

## BEHAVIORAL, ENERGETIC, AND CONSERVATION IMPLICATIONS OF FORAGING PLASTICITY DURING MIGRATION

JEFFREY DAVID PARRISH

**Abstract.** Dietary plasticity is widespread and frequent in many landbird species during migration and typically involves shifts from stereotyped insectivorous diets during the breeding season to inclusion of other animal or plant matter, especially fruit. As with other forms of behavioral plasticity, flexibility in diet has probably evolved in response to environmental uncertainty, which, I argue, most landbirds encounter in terms of food resource availability during migration. The spatial and temporal uncertainty in insect availability during autumn stopover may have influenced the evolution of dietary flexibility during migration. Experiments and empirical observations from studies on Block Island, Rhode Island, off the northeastern coast of North America demonstrate that seasonal dietary shifts to fruit can strongly affect *en route* foraging behavior, habitat use, and migratory departure decisions. Migrants feeding on fruit use less expensive foraging behaviors, encounter more "prey" items per unit time, and perform fewer search movements than when feeding on insects. Furthermore, fruit removal experiments revealed that the presence of fruit influenced the habitats selected by frugivorous migrants such as Yellow-rumped Warblers (*Dendroica coronata*) during autumn. Because of seasonal frugivory, many species are selecting habitats that are different from those selected at other times of the year. Furthermore, dietary shifts also play a major role in migrant energy budgets during stopover by increasing energy intake while decreasing the energy expended during stopover foraging. Experiments with Red-eyed Vireos (*Vireo olivaceus*) and *Catharus* thrushes suggest dietary plasticity can increase energy intake and facilitate lipogenesis in species capable of assimilating novel diet types. Use of more temporally and spatially stable fruit resources may also decrease searching and handling time, and decrease energy expenditure during stopover foraging, resulting in positive net energy budgets for migrants. Aspects of migrant biology that change during the annual cycle, such as dietary shifts to fruit, must be integrated into conservation plans for landbird populations during migration.

**Key Words:** diet, energy budgets, foraging behavior, frugivory, plasticity, resource abundance, stopover ecology.

The behavioral ecology of nearctic-neotropical landbirds during migration is not a simple extension of the breeding or wintering season biology. Environmental and physiological pressures, such as increased energetic demand from nocturnal flights or unpredictable variation in habitat and resource availability, may be quite different during migration than at other periods during the annual cycle. These pressures have strong implications for the evolution of migrant behavior, life history, and population dynamics (Moore 1991a). One mechanism used by migrants to cope with these pressures is the ability to be flexible in behavior during migration. Migrating landbirds demonstrate this behavioral plasticity in a variety of ways, including flexibility in habitat selection, foraging maneuvers, and social interactions. An additional strategy used by many species is dietary plasticity, particularly visible as an expansion from insectivory during the breeding season to a diet including large proportions of fruit during migration. This dietary plasticity can profoundly influence the behavior, energy budgets, and ultimately the conservation of migrant landbirds during stopover periods.

### BEHAVIORAL PLASTICITY

Behavioral plasticity has received extensive theoretical and empirical attention (e.g., Klopfer

and MacArthur 1960, Klopfer 1967, Levins 1968, Stephens and Charnov 1982; Greenberg 1984a,c, 1987a, 1990; Ford et al. 1990, Martin and Karr 1990). Plasticity can be viewed as more than the simple antithesis of specialization (Morse 1980a), as has been suggested in the earlier use of the term (Klopfer and MacArthur 1960). Earlier, "plasticity" was used to define the resource or behavioral breadth of an organism, but Morse (1980a) first suggested that the concept of plasticity extends beyond the generalist and specialist dichotomy. He suggested that stereotypy and plasticity were the exploitation of resources under changing conditions in consistent and variable manners, respectively, and that plasticity was characterized by behavior that lacked long-term predictability in time or space. Greenberg (1990) proposed a further, functional definition: plasticity is the flexibility of organisms of the same genotype to vary in phenotype in the face of change. This definition of plasticity best suits the changing biology of nearctic-neotropical migrant landbirds, given their very diverse behavioral repertoire when experiencing spatio-temporally unpredictable environments.

Environmental instability can influence the evolution of behavioral and life history strategies through random shifts in direction and magnitude of selection pressures (Alerstam and Enckell 1979, Real 1980, Thompson 1991,

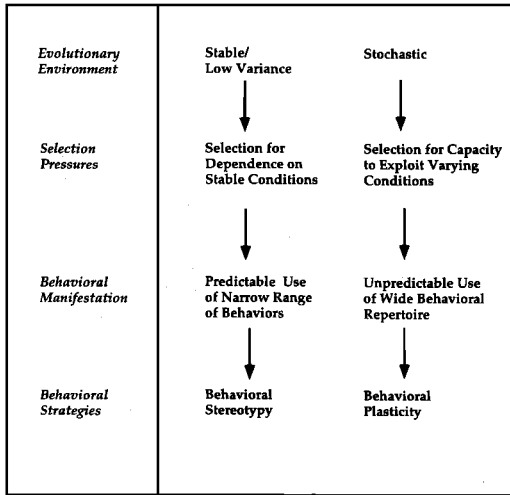


FIGURE 1. Evolutionary environment and selection pressures under which behavioral stereotypy or plasticity may evolve.

Schmitt 1994). Species faced with such frequent instabilities in selection pressure are left with few evolutionary behavioral options beyond the ability to diversify behaviors (Real 1980, Mangel and Clark 1988, Sherry 1990; Fig. 1). When confronted with uncertainty of expected fitness due to unpredictably changing environmental conditions, the optimal behavioral strategy for an organism may be the capacity to diversify the use of fitness-related behaviors—behavioral plasticity (Real 1980, Stephens and Charnov 1982, Real and Caraco 1986).

#### ENVIRONMENTAL UNCERTAINTY AND FORAGING PLASTICITY DURING MIGRATION

Though the migratory journey itself may be obligate, migrating landbirds are confronted with great environmental uncertainty between the temperate breeding grounds and tropical wintering areas, and consequently exhibit behavioral plasticity during stopover periods (Martin and Karr 1990, Parrish 1997). After energetically demanding nocturnal flights, migrants are frequently forced to stop in unfamiliar habitats to refuel for subsequent migratory efforts. During this journey, habitats, weather conditions, and the quality and availability of some resources change unpredictably (Moore 1991a; Fig. 2). Although food resource availability at this time is typically declining (Fig. 2), it does so in a manner heavily dependent on environmental conditions at the precise time and location of foraging (Parrish 1996). Furthermore, extrinsic factors such as unpredictable weather (especially wind velocity and direction) may force migrants to fly undesirable

trajectories and settle in unprofitable, or at least unexpected, stopover sites (e.g., Able 1977, Hutto 1985b, Lindström and Alerstam 1986, Moore and Simons 1992a). For example, the large abundances of migrants on coastal chenier islands of the Gulf of Mexico and glacial moraine islands off the New England coast are dependent on the frequent yet irregular fronts that displace migrating passerines and force birds to settle in areas that stray from "preferred" continental migratory paths (e.g., Able 1977, Moore et al. 1990, Morris et al. 1994, Parrish 1997). Moreover, resting and restoration of lipid reserves must occur under high, yet unpredictable predation risk. Several species of falcon appear to synchronize their migration with peak movements of migratory passerines, yet their abundance and distribution in any given location can not easily be predicted (Metcalf and Furness 1984, Moore et al. 1990, Aborn 1994). The probabilities of surviving *en route* contingencies are diminished by the poor energetic condition of many passage migrants upon arrival at a stopover site. Low energy reserves and the need to replenish them limit the energy and time available for efficient habitat selection, resource acquisition, and predator avoidance during stopover (Moore et al. 1990). To cope with these constraints, migrants may exhibit behavioral plasticity during migration in their habitat selection (Parnell 1969, Bairlein 1983, Winker et al. 1992a), foraging behavior (Hutto 1981, Loria and Moore 1990, Martin and Karr 1990), and dietary shifts (Berthold 1976a,b; Wheelwright 1988, White and Stiles 1990, Willson 1991, Parrish 1997).

#### FRUGIVORY THROUGHOUT THE NONBREEDING PERIOD

Throughout the nonbreeding period many species of landbird migrants range widely in the degree of dietary plasticity. Records of diet shifts to frugivory, for example, are widespread throughout both the spring and autumn migrations and overwintering periods for a variety of taxa (Appendix). During autumn migration, some warbler species, such as American Redstarts (see Appendix for scientific names of all nearctic-neotropical migrants) at northern stopover sites, continue to feed when possible on insect types similar to those used during breeding (Parrish 1997). Other species may shift to use additional insect types, responding to diminishing nutrient demands of reproduction and the changing availability of insect prey during autumn, such as the shift from lepidopteran larvae to extensive use of Diptera and Homoptera by some Palearctic warblers (Bibby and Green 1981, 1983) or Hymenoptera by many neotropical migrants at a northern site (Parrish 1997).

