

A TEN-YEAR STUDY OF THE STOPOVER PATTERNS OF MIGRATORY PASSERINES DURING FALL MIGRATION ON APPLEDORE ISLAND, MAINE¹

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Abstract. This study examined the autumnal stopover patterns of migratory passerines on Appledore Island, Maine, from 1983 to 1992. We recaptured 13.4% of migratory passerines at least one day after initial capture with species averages ranging from 2.8% in Eastern Wood-Pee-wee (*Contopus virens*) to 33.5% in Philadelphia Vireos (*Vireo philadelphicus*). Most observed stopovers were less than four days. Young birds were more prevalent than adults in all species studied. Among Red-eyed Vireos (*Vireo olivaceus*), Black-and-white Warblers (*Mniotilta varia*), and Northern Waterthrushes (*Seiurus noveboracensis*) young birds were more likely to be recaptured than adults. Young Northern Waterthrushes had significantly longer stopovers than adults. No difference in recaptures was detected between the sexes in any species studied. Most of the birds captured were lean (fat class 0 or 0.5) at initial capture. In several species, young birds were significantly leaner both in terms of fat class and mass than adults. Most species studied experienced significant increases in fat class and mass during stopovers. We did not find significant differences in mass or fat increases between age groups or between the sexes in any species studied. Cape May Warblers (*Dendroica tigrina*), Black-and-white Warblers, and American Redstarts (*Setophaga ruticilla*) did not exhibit any differences in recaptures, stopover lengths, or mass increases among years. Northern Waterthrushes exhibited significant differences in recaptures and Red-eyed Vireos exhibited differences in recaptures and mass increases among years during this study.

Key words: Migration; stopover biology; Neotropical landbird migrants; fat deposition; North Atlantic.

INTRODUCTION

Recent apparent declines in Neotropical migrant populations (Robbins et al. 1989) make understanding the annual cycle of these organisms essential (Keast and Morton 1980, Hagan and Johnston 1992). The deforestation of wintering grounds and the destruction and fragmentation of breeding areas pose two serious habitat constraints for passerine conservation. Moore et al. (1990) suggest that the availability of suitable stopover habitat may pose a third habitat constraint. Thus studies investigating the biology and behavior of migrants at stopover sites may prove

to be an integral part of the conservation of these declining migratory species.

Most studies of the stopover biology of migratory passerines in North America have been conducted along the northern coast of the Gulf of Mexico and have focused on spring migration (Rappole and Warner 1976, Moore and Kerlinger 1987, Loria and Moore 1990, Kuenzi et al. 1991). Forsyth and James (1971) recognized the importance of studying migration in different geographical locations to observe the overall pattern of migration. The movement during fall migration of large numbers of migratory passerines both along the coast and over the water of the Western North Atlantic has been well documented (Drury and Keith 1962, Richardson 1972, McClintock et al. 1978, Williams and Williams

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1978). Although numerous studies have focused on the timing and patterns of fall migration along the Atlantic coast (Baird et al. 1958, Baird et al. 1959, Nisbet et al. 1963, Murray 1966), only scanty information is available on the stopover biology of migratory passerines on the Atlantic coast.

Coastal banding stations have reported high proportions of young individuals in the population during fall migration (Baird and Nisbet 1960, Drury and Keith 1962, Murray 1966), however, little is known about differences between adults and juveniles in stopover biology. During the fall, juveniles are facing their first migratory flight and therefore it is possible that they will require additional time to build adequate fat stores compared to adults. Young birds may be less efficient foragers than adults, they may take longer to acclimate to novel habitats, or they may need an additional margin of safety for migratory flight. Studies of differences in the stopover biology of males and females are few in number. Ellegren (1991) did not find any difference in the recapture of males and females in Sweden. Because both males and females of many Neotropical species defend winter territories (Rappole and Warner 1980), it is possible that similar pressures during fall migration will result in similar patterns of stopover in these species.

In this study on a small island in the Gulf of Maine frequented by many migrants during fall migration, we addressed the following questions: (1) Do differences in stopover patterns exist between species? (2) Do males and females have the same stopover patterns? (3) Do young and adult birds have similar patterns of stopover? (4) Does the energetic condition such as mass and fat class of migrants upon arrival affect the observed patterns of stopover? (5) Do migrants experience a change in energetic condition during stopover on Appledore Island, Maine?

STUDY SITE AND METHODS

Our field site is Appledore Island, Maine (42°58'N 70°36'W), a 33.6-ha island in the Gulf of Maine. Appledore Island is the largest island in the Isles of Shoals, a group of nine small islands and several ledges 14.5 km southeast of Portsmouth, New Hampshire, and 9.7 km from the nearest point of the mainland. While most of the islands in the Isles of Shoals are sparsely vegetated and much of their area is composed of exposed rock, Appledore Island is well vegetated with a variety

of vegetation types. More information on the field site is given in Morris et al. (1994).

We gathered data between mid-August and late September from 1983 to 1992. Weather permitting, we operated six to ten mist nets (12 × 2.6 m, 4 shelves, 30 mm mesh) during most of the daylight hours, with the mist nets opened just before sunrise, closed around sunset, and checked approximately every 30 min throughout the day. Mist nets were located in the same locations each year to reduce between-year variation in sampling. We banded birds with a standard U.S. Fish and Wildlife Service aluminum band as they were brought to a central location. For each bird captured and recaptured, we recorded age, sex (whenever possible), the amount of skull pneumatization, unflattened wing chord, fat class, and mass. In the case of recaptures, we did not refer to the initial data sheets, so measurements were not influenced by information recorded previously. We determined age and sex based on guidelines of the U.S. Fish and Wildlife Service (1977), Wood and Beimborn (1981), and Pyle et al. (1987). Fat class in this study refers to the categorical quantification of subcutaneous fat determined by blowing feathers aside to view the furcula (interclavicular fossa) and the sides of the abdomen. The fat classification system we use is similar to that described by Cherry (1982): 0 = no visible fat reserves; 0.5 = traces of fat visible; 1 = fat lining the furcula, but concave, and small reserves of fat on the sides of the abdomen; 2 = fat filling the furcula, but not mounded, and a continuous sheet of fat visible on the sides of the abdomen; 3 = fat filling the furcula and generally slightly mounded and abdominal fat mounded; 4 = furcular and abdominal fat reserves mounded and convex. Because only one or two individuals were assigned a fat class of 4 each season, we analyzed the birds with fat classes of 3 and 4 together. Differences in fat classification between observers can be substantial (Krementz and Pendleton 1990). However, we attempted to reduce the effects of inter-observer variation in two ways: 1) all classifications were made by only three observers, one of whom was responsible for at least three-quarters of the observations; and 2) numerous classifications were checked for between-observer consistency each banding season. From 1983 to 1989, we used a Pesola 50 g spring balance to determine mass to the nearest 0.1 g. From 1990 to 1992, we used an Ohaus electronic balance (Model CT-200) to determine mass to the nearest 0.01 g.

