FORAGING BEHAVIOR OF AMERICAN REDSTARTS IN BREEDING AND WINTERING HABITATS: IMPLICATIONS FOR RELATIVE FOOD AVAILABILITY[1]

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Abstract. We investigated food availability for a long-distance migrant species, the American Redstart (*Setophaga ruticilla*), in both its summer breeding habitat in New Hampshire and in its winter habitat in Jamaica. We used four components of foraging behavior (prey attack rate, foraging speed, time spent foraging, and foraging maneuver use) as indicators of the relative availability of prey in the two seasons.

Redstarts attacked prey at a significantly greater rate in summer than in winter, indicating that foraging birds encountered prey more frequently in summer. The winter prey-encounter rate was low even though redstarts moved almost twice as fast while foraging in winter as in summer. Male redstarts also spent more time foraging in winter (85%) than in summer (43–65%), possibly to balance the low rate at which they encountered prey. In winter, redstarts used more foraging maneuvers that were directed towards small flying prey, whereas in summer they used maneuvers that resulted in the capture of relatively large and presumably energy-rich prey such as lepidopteran larvae. That wintering redstarts foraged faster, attacked prey less often, and spent more time foraging than those in summer indicates that the winter is a period of relative food scarcity for this species, whereas the breeding season is a period of greater resource abundance.

Key words: Foraging behavior; American Redstart; Setophaga ruticilla; Neotropical migrant; prey availability; Jamaica.

INTRODUCTION

Food is often considered the resource most likely to limit bird populations (Lack 1966, Wiens 1989), and has been implicated as an important limiting resource for passerine taxa as diverse as corvids (Hogstedt 1980, 1981), sparrows (Pulliam and Dunning 1987, Arcese and Smith 1988), warblers (Rodenhouse and Holmes 1992) and finches (Smith et al. 1978, Schluter 1982). Migratory birds could experience food limitation in winter (Alerstam and Hogstedt 1982, Fretwell 1986), in summer (Probst 1986, Holmes et al. 1986, Martin 1987, Sherry and Holmes 1992), or during both periods (Cox 1985, Sherry and Holmes, in press a). To date, however, there have been few attempts to compare summer and winter food availability for any long-distance migratory species.

The lack of information on food availability for migrant songbirds largely results from the difficulties of measuring prey abundance for these

small, mainly insectivorous species. No direct method of estimating prey availability is free from potential biases (Cooper and Whitmore 1990), and these biases may be exacerbated when comparisons are made between seasons, habitats, and prey communities. Furthermore, insectivorous birds usually consume a variety of prey types, which often differ in motility, crypsis, size and palatability (Sherry 1984, Holmes and Schultz 1988, Hutto 1990). Prey availability is affected by all of these factors, as well as the overall abundance of prey items. Thus, no prey sampling or census method directly assesses the prey availability actually experienced by foraging birds (Wolda 1990).

An alternative way to obtain information on food availability is to examine how the birds themselves search for and capture food, because foraging behavior often reflects in predictable ways the types and abundances of available prey (Hutto 1990). At least four components of foraging behavior can provide information on food availability. First, prey attack rates are an indication of how often prey are encountered by foraging individuals (Davies and Houston 1981, Price 1981, Blancher and Robertson 1987, Thiollay 1988). This relationship has been ver-

ified by experimental work with insectivorous warblers, which demonstrated that attack rates increase with increasing prey abundance (Hutto 1990).

Second, the rate at which birds move while foraging ("foraging speed") can be used as an indicator of the intensity of foraging effort (Robinson and Holmes 1982). By foraging faster, birds search a greater amount of substrate, and thereby increase their prey encounter rate. Third, the amount of time allocated to active foraging should increase both during times of high energy demand and during periods of low food availability. Estimates of the time spent foraging should thus provide an indirect measure of prey availability. Fourth, birds use different classes of attack maneuvers to catch different types of prey: for example, many warblers use sallies to capture flying prey such as adult Diptera, whereas gleans are often used to obtain sedentary prey such as lepidopteran larvae (Bennett 1980, Robinson and Holmes 1982). The proportional use of different types of foraging maneuver thus gives information about the types of prey taken.

In this study we examined the foraging behavior of the American Redstart, a long-distance migrant, paruline warbler, in its temperate breeding habitat in New Hampshire and in a tropical wintering area in Jamaica. We reasoned that if we found seasonal differences in redstart foraging behavior, we could identify periods of relatively low food availability by a conjunction of low attack rates, high foraging speed, greater time spent foraging, and low prey quality. While none of these behavioral parameters alone is a sufficiently reliable index of resource levels, when considered in concert they provide insight into differences in the relative availability of food resources between seasons.