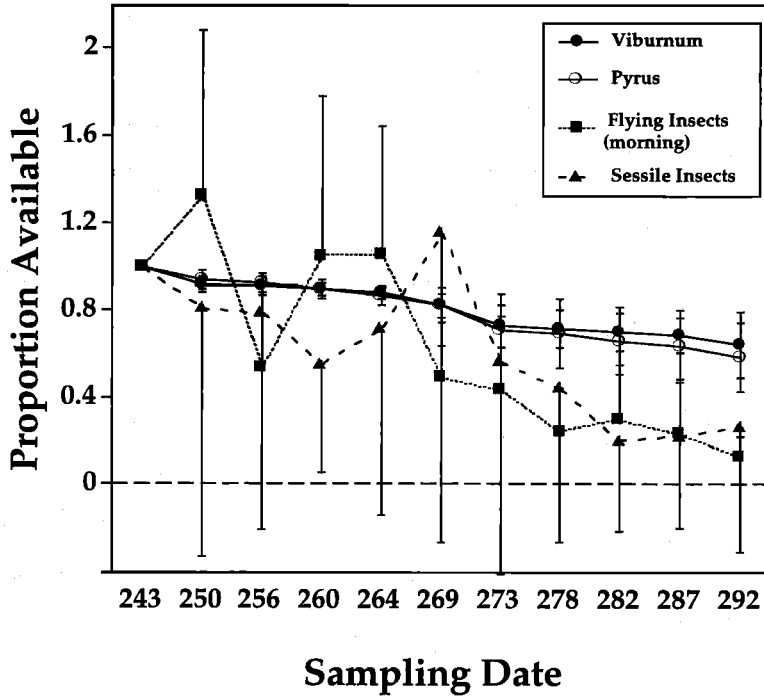


FIGURE 2. Decline in fruit and insect resources sampled at ten sites during autumn migration on Block Island in 1994. Fruit species sampled were *Viburnum recognitum* and *Pyrus melanocarpa*, and insects were sampled as flying insects (through sticky traps) and sessile insects (through branch fumigation counts). Error bars represent one standard deviation and demonstrate high variances about the mean for insect resources throughout the season. Sampling dates are 31 August (Julian date 243) through 19 October (Julian date 292).

Still other migrants may begin to feed on non-insect arthropods, e.g., marine amphipods and other invertebrates taken by Yellow-rumped Warblers late in migration (J. Parrish, pers. obs.). Perhaps the most widespread pattern of diet shifts, however, is that from largely insectivorous diets to include high proportions of fruit, as is common among many migrant thrushes (Turdidae), vireos (Vireonidae), mimids (Mimidae), and wood-warblers (Parulidae). Such extensive frugivory during autumn migration has been

widely documented in both palearctic and nearctic migration systems (e.g., Izhaki and Safrieli 1985, Johnson et al. 1985, Jordano 1988, White and Stiles 1990, Levey and Stiles 1992, Parrish 1997). Because diet shifts to fruit represent an inclusion of resources differing extensively in distribution and nutritional content (Table 1), and because these shifts are almost complete in some migrating landbird species, they present an important opportunity to explore the consequences of seasonal dietary changes for the be-

TABLE 1. QUALITATIVE COMPARISON OF RELATIVE NUTRIENTS AND DISTRIBUTION OF FRUIT AND INSECT RESOURCES FOR MIGRATORY LANDBIRDS (SUMMARIZED FROM MOERMOND AND DENSLOW 1985)

Character	Fruit	Insects
Protein content	Low	High
Carbohydrate content	High	Variable
Fat content	Low in northern latitudes (some species with high lipid content)	High
Rate of autumnal decline	Slow, present through much of autumn	Rapid, variable and unpredictable
Distribution	Clumped; patchy	Variable; not clumped. High spatial and temporal variance
Ease of capture	High	Low
Detectability	High	Variable

TABLE 2. DIET OF RED-EYED VIREO AND *CATHARUS* THRUSHES DURING AUTUMN MIGRATION ON BLOCK ISLAND, RHODE ISLAND, ON THE NORTHWESTERN ATLANTIC COAST (1993–1995), AND DURING SPRING MIGRATION ON HORN ISLAND, MISSISSIPPI, ON THE GULF OF MEXICO COAST (1994–1995) BASED ON ANALYSES OF FECAL SAMPLES FROM MIST-NETTED BIRDS

Species	Autumn migration				Spring migration		
	No. fecal samples (N)	No. samples with insects (%)	No. samples with fruit (%)	Mean % fruit per sample	No. fecal samples (N)	No. samples with insects (%)	No. samples with fruit (%)
Red-eyed Vireo	194	185 (95)	194 (100)	73.9	311	246 (79)	158 (51)
Veery	15	9 (60)	15 (100)	82.7	98	67 (68)	70 (71)
Gray-cheeked Thrush	8	5 (63)	8 (100)	85.0	41	30 (73)	32 (78)
Swainson's Thrush	23	16 (70)	22 (96)	80.0	103	65 (63)	84 (82)
Hermit Thrush	94	67 (71)	94 (100)	83.6	9	4 (44)	7 (78)
Total	334	282 (84)	333 (99.7)		562	412 (73)	351 (62)

Notes: Mean percent fruit per sample during autumn migration based on visual approximation with microscope to nearest 10%. Spring migration data from J. Clark and F. Moore (unpubl. data).

havior, energetics, and conservation of nearctic—neotropical migratory landbirds.

Frugivory is not limited to the temperate zone during autumn migration. Some neotropical migrant species remain frugivorous along tropical migratory routes during autumn even as insects become more abundant at more southerly latitudes during the tropical wet season. For example, during their southern migration throughout southern Mexico, Red-eyed Vireos consume fruits of *Phytolacca rivinoides*, a tropical shrub whose fruiting phenology appears timed with nearctic breeding landbird migrations (Winker 1995). Moreover, the omnivorous diets of overwintering neotropical migrants within the tropics are well documented (e.g., Howe 1977; Greenberg 1981, 1993; Wheelwright et al. 1984; Blake and Loiselle 1991, 1992a; Poulin et al. 1994; see Appendix). However, most investigations in the Neotropics of migrant frugivory have been limited to the roles of overwintering landbirds as seed dispersers (e.g., Olson and Blum 1968, Leck 1972, Howe 1977, Howe and DeSteven 1979) or the influence of fruit on wintering habitat use (Willson et al. 1982, Martin 1985, Blake and Loiselle 1992b). Information is now available for a few species of the importance of fruit in meeting the energy demands of transient migrants within the tropics (Morton 1973, Greenberg et al. 1995a).

During the northward spring migration in the tropics, some neotropical migrant species such as Wood Thrushes and Swainson's Thrushes are reported to shift diets to fruits that become abundant during the tropical dry season, presumably to satisfy the need for lipogenesis (Martin 1985, Blake and Loiselle 1992a). Spring frugivory can also occur within the temperate zone, but this phenomenon and its importance are understudied (Appendix). Where fruits are available as a result of late winter fruiting plants or remnant

fruits from the preceding autumn, many migrants may continue to utilize fruits in attempts to meet energetic demands during spring migration (Willson 1991; J. Clark and F. Moore, unpubl. data; Table 2, Appendix). With selective pressures for early arrival on the breeding grounds for acquisition of mates and territories (Francis and Cooke 1986, Marra et al. 1998), earlier spring migration prior to adequate or reliable insect emergence may be possible through dietary supplementation with spring fruits.

Data from the coast of the Gulf of Mexico suggests that spring frugivory is quite different from that of autumn migration (J. Clark and F. Moore, unpubl. data). For example, fruits are not as abundant among patches in spring, and are generally poorer in nutritional quality compared to autumn (J. Clark, F. Moore, and J. Parrish, unpubl. data). Perhaps as a result of these resource differences and the time constraints of spring migration (Francis and Cooke 1986, Morris et al. 1994, Marra et al. 1998), neotropical migrants do not appear to gain significant mass during spring frugivory compared to autumn (Parrish 1997; J. Clark and F. Moore, unpubl. data). Moreover, 22 of 25 species demonstrating spring frugivory at this southern temperate latitude showed a pattern of more extensive frugivory in fat migrants than in lean migrants (J. Clark and F. Moore, unpubl. data).

Although fruit may be available to migrant landbirds at some sites in spring, many species during the northward migration appear to be returning to insectivorous diets typical of the breeding season, thereby showing the mirror image of autumnal diet shifts (Table 2, Appendix). Yet, in some species (e.g., Northern Waterthrushes, Yellow Warblers, and Common Yellowthroats) frugivory appears common during migration and less frequent during the wintering period, suggesting an advantage to seasonal dietary plasticity

during migration (Parrish 1997; Appendix). That in many species there exists some level of frugivory during most of the annual cycle suggest that neotropical migrants may be more correctly viewed as omnivores that exhibit only seasonal stereotypy on insects during reproduction, while being plastic in their diets during the remainder of the year (Levey and Stiles 1992, Levey 1994). This view has previously been suggested by Levey and Stiles (1992), who proposed that nearctic-neotropical migrant landbirds are descended from neotropical taxa that exhibit seasonal altitudinal or intratropical migration in response to changing fruit and nectar availability at forest edge, canopy, and seasonally dry habitats. The tracking of seasonal fruit and nectar resources, they suggest, may have been influential in the very evolution of the nearctic-neotropical migration system of passerine birds (Levey and Stiles 1992). This broader view of neotropical migrants as tropical omnivores in both their evolutionary origin and in their behavioral ecology during the majority of the annual cycle (Levey 1994), may be a more appropriate context in which to explore the implications of dietary plasticity during migration.

#### CONSTRAINTS ON DIETARY PLASTICITY

That migrating species vary in extent of dietary plasticity shown during the nonbreeding period suggests that certain physiological, morphological, or environmental constraints determine the capacity to exploit novel diet types. First, nutritional requirements of migrant species change over the annual cycle. For example, needs for dietary protein, particular amino acids, and minerals probably change between breeding (for the production of eggs and feeding of young) and migration (Izhaki 1992). However, most migrant populations experience some depletion of muscle mass during migratory efforts (Lindström 1991, Lindström and Piersma 1993), as well as partial or full replacement of plumage prior to or during migration (King 1974, Winker et al. 1992a). Protein needs during migration may therefore still exist, albeit to a lesser degree. Moreover, diet choice for the combination of nutrients and secondary compounds (Izhaki and Safriel 1989, Izhaki 1992) that optimizes lipogenesis in migrating birds should be under heavy selective pressure during stopover. The morphology and physiology of a taxon can further limit its capacity to exploit new diet types, thereby determining the extent of dietary plasticity. For example, certain birds may be unable to process seeds or certain fruit sizes because they lack the bill dimensions or jaw musculature for access to and ingestion of available resources (Moermond and Denslow 1985, Jordano 1987), or because gut length (Jordano 1987) or diges-

tive strategies (Martinez del Río and Karasov 1990, Levey and Duke 1992, Place and Stiles 1992, Levey and Karasov 1994) control the assimilation of ingested foods. Moreover, these physiological and morphological characters have a phylogenetic context which can limit the capacity of certain taxa for dietary plasticity.

