURE 2. Mean degree of frugivory (mean percent fruit volume per fecal sample) in relation to mean body mass of sampled species during autumn migration, 1993–1995 on Block Island, Rhode Island. Body masses are from Clench and Leberman (1978).

71% of *Catharus* thrushes gained mass on Block Island (Table 2). The proportion of recaptured individuals gaining mass was positively correlated with the recapture rates for a given species ($r = 0.49, n = 17, P = 0.046$).

Recapture analyses for species with $n > 3$ revealed significant changes in mass, energetic condition, and fat score for several species (Table 2). Nine (52.9%) of the recaptured species significantly improved their energetic status from first to last capture. Significant gains in mass, energetic condition, and fat score occurred in the Gray-cheeked Thrush, Swainson's Thrush, Veery, Hermit Thrush, Red-eyed Vireo, Phila-

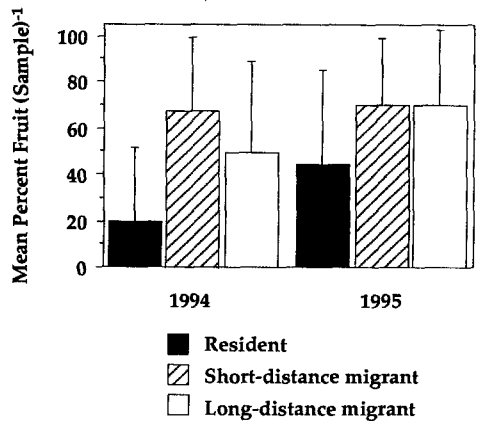


FIGURE 3. Degree of frugivory during autumn, 1994 and 1995 in landbirds differing in migratory status. Bird species were classified as residents, short-distance migrants, or long-distance migrants according to Hussell et al. (1992) and Rappole et al. (1993).

TABLE 2. Percent of individuals recaptured, mean stopover length, percent of individuals gaining mass, and differences in energetic status between first and last captures of migrating landbirds recaptured on Block Island, Rhode Island between 1969–1995. All significant differences in energetic status changes between captures are positive.