METHODS

Summer observations were made from 20 May to 6 July 1990 on a 180-ha plot in the Hubbard Brook Experimental Forest, West Thornton, New Hampshire (Sherry and Holmes 1985). The vegetation at the Hubbard Brook site consisted of mature second-growth northern hardwoods forest dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*).

Winter observations were made in March and in October–November 1990 on three gridded plots totaling ~25 ha near Luana Point, approx-

imately 13 km west of Black River, St. Elizabeth Parish, Jamaica (Holmes et al. 1989). This study area was located within a monospecific black mangrove (*Avicennia germinans*) woodland that had a dense, virtually contiguous canopy between 8 and 15 m above the ground, but little vegetation at lower strata (Parrish and Sherry 1994). The site was submerged by up to one meter of water in October–November, but was mostly dry in March. Although the leafy canopy cover within the mangroves decreased in the late winter dry season (Parrish and Sherry 1994), the mangroves retained substantial green foliage throughout the year. Previous work has demonstrated that mangroves contain high densities of adult male American Redstarts relative to other Jamaican habitat types (Holmes et al. 1989, Sliwa 1991), and thus our winter study site was presumably located within a high quality wintering habitat (Sherry and Holmes, in press b).

Redstarts at both Hubbard Brook and Luana Point were individually color-banded and their territories mapped. To reduce variance due to between-sex differences in redstart foraging behavior (Holmes 1986), we report observations only on male redstarts. Similar proportions of adult and yearling males were observed in all sampling periods. Although yearling male redstarts are female-like in appearance, these individuals could often be identified as male by plumage characteristics (Pyle et al. 1987) or by song behavior during the breeding season. Data from the few female-plumaged birds that could not be visually sexed in the field were excluded from analyses.

Each of our observations were assigned to one of five sampling periods, "early winter" (late October–early November) and "late winter" (March), and three summer periods, "prebreeding," "incubation" (including the nest building and laying periods), and "nestling" periods. Data on summer males whose breeding status was not known were not included in analyses.

To obtain foraging and time budget behavior sequences, we moved systematically through each study plot until we encountered a male redstart. We then followed that individual for as long as it remained in sight, and dictated a constant narrative of its movements, prey attacks, and other behaviors into a portable tape recorder. The recorded data on movements, prey-attacks, and other behaviors were later transcribed, using a stopwatch to measure the time between events.

Multiple observations of attack rates and foraging speeds from a single individual were averaged within sampling periods, so that each individual was represented in statistical comparisons of these parameters by only one mean value within each period. Individuals were often observed again in subsequent periods within a season, but no single individual was seen in both summer and winter. In both seasons, observations were obtained throughout the daylight hours, but were concentrated between 06:00–12:00.

Attack rate. The rate at which redstarts attacked prey was determined for each observational sequence by dividing the number of prey attacks by the amount of time spent actively moving about in search of prey. We defined a "prey attack" as a directed movement towards a potential prey item (i.e., one of the five foraging maneuver classes defined below). Observational sequences during which fewer than two attacks took place were not included in attack rate calculations.

Foraging speed. Movements made by redstarts while searching for prey were classified into three categories following Robinson and Holmes (1982, 1984): hops, short flights ($\leq$ 1 m), and long flights ($>$ 1 m). The rates (number/min foraging) of each of these three categories were summed to determine the total rate of movement while foraging, which we define as "foraging speed."

Foraging time. The amount of observation time allocated to foraging was estimated for each individual by recording the predominant activity during successive five second intervals within each observation sequence. This short, standardized sampling interval was necessary because redstarts rapidly switched between behaviors, and we wished to avoid making subjective judgments about exactly when a given behavior began or ended (Tyler 1979). Redstarts were considered to be foraging if they were actively moving about in search of prey. Non-foraging activities included stationary singing, aggressive or courtship behavior, preening, and stationary vigilance. Seasonal differences in the conspicuousness of male redstart behaviors such as singing may have influenced the detectability of the individuals we studied. We avoided biasing our samples towards conspicuous behaviors by following individual males for as long as possible, and by observing the behavior of many different male redstarts. Note, however, that although we sampled time budgets across the daylight period in both seasons, our total observation time was short relative to the total time available for redstart activity, and thus our time budget figures should be considered as approximations of redstart time allocation.

Foraging maneuvers. Prey-attack maneuvers were classified into five categories after Remsen and Robinson (1990): (1) gleans (attacks from a stationary or hopping position directed towards stationary prey items); (2) sally-hovers (attacks from a hovering position directed towards stationary prey items); (3) sally-strikes (attacks from a flying position directed towards stationary prey items, without a hovering pause); (4) sallies (flights from a perch to attack flying prey items); and (5) flutter-chases (flying attacks directed towards a flying or falling prey item which has been flushed or dislodged). As an analysis of the frequencies of transitions between maneuvers showed that there was little sequential dependence among the maneuver types recorded within a single observational sequence (Lovette, unpubl. data), we pooled all the maneuvers we observed within each sampling period.