Psychological factors and social interactions may also play a role in determining the extent of dietary plasticity. Certain warbler and sparrow species, for example, exhibit an intrinsic "neophobia," or an aversion to novel environments or objects (see Greenberg 1990 for review). Such psychological bases for the limitation or expansion of foraging behavior appear qualitatively related to the extent of frugivory shown during the nonbreeding season: the neophobic Chestnut-sided Warbler seems less likely to demonstrate frugivory in the tropics than its neophilic congener, the Bay-breasted Warbler (Greenberg 1979). Similar patterns appear to exist in other *Dendroica*. For example, Black-throated Blue warblers are highly plastic in their diets during migration and the overwintering period, and they appear more flexible in foraging site selection during breeding periods than congeneric Black-throated Green Warblers, which remain predominantly insectivorous during migration and are more stereotypic in microhabitat selection in both the tropics and the breeding season (Whelan 1989, Greenberg 1992, Parrish 1995b; C. J. Whelan and J. D. Parrish, unpubl. data). Competition for resources among and between species can further limit the possibilities of using additional resource types during stopover (Sealy 1988, 1989; Moore and Yong 1991).

The nutritional composition and distribution of resources during migration, however, may be most decisive in determining which species are plastic, why this plasticity has evolved, and what consequences dietary plasticity may have for the conservation of migratory landbirds during migration. Fruit and insect resources differ in their nutrient composition and distribution in space and time during autumn, the principal migration season characterized by dietary shifts to frugivory in the northern temperate zone (Table 1; but see discussion of spring frugivory above). Insects, in contrast to most fruits, are generally high in protein, but vary extensively in the amounts of carbohydrate per gram relative to fruits (Morton 1973, Moermond and Denslow 1985). Moreover, most fruits available to *en route* landbirds in northern temperate stopover areas are lower in percentage of digestible lipids than available insects (Stiles 1980a, Johnson et al. 1985, Moermond and Denslow 1985, Borowicz 1988; but see Conway et al. 1994). Thus fruits may present a valuable source of carbo-

hydrates, but a variable reward in lipid composition between plant species (Morton 1973, Johnson et al. 1985). These fruit species can also vary in nutrient, caloric, and water content over the season (Stiles 1980a, Johnson et al. 1985, White 1989). The distribution of fruit and insect resources are also extremely different in ways that influence the relative value of the two resource types for migrants. Fruits are typically patchily distributed and spatially aggregated over a variety of scales. Individual infructescences in some plants such as *Viburnum* spp. and *Sambucus* spp. can hold over 1000 individual fruits, and these plants also tend to occur in aggregated groups within a habitat (Levey 1988, 1990), perhaps as a result of avian dispersal effects on seed shadows (Levey 1991, Willson and Whelan 1990). Insects, in contrast, are more variable and widely distributed than fruits (Wolda 1978, 1988), especially during autumn in northern temperate zones (Fig. 2; J. Parrish, unpubl. data). Insects are also more difficult to detect due to cryptic coloration or mimicry, as opposed to the brightly colored displays of fruiting shrubs that serve as advertisement for seed dispersal (Willson and Thompson 1982, Willson and Whelan 1990, Willson et al. 1990). Furthermore, insects are usually active and mobile, and often possess escape mechanisms to evade predation, whereas fruits are sessile and present little difficulty for a hyperphagic migrating landbird. Temporal distributions of insects and fruit also vary over the autumn period, with the decline in insect resources being much more rapid and unpredictable over the migration period than that of fruit resources (Fig. 2; J. Parrish, unpubl. data). I suggest that these differences in display and spatial distribution render insects a much more "expensive" foraging resource than fruits during autumn migration in terms of searching time, handling time and energy expenditure (Parrish 1996).

#### DEBATE OVER THE IMPORTANCE OF FRUIT TO MIGRATING LANDBIRDS

Despite the extensive frugivory noted in many migrating species, many researchers have suggested that fruit plays only a minor role in lipid deposition by migrant birds during stopover periods (Berthold 1976a,b; Izhaki and Safriel 1990). In early feeding experiments, Berthold (1976a,b) found that any mass gain by captive Blackcaps (*Sylvia atricapilla*) during the experimental period was closely tied to a decrease in ingested vegetable matter and an increase in the proportion of animal food in the diet. Moreover, when European Blackbirds (*Turdus merula*), European Robins (*Erithacus rubecula*), and Garden Warblers (*Sylvia borin*) were fed exclusively fruit diets,

they suffered precipitous declines in body mass and fat levels that were only reversed when they were returned to animal diets. Berthold concluded that his findings were incompatible with the hypothesis that fruits are important to migrant passerines during migration, allowing only that fruit may be beneficial as a supplementary food for transient birds lacking any other food.

There is conflicting evidence, however, which suggests that fruit is of greater importance to the energetic condition of migrating songbirds than proposed by earlier workers. The occurrence of frugivory in *en route* migrants is frequent and extensive in both the Palearctic (Mead 1966, Blondel 1969, Fry et al. 1970, Ferns 1975, Thomas 1979; Herrera 1981, 1984; Jordano 1981, Stoate and Moreby 1995) and the Nearctic (Baird 1980, Stiles 1980a, Rybczynski and Riker 1981, Johnson et al. 1985, Parrish 1997). More importantly, there are potential associations between avian use of fruit and fruiting habitats, and higher body mass. For example, Thomas (1979) showed that frugivorous Garden Warblers feeding on the fig *Ficus carica* in southern Portugal during migration weighed significantly more than insectivorous conspecifics feeding in reed beds at the same site. Yet most convincing is the evidence presented by Simons and Bairlein (1990) and Bairlein (1990), who experimentally investigated the contradiction between Berthold's findings and the high incidence of frugivory in palearctic migrants, using Garden Warblers feeding on lipid-rich fruits. Birds were able to gain mass on fruit diets, suggesting that non-animal food resources may be more important to stopover mass gain than was once considered. Indeed, Willson (1991) has called for a renewal of interest and a re-questioning of the importance of fruit to the biology of passage migrant landbirds.

#### BEHAVIORAL AND ENERGETIC CONSEQUENCES OF FRUGIVORY DURING MIGRATION—A CASE STUDY AND EXAMPLES

Flexible, plastic diets that include frugivory can have direct consequences for nearctic-neotropical landbird migrant foraging behavior, habitat selection, and energy budgets during *en route* stopover. The influence of diet on these facets of migrant biology has been the focus of empirical observation studies and experimental work during autumn migration on Block Island, Rhode Island.

#### STUDY SITE AND METHODS

Block Island is a 2900 ha glacially deposited landmass 18 km off the coast of southern New England, where northwesterly winds associated with cold fronts force migrants to concentrate on offshore islands (Able

1977). The site is composed of three basic habitat types: contiguous northern bayberry (*Myrica pensylvanica*) from 1 to 2.5 m in height, maritime scrub (from 2–4 m high and predominantly *Pyrus melanocarpa*, *Viburnum recognitum*, *Amelanchier* spp., *Myrica pensylvanica*, *Rosa* spp., and *Rubus* spp.), and older orchard scrub (measuring 4–7 m and composed of maritime scrub species, but also with high densities of *Prunus serotina* and *Pyrus malus*). Ten 12-m mist nets (32-mm mesh) were used in the maritime scrub habitat to sample individual migrants for diet, experimentation, and general monitoring of stopover population ecology. I focused these studies of seasonal frugivory on the maritime scrub habitat because of its high density yet relatively low diversity of fruit and fruiting shrubs, which has facilitated experimental approaches toward understanding diet shifts.

Red-eyed Vireos and *Catharus* thrushes (*C. ustulatus*, *C. minimus*, *C. fuscescens*, and *C. guttata*) were chosen as focal species for experiments because of their abundance, ease of acclimation to captivity, and extremely frugivorous diets. I determined the trends in body mass and fat condition of these focal species during autumn migration by analyzing capture data from the same location. Analyses of energetic condition changes were made on recaptured individuals netted on Block Island from 1969–1995 by Mrs. F. D. Lapham and the author (Table 3). I conducted diet surveys of the focal species with individuals netted during the autumns of 1993–1995. Birds were removed from mist nets and placed into transport bags (Parrish et al. 1994), which allowed collection of fecal samples of captured birds to estimate later the degree of frugivory to the nearest 10% in bird diets before capture (e.g., Jordano and Herrera 1981). I acquired large numbers of samples with this technique, providing an estimate of frugivory for focal experimental species (Table 2). The patterns of dietary data (Table 2) and energetic condition (Table 3) for these focal species suggest that they were gaining mass in the field on highly frugivorous diets while resting on Block Island.