Minimum length of stopover, determined by subtracting the initial date of capture from the date of last recapture, follows Cherry (1982), Moore and Kerlinger (1987), and Ellegren (1991). Thus, a one-day stopover refers to a stopover of one night and part of two days. This method differentiates between passage migrants, birds that suspend migration only during the day but presumably continue migration that night, and migrants that suspend migration for at least one night. Several other authors (e.g., Borror 1948, Bairlein 1985, Biebach et al. 1986, Lavee et al. 1991) also include the day of initial capture in the minimum length of stopover. Thus, when comparing these minimum stopover lengths to those in other papers, it is important to compare the method of calculating length of stopover. Either method results in a conservative estimate of the time a migrant stopped because we could not assume that the date of initial capture was the first day of a stopover, nor could we assume that the final recapture occurred on the last day of a stopover (Cherry 1982, Biebach et al. 1986, Moore and Kerlinger 1987). Additionally, average stopover lengths would be biased if residents as well as migrants of the same species were included in the analysis; therefore, we have eliminated from this study confirmed regular breeders on Appledore Island including Common Yellowthroats (*Geothlypis trichas*), Yellow Warblers (*Dendroica petechia*), and Eastern Kingbirds (*Tyrannus tyrannus*) (Borror and Holmes 1990).

Mass changes were calculated for individuals recaptured at least one day after initial capture by subtracting initial mass from the final mass. In many passerine species, males tend to be larger than females. Males also often have longer wing chords than do females (Pyle et al. 1987). To compare increases in mass, we calculated the percent change during stopover using the following formula: percent change = (final mass - initial mass) · initial mass⁻¹ · 100%. This method reduces the possibility of sex- or age-related size differences influencing observed differences in mass. Daily percent increases in mass were calculated by dividing the percent gain by stopover length. Following Winker et al. (1992a), we used simple linear regression to investigate the relationship of condition and time of capture for all individuals captured. Condition was calculated as mass · (wing³)⁻¹ · 10,000. Using these equations, we estimated the net daily mass increases of our most frequently captured species using the average mass and wing chord for each species and av-

erage day length during banding station operation. Because unflattened wing length was taken during banding, our estimates may be slightly different than those of Winker et al. (1992a) who used flattened wing length in their calculations.

Flight range estimates were computed using the flight performance calculations of Pennycook (1989). The wing span averages were obtained from specimens in the Cornell University Vertebrate Collections and from a tower kill in New Hampshire. The average wingspans are as follows: Red-eyed Vireos (*Vireo olivaceus*): 248.9 ± 9.4 mm (*n* = 11); male American Redstarts (*Setophaga ruticilla*): 191.1 ± 6.8 mm (*n* = 6); female American Redstarts: 186.9 ± 1.8 mm (*n* = 4); and Ovenbirds (*Seiurus aurocapillus*): 233.5 ± 15.1 mm (*n* = 16). Estimates reflect still air and a flight altitude of 1000 m (Nisbet 1963). Although offshore movements have been recorded at altitudes equal to and greater than 2000 m (Richardson 1972, Williams and Williams 1978), we do not know the direction or height of migratory movements from this island. The fat free masses used for these analyses were obtained from Rogers and Odum (1964, 1966).

Significance levels of statistical tests on the initial condition of migrants denote one-tailed probabilities to reflect our expectation of more recaptures of leaner birds than fatter ones. Similarly, we expected birds to experience fat and mass increases during stopover and therefore we report one-tailed probabilities from those tests. All other statistical tests reflect two-tailed probabilities. In the case of two-sample *t*-tests, we did not assume equal variance and therefore we present results using degrees of freedom corrected for unequal variance. The mass change data were log transformed to normalize the distributions and equalize variances prior to performing *t*-tests. All significance levels were adjusted by sequential Bonferroni corrections for multiple tests.

RESULTS

GENERAL PATTERNS

During the ten fall migration periods studied, we banded 14,324 migrant passerines of 77 species, 202 non-passerine migrants of ten species, and 3,374 individuals of 15 species of confirmed breeding or resident species. We present results here from the 33 migrant passerine species regularly captured during this study (Table 1).

We recaptured 13.4% of the migratory passerines at least one day after initial capture, with

TABLE 1. Stopover patterns and age composition of frequently captured species^a of migratory passerines during fall migration on Appledore Island, Maine.

Species	Total captured	Recaptured ^b # (%)	Stopover $\bar{x} \pm 1SD$ (dd)	Range (dd)	Young ^c %
Eastern Wood-Pewee <i>Contopus virens</i>	176	5 (2.8)	3.6 \pm 1.3	2-5	81.8
Least Flycatcher <i>Empidonax minimus</i>	414	22 (5.3)	3.1 \pm 2.3	1-9	98.8
"Traill's" Flycatcher <i>E. alnorum</i> and <i>E. traillii</i>	428	37 (8.6)	2.9 \pm 1.7	1-7	96.2
Yellow-bellied Flycatcher <i>E. flaviventris</i>	442	43 (9.7)	2.7 \pm 1.9	1-8	97.1
Red-breasted Nuthatch <i>Sitta canadensis</i>	378	61 (16.1)	3.0 \pm 2.7	1-17	81.7
Veery <i>Catharus fuscescens</i>	275	38 (13.8)	3.1 \pm 2.1	1-10	80.4
Swainson's Thrush <i>C. ustulatus</i>	136	15 (11.0)	2.5 \pm 1.7	1-7	86.8
Cedar Waxwing <i>Bombycilla cedrorum</i>	637	22 (3.5)	4.6 \pm 5.0	1-24	88.4
Warbling Vireo <i>Vireo gilvus</i>	58	7 (12.1)	3.1 \pm 2.5	1-7	98.2
Philadelphia Vireo <i>V. philadelphia</i>	164	55 (33.5)	3.4 \pm 1.9	1-8	98.2
Red-eyed Vireo <i>V. olivaceus</i>	1,450	328 (22.4)	3.5 \pm 2.6	1-15	93.1
Blue-winged Warbler <i>Vermivora pinus</i>	136	20 (14.7)	3.2 \pm 2.0	1-7	100.0
Tennessee Warbler <i>V. peregrina</i>	166	29 (17.5)	2.2 \pm 2.1	1-9	75.5
Nashville Warbler <i>V. ruficapilla</i>	127	13 (10.2)	2.2 \pm 1.1	1-5	97.6
Chestnut-sided Warbler <i>Dendroica pensylvanica</i>	130	9 (6.9)	1.9 \pm 1.2	1-4	97.7
Magnolia Warbler <i>D. magnolia</i>	223	12 (5.4)	1.8 \pm 1.6	1-6	92.4
Cape May Warbler <i>D. tigrina</i>	622	63 (10.1)	2.9 \pm 2.1	1-9	96.5
Black-throated Blue Warbler <i>D. caerulescens</i>	116	12 (10.3)	1.6 \pm 0.5	1-2	97.4
Yellow-rumped Warbler <i>D. coronata</i>	77	7 (9.1)	4.3 \pm 3.8	1-11	97.4
Prairie Warbler <i>D. discolor</i>	55	2 (3.6)	4.5 \pm 0.7	4-5	96.4
Bay-breasted Warbler <i>D. castanea</i>	198	41 (20.7)	4.8 \pm 4.0	1-18	89.9
Blackpoll Warbler <i>D. striata</i>	170	5 (2.9)	1.8 \pm 1.8	1-5	76.5
Black-and-white Warbler <i>Mniotilta varia</i>	464	104 (22.2)	3.3 \pm 2.5	1-17	94.0
American Redstart <i>Setophaga ruticilla</i>	1,635	226 (13.8)	2.7 \pm 2.2	1-18	92.8
Ovenbird <i>Seiurus aurocapillus</i>	317	50 (15.8)	4.7 \pm 3.4	1-17	98.4
Northern Waterthrush <i>S. noveboracensis</i>	2,103	396 (18.8)	4.0 \pm 2.9	1-17	76.6
Mourning Warbler <i>Oporornis philadelphia</i>	187	21 (11.2)	3.0 \pm 2.7	1-13	95.7
Wilson's Warbler <i>Wilsonia pusilla</i>	295	19 (6.4)	2.6 \pm 1.1	1-5	98.6
Canada Warbler <i>W. canadensis</i>	245	20 (8.2)	3.4 \pm 2.3	1-10	86.5
Yellow-breasted Chat <i>Icteria virens</i>	62	3 (4.8)	3.3 \pm 1.5	2-5	95.2
Rose-breasted Grosbeak <i>Pheucticus ludovicianus</i>	62	5 (8.1)	4.2 \pm 3.0	2-8	98.4
White-throated Sparrow <i>Zonotrichia albicollis</i>	84	9 (10.7)	3.7 \pm 3.6	1-13	100.0
Northern Oriole <i>Icterus galbula</i>	314	20 (6.4)	3.0 \pm 2.5	1-9	— ^d