Comparisons of attack rates, foraging speeds, and foraging time among sampling periods and between seasons were made using analysis of variance (ANOVA) and multivariate analysis of variance procedures (MANOVA; SAS 1987). Where a single degree of freedom is indicated in comparisons of summer and winter data, the analyses were performed after the observations within each season were pooled. Foraging time frequency data were arcsine transformed before analysis. Differences in foraging maneuver use were tested by chi-square on the total counts of all maneuvers observed within each sampling period. For comparisons between seasons, we pooled within-season observations even though significant within-season variation existed in some cases (see below).

RESULTS

We quantified the attack rates, foraging speeds, time budgets, and foraging maneuver use of 33 male redstarts in summer and 58 male redstarts in winter.

PREY ATTACK RATES

Within-season variation. In summer, foraging male redstarts attacked prey at a mean rate of about 5 attacks/minute (Fig. 1A). There was no
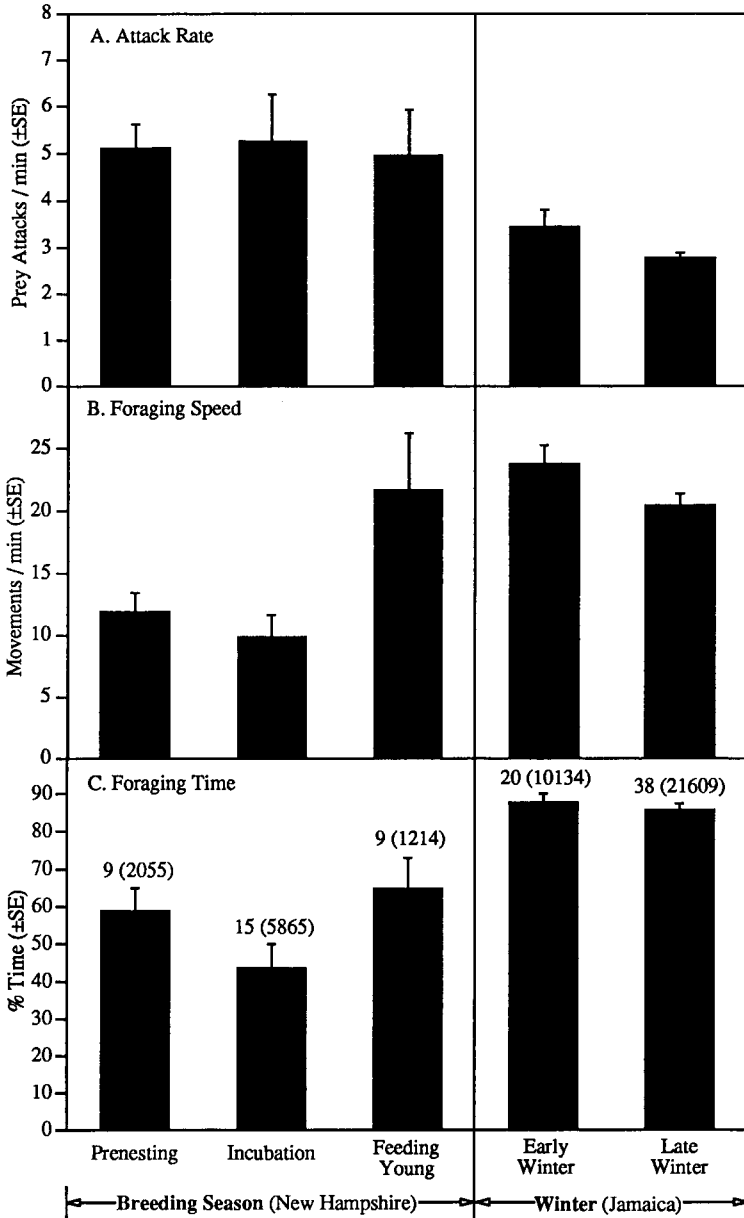
FIGURE 1. Prey attack rates (A), movement rates while foraging (B), and proportion of time devoted to foraging (C) by male American Redstarts in winter and summer habitats. Sample sizes for foraging time are number of individuals observed and total number of seconds of observation (in parentheses). Sample sizes for prey attack and movement rates are given in Table 1.

significant difference in attack rate across the three stages of the breeding cycle ($F = 0.02$, df = 2, $P < 0.98$). This mean summer attack rate is similar to that reported by Robinson and Holmes (1982), who found that redstarts at Hubbard Brook attacked prey at a mean rate of 5.6 attacks/minute.