Because of potential, yet undocumented, differences in the temporal distribution of fruit and insect resources that could influence the behavior and energetics of *en route* migrants, I documented the relative decline over the autumn migration season of the two resources on Block Island during 1994. Flying insects in the 2–4 m coastal scrub habitat were monitored during morning and afternoon intervals with Tanglefoot®-coated boards (22 cm × 22 cm; Cooper and Whitmore 1990, Wolda 1990, Kuenzi et al. 1991) placed at 1-, 1.5-, and 2-m height intervals at ten points spread through the study area. I also monitored sessile insect abundance by bagging randomly chosen, 0.5-m branches from northern bayberry and northern arrowwood (*Viburnum recognitum*) at the same ten points and fumigating them with permethrin (Morse 1976, Wolda 1990). Fruit crops (ripe fruits per designated branch segment) of tagged 0.5-m branches of northern arrowwood and black chokeberry (*Pyrus melanocarpa*) were also monitored. Fruit abundances on five branches of each plant species were followed throughout the season at five of the insect monitoring points in the study site. Resource measurements were made

TABLE 3. ENERGETIC CONDITION CHANGES AND STOPOVER LENGTH OF VIREO OLIVACEUS AND CATHARUS THRUSHES ON BLOCK ISLAND, RHODE ISLAND, DURING AUTUMN MIGRATION BASED ON INDIVIDUALS RECAPTURED WITHIN ONE SEASON BETWEEN 1970–1995

Species	N	Mass (g)		t	Fat score		t	Stopover length (days)	
		first capture	last capture		first capture	last capture		first capture	last capture
Red-eyed Vireo	308	18.3 ± 2.5	19.9 ± 3.3	-10.9***	1.5 ± 2.5	1.9 ± 1.1	-9.0***	4.5 ± 4.4	4.3 ± 4.4
Veery	95	32.9 ± 3.7	35.7 ± 5.1	-6.3***	1.2 ± 1.0	1.9 ± 1.1	-6.6***	4.3 ± 3.0	4.3 ± 3.0
Gray-cheeked Thrush	98	33.5 ± 4.3	37.3 ± 5.9	-8.2***	1.6 ± 1.2	2.4 ± 1.2	-8.0***	4.3 ± 2.8	4.3 ± 2.8
Swainson's Thrush	110	30.6 ± 3.1	33.2 ± 4.3	-6.7***	1.0 ± 0.9	1.9 ± 1.2	-6.7***	5.1 ± 4.0	5.1 ± 4.0
Hermit Thrush	121	30.0 ± 2.4	31.2 ± 5.8	-2.6*	0.8 ± 0.8	1.3 ± 1.0	-6.9***	4.6 ± 3.8	4.6 ± 3.8

\* = P < 0.05; \*\*\* P < 0.001.

on average every four days during the period from 2 September–25 October.

#### RESOURCE VARIATION

Resource abundance data from 1994 (Fig. 2) indicated dramatic differences in the overall rate of decline of insect and fruit resources available to migrants at this northern temperate stopover site. When expressed as a percentage of the original count remaining during the season, insects declined at a much faster rate over autumn than did fruits. Moreover, insect resources were more stochastic in their temporal availability during the season, an expected pattern given the dependence of many orders on appropriate temperature and wind regimes for flight (Wolda 1988). The variance among ten sampling sites, represented in Fig. 2 by standard deviation error bars at each temporal point, illustrates the high spatial variability of insect resources relative to the two principal fruit species used by most landbird migrants. Thus for a fat-depleted, inexperienced, recently arrived migrant, fruit resources may be more reliable in both space and time than are insects.

#### BEHAVIORAL IMPLICATIONS

Shifts in diet to fruit can influence many facets of migrating songbird behavior in ways that affect energetic and habitat requirements as well as migratory strategies during migration. For example, the foraging behavior of many landbird species during stopover is characterized by the use of an expanded range of foraging maneuvers (Martin and Karr 1990). Dietary plasticity can produce these observed expansions in foraging behavior, whether they are increased ranges of substrates from which prey are taken, an expanded repertoire of foraging maneuvers, altered foraging rates, or shifted foraging-site selection. When diet is altered, foraging behavior may subsequently change in response to the novel distribution and accessibility of new prey items, thereby explaining observed differences in foraging activity during stopover periods. For example, the clumped and stationary distribution of fruits may lower foraging rates and increase stationary foraging by frugivorous migrants, while allowing them to use energetically less expensive non-aerial maneuvers with greater frequency than is required during insectivory. To test the hypothesis that foraging behavior would differ between fruit and insect diets during stopover, foraging *en route* migrants were observed on Block Island during 1994. Search and attack rates and proportions of different foraging behaviors used (based on methods of Remsen and Robinson [1990]) were determined for each diet type from 5 September through 16 October as

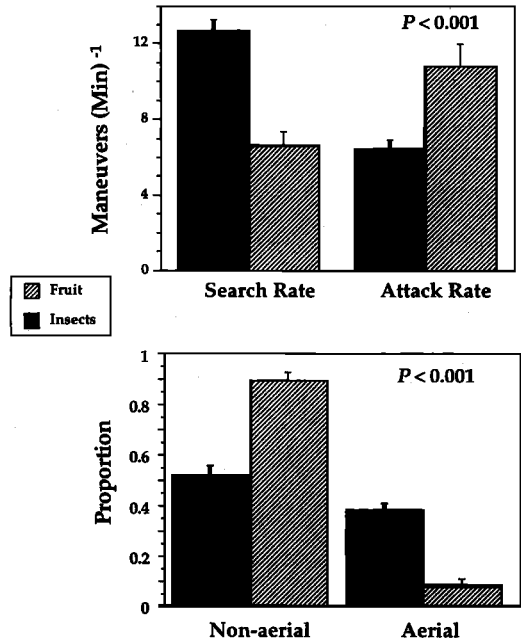


FIGURE 3. Foraging behavior of migrant landbirds on fruit and insect diets during autumn, 1994, on Block Island, Rhode Island. Foraging behaviors observed include the average search and attack rates of foraging birds, and the proportion of aerial versus non-aerial attack maneuvers used by migrants on fruit and insect diets. Aerial maneuvers included sallies, sally-hovers, sally-strikes, and leaps, whereas non-aerial maneuvers consisted of gleans, reaches, hangs, and lunges, according to Remsen and Robinson (1990) and Parrish (1996).

part of a larger study of migrant foraging behavior (Parrish 1996). Birds were classified as foraging on fruit or insects based on observations of the resources at which foraging maneuvers were directed; such classification was possible since birds rarely switched between insect and fruit resources within one foraging bout observation (Parrish 1996). Based on 372 observed foraging sequences, search rates were lower and attack rates were higher for fruit diets than for insect resources, suggesting more frequent "prey" encounters as a result of the clumped nature of fruit (search rates:  $t = 4.47$ ,  $P < 0.001$ ; attack rates:  $t = 4.90$ ,  $P < 0.001$ ; Fig. 3). Moreover, energetically costly aerial attack maneuvers were used more frequently during insectivory than during frugivory ( $\chi^2 = 31.45$ ,  $P < 0.001$ ; Fig. 3). These data suggest that diet shifts to fruit may afford landbirds that are physiologically capable of dietary plasticity the opportunity to maintain caloric intake with lower energetic expenditure during foraging. Thus diet can affect foraging behavior in ways that may, in



turn, influence energy balance during stopover periods.

With shifts in diet choice during the nonbreeding season, many species may also shift their habitat selection behavior. For example, work from both the tropical wintering grounds and temperate migration sites suggests that frugivorous migrants may select nonbreeding habitats on the basis of fruit availability alone. In the Neotropics, Blake and Loiselle (1992b) found that numbers of frugivorous overwintering migrants in Costa Rican rainforest were greatest in the sites where fruit was most prevalent. Further work by Martin (1985) revealed that migrating birds in Panama concentrated in second-growth forests perhaps due to the greater abundances of accessible fruits in those areas. In the Palearctic, wintering European warblers were also found in greater densities in habitats with the greatest abundance of fruits, to the extent that Herrera (1985) suggested that those migrants, as seed dispersers, were significant modifiers of their own habitats. Large-scale experiments with wintering distribution of palearctic migrants in olive orchard landscapes of southern Spain have demonstrated that overwintering landbirds track fruit availability and that migrant and fruit abundances are closely linked (Rey 1995).

Less well-studied is the relationship between novel diet types, such as fruit, and the habitat selection of *en route* migrants. Bairlein (1983) hypothesized that the change in habitats used by Blackcaps on migration in Germany resulted from including more fruit in their diet during migration than during the breeding season. Bibby and Green (1981, 1983) showed that a more specific habitat use of marshland reed beds was correlated with a diet shift in Sedge Warblers (*Acrocephalus schoenobaenus*) to the plum-reed aphid *Hyalopterus pruni* during migration. Moreover, Garden Warblers on migration occurred in highest densities in the presence of *Ficus carica* in southern Portugal (Thomas 1979).

Yet the influence of fruit on stopover habitat selection in nearctic-neotropical migration systems has not been as thoroughly explored. Blake and Loiselle (1991) noted a shift in the abundance of temperate migrants in tropical lowland habitats of Costa Rica simultaneous with the peak of fruit abundances. In a comparative study between northern temperate zones during migration and Panamanian rainforest, Willson et al. (1982) showed migrating frugivores at the northern migration site to be more common in light gaps, where fruits were more abundant than in the forest interior. In other correlative studies, Martin and Karr (1986) and Blake and Hoppes (1986) showed that habitat selection of frugivorous *en route* migrants was correlated with for-

est gap understory sites, where fruit abundance was concentrated during autumn. I have found similar patterns for certain species during autumn stopover in coastal maritime scrub habitats on Block Island, where fruiting shrub densities are exceedingly high (J. Parrish, unpubl. data). For example, Red-eyed Vireos, a highly frugivorous species (Table 2), are captured over ten times more frequently in coastal maritime scrub than in old orchard habitat on Block Island, with the former habitat type having a greater density of fruiting shrubs (t-test,  $P < 0.05$ ). Furthermore, the Yellow-rumped Warbler, a species that feeds heavily on northern bayberry fruits during the winter, also appears to base its habitat use on fruit resources. This migrant species possesses specific adaptations for processing of the fatty esters surrounding bayberry pericarp (Yarbrough and Johnston 1965, Wilz and Giampa 1978, Place and Stiles 1992). However, these warblers actually begin their diet shift while on migration through northern temperate latitudes (Parrish 1997), and occur in greatest densities in habitats where bayberry plants predominate (J. Parrish, unpubl. data). On Block Island, overall migrant capture rates were higher in bayberry habitats than in coastal shrubland during autumn migration, 1995 (Wilcoxon sign rank test,  $z = -2.67$ ,  $P = 0.008$ ; Fig. 4). This pattern was most apparent in the latter half of the migration period (after the first week in October at the site; calendar date = 282, Fig. 4), when Yellow-rumped Warbler abundances increased rapidly and typically constituted over 35% of all daily migrant captures on Block Island.