^a Species with at least 50 new captures from 1983 to 1992.

^b Number of individuals recaptured at least one day after initial capture (percent).

^c Percent of total captures classified as young. Young refers to hatch-year individuals.

^d Northern Orioles often cannot be reliably aged.

the species means of individuals recaptured ranging from 2.8% in Eastern Wood Pewee (*Contopus virens*) to 33.5% in Philadelphia Vireos (*Vireo philadelphia*; Table 1). Most recaptured migrants had short observed stopovers with almost 75% of all individuals recaptured within four days of initial capture (Table 1).

Young birds (hatch-year individuals) were much more prevalent than adults (after-hatch-year individuals) on Appledore Island (Table 1). Although most species showed patterns of young birds accounting for more than 90% of individuals captured, young Tennessee Warblers (*Vermivora peregrina*), Blackpoll Warblers (*Dendroica striata*), and Northern Waterthrushes (*Seiurus noveboracensis*) accounted for less than 80% of the individuals captured (Table 1). Ad-

ditionally, young Eastern Wood-Pewees, Red-breasted Nuthatches (*Sitta canadensis*), and Veerys (*Catharus fuscescens*) accounted for less than 82% of individuals captured. In most species, young birds were recaptured more frequently than adults, although this pattern was significant only among Red-eyed Vireos, Black-and-white Warblers, and Northern Waterthrushes. Differences in stopover lengths between young and adult birds were highly variable (Table 2). The Northern Waterthrush was the only species in which we found a significant difference between the age groups, with young birds having significantly longer stopover lengths than adults ($U = 8178.0$, $P < 0.05$).

We found no significant difference in the proportion of males and females recaptured among

TABLE 2. Initial mass, proportion of migrants recaptured, and mean minimum length of stopover during the fall by age for seventeen species of migratory passerines regularly captured on Appledore Island, Maine.

	Young birds				Adult birds				C ^c
	n	Initial mass (g) ^a	Recaptured ^b # (%)	Stopover $\bar{x} \pm$ 1SD (dd)	n	Initial mass (g) ^a	Recaptured ^b # (%)	Stopover $\bar{x} \pm$ 1SD (dd)	
Eastern Wood-Pewee	144	13.0 ± 1.2	5 (3.5)	3.6 ± 1.3	32	14.4 ± 1.2	0 (0.0)	—	2.0
Traill's Flycatcher	409	12.9 ± 1.5	36 (8.8)	2.8 ± 1.6	16	13.0 ± 1.3***	0 (0.0)	—	2.9
Yellow-bellied Flycatcher	428	10.5 ± 0.9	43 (10.1)	2.7 ± 1.9	13	10.2 ± 0.9	0 (0.0)	—	2.7
Red-breasted Nuthatch	303	10.0 ± 0.8	48 (15.8)	2.8 ± 2.7	68	9.9 ± 0.7	10 (14.7)	3.4 ± 2.5	0.1
Veery	221	33.4 ± 3.3	35 (15.8)	2.9 ± 2.7	54	34.1 ± 4.3	3 (5.6)	4.7 ± 4.6	4.5
Swainson's Thrush	118	30.6 ± 3.0	15 (12.7)	2.5 ± 1.7	18	30.6 ± 3.0	0 (0.0)	—	4.6
Cedar Waxwing	562	33.7 ± 3.3	20 (3.6)	3.5 ± 2.4	74	32.6 ± 2.9	2 (2.7)	16.5 ± 10.6	0.2
Red-eyed Vireo	1,350	17.6 ± 1.9	319 (23.6)	3.5 ± 2.6	100	18.4 ± 2.1**	7 (7.0)	3.3 ± 2.8	18.5**
Tennessee Warbler	123	8.9 ± 0.9	24 (19.5)	2.5 ± 2.2	40	9.6 ± 1.2*	5 (12.5)	1.2 ± 0.5	1.1
Magnolia Warbler	206	7.8 ± 0.7	12 (5.8)	1.8 ± 1.6	17	7.9 ± 0.6	0 (0.0)	—	2.0
Cape May Warbler	600	9.4 ± 0.9	62 (10.3)	2.9 ± 2.1	22	9.8 ± 1.1	1 (4.6)	3	1.0
Bay-breasted Warbler	178	10.9 ± 1.0	35 (19.7)	4.4 ± 3.2	20	11.2 ± 1.2	6 (30.0)	7.2 ± 6.8	1.1
Blackpoll Warbler	130	11.1 ± 1.2	2 (1.5)	1.0 ± 0.0	40	11.5 ± 0.9	3 (7.5)	2.3 ± 2.3	-3.1
Black-and-white Warbler	436	10.5 ± 1.4	102 (23.4)	3.3 ± 2.5	28	10.3 ± 1.2	1 (3.6)	1	8.3*
American Redstart	1,515	8.1 ± 0.8	213 (14.1)	2.8 ± 2.3	118	8.3 ± 0.6**	12 (10.2)	2.4 ± 1.0	1.5
Northern Waterthrush	1,606	17.2 ± 2.0	359 (22.4)	4.1 ± 2.9	492	17.8 ± 2.2***	36 (7.3)	2.9 ± 2.5	65.4**
Canada Warbler	212	9.7 ± 1.0	19 (9.0)	3.4 ± 2.4	33	9.9 ± 0.9	1 (3.0)	3	1.7

Initial mass (g) of all individuals captured. Significance levels report the results of two-sample *t*-tests on the initial mass between adults and young birds. **P* < 0.05, ***P* < 0.01, ****P* < 0.001 after sequential Bonferroni correction for multiple tests.
^a Number of individuals recaptured at least one day after initial capture (percent of total captured).
^b Results of a G-test between proportion of young and adult birds recaptured.

any species studied (Table 3). Differences between males and females in stopover length were highly variable. While among Northern Orioles (*Icterus galbula*) males had significantly longer observed stopovers than females ($U = 7.5$, $P < 0.05$), females had significantly longer stopovers than males among American Redstarts ($U = 4700$, $P < 0.05$) and Red-breasted Nuthatches ($U = 263$, $P < 0.05$).