Species (n)	Percent recaptured	Stopover length ^a (days)	Percent gaining mass	Mass (g) ^b		Energetic Condition ^{a,b}		Fat Score ^a	
				First capture	Last capture	First capture	Last capture	First capture	Last capture
Ruby-crowned Kinglet (13)	5.0	2.6 (2.6)	30.8	6.09 (0.52)	6.15 (0.64)	3.48 (0.50)	3.51 (0.46)	0.93 (0.58)	1.08 (1.20)
Golden-crowned Kinglet (25)	0.5	3.4 (2.8)	40.0	5.83 (0.59)	5.70 (0.55)	3.35 (0.29)	3.30 (0.30)	0.96 (0.81)	0.76 (0.69)
Gray-cheeked Thrush (98)	8.3	4.3 (3.1)	80.6	33.39 (4.12)	37.33 (6.02)**	3.53 (0.47)	3.94 (0.63)**	1.62 (1.20)	2.42 (1.21)**
Swainson's Thrush (110)	10.2	5.1 (4.0)	73.6	30.64 (3.09)	33.20 (4.30)**	3.61 (0.48)	3.91 (0.58)**	1.00 (0.90)	1.90 (1.20)**
Hermit Thrush (121)	7.2	4.3 (4.8)	73.6	29.95 (2.43)	31.19 (5.83)*	4.28 (0.41)	4.46 (0.86)**	0.80 (0.81)	1.33 (0.96)**
Veery (95)	12.2	4.3 (3.0)	75.8	32.85 (3.68)	35.74 (5.07)**	3.94 (0.48)	4.29 (0.64)**	1.18 (1.03)	1.93 (1.14)**
Red-eyed Vireo (307)	5.9	4.5 (4.4)	71.0	18.39 (2.27)	19.96 (3.11)**	4.06 (0.53)	4.41 (0.69)**	1.34 (1.03)	1.89 (1.12)**
Philadelphia Vireo (13)	<0.0	4.4 (2.6)	61.5	11.91 (1.57)	13.10 (2.08)*	4.66 (0.66)	5.19 (0.97)*	1.23 (1.24)	2.08 (1.26)*
Black and White Warbler (5)	1.4	4.6 (2.6)	40.0	10.96 (0.67)	10.82 (0.95)	3.86 (0.41)	3.81 (0.39)	1.80 (0.84)	1.20 (1.10)
Black-throated Blue Warbler (35)	14.9	4.3 (2.4)	45.7	9.08 (0.73)	9.13 (0.78)	4.07 (0.49)	4.09 (0.50)	0.62 (0.83)	0.70 (0.82)
Magnolia Warbler (6)	<0.0	6.3 (5.2)	66.7	9.48 (2.03)	9.63 (1.52)	5.50 (1.29)	5.56 (0.87)	2.33 (1.51)	2.00 (1.41)
Yellow-rumped Warbler (166)	1.1	6.2 (5.4)	63.3	12.53 (1.24)	13.08 (1.41)**	3.76 (0.43)	3.93 (0.49)**	1.12 (0.98)	1.45 (1.14)**
Blackpoll Warbler (4)	<0.0	3.5 (2.9)	50.0	13.23 (2.01)	13.40 (1.76)	3.55 (0.52)	3.61 (0.59)	1.75 (1.50)	1.62 (1.11)
Ovenbird (18)	10.3	7.2 (6.4)	66.7	20.32 (2.56)	21.20 (3.19)*	5.28 (0.96)	5.51 (1.10)*	1.47 (1.08)	1.36 (1.25)
Northern Waterthrush (39)	28.3	5.9 (5.7)	79.5	17.27 (1.96)	18.84 (2.23)**	4.59 (0.71)	5.01 (0.84)**	1.50 (1.16)	1.90 (1.08)*
Yellow-breasted Chat (4)	<0.0	5.2 (4.7)	50.0	25.45 (4.01)	27.42 (1.73)	6.57 (0.96)	7.12 (0.89)	1.25 (0.87)	1.88 (1.03)
American Redstart (15)	5.4	4.9 (3.7)	46.7	8.34 (0.65)	8.17 (0.76)	3.91 (0.57)	3.82 (0.41)	1.20 (1.07)	1.23 (1.03)

^a Mean (\pm SD).

^b Energetic Condition index = mass-10⁶-wing chord⁻³.

* $P < 0.05$, ** $P < 0.01$; two-tailed paired t -test.

delphia Vireo, Yellow-rumped Warbler, Ovenbird, and Northern Waterthrush (Table 2).

If a species did not show mass gains in recapture analyses, non-recaptured individuals still may have gained sufficient energy stores within one day to depart Block Island for further migratory flight (Winker et al. 1992). To determine if such diurnal mass gain occurred, I regressed time of capture against energetic condition for all 17 of the recaptured species. Only Red-eyed Vireos displayed significantly positive diurnal changes in the energetic condition index ($F_{1,220} = 8.03, r^2 = 0.04, P < 0.01$), although Hermit Thrushes approached a significant positive relationship ($F_{1,149} = 3.66, r^2 = 0.02, P = 0.058$). Both of these species also showed significant energy gains by recapture analyses (Table 2). Linear regression failed to show significant diurnal energy changes for any other species.

PATTERNS OF ENERGETIC CONDITION IN RELATION TO DIET

I conducted further analyses to quantify the relationship of diet with energetic condition and stopover length at the species level. I classified the 17 species with recapture data as omnivores and insectivores as in Table 1. Recapture rate of omnivores and insectivores on Block Island did not differ (Mann-Whitney $U = 19.0, P = 0.42$), but high proportions of *Catharus* thrushes and both *Seiurus* species were recaptured (Table 2). Stopover length also did not vary significantly between omnivores ($\bar{x} = 5.05 \pm 1.06$ days, $n = 13$) and insectivores ($\bar{x} = 3.89 \pm 1.09$ days, $n = 4, U = 14.0, P = 0.17$). However, a greater proportion of recaptured omnivores ($\bar{x} = 66.00 \pm 11.49\%$) than insectivores ($\bar{x} = 39.38 \pm 6.53\%$) gained mass during stopover on Block Island ($U = 1.0, P < 0.01$).