Moving beyond correlational analyses, I have conducted fruit removal experiments in coastal shrubland habitats to determine if the presence of fruit in conjunction with seasonal frugivory is responsible for habitat use during migration. I removed all bird-dispersed fruits from 30 m × 30 m plots and mist netted migrants within control and removal plots to compare resulting bird abundances. Results indicated that migrant habitat use by highly frugivorous species was strongly influenced by the presence of fruit in a habitat. For example, Yellow-rumped Warblers (which are highly frugivorous) were more abundant in control plots within bayberry habitats, where fruit was present, than in treatment plots, where fruit had been removed (Wilcoxon sign rank test,  $z = -3.008$ ,  $P = 0.003$ ; Fig. 4). Few such experiments have been conducted, yet they are critical to determine the habitat selection mechanisms used during migration and the extent to which these are modified by dietary plasticity (Morse 1985).

Migratory strategies of *en route* migrants, including departure decisions and, therefore, stop-

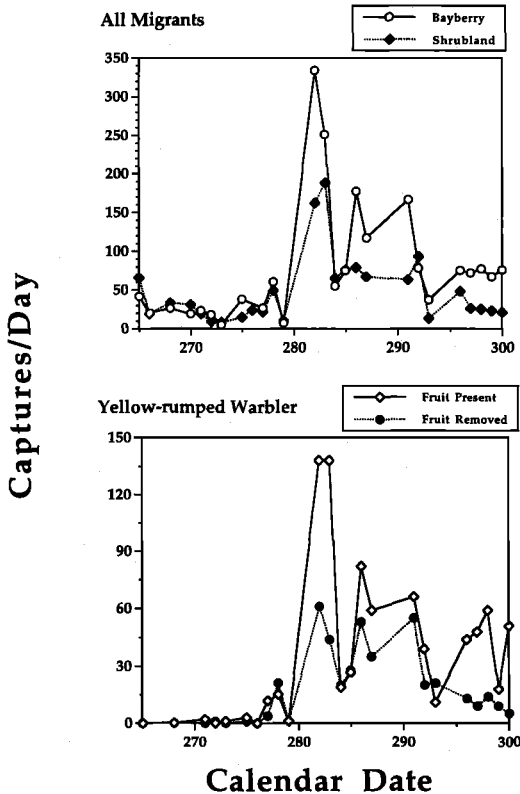


FIGURE 4. Habitat use by migrant landbirds during autumn, 1995, on Block Island, Rhode Island. Top figure represents the total number of captures of all migrant species in bayberry and coastal shrubland species. Bottom figure illustrates responses (distribution of mist-net captures per day) in habitat use by highly frugivorous Yellow-rumped Warblers to a fruit removal experiment within bayberry habitats.

over length, can also fluctuate with seasonally changing dietary needs. Such an effect is proximately controlled by time and energetic constraints, which ultimately can be influenced by the food resources used during migration. For example, Palearctic *Acrocephalus* warblers show differences in dietary plasticity during migration (Bibby and Green 1981, 1983). Sedge Warblers are stereotyped in their insectivorous diets, feeding on plum-reed aphids. As a result of this narrow, stereotyped diet, Sedge Warblers migrate more rapidly, gain more mass at each stopover site, and fly further per migratory flight than the more dietarily plastic Reed Warbler (*A. scirpaceus*; Bibby and Green 1981). Bibby and Green suggested that the degree of dietary plasticity during migration was influential in the evolution of migration strategies by these congeners.

In general, migrant stopover length is inversely proportional to energetic condition on arrival;

that is, migrants will continue their journey (exhibit migratory flight behavior) once they have gained sufficient mass (Biebach et al. 1986, Moore and Kerlinger 1987, Loria and Moore 1990, Lavee et al. 1991, Kuenzi et al. 1991, Yong and Moore 1993). Others (Rappole and Warner 1976, Gwinner et al. 1984, Terrill 1990) have suggested that birds that are unable to replenish fat reserves in a stopover location will depart the site sooner in search of better foraging opportunities. Dietary plasticity can facilitate or slow migrant weight gain during stopover, depending on individuals' abilities to process the novel diet types and the availability of seasonally preferred foods. I therefore predicted that diet could proximately influence the migratory strategies of frugivorous landbirds as measured by the caged migratory restlessness activity (*Zugunruhe*) of focal individuals. I measured the nocturnal activity of experimental Red-eyed Vireos ( $N = 80$  birds) and *Catharus* thrushes ( $N = 59$  birds) between sunset and sunrise in holding cages with electronic activity-recording perches. Birds were subjected to four-day ad libitum diet treatments of exclusively insects (mealworms, *Tenebrio molitor*), exclusively fruit diets (fruits of *Phytolacca americana*, *Viburnum recognitum*, and *Pyrus melanocarpa*), and a mixed control diet of all food items. Red-eyed Vireos showed a strong inverse relationship between energetic condition and migratory behavior by increasing their nocturnal activity significantly when placed on fruit diets, which lowered their energetic condition (activity experiments analyzed by ANOVA; treatment effect:  $F = 5.88$ ,  $P < 0.01$ ; Figs. 5–6). This response suggests departure behavior in search of more suitable sites where mass gain is more assured (sensu Terrill and Ohmart 1984, Terrill 1990). In contrast, *Catharus* thrushes showed migratory activity independent of diet types (ANOVA; treatment effect:  $F = 0.16$ ,  $P = 0.85$ ; Fig. 5). These results demonstrate the influence of dietary plasticity on the migratory strategy of the Red-eyed Vireo, but suggest that fruit diets are essentially equal to insect diets with regard to factors influencing *Catharus* thrush migratory strategies.

#### ENERGETIC IMPLICATIONS

Diet shifts occurring during migration can have profound implications for energy budgets of passage landbirds by influencing rates of mass change, optimal fat load, and energetic condition at departure. Although most studies of stopover ecology are concerned with the importance of energy intake during stopover in terms of hyperphagia (Loria and Moore 1990), optimal *en route* foraging (Moore and Simm 1985), and alternative diet choice (e.g., Berthold 1976a,b;

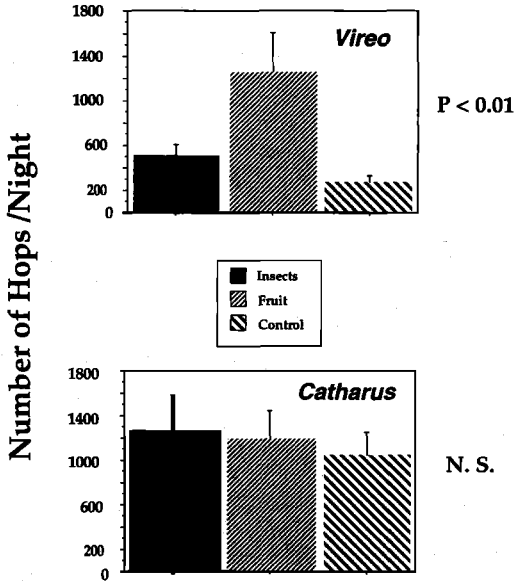


FIGURE 5. Mean ( $\pm$  SD) nocturnal migratory activity in Red-eyed Vireos and *Catharus* thrushes fed four-day, ad libitum insect diets (*Tenebrio* larvae), fruit diets (*Viburnum recognitum*, *Phytolacca americana*, and *Pyrus melanocarpa*), or a control diet of fruits and insects. Activity was measured as the mean number of perch hops recorded in caged birds between sunset and sunrise, and was analyzed using analysis of variance.

Graber and Graber 1983; Bairlein 1990), few have considered the additional factor involved in any net energy budget equation: energy expenditure during stopover. Graber and Graber (1983) suggested some of their spring foraging observations of warblers in areas with insufficient food resources were consistent with the

concept of energy conservation during *en route* foraging. Additionally, for migrant hummingbirds, which have different physiological options for energy budget maintenance, Hiebert (1991) has suggested the importance of maximizing energy conservation and minimizing time for pre-migratory fattening through seasonal use of torpor. Yet in migratory passerines, little consideration has been given to the role of minimizing energy expenditure in realizing net positive energy budgets during stopover. Shifts to diets that help maximize energy intake and minimize energy used during stopover would thus be strongly favored under selection for optimal behavioral strategies in *en route* migrants.

Despite the controversy over the abilities of migrants to maintain themselves on fruit (Berthold 1976a,b; Izhaki and Safriel 1989, Mack 1990, Simons and Bairlein 1990, Izhaki 1992), neotropical migrants maintain high levels of frugivory during stopover and gain mass in the field (e.g., Johnson et al. 1985; Tables 2, 3). Most fruits are generally low in protein and lipids but high in carbohydrates (Snow 1971, Morton 1973, Moermond and Denslow 1985, Debussche et al. 1987, Herrera 1987). However, Bairlein (1985b, 1987a) has shown that captive Garden Warblers recover from an initial mass loss on forced low-protein diets (simulating frugivory) by increasing their daily food intake and improving assimilation efficiency of fat and carbohydrates. Moreover, birds fed high carbohydrate diets when under fat-reduced diet treatments did not lose body mass. Subsequently, Bairlein (1990) also demonstrated experimentally that laboratory Garden Warblers could gain mass on fruit diets during migration through a series of changes in fruit selection and physio-

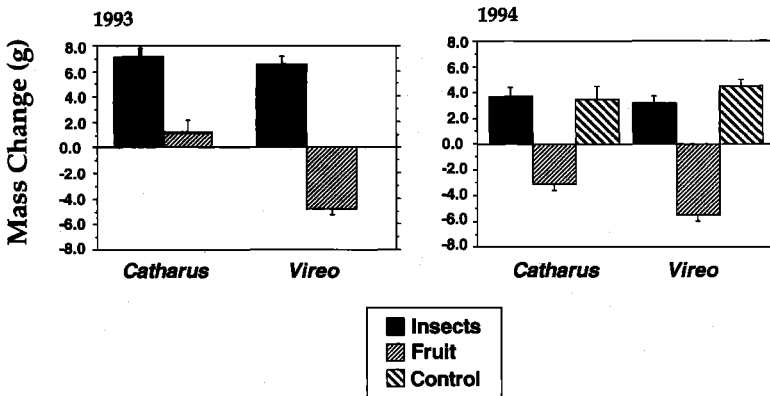


FIGURE 6. Mean ( $\pm$  SD) mass change by caged Red-eyed Vireos and *Catharus* thrushes fed four-day, ad libitum diets of insects (*Tenebrio* larvae), fruits (*Viburnum recognitum*, *Phytolacca americana*, and *Pyrus melanocarpa*) or a control diet of both insect and fruit resources. Preliminary experiments in 1993 included only exclusive fruit and insect diets.

logical processing. Thus birds may change food intake quantities, increase assimilation efficiency, and seek those fruits that allow them to maintain or gain weight on predominantly fruit diets, strengthening the argument that inclusion of fruit in the diet may benefit some species by providing greater energy intake during migration.