ENERGETIC CONDITION

Over half (51.6%) of all birds captured were lean (fat class 0 or 0.5) at first capture. Differences in initial fat stores between adult and young birds were mixed. Among Cedar Waxwings (*Bombus cedrorum*), adults encountered on Appledore were leaner than young birds ($\chi^2 = 23.6$, $df = 1$, $P < 0.001$). However, young Tennessee Warblers, Northern Waterthrushes, and American Redstarts were leaner in terms of fat class than adults ($\chi^2 = 10.4$, $df = 1$, $P < 0.05$; $\chi^2 = 12.5$, $df = 1$, $P < 0.01$; $\chi^2 = 11.8$, $df = 1$, $P < 0.05$, respectively). When comparing the initial mass of adult and young individuals, five species showed significantly higher mass in adults (Table 2). We did not find differences in fat stores between males and females in most species studied. However, among American Redstarts males were more likely to be lean than females ($\chi^2 = 15.5$, $df = 1$, $P < 0.01$). Mass differences were more pronounced between the sexes (Table 3). Males averaged a significantly higher initial mass than females in ten species studied.

Lean birds were generally more likely to be recaptured than fat ones, although this trend was significant in only three species studied. Red-eyed Vireos which were later recaptured were leaner in terms of fat class upon initial capture than those captured only once ($\chi^2 = 85.2$, $df = 1$, $P < 0.001$). Northern Waterthrushes and Veerys exhibited the same pattern ($\chi^2 = 8.5$, $df = 1$, $P < 0.05$; $\chi^2 = 7.9$, $df = 1$, $P < 0.05$, respectively). Initial fat class does not appear to influence the length of stopover in most of the species studied. However, lean Red-eyed Vireos had average stopover lengths one day longer than fat birds ($KW = 14956$, $P < 0.05$). Analyses on the relationship between initial mass and the recapture of migrants yielded similar results. Eastern Wood-Pewees ($t = 6.2$, $df = 5$, $P < 0.05$), "Traill's" Flycatchers (*Empidonax traillii* and *E. alnorum*; $t = 3.1$, $df = 50$, $P < 0.05$), Yellow-bellied Flycatchers (*E. flaviventris*; $t = 3.0$, $df =$

63, $P < 0.05$), Veerys ($t = 3.4$, $df = 60$, $P < 0.05$), Philadelphia Vireos ($t = 3.1$, $df = 118$, $P < 0.05$), Red-eyed Vireos ($t = 9.0$, $df = 631$, $P < 0.001$), Chestnut-sided Warblers (*Dendroica pensylvanica*; $t = 4.4$, $df = 16$, $P < 0.01$), and Northern Orioles ($t = 3.8$, $df = 21$, $P < 0.05$) that were recaptured had lower initial masses than individuals of the same species that were captured only once. We did not find any relationship between the initial mass and the length of stopover in any species studied.

Males and females later recaptured on Appledore Island did not differ significantly in initial fat class among any species in this study. However, among individuals recaptured, male Red-eyed Vireos ($t = 4.0$, $df = 33.4$, $P < 0.01$), American Redstarts ($t = 3.6$, $df = 206.5$, $P < 0.01$), and Mourning Warblers (*Oporornis philadelphia*; $t = 5.6$, $df = 5$, $P < 0.05$) had higher average initial masses than females of the same species (Table 3).

Most species of migrants studied experienced increases in both mass and fat class between initial and final capture on Appledore Island although there was substantial variation among individuals (Table 4). While not all tests showed significant increases, there were no cases with significant trends of decreasing body condition during stopover. To reduce the effects of individuals with long stopovers and large changes in mass, daily percent mass changes were computed. Most species also experienced average daily percent increases in mass (Table 4). Five species exhibited average daily decreases in mass, but none of these decreases were significant. No species studied exhibited significant differences in mass change by age or by sex.

We recaptured 374 migrants more than once during stopover on Appledore Island. Graphical representations indicate that mass increases are not linear between first capture and final recapture. However, there is no evidence to support an initial phase of mass decrease followed by mass increase at this stopover site. Most of these individuals experienced a mass increase between initial capture and first recapture (Sign Test $P < 0.001$) as well as between first recapture and final recapture ($P < 0.001$). As with total mass increases, we did find variation among species. Among the species frequently recaptured more than once, both Red-eyed Vireos (REVI) and Northern Waterthrushes (NOWA) significantly increased in mass between initial capture and

TABLE 3. Initial mass, proportion of individuals recaptured, and mean minimum length of stopover during the fall by sex for fifteen species of migrants regularly captured on Appledore Island, Maine.

	Females			Males				
	n	Initial mass (g) ^a	Recaptured ^b # (%)	Stopover $\bar{x} \pm 1SD$ (dd)	n	Initial mass (g) ^a	Recaptured ^b # (%)	Stopover $\bar{x} \pm 1SD$ (dd)
Least Flycatcher	269	9.4 ± 0.8	14 (5.2)	2.9 ± 2.1	112	10.2 ± 0.8***	6 (5.4)	2.7 ± 1.9
Yellow-bellied Flycatcher	270	10.2 ± 0.8	31 (11.5)	2.8 ± 1.9	156	10.9 ± 0.8***	10 (6.4)	1.9 ± 1.2
Red-breasted Nuthatch	192	9.8 ± 0.7	29 (15.1)	4.1 ± 3.4	182	10.2 ± 0.7***	32 (17.6)	2.0 ± 1.3
Red-eyed Vireo	221	17.0 ± 1.6	48 (21.7)	3.5 ± 2.7	120	18.3 ± 2.0***	20 (16.7)	2.6 ± 1.5
Blue-winged Warbler	69	9.2 ± 1.3	14 (20.3)	2.9 ± 2.0	62	9.1 ± 1.1	6 (9.7)	3.8 ± 2.0
Tennessee Warbler	25	8.5 ± 1.0	5 (20.0)	1.6 ± 0.9	23	9.3 ± 1.2	4 (17.4)	1.3 ± 0.5
Nashville Warbler	70	7.8 ± 0.8	8 (11.4)	2.0 ± 0.8	55	8.1 ± 0.8	5 (9.1)	2.4 ± 1.7
Magnolia Warbler	79	7.6 ± 0.6	7 (8.9)	1.4 ± 1.1	112	7.9 ± 0.6	4 (3.6)	1.5 ± 0.6
Cape May Warbler	336	9.3 ± 0.8	33 (9.8)	3.1 ± 2.2	285	9.5 ± 0.9*	30 (10.5)	2.7 ± 1.9
Black-throated Blue Warbler	61	8.8 ± 0.7	5 (8.2)	2.0 ± 0.0	55	9.4 ± 0.9**	7 (12.7)	1.3 ± 0.5
Black-and-white Warbler	247	10.5 ± 1.3	55 (22.3)	3.5 ± 2.7	217	10.5 ± 1.4	48 (22.1)	2.0 ± 2.3
American Redstart	817	7.9 ± 0.8	117 (14.3)	3.0 ± 2.3	781	8.3 ± 0.9***	100 (12.8)	2.4 ± 2.1
Mourning Warbler	49	11.4 ± 1.3	3 (6.1)	3.0 ± 1.7	62	12.3 ± 1.2**	8 (12.9)	2.3 ± 1.0
Wilson's Warbler	120	7.3 ± 0.7	9 (7.5)	3.0 ± 1.0	151	7.5 ± 0.7**	7 (4.6)	2.0 ± 1.2
Canada Warbler	127	9.6 ± 1.1	11 (8.7)	3.1 ± 1.6	103	9.9 ± 0.9	8 (7.8)	3.5 ± 3.1
Northern Oriole	181	33.5 ± 3.7	14 (7.7)	2.1 ± 1.8	123	35.3 ± 3.7***	5 (4.1)	5.6 ± 2.8