I compared the total change, rate of change (score/day) and the percent change in energetic condition index and fat score between the two diet types. All three measures differed significantly between omnivores and insectivores for both energetic condition and fat score (Table 3). Omnivores showed positive energy changes, whereas insectivores declined in energetic condition and lost fat stores during stopover.

In regressions of the mean energetic condition of recaptured individuals against the degree of frugivory of a species, neither fat score nor energetic condition at first capture varied with extent of frugivory in Nearctic migrants (Table 4).

TABLE 3. Differences in energetic condition and fat score changes between omnivores and insectivores on Block Island, Rhode Island during autumn migration, 1970-1995. Energetic condition and fat score indices are independent of body size, and changes in these indices are directly comparable across taxonomic groups.

Diet ^a	Energetic Condition ^b mean (\pm SD)			Fat score mean (\pm SD)		
	Change	Rate (score/day)	Percent change (% original score)	Change	Rate (score/day)	Percent change (% original score)
Omnivores ($n = 1,026$)	0.28 \pm 0.18	0.04 \pm 0.04	6.96 \pm 3.93	0.41 \pm 0.39	0.06 \pm 0.12	41.78 \pm 36.00
Insectivores ($n = 54$)	-0.05 \pm 0.06	-0.04 \pm 0.01	-0.72 \pm 1.71	-0.13 \pm 0.36	-0.10 \pm 0.10	-5.59 \pm 36.97
F	3.58**	4.08**	3.73**	2.50*	2.38*	2.29*

^a Diet classifications: omnivore = mean percent fruit volume per fecal sample greater than 33%; insectivore less than or equal to 33% fruit volume per sample.
^b Energetic Condition index = mass $\cdot 10^6$ wing chord⁻³.
^c Two-tailed, unpaired *t*-test. * $P < 0.05$, ** $P < 0.01$.

TABLE 4. Results of linear regression analyses between mean volumetric proportion of fruit in fecal samples for each species and indices of the species' energetic status.

Energetic Status Index	Slope	r ²	F
Energetic Condition (EC)			
Energetic condition at first capture	0.92	0.17	3.05
Energetic condition at last capture	1.36	0.29	6.06*
Total EC change	0.45	0.66	29.54***
Percent EC change	10.52	0.70	34.20***
Fat Score			
Fat score at first capture	0.05	<0.01	0.03
Fat score at last capture	0.93	0.54	17.87***
Total fat score change	0.85	0.56	18.96***
Percent fat score change	81.02	0.58	20.94***

* $P < 0.05$, *** $P < 0.001$.

However, both energetic condition and fat score at last capture showed a significant positive increase with the mean degree of frugivory for a species (Table 4). The total change and percent change in energetic condition and fat score also increased significantly with the amount of fruit in the diet (Table 4). I further regressed the rate of change in fat score and energetic condition per day against the amount of fruit in the diet (Fig. 4). The degree of frugivory explained 72% and 57% of the variance in the rate of change in energetic condition and fat score, respectively. Both measures increased significantly with frugivory (Fig. 4).

DISCUSSION

Nearctic-Neotropical migratory landbirds demonstrated dietary expansion to include fruit during migration on Block Island. Frugivory was widespread across the migrant community, frequent in occurrence within species, and extensive within individuals. Moreover, extensive frugivory corresponded with significant mass gain prior to departure in many species. A significant positive relationship existed between the degree of frugivory and a species' change in energetic condition on Block Island. These results suggest that the degree of frugivory in Nearctic-Neotropical migratory landbirds is more extensive during autumn migration than previously assumed, and strategies of dietary plasticity may enhance migrants' abilities to gain mass during migration (Bairlein 1990, Stoate and Moreby 1995).