I have experimentally tested this idea that fruit is included in the diet to maximize energy intake by conducting feeding trials with transient Red-eyed Vireos and *Catharus* thrushes subjected to four-day treatments of fruit, insect, or mixed diets as in the migratory activity experiments above (Parrish 1996). In order to isolate energy intake from energy expenditure, I conducted feeding experiments in small holding cages (28 cm on all sides) that minimized energy expended by experimental individuals. In experiments conducted in 1993, *Catharus* thrushes ( $N = 21$ ) gained significantly more mass on insect diets than on fruit diets, but did maintain or gain mass slightly on exclusively fruit diets (ANOVA; treatment  $\times$  genus effect:  $F = 26.8$ ,  $P < 0.01$ ; Fig. 6), supporting the hypothesis that fruit can provide some energy intake benefits during stopover. Red-eyed Vireos, in contrast, always lost mass on fruit diets. In 1994, I added an additional treatment of mixed, ad libitum fruits and insects to experiments. In 1994, *Catharus* thrushes ( $N = 24$ ) on average gained weight on mixed diets and insect diets. As in 1993, Red-eyed Vireos tested in 1994 ( $N = 29$ ) also declined in energetic condition when provided with strictly fruit diets (ANOVA; treatment  $\times$  genus interaction:  $F = 3.75$ ,  $P = 0.026$ ; Fig. 6), despite high levels of frugivory on the same fruits in the wild (Table 2). Mass gain did occur, however, when individual vireos fed on either insect and mixed control diets. A significant Bonferroni post hoc test demonstrated greater mass gain on average in mixed diets, where both fruit and insects were available ad libitum, compared to diet treatments of ad libitum insects alone ( $P = 0.017$ ), suggesting a potential adaptive advantage to mixing diets by way of dietary plasticity during autumn migration (e.g., Pennings et al. 1993, Bairlein 1990; Fig. 6). These results with long-distance nearctic-neotropical migrants contrast with Berthold's (1976a,b) conclusions from the Palearctic, which suggest no increased energetic intake is possible for migrants on mixed or frugivorous diets. It is unknown at this time precisely what factors are responsible for the maintenance of extensive frugivory in Red-eyed Vireos in the wild, since experimental evidence suggests that large amounts of mass gain do not seem possible on exclusively fruit diets. However, the discrepancy between field patterns and feeding trial experiments may lie, at least in part, in

the energy expended by Red-eyed Vireos when foraging on insect versus fruit diets.

Because of the differences between fruit and insect resources in the distribution, ease of capture, and rate of decline during the autumn migration period (Table 1, Fig. 2), I suggest that birds foraging on fruit expend significantly less energy during stopover foraging than those feeding exclusively on insects. Fruits are stationary, clumped, highly visible, and more predictably available than insects throughout autumn. These characters enable frugivorous migrants to remain virtually stationary in a patch of fruiting shrubs (Parrish 1996; Fig. 3) where they are limited in energy intake only by competition (Sealy 1989, Moore and Yong 1991) or by morphological or physiological constraints such as gut passage time or digestion and assimilation capabilities (e.g., Jordano 1987, Levey and Karasov 1989, Levey and Duke 1992).

I suggest that selection for minimization of energy expenditure during stopover has influenced the evolution of dietary plasticity during migration. Diet shifts to fruit allow many migrant species to minimize the time and energy needed for foraging on "expensive" diet types such as insects. The different energy requirements for foraging on fruit and insect resources may, in effect, alter the relative profitabilities of the two diet types, thereby influencing the proximate foraging decisions of migrant landbirds during stopover. Even for species which are incapable of efficiently assimilating exclusive diets of northern temperate zone fruits into lipid reserves (e.g., Red-eyed Vireos), bouts of insectivory for lipogenesis need only be infrequent and of short duration when caloric intake is subsidized by ingestion of easily acquired fruit resources. Preliminary feeding experiments with Red-eyed Vireos on limited and ad libitum treatments of insect diets support the idea that only small quantities of insects are necessary to effect significant weight gains and increases in fat loads (see also Izhaki and Safriel 1989). The reduction in energy expenditure during stopover foraging through dietary shifts to fruit can, in theory, be as important in effecting positive net energy balances during stopover periods as is maximization of energy intake through hyperphagia. Although the foraging observations reported herein suggest important energy savings during foraging on fruit, in practice, no study to date has tested experimentally the hypothesis that frugivory during migration significantly reduces the cost of stopover foraging relative to strictly insectivorous diets. A combination of energy expenditure reduction and an increase in energy intake and assimilation suggests that di-

etary plasticity actively facilitates successful stopover refueling for migrating landbirds.

#### IMPLICATIONS OF BEHAVIORAL PLASTICITY FOR THE CONSERVATION OF NEOTROPICAL MIGRANTS DURING *EN ROUTE* PERIODS

Because it affects aspects of migratory behavior that are important for a successful migration, such as habitat selection, foraging performance, and energetic budgets, dietary plasticity is clearly a phenomenon of direct importance to the conservation of migrant landbird populations. Shifts in diet can generate new resource needs, different energetic priorities, and novel behaviors for *en route* migrants that are entirely different from those used by the same species on the breeding or wintering grounds. Birds that are plastic in their diets will, as a result of their new resources, show changes in behavior that have important consequences for reversing declines of migrant populations. For example, changes that occur in *en route* habitat selection as a result of diet shifts can completely shift priorities for protection of migratory bird habitats that are based only on knowledge of breeding and wintering season biology. That certain thrush species breed principally in extensive hardwood and mixed coniferous-deciduous forests and winter in extensive tropical forest would certainly mask patterns of habitat use during migration through the northern temperate zone, when many species are highly abundant in small-statured coastal fruiting scrub (Parrish 1996, unpubl. data). Because of behavioral plasticity in the life cycles of migratory bird species, efforts to maintain the health and existence of desirable stopover habitat during migration require an understanding of transient migrants' needs during migration that is independent of breeding or wintering season behavior.

Furthermore, as the effects of dietary plasticity on habitat selection and use during migration continue to be illuminated, the present and future availability and vulnerability of these important stopover habitats must be considered in conservation decisions for migratory landbirds. For example, coastal habitats have long been considered important for songbird migration as a result of geographic and wind patterns that concentrate large numbers of species and individuals along coastal areas (e.g., Moore and Simons 1992a). Furthermore, coastal habitats are the areas most heavily used by hatching-year birds (perhaps due to navigational errors or inexperience; Ralph 1971, 1981), which annually recruit into the reproductive population and therefore are important first steps for recovery from declines. The evidence presented above suggests that fruit resources, which tend to be

extremely common in coastal shrubland habitats, are very important for meeting the energy demands necessary for a successful migration.

Yet coastal habitats, especially along the eastern and southern seaboard of the United States, face unrelenting pressures for development, resulting from urban expansion, tourism, agriculture, and non-random population growth in coastal vicinities (Cullitan et al. 1990, Mabe and Watts *this volume*, Simons et al. *this volume*). Such degradation and destruction of migratory corridors along coastal North America represents a significant threat to migrating landbirds. Moreover, popular perception of shrubland habitats among coastal human communities is generally low (due to the high abundance in these habitats of thorny plants and poison ivy, *Rhus radicans*), resulting in land use matrices with little remaining of the fruit-bearing shrubland preferred by many migrating songbirds. Protection of existing maritime shrubland habitats and stewardship efforts aimed at managing for successional stages typified by an abundance of fruiting plants are encouraged given the importance of fruit in the diets and behaviors of many species. This example of fruit-bearing coastal shrubland demonstrates that the relative conservation value of habitats for landbirds is also a dynamic character, altered by seasonal dietary plasticity in the foraging behavior of nearctic-neotropical migrants.

Dietary plasticity, exemplified here as dietary shifts from insectivory to frugivory, illuminates an important, yet disturbing conclusion: *en route* migratory landbirds may possess completely different biologies than those with which we are familiar at other times of the year. Autumn and spring migrations are more than simple short-term links between reproduction and winter maintenance. They present additional, novel challenges to conservation biologists concerned with holistic approaches to migratory bird conservation. Until we recognize the patterns, causes, and consequences of seasonal changes, such as diet shifts, in the biological identity of landbird migrants, we will compromise any management efforts exerted during other periods of the annual cycle. Unbalanced approaches to conservation of migratory landbirds that are biased toward the breeding or wintering period may provide increased reproductive success or overwinter survival, benefits that could be lost in temporal population "sinks" during migration. Consideration of a broader view of nearctic-neotropical migrants (Levey 1994) that attempts to avoid temperate biases and accepts the changing biologies of these species throughout the annual cycle will be critical for migrant landbird conservation giv-

en the political, cultural, and biological boundaries over which these landbirds cross.