We found more variation in attack rates within the winter than within the summer: attack rates differed significantly between the early and late winter sampling periods ($F = 4.70$, df = 1, $P < 0.04$). Male redstarts attacked prey at an average rate of 3.2 attacks/minute in the early winter,

TABLE 1. Foraging speeds of male American Redstarts in summer at Hubbard Brook Experimental Forest, New Hampshire and in winter at Luana Point, Jamaica.

| Period | $n^a(t)^b$ | Movement rates (mean number of movements/min $\pm$ SE) | | | |
		Hops	Short flights	Long flights	Foraging speed
Summer:					
Pre-nesting	10 (2,119)	7.5 $\pm$ 1.3	2.0 $\pm$ 0.5	2.4 $\pm$ 0.5	11.9 $\pm$ 1.5
Incubation	15 (5,460)	7.0 $\pm$ 1.5	1.4 $\pm$ 0.3	1.4 $\pm$ 0.3	9.8 $\pm$ 1.9
Nestling	10 (1,443)	15.3 $\pm$ 3.6	4.4 $\pm$ 1.1	1.9 $\pm$ 0.4	21.6 $\pm$ 4.5
Winter:					
Early winter	22 (10,059)	18.0 $\pm$ 1.6	3.7 $\pm$ 0.3	1.9 $\pm$ 0.2	23.7 $\pm$ 1.5
Late winter	36 (21,609)	16.3 $\pm$ 0.9	2.5 $\pm$ 0.3	1.6 $\pm$ 0.1	20.4 $\pm$ 1.0

^{a} n = number of individuals observed.
^{b} t = cumulative number of seconds of observation.

and 2.8 attacks/minute in late winter, after the onset of the dry season at our Jamaican site (Fig. 1A).

Between-season comparison. Although attack rates varied within the winter, they were lower in both winter periods than during any of the summer periods (Fig. 1A). The pooled summer mean attack rate was significantly greater than both the early winter ($F = 5.29$, df = 1, $P < 0.025$) and the late winter ($F = 19.40$, df = 1, $P < 0.001$) attack rates. Overall, winter attack rates were about 60% of those in summer (Fig. 1A), suggesting that in winter, foraging redstarts encounter potential prey items at a considerably lower rate than they do in summer.

FORAGING SPEED

Within-season variation. Redstarts move rapidly while foraging, and their movement rates are high even compared with other Hubbard Brook warblers (Robinson and Holmes 1982). In this study, we found that the foraging speed of male redstarts varied both within and between seasons. In summer, there was significant variation across breeding stages in hop ($F = 4.05$, df = 2, $P < 0.027$) and short flight ($F = 6.16$, df = 2, $P < 0.005$) rates, but not in long flight rates ($F = 1.37$, df = 2, $P < 0.27$). The overall foraging speed (which represents the sum of all three types of movement) roughly doubled during the nestling period relative to the earlier stages of the breeding cycle. This increase during the nestling period to the rapid pace of 20 movements/minute contributed to the significant variation in foraging speed we found among the summer breeding stages ($F = 5.08$, df = 2, $P < 0.01$; Fig. 1).

In winter, movement rates were more consistent between the early and late winter sampling periods (Table 1). Short flight rates were significantly greater in early winter ($F = 6.36$, df = 1, $P < 0.02$), but rates of hops ($F = 1.24$, df = 1, $P < 0.27$), long flights ($F = 1.16$, df = 1, $P < 0.29$), and overall foraging speed ($F = 3.70$, df = 1, $P > 0.05$) did not differ between the two winter periods (Table 1).

Between-season comparison. The foraging speeds of male redstarts in winter were similar to those of summer males feeding young, and were almost twice as fast as the foraging speeds of the earlier parts of the breeding season (Fig. 1B). When the pooled summer stages were contrasted with the pooled winter stages, two of the four movement categories were significantly faster in winter: hop rates ($F = 24.47$, df = 1, $P < 0.001$) and total foraging speed ($F = 9.37$, df = 1, $P < 0.005$). Short flight ($F = 1.37$, df = 1, $P > 0.25$) and long flight rates ($F = 0.31$, df = 1, $P > 0.58$) did not differ between seasons.

FORAGING TIME

Within-season variation. In summer, male redstarts spent the least amount of time foraging during the incubation period (44%), and spent more time foraging both earlier in the season during the pre-nesting period (59%) and late in the season during the nestling period (65%). This variation among the summer periods approached statistical significance ($F = 2.82$, df = 2, $P < 0.075$). In winter, the amount of time spent foraging did not differ between the two sampling periods ($F = 0.81$, df = 1, $P > 0.372$). In winter, male redstarts searched for prey about 85% of the time (Fig. 1C).