DIETARY PATTERNS

Many of the species reported here are known to consume fruit (Malmborg and Willson 1988,

White and Stiles 1990). However, this is one of the first quantitative accounts of frugivory during migration that covers many species, including several warblers, vireos, and sparrows. The degree to which each of these species used fruit also is unprecedented: some fruit material occurred in over 85% of the fecal samples collected, and the average proportion of a fecal sample that was fruit for any one species reached a maximum of 96%. These results suggest that even species once thought to be stereotypically insectivorous (e.g., Black-throated Green Warblers or Northern Waterthrushes) use fruit resources to some extent during migration. Dietary plasticity was thus a widespread phenomenon during autumn migration, presumably in response to heightened energetic demand (Bairlein and Gwinner 1994) and/or variable resource abundances during migration (Parrish 1997).

Several highly omnivorous species exploited *Viburnum* more than other species of fruit, perhaps because of its high abundance on Block Island (Parrish 1997, in press) and its high lipid and energy content (White 1989, Parrish 1997). Of particular interest, however, is the almost exclusive use by Yellow-rumped Warblers of the waxy fruits of *Myrica pensylvanica*. No other migrant used *Myrica* as frequently or extensively as *D. coronata*. The relationship between *Myrica* and Yellow-rumped Warblers is one of the few in this system that approached the level of exclusivity reported for some tropical-fruit-bird interactions (Herrera 1981). Species that only occasionally ingested fruit often foraged solely on *Viburnum* or *Myrica*, probably as a result of the predominance of these two fruits on

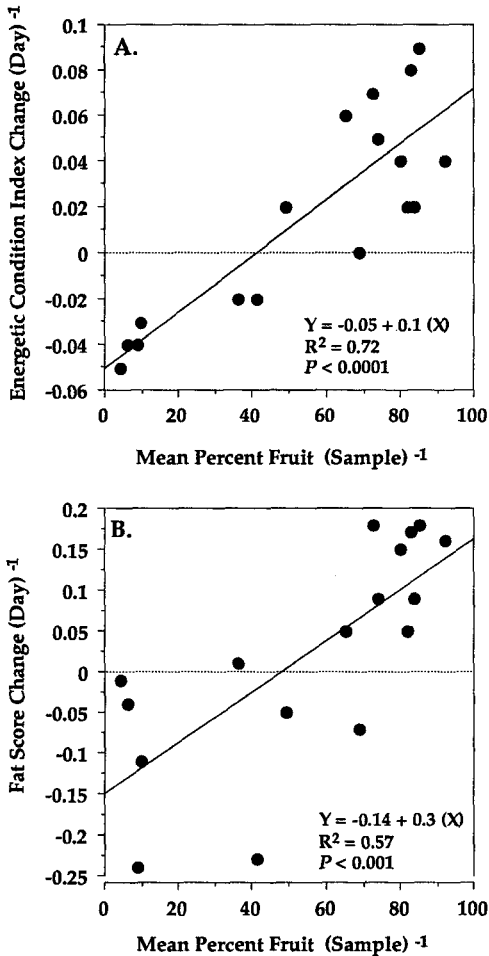


FIGURE 4. Relationship between rate of change in energetic condition (mass-100,000-wing chord⁻³) and fat score, versus degree of frugivory for recaptured species on Block Island, Rhode Island during autumn migration, 1993–1995. Degree of frugivory was measured as the mean percent fruit volume per fecal sample. Energetic condition and fat score are means from birds recaptured within one autumn migration on Block Island. Sample sizes as in Table 2.

Block Island (Parrish 1997, in press) and their small size relative to the bill morphology of most migrant landbirds (Wheelwright 1985). Although *Viburnum* and *Myrica* fruits were consumed heavily at the site, these fruit species also were highly abundant. Absolute preferences (disproportionate use relative to abundance) therefore can only be inferred outside of the context of fruit abundance.