#### ACKNOWLEDGMENTS

I thank the following for their dedication, assistance, and companionship in the field: S. Comings, M. Whitman, C. Fuller, M. Grady, G. Lowe, S. Oppenheimer, A. Panjabi, A. Parker, A. Parrish, G. Turano, A. Williams, D. Workman, and numerous Earthwatch Research Corps volunteers. Mrs. Elise and Helen Lapham graciously allowed use of unpublished data and access to the field site. J. Clark and F. Moore allowed use of spring migration frugivory data to demonstrate the extent of dietary plasticity. Experimental cages were provided by R. L. Holberton and K. P. Able. Logistical support was generously provided by Mr. and Mrs. William Comings, Mr. and Mrs. Larry Smith, Mr. and Mrs. A. Angelbeck, Ms. Maureen Gary, and the Block Island Field Office of The Nature Conservancy. N.

Wheelwright revealed the value of working with *Catharus* thrushes, D. Levey and J. Zurovchak provided stimulating discussions, and T. Kunz provided generous use of supplies, laboratory space, and ideas on experimental design with doubly labeled water techniques. D. H. Morse, F. R. Moore, R. L. Holberton, J. Rotenberry, and the Migratory Bird Group at the University of Southern Mississippi provided valuable comments on early drafts of the manuscript. Travel to the Stopover Ecology Symposium in Missoula, MT, was provided by a student travel award from the American Ornithologists Union. Field work was aided by a Earthwatch Research Grant, and a pre-doctoral fellowship and Dissertation Improvement Grant (IBN-9411650) to the author from the National Science Foundation. Sincere appreciation is extended to Frank Moore for the opportunity to take part in this migration symposium. This paper is dedicated to the memory of Mr. Peter Tortorigi.

#### APPENDIX. SPECIES OF NEARCTIC-NEOTROPICAL MIGRATORY LANDBIRDS KNOWN TO DEMONSTRATE FRUGIVORY DURING THE NON-BREEDING PERIOD

Species	Extent of Frugivory <sup>a</sup>			References		
	Autumn migration	Tropic winter	Spring migration	Autumn migration	Tropic winter	Spring migration
Yellow-billed Cuckoo <i>Coccyzus americanus</i>	+	+	++	10 <sup>b</sup>	9	12 <sup>b</sup>
Black-billed Cuckoo <i>Coccyzus erythrophthalmus</i>	0	+		10 <sup>b</sup>	9	
Olive-sided Flycatcher <i>Contopus borealis</i>		0			1, 9, 11, 24	
Eastern Wood Pewee <i>Contopus virens</i>	+	+/0	++	13	1, 2, 9, 11	12 <sup>b</sup>
Western Wood Pewee <i>Contopus sordidulus</i>			+/0			9/11, 24
Eastern phoebe <i>Sayornis phoebe</i>	++	+		10 <sup>b</sup> , 16	9, 11, 13	
Say's phoebe <i>Sayornis saya</i>		0			9, 11	
Gray Flycatcher <i>Empidonax wrightii</i>		+/0			9/11	
Dusky Flycatcher <i>Empidonax oberholseri</i>		+/0			9/11	
Hammond's Flycatcher <i>Empidonax hammondi</i>		+/0			9/11	
Least Flycatcher <i>Empidonax minimus</i>	++	+		10 <sup>b</sup>	9, 22	
Acadian Flycatcher <i>Empidonax virescens</i>	++	++	+	10 <sup>b</sup>	9, 11, 24, 25 <sup>b</sup>	12 <sup>b</sup>
Traill's Flycatcher <i>Empidonax traillii</i>	++	++		10 <sup>b</sup>	9, 11, 25 <sup>b</sup>	
Ader Flycatcher <i>Empidonax alnorum</i>		+			1, 9, 11	
Yellow-bellied Flycatcher <i>Empidonax flaviventris</i>	++	+	++	10 <sup>b</sup>	9, 11	12 <sup>b</sup>
Western Flycatcher <i>Empidonax difficilis</i>		+/0			9/11	
Ash-throated flycatcher <i>Myiarchus cinerascens</i>		+/0			9/11	
Great crested Flycatcher <i>Myiarchus crinitus</i>	++	++	+	10 <sup>b</sup>	8, 9, 11, 25 <sup>b</sup>	12 <sup>b</sup>

## APPENDIX. CONTINUED

Species	Extent of Frugivory <sup>a</sup>			References		
	Autumn migration	Tropic winter	Spring migration	Autumn migration	Tropic winter	Spring migration
Scissor-tailed Flycatcher <i>Tyrannus forficatus</i>		++			9, 11	
Cassin's Kingbird <i>Tyrannus vociferans</i>		+/0			9/11	
Western Kingbird <i>Tyrannus verticalis</i>		+			9, 11	
Eastern Kingbird <i>Tyrannus tyrannus</i>		++	++	16	1, 5, 9, 11, 25 <sup>b</sup>	12 <sup>b</sup>
Tree Swallow <i>Tachycineta bicolor</i>	++	+	+	13	9	13
Violet-green swallow <i>Tachycineta thalassina</i>		0			9	
Purple Martin <i>Progne subis</i>		0			9	
Bank Swallow <i>Hirundo rustica</i>		0			9	
Northern Rough-winged Swallow <i>Stelgidopteryz serripennis</i>		0			9	
Cliff Swallow <i>Hirundo pyrrhonata</i>		+			9	
Barn Swallow <i>Riparia riparia</i>		0			9	
House Wren <i>Troglodytes aedon</i>	++	0	++	10 <sup>b</sup>	9	12 <sup>b</sup>
Marsh Wren <i>Cistothorus palustris</i>		0			9	
Sedge Wren <i>Cistothorus platensis</i>		0			9	
Winter Wren <i>Troglodytes troglodytes</i>	0	0		10 <sup>b</sup>	9	
Ruby-crowned Kinglet <i>Regulus calendula</i>	+	+	0	10 <sup>b</sup>	9	12 <sup>b</sup>
Blue-gray Gnatcatcher <i>Poliopitila caerulea</i>		0	0		9	12 <sup>b</sup>
Eastern Bluebird <i>Sialia sialis</i>	++	+		16, 20	3, 4, 9	
Western Bluebird <i>Sialia mexicana</i>		+			9	
Mountain Bluebird <i>Sialia currucoides</i>		+			9	
Townsend's Solitaire <i>Myadestes townsendi</i>		+			9	
Wood Thrush <i>Hyocichla mustelina</i>	++	++	++	10 <sup>b</sup> , 13, 14, 15, 16, 18 <sup>b</sup> , 20, 21	5, 7, 9, 11, 25 <sup>b</sup>	12 <sup>b</sup> , 25 <sup>b</sup>
Veery <i>Catharus fuscescens</i>	++	++	++	10 <sup>b</sup> , 13, 14, 16, 18 <sup>b</sup> , 20, 21	5, 9, 11, 25 <sup>b</sup>	12 <sup>b</sup>
Swainson's Thrush <i>Catharus ustulatus</i>	++	++	++	10 <sup>b</sup> , 13, 14, 15, 16, 18 <sup>b</sup> , 20, 21	5, 6, 7, 9, 11, 13, 17, 25 <sup>b</sup>	12 <sup>b</sup>
Gray-cheeked Thrush <i>Catharus minimus</i>	++	++	++	10 <sup>b</sup> , 13, 14, 16, 18 <sup>b</sup> , 20, 21	5, 9, 11, 25 <sup>b</sup>	12 <sup>b</sup>
Hermit Thrush <i>Catharus guttata</i>	++	++	++	10 <sup>b</sup> , 13, 14, 15, 16, 18 <sup>b</sup> , 20, 21	9	12 <sup>b</sup> , 13
American Robin <i>Turdus migratorius</i>	++	++	++	10 <sup>b</sup> , 13, 14, 15, 16, 18 <sup>b</sup> , 20, 21	3, 4, 9, 11	13
Gray Catbird <i>Dumetella carolinensis</i>	++	++	++	10 <sup>b</sup> , 13, 14, 15, 16, 18 <sup>b</sup> , 20, 21	7, 9, 11, 25 <sup>b</sup>	12 <sup>b</sup>
Sage Thrasher <i>Oreoscoptes montanus</i>		+			9	
Cedar Waxwing <i>Bombycilla cedrorum</i>		++	++	10 <sup>b</sup> , 13, 16, 18 <sup>b</sup> , 20	9	12 <sup>b</sup> , 13