Between-season comparison. Male redstarts spent significantly more time foraging in winter than in summer ($F = 65.94$, df = 1, $P < 0.001$).

TABLE 2.   Proportional use of foraging maneuvers by male American Redstarts in summer in New Hampshire and in winter in Jamaica.

Period	n^b	Maneuvers (%)					Aerial attacks (%)[a]
		Glean	Sally-Hover	Sally	Sally-Strike	Flutter-Chase	
Summer:							
Pre-nesting	129	40	12	23	24	4	26
Incubation	130	34	6	34	22	4	38
Nestling	74	37	17	8	32	6	14
All summer observations	333	36	11	24	25	4	28
Winter:							
Early winter	389	22	18	22	19	19	40
Late winter	692	29	18	29	13	12	41
All winter observations	1,081	26	18	26	15	14	41

[a] Attacks directed towards flying prey (sallies + flutter-chases).
[b] n = number of maneuvers observed.

Even when provisioning young, male redstarts spent only 65% of their time foraging, compared with about 85% in the winter (Fig. 1C).

FORAGING MANEUVERS

Within-season variation. The proportional use of the five classes of foraging maneuvers differed significantly both within summer ($\chi^2 = 22.16$, df = 8, $P < 0.01$) and winter sampling periods ($\chi^2 = 23.13$, df = 4, $P < 0.01$; Table 2). In summer, the proportional use of sallies differed the most between stages of the breeding cycle: sallies were common early in the season during the pre-nesting and incubation periods, when they represented 23% and 34%, respectively, of the maneuvers observed, but they were rare during the nestling period (8% of maneuvers observed). Similarly, attack maneuvers directed towards aerial prey (sallies and flutter-chases) were more frequent in the first two summer periods.

The proportional use of foraging maneuvers found in the present study differ from those reported by Robinson and Holmes (1984). These differences my stem from annual variation in the types of prey taken by breeding redstarts, or it may reflect differences in the classification of maneuvers between the two studies. In particular, we used an additional maneuver category (sally-snatches) not used by Robinson and Holmes (1984), and we may have included in this category maneuvers that they would have lumped in their "flutter-chase" category.

In winter, attack maneuvers were more consistent, with no single type of maneuver showing a large shift in frequency between early and late winter (Table 2).

Between-season comparison. The pooled summer maneuver frequencies differed significantly from those in winter ($\chi^2 = 54.9$, df = 4, $P < 0.01$). Maneuvers directed at aerial prey were more frequent in winter (41%) than in summer (28%). These differences resulted from changes in the proportional use of three types of maneuvers: gleans were more common in summer than in winter, whereas sally-hovers and flutter-chases were more common in winter (Table 2).

In both seasons, most prey items were too small to be visually identified in the field, and therefore we did not attempt to quantify the actual prey types captured. However, in summer we often observed redstarts consuming large prey such as lepidopteran larvae and adult tipulid flies, whereas in winter prey items were rarely observed (Lovette, pers. observ.). This difference is consistent with stomach content analyses from the two sites, which have indicated that redstarts consume small prey such as dipterans, hymenopterans, homopterans, and adult Lepidoptera in winter, and more large Diptera and larval Lepidoptera in summer (T. W. Sherry, unpubl. data).

DISCUSSION

Many migratory birds experience seasonal shifts in food resources as they move between breeding and wintering areas. Some species, such as the Bay-breasted Warbler (*Dendroica castanea*; Greenberg 1984) and Worm-eating Warbler (*Helmitheros vermivorus*; Greenberg 1987), conspicuously switch between different food sources in the two seasons. Other species, such as the Yellow Warbler (*Dendroica petechia aestiva*), use similar foraging methods in both summer and
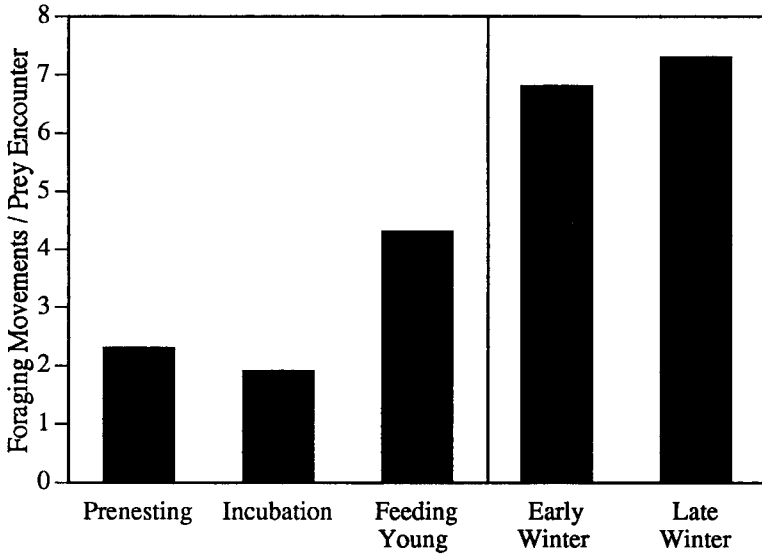
FIGURE 2.   Ratio of foraging movements to prey attacks for male American Redstarts in summer and winter. Movement : attack ratio was derived by dividing mean foraging speed within a period by the mean attack rate within that period.