^aSD \pm 1SD for all individuals captured. Significance levels report the results of two-sample t-tests on the initial mass between females and males. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ after sequential Bonferroni correction for multiple tests.

^b Number of individuals recaptured at least one day after initial capture (percent of total captured).

TABLE 4. Changes in mass and fat class by migratory passerines stopping over on Appledore Island, Maine.

	<i>n</i>	Mass change (g)	Daily mass change (g)	Mass change (%)	Daily mass change (%)	Daily mass change (%)	Change in fat class
Least Flycatcher	22	0.6 ± 0.8*	0.1 ± 0.4	5.6 ± 8.3	0.8 ± 4.2	0.5 ± 0.7	
“Trail’s” Flycatcher	37	1.5 ± 1.7***	0.4 ± 0.5**	12.1 ± 13.7***	3.2 ± 4.4**	0.7 ± 0.9**	
Yellow-bellied Flycatcher	43♦	0.6 ± 1.1**	0.2 ± 0.6	6.3 ± 10.8**	2.0 ± 5.6	0.3 ± 0.7	
Red-breasted Nuthatch	61♦♦	0.1 ± 0.8	0.0 ± 0.5	1.2 ± 8.6	-0.3 ± 5.2	0.2 ± 0.7	
Veery	38	1.6 ± 2.8*	0.4 ± 0.9	5.1 ± 13.7*	1.4 ± 2.9	0.7 ± 1.1*	
Swainson’s Thrush	15♦♦	1.2 ± 2.0	0.5 ± 1.3	3.8 ± 6.3	1.6 ± 4.2	0.3 ± 0.6	
Cedar Waxwing	22♦	0.6 ± 2.8	0.2 ± 0.9	2.0 ± 8.2	0.7 ± 5.6	0.3 ± 0.7	
Philadelphia Vireo	55	0.9 ± 1.1***	0.3 ± 0.5**	8.0 ± 10.1***	2.3 ± 4.2**	0.5 ± 0.8***	
Red-eyed Vireo	328	1.6 ± 2.2***	0.4 ± 0.7***	9.8 ± 13.5***	2.3 ± 4.3***	0.7 ± 1.1***	
Blue-winged Warbler	20	1.1 ± 1.4*	0.2 ± 0.5	13.1 ± 17.6*	2.3 ± 5.4	0.6 ± 1.2	
Tennessee Warbler	29♦	0.8 ± 0.8***	0.5 ± 0.5**	9.7 ± 9.6***	5.4 ± 5.6***	0.7 ± 1.1	
Nashville Warbler	13	0.5 ± 0.8	0.2 ± 0.3	6.7 ± 10.1	2.1 ± 4.1	0.7 ± 0.8	
Magnolia Warbler	12	0.2 ± 0.8	-0.1 ± 0.4	1.9 ± 10.1	-1.1 ± 5.8	0.3 ± 1.0	
Cape May Warbler	63♦♦	0.2 ± 0.8	0.0 ± 0.4	2.4 ± 8.8	-0.3 ± 4.0	0.2 ± 0.6	
Black-throated Blue Warbler	12♦	-0.0 ± 0.7	-0.1 ± 0.4	-0.1 ± 7.5	-0.8 ± 4.8	0.0 ± 0.6	
Bay-breasted Warbler	41	0.6 ± 1.2*	0.2 ± 0.5	5.9 ± 11.6*	1.6 ± 4.3	0.3 ± 0.7	
Black-and-white Warbler	102	0.6 ± 1.1***	0.2 ± 0.5**	6.4 ± 10.7***	2.0 ± 4.4***	0.3 ± 0.7**	
American Redstart	224♦	0.2 ± 0.7*	0.0 ± 0.4	2.1 ± 8.2*	0.3 ± 4.4	0.1 ± 0.6	
Ovenbird	50	1.8 ± 2.6***	0.4 ± 1.2	10.0 ± 13.3***	2.1 ± 6.2	0.6 ± 0.9**	
Northern Waterthrush	395♦	1.2 ± 1.8***	0.3 ± 0.6***	7.4 ± 10.7***	1.8 ± 3.7***	0.3 ± 0.9***	
Mourning Warbler	21♦♦	0.7 ± 1.1	0.1 ± 0.5	6.6 ± 10.2	1.6 ± 4.6	0.3 ± 0.6	
Wilson’s Warbler	19♦♦	-0.0 ± 0.5	-0.0 ± 0.2	0.4 ± 7.6	-0.4 ± 3.3	0.1 ± 0.6	
Canada Warbler	20	0.6 ± 1.1	0.1 ± 0.4	7.1 ± 11.9	1.7 ± 4.7	0.4 ± 0.7	
Northern Oriole	20♦	3.3 ± 4.1*	1.2 ± 1.3*	5.9 ± 11.6*	3.7 ± 4.0*	0.6 ± 0.9	

♦ *n* for mass change is the given *n* - 1 (One individual was not reweighed).♦♦ *n* for difference in fat class is the given *n* - 1 (One individual was missing a fat class).* *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001 after Bonferroni correction for multiple tests. Paired *t*-tests were performed on all changes in mass. Wilcoxon signed rank tests were performed on fat class data.

TABLE 5. Summary of condition increase based on initial condition of individuals and time of initial capture using linear regression models (following Winker et al. 1992a). *b* and *m* are directly from the model $y = mx + b$ where *y* is the initial condition of migrants ([mass/wing³]*10,000), *x* is time of capture (in hundredth-hours), *b* is the *y*-intercept, and *m* is the slope. The correlation coefficient (*r*) is given to show the strength of the relationship between condition and time and *F*-statistics indicate how well the linear regression model fits the data.