## APPENDIX. CONTINUED

Species	Extent of Frugivory <sup>a</sup>			References		
	Autumn migration	Tropic winter	Spring migration	Autumn migration	Tropic winter	Spring migration
White-eyed Vireo <i>Vireo griseus</i>	++	++	++	10 <sup>b</sup> , 13	2, 7, 9, 11, 22	12 <sup>b</sup> , 13
Bell's Vireo <i>Vireo bellii</i>		+			9	
Black-capped Vireo <i>Vireo atricapillus</i>		+			9	
Yellow-throated Vireo <i>Vireo flavifrons</i>		+	++		9, 11, 22	12 <sup>b</sup>
Gray Vireo <i>Vireo vicinior</i>		+			9	
Solitary Vireo <i>Vireo solitarius</i>	++	++		10 <sup>b</sup> , 13c	2, 9	
Warbling Vireo <i>Vireo gilvus</i>	++	+		10 <sup>b</sup> , 13, 16, 20	2, 9	
Red-eyed Vireo <i>Vireo olivaceus</i>	++	++	++	10 <sup>b</sup> , 13, 14, 15, 16	2, 9, 11, 23 <sup>b</sup> , 25 <sup>b</sup>	12 <sup>b</sup>
Philadelphia Vireo <i>Vireo philadelphicus</i>	++	+		10 <sup>b</sup> , 13, 15,	9	
Prothonotary Warbler <i>Protonotaria citrea</i>		++	+		5, 8, 9, 11, 23 <sup>b</sup>	12 <sup>b</sup>
Golden-winged Warbler <i>Vermivora chrysoptera</i>		0			9, 11	
Blue-winged Warbler <i>Vermivora pinus</i>		0/+	0		9, 11/25 <sup>b</sup>	12 <sup>b</sup>
Tennessee Warbler <i>Vermivora peregrina</i>	+	++	+	13	5, 8, 9, 11	12 <sup>b</sup>
Orange-crowned Warbler <i>Vermivora celata</i>	+	0		13	9, 11	
Nashville Warbler <i>Vermivora ruficapilla</i>	++	0		10 <sup>b</sup>	9, 11	
Virginia's Warbler <i>Vermivora virginiae</i>		0			9	
Lucy's Warbler <i>Vermivora luciae</i>		0			9	
Northern Parula <i>Parula americana</i>	++	+	+	10 <sup>b</sup>	9, 22	12 <sup>b</sup>
Black and White Warbler <i>Mniotilta varia</i>	+	0	+	10 <sup>b</sup>	9, 11, 25 <sup>b</sup>	12 <sup>b</sup>
Black-throated Blue Warbler <i>Dendroica caerulescens</i>	++	++		10 <sup>b</sup>	11, 13	
Cerulean Warbler <i>Dendroica cerulea</i>		0	+		9, 11	12 <sup>b</sup>
Blackburnian Warbler <i>Dendroica fusca</i>	+	++		10 <sup>b</sup>	6, 9, 25 <sup>b</sup>	
Chestnut-sided Warbler <i>Dendroica pensylvanica</i>	++	+	+	10 <sup>b</sup>	9, 11, 25 <sup>b</sup>	12 <sup>b</sup>
Cape May Warbler <i>Dendroica tigrina</i>	+	+	++	13	11, 19	12 <sup>b</sup>
Magnolia Warbler <i>Dendroica magnolia</i>	++	+/0	+	10 <sup>b</sup>	22/9, 25 <sup>b</sup> c	12 <sup>b</sup>
Yellow-rumped Warbler <i>Dendroica coronata</i>	++	++	++	10 <sup>b</sup> , 14, 16, 18 <sup>b</sup> , 20, 21	9, 11, 19	12 <sup>b</sup> , 13
Black-throated Gray Warbler <i>Dendroica nigrescens</i>		0			9	
Townsend's Warbler <i>Dendroica townsendi</i>		0			9	
Hermit Warbler <i>Dendroica occidentalis</i>		0			9	
Black-throated Green Warbler <i>Dendroica virens</i>	++	+	0	10 <sup>b</sup>	9, 22	12 <sup>b</sup>



## APPENDIX. CONTINUED

Species	Extent of Frugivory <sup>a</sup>			References		
	Autumn migration	Tropic winter	Spring migration	Autumn migration	Tropic winter	Spring migration
Golden-cheeked Warbler <i>Dendroica chrysoparia</i>		0			9, 25 <sup>b</sup>	
Yellow-throated Warbler <i>Dendroica dominica</i>		0			9	
Grace's Warbler <i>Dendroica graciae</i>		0			9	
Prairie Warbler <i>Dendroica discolor</i>		+	0		9	12 <sup>b</sup>
Bay-breasted Warbler <i>Dendroica castanea</i>	+	++	+	13	9, 11, 19, 25 <sup>b</sup>	12 <sup>b</sup> , 13
Blackpoll Warbler <i>Dendroica striata</i>	++	+	+	10 <sup>b</sup>	9	12 <sup>b</sup>
Pine Warbler <i>Dendroica pinus</i>		+			9	
Palm Warbler <i>Dendroica palmarum</i>	++	0		10 <sup>b</sup>	9, 11	
Yellow Warbler <i>Dendroica petechia</i>	++	0	++	10 <sup>b</sup>	9, 11	12 <sup>b</sup> , 13
Mourning Warbler <i>Oporornis philadelphia</i>	++	0		10 <sup>b</sup>	9, 11, 25 <sup>b</sup>	
MacGillivray's Warbler <i>Oporornis tolmiei</i>		0			9, 11	
Connecticut Warbler <i>Oporornis agilis</i>	+	0		10 <sup>b</sup>	9	
Kentucky Warbler <i>Oporornis formosus</i>		0/+	+		11/9, 25 <sup>b</sup>	12 <sup>b</sup>
Canada Warbler <i>Wilsonia canadensis</i>	+	0		10 <sup>b</sup>	9, 11, 25 <sup>b</sup>	
Wilson's Warbler <i>Wilsonia pusilla</i>	+	0/+		10 <sup>b</sup>	11/9	
Hooded Warbler <i>Wilsonia citrina</i>	+	0	+	10 <sup>b</sup>	9, 11, 25 <sup>b</sup>	12 <sup>b</sup>
Worm-eating Warbler <i>Helmitheros vermivorus</i>		0/+	+		9, 11/25 <sup>b</sup>	12 <sup>b</sup>
Swainson's Warbler <i>Limnothlypis swainsonii</i>		?	+			12 <sup>b</sup>
Ovenbird <i>Seiurus aurocapillus</i>	++	+	+	10 <sup>b</sup>	11, 25 <sup>b</sup>	12 <sup>b</sup> , 13
Louisiana Waterthrush <i>Seiurus motacilla</i>		0	+		9, 11, 25 <sup>b</sup>	12 <sup>b</sup>
Northern Waterthrush <i>Seiurus noveboracensis</i>	++	0	+	10 <sup>b</sup>	9, 11, 25 <sup>b</sup>	12 <sup>b</sup>
Common Yellowthroat <i>Geothlypis trichas</i>	++	0	+	10 <sup>b</sup>	11	12 <sup>b</sup>
Yellow-breasted Chat <i>Icteria virens</i>	++	0/+	++	10 <sup>b</sup> , 20	11/9	12 <sup>b</sup>
American Redstart <i>Setophaga ruticilla</i>	0	0	+	10 <sup>b</sup>	9, 13	12 <sup>b</sup>
Rose-breasted Grosbeak <i>Pheucticus ludovicianus</i>	++	++	++	10 <sup>b</sup> , 20,	3, 5, 9, 11, 13	12 <sup>b</sup>
Black-headed Grosbeak <i>Pheucticus melanocephalus</i>		+			9	
Blue Grosbeak <i>Guiraca caeurula</i>		++	++		3, 9	12 <sup>b</sup>
Indigo Bunting <i>Passerina cyanea</i>		++	++		3, 9	12 <sup>b</sup>
Lazuli Bunting <i>Passerina amoena</i>		0			9	
Savannah Sparrow <i>Passerculus sandwichensis</i>		0			9	

## APPENDIX. CONTINUED

Species	Extent of Frugivory <sup>a</sup>			References		
	Autumn migration	Tropic winter	Spring migration	Autumn migration	Tropic winter	Spring migration
Vesper Sparrow		0			9	
<i>Poocetes gramineus</i>						
Lark Sparrow		0			9	
<i>Chondestes grammacus</i>						
Chipping Sparrow	+	0		10 <sup>b</sup>	9	
<i>Spizella passerina</i>						
Clay-colored Sparrow		0			9	
<i>Spizella pallida</i>						
Brewer's Sparrow		0			9	
<i>Spizella breweri</i>						
White-crowned Sparrow	++	0	+	10 <sup>b</sup> , 15,	9	13
<i>Zonotrichia leucophrys</i>						
Lincoln's Sparrow	++	0		10 <sup>b</sup>	9	
<i>Melospiza lincolni</i>						
Bobolink		0			9	
<i>Dolichonyx oryzivorus</i>						
Orchard Oriole		++	++	20	4, 5, 9,	12 <sup>b</sup>
<i>Icterus spurius</i>						
Northern Oriole	++	++		10 <sup>b</sup> , 14, 20	4, 5, 9, 13	
<i>Icterus galbula</i>						
Scarlet Tanager	++	++	++	10 <sup>b</sup> , 14, 16	3, 5, 6, 7, 9,	12 <sup>b</sup>
<i>Piranga olivacea</i>					11, 25 <sup>b</sup>	
Western Tanager		+			9	
<i>Piranga ludoviciana</i>						
Summer Tanager	+	++	++	20	3, 5, 6, 9, 11,	12 <sup>b</sup>
<i>Piranga rubra</i>					25 <sup>b</sup>	

Notes: Where there is strong disagreement among the literature sources, both scores of frugivory and their respective references are provided. Source reference list includes earlier studies that reviewed diets during the wintering period (9, 11, 19; see below) and complete reference lists for frugivory in landbird migrants while wintering in the tropics can be obtained there.

<sup>a</sup> Extent of frugivory determined by counts of the number of primary literature records (as in Levey and Stiles 1992) or based on categorization of data from quantitative studies. During spring migration, few studies have attempted to document frugivory, and the extent of frugivory is therefore based predominantly on an unpublished study from J. Clark and F. Moore from the Gulf coast. For autumn migration and for tropical wintering periods, the extent of frugivory was determined as follows: (0) = no reports of frugivory or 0–5% of samples in quantitative studies containing fruit; (+) = 2–5 different records of frugivory from the literature or 5–25% of samples in quantitative studies containing fruit; and (++) = >5 different records of frugivory from the literature or > 25% of samples in quantitative studies containing fruit.

<sup>b</sup> Quantitative study using diet/fecal analyses in which frequency of frugivorous samples was determined.

<sup>c</sup> Source references: (1) Fitzpatrick 1980; (2) Barlow 1980; (3) Faaborg 1980; (4) Hutto 1980; (5) Willis 1980; (6) Hilty 1980; (7) Rappole and Warner 1980; (8) Morton 1980; (9) Rappole et al. 1993; (10) Parrish 1996; (11) Levey and Stiles 1992; (12) J. Clark and F. Moore, unpubl. data; (13) J. Parrish, pers. obs.; (14) Blake and Hoppes 1986; (15) Rybczynski and Riker 1981; (16) Davidar and Morton 1986; (17) Howe 1981; (18) White and Stiles 1990; (19) Greenberg 1979; (20) Stiles 1980; (21) Malmberg and Willson 1988; (22) Greenberg et al. 1995a; (23) Poulin et al. 1994; (24) Sherry 1984; (25) Blake and Loiselle 1992a.