Insects made up only a minor volumetric fraction of sampled fecal material in many species.

For those species capable of frugivory, only small volumes of insect resources may actually be needed to meet protein and additional lipogenic demands during migration. For example, fruits may assist in meeting metabolic needs and increasing energetic stores (Foster 1987, Witmer 1994), thereby lowering the insect volume required for protein and additional fat deposition.

Dietary patterns in this study were recorded from a high proportion of young birds typically found in migrant populations in coastal regions of North America ("the coastal effect," *sensu* Ralph 1978). Migrant behavioral ecology at such sites is particularly relevant, because coastal locations are known to be spatial bottlenecks for migrant populations (Moore et al. 1995). Thus, ecological phenomena at these sites become particularly important in understanding aspects of migrant ecology that influence behavioral responses to migration demands for large proportions of the population. Furthermore, frugivory also is common in interior continental regions (Whelan and Willson 1994) where older individuals of migrant populations are known to be abundant. Frugivory may therefore not be an age-dependent behavior, although I lacked sufficient data for statistical comparison of the diets of young and old birds at Block Island. In addition, few studies are yet available that extensively quantify migrant diets in relation to energetic condition at inland sites, where fruit is often less abundant than at coastal sites such as Block Island. Until such data are available, results from Block Island must be carefully extrapolated to other sites and migrant communities.

Reports of frugivory are not limited to autumn migration, and frugivory is frequently reported in these taxa during the overwintering period, especially during the tropical dry season (Greenberg 1981, Blake and Loiselle 1992). Adults of some species (e.g., Hermit Thrush and Wood Thrush) begin frugivory during fledging periods immediately after the nutrient or energetic constraints of reproduction are relaxed (pers. observ.). Frugivory also is prevalent during spring migration on fruits that remain from the previous autumn or winter in both the Temperate (Willson 1990, J. Clark and F. Moore, pers. comm.) and Tropical Zones (Blake and Loiselle 1992, Stoate and Moreby 1995). Perceptions of Nearctic-Neotropical landbird migrants as strict insecti-

vores across all taxa may therefore be an incorrect generalization (Levey 1994).

ENERGETIC CONDITION AND MIGRATORY STRATEGIES ON BLOCK ISLAND

The large volume of migrants that encounters Block Island has been forced off the mainland coast by low pressure systems. Many species subsequently reorient northward to return to the mainland (Able 1977). Consequently, it is possible that many birds depart the island within 24 hr of arrival if sufficient energy stores can be gained during the day (Winker et al. 1992). Regressions of energetic condition versus time of capture suggest that energy gains within one day are negative or insignificant in all but two species, the Red-eyed Vireo and Hermit Thrush. Unless their reoriented flight was short and capable of being fueled solely by previously accrued, arrival fat stores, it is doubtful that any species gained sufficient mass during foraging within one day for long-distance nocturnal migrations. Stays of longer than one day are probably necessary for most species to gain significant mass at the site.

Decisions to stay or depart may be based on a balance of factors including remaining energetic stores upon arrival (Moore 1990), meteorological conditions (Alerstam 1979), and the likelihood of mass gain in the dense fruiting shrubland of Block Island (Biebach 1990). Many migrant species remaining on Block Island exhibited significant positive gains in energetic condition and fat scores during stopover, suggesting that if they remained to feed at the site, significant lipid deposition could occur (Table 2). If likelihood of mass gain is an important metric for decisions to remain on Block Island or to depart in attempts to find another suitable stopover site, then recapture rates should increase with the proportion of birds gaining mass, assuming that birds can assess such critical features during migration (Moore et al. 1995). There was a significant positive relationship between likelihood of recapture and proportion of individuals of a species gaining mass on Block Island, suggesting that birds may have made stopover decisions based on the probability of mass gain. Although there was no relationship between proportion of recaptures and extent of frugivory of a species, the *Catharus* thrushes and *Seiurus* warblers both showed high degrees of frugivory, mass gain, and recapture rates (Ta-

bles 1 and 2), suggesting that the fruit-bearing coastal shrubland of Block Island was a suitable stopover area during migration for these species.