Species	<i>n</i>	<i>b</i>	<i>m</i>	<i>r</i>	<i>F</i> ^a	Daily condition change ^b	Net daily change (g) ^c
Least Flycatcher	413	0.106	0.0000198	0.20	16.5***	0.0268	0.17
“Trail’s” Flycatcher	428	0.387	0.0000150	0.17	11.9**	0.0318	0.41
Yellow-bellied Flycatcher	440	0.380	0.0000195	0.17	13.6**	0.0263	0.21
Red-breasted Nuthatch	377	0.329	0.0000112	0.13	6.5	0.0152	-0.01
Veery	273	0.370	0.0000153	0.15	6.2	0.0201	0.28
Swainson’s Thrush	134	0.329	0.0000116	0.13	2.2	0.0157	0.03
Cedar Waxwing	636	0.405	0.0000192	0.16	17.2***	0.0259	0.52
Philadelphia Vireo	163	0.383	0.0000252	0.15	3.7	0.0340	0.43
Red-eyed Vireo	1,444	0.354	0.0000209	0.15	32.8***	0.0283	0.52
Blue-winged Warbler	134	0.424	0.0000290	0.15	2.9	0.0392	0.37
Tennessee Warbler	163	0.347	0.0000150	0.13	2.7	0.0202	0.09
Nashville Warbler	127	0.429	-0.0000002	0.00	0.0	-0.0002	-0.36
Magnolia Warbler	223	0.378	0.0000214	0.14	4.5	0.0288	0.21
Cape May Warbler	616	0.323	0.0000152	0.15	13.2**	0.0206	0.15
Black-throated Blue Warbler	116	0.387	-0.0000047	0.04	0.2	-0.0062	-0.65
Bay-breasted Warbler	197	0.284	0.0000116	0.11	2.5	0.0157	0.09
Black-and-white Warbler	464	0.321	0.0000216	0.16	12.3**	0.0291	0.41
American Redstart	1,619	0.330	0.0000165	0.16	42.9***	0.0223	0.15
Ovenbird	315	0.500	0.0000195	0.10	3.3	0.0263	0.11
Northern Waterthrush	2,095	0.393	0.0000329	0.23	112.3***	0.0444	1.01
Mourning Warbler	186	0.542	0.0000320	0.18	6.0	0.0432	0.35
Wilson’s Warbler	294	0.462	0.0000137	0.10	2.8	0.0185	-0.05
Canada Warbler	244	0.363	0.0000307	0.24	14.5**	0.0415	0.61
Northern Oriole	313	0.432	0.0000273	0.18	10.0*	0.0369	1.17

^a Significance levels reflect Bonferroni corrections for multiple tests * *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001.
^b Daily condition changes are based on the average daylength during banding station operation.
^c Net daily changes use the regression model to estimate change in mass based on the average wing length of individuals captured. These values also reflect overnight mass loss calculated as 4.5% of initial mass (based on species averages).

first recapture (REVI: *P* < 0.001; NOWA: *P* < 0.01) as well as between first recapture and final recapture (REVI: *P* < 0.001; NOWA: *P* < 0.001). However, American Redstarts did not significantly increase in mass in either period (initial capture to first recapture: *P* = 1.0; first recapture to final recapture: *P* = 0.47).

Linear regression models of initial condition and time of initial capture were also used to investigate the likelihood that individuals were increasing mass during stopover. Results of these analyses also support mass increases by migrants during stopover on Appledore Island (Table 5). Eight species that exhibited significant mass increases by recaptures also exhibited significant increases by linear regression. Veerys, Philadelphia Vireos, Blue-winged Warblers (*Vermivora pinus*), and Ovenbirds did not show significant mass increases using linear regression although recaptured individuals exhibited significant mass

increases during stopover. Conversely, Cedar Waxwings, Cape May Warblers, and Canada Warblers (*Wilsonia canadensis*) had significant positive slopes to their regression lines although recaptured individuals did not significantly increase in mass. As with mass changes by recaptured migrants, there were no species with significant negative slopes to the linear regression models suggesting that no species is significantly decreasing mass on Appledore.

Mass increases during stopover translate into increased potential flight ranges. Flight range estimates for individuals captured only once were slightly longer than the ranges estimated using the initial mass of individuals later recaptured (Fig. 1). For all three species studied, the flight ranges estimated from the final mass of individuals recaptured were longer than either category described above. This was especially true for Red-eyed Vireos and Ovenbirds, two of the species

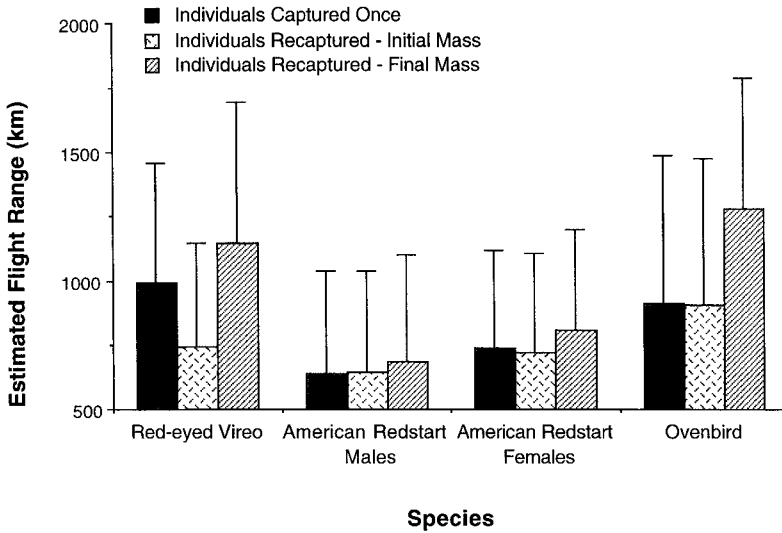


FIGURE 1. Estimated flight ranges for Red-eyed Vireos, American Redstarts, and Ovenbirds. Estimates were computed using Pennyquick's (1989) flight model and reflect still air and the average mass of the sampled population. Error bars reflect the flight range of individuals with average mass + 1 SD. Sample sizes of individuals captured once are as follows: Red-eyed Vireos: $n = 1119$; male American Redstarts: $n = 677$; female American Redstarts: $n = 694$; and Ovenbirds: $n = 265$. Sample sizes of individuals later recaptured are as follows: Red-eyed Vireos: $n = 326$; male American Redstarts: $n = 100$; female American Redstarts: $n = 116$; and Ovenbirds: $n = 50$.

with relatively large mass increases during stopover on Appledore Island (Table 4).