winter (Wiedenfeld 1992). In this study, we found that although American Redstarts use a similar general foraging strategy in both seasons, there are differences between seasons in their attack rates, foraging speed, amount of time spent foraging, and types of prey consumed. This variation in redstart foraging behavior provides insights into differences in prey availability between summer and winter.

Prey attack rates of male redstarts were significantly lower in winter than during any part of the breeding season. Although attack rates were low in winter, redstarts foraged at greater speeds and hence presumably searched more substrate per unit time than in the breeding season. By dividing the mean foraging speed by the mean attack rate for each sampling period, we estimated the number of foraging movements required for a bird to encounter a prey item in each season. This movement : attack ratio was highest in winter, intermediate during the nestling stage, and lowest in the early stages of the breeding season (Fig. 2).

Both the low winter attack rate and the high winter movement : attack ratio implicate the winter as a period of relatively low prey availability for redstarts. Similarly, in a comparison of temperate and tropical guilds of insectivorous birds, Thiollay (1988) found that tropical birds

had lower attack rates than did species foraging on similar types of prey at temperate latitudes, which he attributed to lower prey availability in the tropics. In contrast, Wiedenfeld (1992) found that Yellow Warblers had similar attack rates in their temperate breeding habitats and the tropical mangrove forests where they winter, suggesting that prey availability for this species may be more constant between seasons than it is for redstarts.

In summer, the movement rates of male redstarts appeared to vary in concert with the energetic demands imposed by feeding young, as male redstarts more than doubled their foraging speed after they began provisioning nestlings. Their winter foraging speed was similar to this rapid nestling-stage rate, a further suggestion that winter food resources may be low relative to demand.

Although time budget sample sizes were small, the data suggest that male redstarts devote more time to foraging in winter than in summer. This seasonal difference may stem in part from the time constraints of mate attraction, pairbond maintenance, and territoriality that are present in summer but not in winter; during the summer, male redstarts devoted much of their time to stationary singing, especially in the prenesting and nesting stages of the breeding season. Al-

though redstarts engage in agonistic interactions in winter, they do not sing, but rather emit chip-notes while foraging (Holmes et al. 1989), and thus in winter relatively less time is devoted exclusively to territory maintenance.

Time budgets of insectivorous birds resident in the tropics indicate that these species may spend up to 95% of their time foraging (Ricklefs 1971, Marcotullio and Gill 1985). Insectivorous birds at temperate latitudes, however, seem to spend less time foraging, even while breeding. For example, adult juncos (*Junco phaeonotus*) devote less than 75% of their time to foraging when feeding nestlings (Weathers and Sullivan 1989), and male Willow Flycatchers (*Empidonax trailii*) spend a proportion of their time during the breeding season "loafing" (Ettinger and King 1980). Redstarts appear to follow the time budget pattern of tropical residents while wintering in Jamaica, when they spend about 85% of the time foraging, and the temperate pattern while breeding, when the proportion of time they spend foraging ranges between 43% and 56%.

This inter-seasonal shift in time allocation probably reflects differences in the composition and/or availability of prey resources between the two seasons. The small flying insects taken more often during the winter (T. W. Sherry, unpubl. data) probably require more time to find and capture, and provide less energy per prey item than do the types of prey taken in the breeding season. Lepidopteran larvae and tipulid flies, the types of prey fed most frequently to redstart nestlings (Omland and Sherry 1994), are large prey items that are energy-rich relative to the smaller prey that predominate in the redstart's winter diet.

Insects attacked in winter were flushed from their resting places on foliage more often than the insects attacked in summer. When foraging, male redstarts frequently use a characteristic "tail-fanning" behavior that flashes brightly-colored patches of their plumage, which may flush prey items from hiding (Robinson and Holmes 1982). Although we did not quantify these "tail-fans," they appeared to be more common in winter when the "flutter-chase" maneuvers were more frequent. The "tail-fanning" behavior of foraging redstarts may thus be particularly advantageous in the winter when prey are relatively scarce, and when those most available are small flying prey which can be flushed by the rapid movement rates of foraging redstarts.