ENERGETIC CONDITION AND DIET DURING MIGRATION

Species consuming large quantities of fruit improved their energetic status on Block Island, whereas insectivores declined in both energetic condition and fat score (Table 3, Fig. 4). Similar patterns have been reported for Palearctic migrants in spring by Stoate and Moreby (1995) and in Spain by Jordano (1988). Insectivores in the energetic condition analyses reported here for Block Island were few in number, represented by four species. It is possible that lack of improvement in energetic status for this group resulted from the smaller sample sizes of insectivorous species in this study, and more data are needed from sites where insectivores are more common.

Two of the four insectivorous species on Block Island were shorter distance migrants, i.e., the Golden-crowned and Ruby-crowned Kinglets. Whereas shorter distance migrants might be expected to have lower fat loads and require less energy gain than longer-distance migrant species due to their different migratory strategies, all four insectivorous species demonstrated *declines* in energetic condition instead of smaller increases as would be expected. Furthermore, regressions of energetic status change against degree of frugivory emphasize that omnivorous species were more capable of improving energetic condition on Block Island, regardless of migratory distance (Table 4, Fig. 4). Regressions of energetic condition against time of capture within a day failed to show significant increases in energetic condition in all but one species, the Red-eyed Vireo, which was itself highly omnivorous. This result refutes the alternative that insectivorous migrants gained sufficient mass within one day to depart Block Island and therefore were not included within recapture samples.

Several hypotheses may be offered to explain the inability of insectivores to achieve energy gain on Block Island. First, the majority of insectivores might depart the island as soon as possible after assessing that conditions are not adequate for refueling. Those insectivores that remain must then attempt energetic gain under potential constraints of competition with omnivores that have remained for refueling (Moore

and Yong 1991). Second, predation may play a role in the ability of insectivores to achieve a positive energy balance (Howe 1979). Insectivores use faster, more active and noticeable maneuvers during foraging than do frugivores (Parrish 1997, in press), and often include behaviors in their repertoire that expose them in space and time to flying predators (falcons and accipiters) whose own migrations coincide with that of landbird migrants (Aborn 1994). Frugivores, in contrast, can perch in one location, move relatively little, and forage amidst dense vegetation without compromising their abilities to encounter fruit "prey" (Parrish 1997, in press). Thus, predation risk may result in birds failing to forage effectively and ultimately impose negative energy budgets (Metcalf and Furness 1984).

Alternatively, dietary plasticity may be the most appropriate strategy in stopover locations where high abundance of fruit resources allows for rapid, continuous energy intake with little energy expenditure. Fruits traditionally have been viewed as a patchy resource for birds (Levey 1988), but the patchy distribution patterns typical of fruit resources in other habitats may effectively dissipate if fruits are a superabundant resource. Evidence that fruit on Block Island is superabundant for migrants includes: (1) in three years of surveys, birds never removed entire fruit crops, and large volumes of fruit crops remained to rot, desiccate, and fall to the ground long after the passage period of migrant birds (Parrish 1997, in press), (2) interspecific and intraspecific aggression at fruit sources was uncommon (Parrish, unpubl. data), and (3) estimates of the percent depletion of the original fruit crop made at the site vary from approximately 25% to 40% in the three most common fruit species used by migrants on Block Island in 1993 and 1994 (Parrish 1997, in press). Fruit on Block Island was widespread such that birds moving from one large infructescence or aggregation of fruiting shrubs to another seldom had to move more than a few meters. Coastal shrubland is therefore characterized by high fruit abundance (Parrish 1997) and, consequently, can represent suitable stopover habitat for omnivorous species.