ANNUAL DIFFERENCES

Several species of migrant had sufficient sample sizes to compare stopover patterns among years (Table 6). Cape May Warblers, Black-and-white Warblers, and American Redstarts did not exhibit any significant differences in the proportions of individuals recaptured, stopover lengths, or mass increases among years. Although Northern Waterthrushes did not exhibit differences in stopover lengths or mass increases among years, they did show significant differences in recaptures among years ($G = 65.4$, $P < 0.001$). Red-eyed Vireos exhibited significant differences among years in recaptures ($G = 86.6$, $P < 0.001$) and mass increases ($F_{9,316} = 3.9$, $P < 0.001$), but not in stopover lengths.

DISCUSSION

On Appledore Island, we investigated several aspects of the stopover biology of Nearctic-Neotropical migratory passerines during fall migration. Some patterns (such as a high proportion of juveniles, short observed stopover lengths, lower mass for individuals later recaptured than

those captured once, and mass increases during stopover seem to hold for many of the species studied. However, other aspects of stopover biology including differences in recaptures and stopover lengths between males and females and between young and adult birds vary among the species studied. Although we attempted several cluster analyses using subsets of the following variables: median time of passage, percent young, percent recaptured, stopover length, habitat, foraging mode, and percent mass increase to examine possible groupings of different aspects of stopover biology, we were unable to detect any discernible associations. Therefore, in the following discussion we present several components of stopover biology in single factor analysis, however, many of these factors may still be interrelated and may be confounding in their effect on the stopover biology observed within a species.

The reported similarities in recaptures, stopover lengths and mass increases among years validate analyses of data from several years together. However, differences in mass increases and recaptures do exist for some species. Annual variation in food availability, competition, and weather patterns certainly affect observed stop-

TABLE 6. Variation in annual average stopover patterns of frequently captured migrants between 1983 and 1992. The given range represents the variation in annual averages.

Species	Stopover (%)		Stopover length (dd)		Mass change (g)	
	Overall mean	Range	Overall mean	Range	Overall mean	Range
Red-eyed Vireo	19.6 ± 9.8	9.9–40.4	3.3 ± 0.6	2.5–4.2	1.6 ± 0.9	0.5–2.9
Cape May Warbler	9.1 ± 3.3	3.5–16.2	2.9 ± 1.1	1.3–4.2	0.2 ± 0.6	-0.7–1.1
Black-and-white Warbler	21.3 ± 6.9	12.0–33.3	3.5 ± 0.9	2.2–5.2	0.7 ± 0.4	0.2–1.3
American Redstart	13.7 ± 4.0	7.8–22.2	2.7 ± 0.4	2.2–3.5	0.5 ± 1.1	-0.1–0.5
Northern Waterthrush	17.7 ± 7.1	9.6–28.4	3.9 ± 0.6	2.5–4.9	1.2 ± 0.4	0.7–1.7

over patterns, although this study does not include data to examine the effects of these factors.

Several factors including distance from initial point of departure (Abramsky and Safriel 1980), distance to final destination (Bairlein 1985, Moore and Kerlinger 1987), adequacy of the habitat and food supply at the stopover site (Biebach et al. 1986), and energetic condition, have been discussed as factors which may affect the stopover behavior observed for a species. With the exception of Red-breasted Nuthatches, Cedar Waxwings, and White-throated Sparrows (*Zonotrichia albicollis*), the migrants included in this study are Nearctic-Neotropical migrants (Rappole et al. 1983). Most of the Nearctic-Neotropical migrant species captured regularly on Appledore Island have breeding ranges which extend into New England and Canada. Although the breeding ranges of several species of migrants including Eastern Wood-Pewee, Red-eyed Vireo, Northern Parula, American Redstart, and Ovenbird extend much further south than Appledore, because of Appledore's location, we suggest that most migrants encountered at our station have traveled from the northern portion of the breeding areas. The most northern area in which any of these migrants regularly winter is south Florida, and most have wintering ranges which extend into Central America, the West Indies, and South America. Therefore, individuals of Nearctic-Neotropical migrant species encountered at Appledore Island can be considered middle-to-long, if not long-distance migrants. Furthermore, migrants captured on Appledore during fall migration presumably have traveled only a fraction of their total migration distance. We suggest that the distance traveled or left to travel during fall migration is not a significant factor in the patterns of stopover between species encountered on Appledore Island. We propose that a complex interaction of factors including migratory route, food availability, competition, and

timing of migration may be responsible for the different recapture rates, stopover lengths, and mass gains among species reported in this study.

ENERGETIC CONDITION

Fat is the main source of fuel for migration (Bertold 1975, Blem 1980). Biebach (1985) and Gwinner et al. (1988) suggest that the suppression of migratory restlessness, and thus the probability of stopover, are critically affected by the energetic condition of a migrant (i.e., its fat stores and mass), as well as by the possibility of foraging and increasing energy stores during stopover. Moore and Kerlinger (1987) found that the probability of stopover by warblers during spring migration on the Gulf coast was related to the migrants' energetic conditions upon arrival, i.e., leaner birds were more likely to stop. If migrants are stopping on Appledore Island to build or rebuild fat stores for migratory flights, we would expect to find: (1) most migrants to have little, if any, fat stores; (2) migrants recaptured to be leaner at first capture than those captured only once; and (3) migrants captured more than once should increase both fat stores and mass. In general, our data support this three-part hypothesis. Over half of all migrants captured on Appledore had either a 0 or a 0.5 fat class and thus could be considered lean. Veerys, Red-eyed Vireos, and Northern Waterthrushes which were recaptured had significantly lower initial fat stores than individuals only captured once. Moreover, among half of the species regularly recaptured, individuals recaptured weighed significantly less than those individuals captured only once. Data presented here reveal that most species studied experienced increases in both fat class and mass during stopover, although the mass gain and the increase in fat stores varied widely among species (Tables 4 and 5). The observed mass increases translate into increased potential flight distances (Fig. 1). This is especially true for those species

with relatively high mass increases like Red-eyed Vireos and Ovenbirds.

Mass increases observed among recaptured individuals in this study were higher in general than those reported from other locations investigating fall stopover (Gulf coast: Rappole and Warner 1980; inland: Winker et al. 1992a, 1992b). However, linear regression models using initial condition and time of capture for all individuals yielded slightly lower mass increases than a wooded inland stopover site (Winker et al. 1992a, 1992b). Because of Appledore Island's location, variation in mass is due not only to the substantial variation among individuals observed at this and other stopover sites, but also to the possibility that individuals are arriving during the day from over the ocean. Such individuals having overflowed the coast at night could arrive on Appledore during daylight hours with lower fat reserves than those that stopped during the night. Individuals arriving during the day with low masses and no opportunity to forage throughout the morning would result in flattened slopes of regression lines and could even decrease the likelihood of finding a significant relationship between condition and time of capture.

Numerous studies of recaptured individuals have reported initial mass losses followed by a period of mass increase (Moore and Kerlinger 1987, Loria and Moore 1990, Kuenzi et al. 1991, Winker et al. 1992b). In this study most individuals had mass increases between initial capture and first recapture as well as between first recapture and final recapture, although mass changes were rarely linear. However, as with total mass increases, we found substantial variation among individuals within species.