The four behavioral indices of food availability, taken together, suggest that redstarts face a reduced insect availability in winter relative to summer. However, male redstarts presumably have reduced energetic costs in winter relative to summer: in winter they are rarely exposed to temperatures below their thermoneutral zone, and they do not need to allocate resources to mate attraction or raising young. The increased day-length redstarts experience during the breeding season also increases the amount of time available for foraging. A more detailed knowledge of this between-season variation in energetic costs is needed to determine the fitness consequences of low winter food availability for redstarts.

This study was limited to only one habitat type in each season. However, the low winter food availability we inferred from these foraging behavior analyses is consistent with known redstart demographic patterns. In winter, habitats vary in suitability for redstarts, as indicated by differences in densities, age and sex composition, and overwinter survival between habitats (Holmes et al. 1989, Sherry and Holmes, in press b). Removal experiments have shown that redstarts compete strongly for winter territories in preferred habitats such as the mangrove forest site where this study was conducted (Marra et al. 1993). However, further information on the factors influencing the overwinter survival of redstarts is required to evaluate whether the low winter resource levels reported here have demographic consequences for American Redstarts and other Neotropical migrants.

ACKNOWLEDGMENTS

LITERATURE CITED

ALERSTAM, T., AND G. HOGSTEDT. 1982. Bird migration and reproduction in relation to habitats for survival and breeding. Ornis Scand. 13:25–37.

ARCESE, P., AND J.N.M. SMITH. 1988. Effects of population density and supplemental food on reproduction in Song Sparrows. J. Anim. Ecol. 57:119–136.

BENNETT, S. E. 1980. Interspecific competition and the niche of the American Redstart (Setophaga ruticilla) in wintering and breeding communities, p. 319–335. In A. Keast and E. S. Morton [eds.], Migrant birds in the Neotropics. Smithsonian Institution Press, Washington, DC.

BLANCHER, P. J., AND R. J. ROBERTSON. 1987. Effect of food supply on the breeding biology of Western Kingbirds. Ecology 68:723–732.

COOPER, R. J., AND R. C. WHITMORE. 1990. Arthropod sampling methods in ornithology, p. 29–37. In M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr. [eds.], Avian foraging: theory, methodology, and applications. Stud. Avian Biol. No. 13.

COX, G. W. 1985. The evolution of avian migration systems between temperate and tropical regions of the New World. Am. Nat. 126:451–474.

DAVIES, N. B., AND A. I. HOUSTON. 1981. Curriers and satellites: the economics of territory defense in the Pied Wagtail, Motacilla alba. J. Anim. Ecol. 50:157–180.

ETTINGER, A. O., AND J. R. KING. 1980. Time and energy budgets of the Willow Flycatcher (Empidonax trailii) during the breeding season. Auk 97:533–46.

FRETWELL, S. D. 1986. Distribution and abundance of the Dickcissel. Current Ornithology, 4:211–242.

GREENBERG, R. 1984. The winter exploitation systems of Bay-breasted and Chestnut-sided Warblers in Panama. Univ. Calif. Publ. Zool. 116:1–107.

GREENBERG, R. 1987. Seasonal foraging specialization in the Worm-eating Warbler. Condor 89:158–168.

HOGSTEDT, G. 1980. Resource partitioning in magpie Pica pica and jackdaw Corvus monedula during the breeding season. Ornis. Scand. 11:110–125.

HOGSTEDT, G. 1981. Effect of additional food on reproductive success in the magpie (Pica pica). J. Anim. Ecol. 50:219–230.

HOLMES, R. T. 1986. Foraging patterns of forest birds: male-female differences. Wilson Bull. 98:196–213.

HOLMES, R. T., AND J. C. SCHULTZ. 1988. Food availability for forest birds: effect of prey distribution and abundance on bird foraging. Can. J. Zool. 66:720–728.

HOLMES, R. T., T. W. SHERRY, AND L. R. REITSMA. 1989. Population structure, territoriality, and overwinter survival of two migrant warbler species in Jamaica. Condor 91:545–561.

HOLMES, R. T., T. W. SHERRY, AND F. W. STURGES. 1986. Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. Ecol. Monogr. 56:201–220.

HUTTO, R. L. 1990. Measuring the availability of food resources, p. 20–28. In M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr. [eds.], Avian foraging: theory, methodology, and applications. Stud. Avian Biol. No. 13.

LACK, D. L. 1966. Population studies of birds. Clarendon Press, Oxford, U.K.

MARCOTULLIO, P. J., AND F. B. GILL. 1985. Use of time and space by Chestnut-backed Antbirds. Condor 87:187–191.

MARRA, P. P., T. W. SHERRY, AND R. T. HOLMES. 1993. Territorial exclusion by a Neotropical migrant bird in winter: a removal experiment with American Redstarts (Setophaga ruticilla) in Jamaica. Auk 110:565–572.