HYPOTHESES FOR THE EVOLUTION OF FRUGIVORY DURING MIGRATION

Results presented here shed light on hypotheses of the evolution of frugivory during migration.

Three nonexclusive hypotheses have been offered to explain why birds consume fruit at this time: (1) resource availability, (2) phylogenetic inertia, and (3) net energy assimilation. Several authors have proposed that birds have evolved endogenous changes in diet preferences in response to shifts in resource abundance (see Bairlein and Gwinner 1994 for review). During autumn, insect abundances presumably decline rapidly and are not present to fuel the migratory flights of diurnally foraging songbirds (Berthold 1976). Simultaneously, fruiting phenologies coincide with migrant bird passage (Thompson and Willson 1979). Birds are therefore presumably forced to feed upon fruits as an alternative diet simply due to lack of availability of preferred insect resources.

Second, Nearctic-Neotropical migratory landbirds may have arisen from tropical taxa that were originally omnivorous in diet (Levey and Stiles 1992). The use of insects during the reproductive period may therefore be a brief seasonally-specialized adaptation that meets protein needs for the production of eggs, feeding of young, and completion of molt prior to migration to the tropics (Morton 1973, Izhaki 1992). The "phylogenetic inertia" hypothesis states that, although they may currently experience benefits from frugivory during migration, migrants are reverting to omnivory, a phylogenetically conservative behavior that may have been the precursor for the evolution of the migratory life history strategy itself (Levey and Stiles 1992). Several taxa exhibiting high degrees of frugivory during migration are probably of tropical origin (Levey and Stiles 1992, Fig. 1). However, many of these species do not maintain the same level of dietary plasticity during the wintering period in the tropics and once again become stereotypically insectivorous during winter residence (e.g., Northern Waterthrushes, Poulin et al. 1994; Swainson's Thrush, Blake and Loiselle 1992). For some, such as Swainson's Thrush, frugivory will then remain low until spring migration through the tropics (Blake and Loiselle 1992).

The third hypothesis, that migrants enhance net energy uptake for lipogenesis when fruit is consumed during migration, has been widely debated (Berthold 1976, Bairlein and Gwinner 1994). Comparisons of the direction and extent of energetic change between omnivorous and insectivorous migrants (Table 3) and regression

analyses of change in energetic stores with degree of frugivory on Block Island (Table 4, Fig. 4) demonstrate an energetic advantage to omnivory during stopover periods. Results published here corroborate findings in Palearctic migrant systems (Bairlein 1990, Stoate and Moreby 1995), and support the "energy assimilation hypothesis."

FRUGIVORY AND LANDBIRD CONSERVATION DURING MIGRATION

Evidence reported here corroborates suggestions by Blake and Loiselle (1992) and Martin (1985) that some migrating birds require fruit resources for successful refueling during stopover periods. Highly omnivorous passage birds on Block Island improved their energetic condition more efficiently than did strictly insectivorous species. Because it facilitates energy gain, I suggest that frugivory in migrant landbirds may distinguish particular fruit-bearing stopover locations as important sites for resting and refueling during migration (Winker et al. 1992, Moore et al. 1995).

Migrating birds that expand their diets to fruit will require different resources and perhaps different habitats (Bairlein 1983, Blake and Loiselle 1991, 1992) during migration than are used at other times of the annual cycle. If migrants select habitats high in fruit abundance during migration as has been suggested (Bairlein 1983, Martin 1985), then second growth habitats and shrubland in coastal regions may be critical for conservation planning during the migration phase of the annual landbird cycle. As human population densities increase disproportionately in coastal regions of North America (Cullitan et al. 1990, Weber 1994), recognition of the dynamic nature of migratory landbird behavior and of seasonal bottlenecks in migratory bird populations during passage through coastal areas will be essential (Moore et al. 1995). Conservation efforts that consider only behaviors of migrants characterizing reproductive periods (such as breeding season insectivory) or the wintering period, while ignoring migration, will jeopardize a holistic and effective conservation strategy (Levey 1994).

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