The observed differences in the amount of mass gained or fat deposited during stopover among species are similar to those reported from other stopover sites (Bibby and Green 1983, Moore and Kerlinger 1987, Safriel and Lavee 1988, Kuenzi et al. 1991). Kuenzi et al. (1991) suggest that different species may use resources available at a stopover site more efficiently than others. On Appledore Island, we found that several species with higher proportions of the population recaptured during stopover also had higher increases in mass. Therefore, probability of stopover and probability of increasing mass are presumably closely related. Furthermore, differences in the possibility of gaining mass during

stopover also may be a factor affecting the different stopover patterns observed between species. Many of the species in which we found no difference in initial mass between individuals captured once and individuals recaptured and those species that did not significantly gain mass and fat are forest specialists which would not find appropriate habitat on Appledore Island. Therefore, these species may continue to another location to replenish fat stores without undertaking a true migratory flight.

If the length of stopover is negatively correlated to the initial fat stores of a migrant then we would expect lean birds to stop longer. Although other studies have found this association (e.g., Cherry 1982) and we found this relation in Red-eyed Vireos, results of this study do not support this relationship in most species studied. It appears that on Appledore Island, once a stopover of more than one day is initiated and a migrant is able to fuel or refuel as evidenced by significant daily mass increases, a migrant may remain at that stopover site until favorable weather conditions allow a migratory flight. This may be particularly true close to an ecological barrier such as the Atlantic Ocean, especially if migrants have a high energetic threshold prior to the initiation of barrier crossing. Furthermore, even birds with large fat stores would be likely to wait for favorable weather before crossing an ecological barrier. If heavy birds are waiting for favorable weather, although their fat stores would allow a migratory flight, stopover would be longer than expected based only on energetic condition. Therefore, we would not find differences in stopover length between lean and fat migrants.

AGE AND SEX

The high proportion of young individuals captured on Appledore Island during fall migration is similar to the findings of other coastal banding stations (Table 1; Baird and Nisbet 1960, Drury and Keith 1962, Murray 1966). Although high percentages of young birds could result from different hatching or survivorship rates of young birds in different areas, or from a reduced stopover rate by adults, these alternatives seem unlikely because Ralph (1981) found much lower percentages of young birds at more inland locations. Ralph (1981) has suggested that high percentages of young migrants along the coast compared to inland stations indicate the periph-

ery of a species' migratory route. Because young Tennessee Warblers, Blackpoll Warblers, and Northern Waterthrushes accounted for approximately 75% of the individuals of each of these species captured in this study, the coast may not be the edge of the migratory route for these three species, rather all three species may have a significant portion of the population migrating over water.

Substantial evidence suggests that Blackpoll Warblers make transoceanic flights from North to South America (Drury and Keith 1962, Nisbet et al. 1963, Nisbet 1970, Richardson 1972; but see Murray 1989). Other species have also been suggested to be transoceanic migrants or to have segments of the population which migrate over the ocean (e.g., Kirtland's Warblers: Mayfield 1988). Radar studies of migration over the Western North Atlantic confirm that many migrants leave the coast of New England and Eastern Canada and fly south over the ocean (Drury and Keith 1962, Richardson 1972, McClintock et al. 1978, Williams and Williams 1978). Computer simulations of migration by small passerines during fall migration by Stoddard et al. (1983) indicate that nonstop flights from as far north as Nova Scotia to the northern coast of South America are possible in less than 100 hours.

More evidence is needed to determine which species are participating in these transoceanic flights from North to South America, but based on the results of this study, Blackpoll Warblers, Tennessee Warblers, and Northern Waterthrushes are likely candidates. The flight range estimates based on average mass increases by Red-eyed Vireos, American Redstarts, and Ovenbirds do not support the possibility of a successful transoceanic crossing for most individuals of these species. Lack of wingspan data prevented estimation of flight ranges for Tennessee Warblers, Blackpoll Warblers, and Northern Waterthrushes.

Because the amount of fat a migrant carries appears to be a determinant of the probability of stopover, differences in initial condition within a population could also lead to different rates of stopover. Because the young birds encountered on Appledore Island had lower fat stores and lower average initial mass than adult birds in several species, it is not surprising that a greater proportion of young birds were recaptured compared to adults (Table 2). However, we did

not find a significant difference in the stopover length between age groups in most species studied.

The higher recapture rates, as well as lower fat stores, among young birds compared to adults in this study are consistent with Ellegren's (1991) study of Bluethroats (*Luscinia svecica svecica*) in Sweden and Veiga's (1986) study of Pied Flycatchers in Spain, although Ellegren also found longer stopover among young birds. The Northern Waterthrush was the only species of migrant in which young birds had significantly longer stopovers than adults (Table 2). Drury and Keith (1962) suggested that a high percentage of young birds along the coast could be due to hesitation or indecision by young birds encountering a large body of water compared to the continuation of migration over water by adults. This suggestion may in part explain the difference in recaptures and stopover length as well, especially in species which migrate over the Atlantic Ocean. For example, young Northern Waterthrushes encountered on Appledore Island have never crossed a major ecological barrier, while it is likely that adults have already made a successful crossing. An alternative explanation for the increased recaptures by young birds might be that young birds are not physiologically prepared to initiate a barrier crossing. The lower fat loads carried by young birds compared to adults in this study also support this alternative.

Both males and females of many species of migrants are known to defend feeding territories against both sexes on their wintering grounds (Rappole and Warner 1980). Because males and females must establish these upon reaching the wintering ground, they may face similar pressures and time constraints during fall migration enroute to these areas. Unless males and females are following different migratory paths we would predict a similar probability of stopover between the sexes in the fall. If both sexes have the same probability of stopover then we should find similar proportions of males and females recaptured. Among most migrant species in this study, males and females did not significantly differ in proportions of individuals recaptured. Our results are similar to those of Ellegren (1991) who found no difference in the proportion of male and female Bluethroats (*Luscinia s. svecica*) recaptured. Additional work by Ellegren (1990) found no difference in migration speed during fall mi-

gration between the sexes in Bluethroats. As the speed of migration includes both the actual flying time and the time spent at stopover sites (Alerstam and Lindstrom 1990), Ellegren's (1990) results suggest that in the fall males and females have similar probabilities and durations of stopover.

In their study of Blackcaps (*Sylvia atricapilla*) and Redstarts (*Phoenicurus phoenicurus*), Lavee et al. (1991) did not find significant differences in stopover length between the sexes in the fall. Ellegren (1990) found that male Bluethroats tended to stay longer than females, although this difference was not significant. In this study, female Red-breasted Nuthatches and American Redstarts averaged longer stopovers than males (Table 3). These results are not unexpected because female American Redstarts that were later recaptured weighed less than males. However, Northern Orioles showed the opposite pattern with males having longer stopovers than females. The observed variability in stopover lengths suggests that stopover length may be affected by numerous factors, which may include age and sex, but also may be due to the initial condition of the individual as well as the particular conditions of weather, food availability, and competition encountered during stopover.

Although it is reasonable to talk about stopover biology among migrants in general, differences among species can be quite remarkable. Therefore, we suggest that studies on stopover biology look not only at general patterns, but also at the biology and behavior of individual species.

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