MARTIN, T. W. 1987. Food as a limit on breeding birds: a life history perspective. Ann. Rev. Ecol. Syst. 18:453–487.

OMLAND, K. E., AND T. W. SHERRY. 1994. Parental care at nests of two age classes of male American Redstart: implications for female mate choice. Condor 96:606–613.

PARRISH, J., AND T. W. SHERRY. 1994. Sexual habitat segregation by American Redstarts wintering in Jamaica: importance of resource seasonality. Auk 111:38–49.

PRICE, T. 1981. The ecology of the Greenish Warbler Phylloscopus trochiloides in its winter quarters. Ibis 123:131–144.

PROBST, J. R. 1986. A review of factors limiting the Kirtland's Warbler on its breeding grounds. Amer. Midl. Nat. 116(1):87–100.

PULLIAM, H. R., AND J. B. DUNNING. 1987. The influence of food supply on local density and diversity of sparrows. Ecology 68:1009–14.

PYLE, P., S.N.G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, CA.

REMSON, J.J.V., AND S. K. ROBINSON. 1990. A classification scheme for foraging behavior of birds in terrestrial habitats, p. 144–160. In M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr. [eds.], Avian foraging: theory, methodology, and applications. Stud. Avian Biol. No. 13.

RICKLEFS, R. E. 1971. Foraging behavior of Mangrove Swallows at Barro Colorado Island. Auk 88:635–651.

ROBINSON, S. K., AND R. T. HOLMES. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. Ecology 63:1918–1931.

ROBINSON, S. K., AND R. T. HOLMES. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. Auk 101:672–684.

RODENHOUSE, N. L., AND R. T. HOLMES. 1992. Results of experimental and natural food reductions for breeding Black-throated Blue Warblers. Ecology 73:357–372.

SAS INSTITUTE. 1987. SAS/STAT guide for personal computers. Version 6th ed. SAS Institute, Cary, NC.

SCHLUTER, D. 1982. Seed and patch selection by Galapagos Ground Finches: relation to foraging efficiency and food supply. Ecology 63:1106–1120.

SHERRY, T. W. 1984. Comparative dietary ecology of sympatric insectivorous Neotropical flycatchers (Tyrannidae). Ecol. Mono. 54:318–358.

SHERRY, T. W., AND R. T. HOLMES. 1985. Dispersion

patterns and habitat responses of birds in northern hardwoods forest, p. 289–309 *In* M. L. Cody [ed.], Habitat selection in birds. Academic Press, Orlando, FL.

SHERRY, T. W., AND R. T. HOLMES. 1992. Population fluctuations in a long distance Neotropical migrant: demographic evidence for the importance of breeding season events in the American Redstart, p. 431–442. *In* J. M. Hagan and D. W. Johnston [eds.], Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, DC.

SHERRY, T. W., AND R. T. HOLMES. In press a. Summer versus winter limitation of populations: conceptual issues and evidence, p 85–120. *In* T. E. Martin and D. M. Finch [eds.], Ecology and management of Neotropical migratory birds: a synthesis and review of the critical issues. Oxford Univ. Press, New York.

SHERRY, T. W., AND R. T. HOLMES. In press b. Quality, population limitation, and conservation of Neotropical-Nearctic migratory birds. Ecology.

SLIWA, A. 1991. Age- and sex-specific habitat and geographic segregation patterns of two New World Wood Warblers (Parulinae) wintering in Jamaica. M.Sc.thesis, Berlin Free Univ., Germany.

SMITH, J.N.M., P. R. GRANT, B. R. GRANT, I. J. ABBOTT, AND L. K. ABBOTT. 1978. Seasonal variation in feeding habits of Darwin's Ground Finches. Ecology 59:1137–1150.

THIOLLAY, J.-M. 1988. Comparative foraging success of insectivorous birds in tropical and temperate forests: ecological implications. Oikos 53:17–30.

TYLER, S. 1979. Time sampling: a matter of convention. Anim. Behav. 27:801–810.

WEATHERS, W. W., AND K. A. SULLIVAN. 1989. Juvenile foraging proficiency, parental effort, and avian reproductive success. Ecol. Monogr. 59:223–246.

WIEDENFELD, D. A. 1992. Foraging in temperate- and tropical-breeding and wintering Yellow Warblers, p. 321–328. *In* J. M. Hagan and D. W. Johnston [eds.], Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, DC.

WIENS, J. A. 1989. The ecology of bird communities. Cambridge Univ. Press, Cambridge, U.K.

WOLDA, H. 1990. Food availability for an insectivore and how to measure it, p. 38–43. *In* M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr. [eds.], Avian foraging: theory, methodology, and applications. Stud. Avian Biol No. 13.