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Source: Northeastern Naturalist, 8(3) : 253-266

Published By: Eagle Hill Institute

URL: https://doi.org/10.1656/1092-6194(2001)008[0253:POMDPM]2.0.CO;2

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2001 NORTHEASTERN NATURALIST 8(3):253-266

# PATTERNS OF MOVEMENT DURING PASSERINE MIGRATION ON AN ISLAND STOPOVER SITE

CAREN E. GELLIN [1] AND SARA R. MORRIS [1,2]

ABSTRACT - We used mist nets to examine the directional movement of 20,019 passerines on Appledore Island, Maine, during spring and fall migration. Based upon the seasonal trend of North American migration, the hypothesis was that migrant birds would be moving north in the spring and south in the fall. Results, however, indicate that in both seasons, birds were more likely to be flying north than south and were more likely to be flying west than east. The data for the most commonly captured species support the directional patterns observed among all individuals. Although all captures as well as captures in the first hour after sunrise indicate northward movement in both seasons, spring captures in the northward direction were significantly more prevalent than fall captures. Therefore, we suggest that the general migratory direction and the presence of an ecological barrier, the Atlantic Ocean, appear to influence the directional capture of stopover migrants. Recaptured birds generally showed a lack of directional movement in both seasons, although subsequent recaptures indicate northward movement by these migrants in the spring. Age did not appear to affect directional movement.

## INTRODUCTION

For passerines that breed in the eastern United States or Canada, there are several different possible migration routes. Fundamentally, the route of any migrant is affected by the relative locations of wintering and breeding areas, pathways with reliable tailwinds (Able 1999, Alerstam 1990, Gauthreaux 1999), and the availability of suitable stopover sites (Moore and Simons 1992). Some birds, such as the Blackpoll Warbler (*Dendroica striata* Forster), can migrate nonstop from northeast Canada to South America by flying eighty hours over the ocean from the western North Atlantic Ocean to the northern coast of South America (Rappole 1995). However, many birds employ a different strategy of shorter migratory flights alternated with intermittent breaks in migration at stopover sites. Stopover sites serve as areas for migrants to rest fatigued muscles and refuel their energy supply as quickly and efficiently as possible so migration can continue (Moore 1999). By stopping periodically to refuel, birds can maintain sufficient energy without greatly increasing their carrying load. Several studies have shown that the level of fat carried by a migrant affects the probability that stopover will occur (Bairlein 1992, Loria and Moore 1990, Moore and Kerlinger 1987, Morris et al. 1996).

While little information is known about stopover ecology, still less is known concerning the direction of movement at stopover sites. Aborn

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and Moore (1997) found that Summer Tanagers (*Piranga rubra* Linneaus) seemed to orient away from water barriers on Horn Island, off the coast of Mississippi. Studies at a stopover location in the Neotropics, however, did not show any significant directed movement among any of the species studied (Winker 1995). Therefore, Winker's study showed that the local, diurnal movements did not reflect the directional migratory movements that occur on a seasonal, latitudinal scale. However, Winker notes that his results (at a slightly inland stopover site) do not imply that migrants behave in the same manner when the stopover site is on the coast.

A general, well-known trend of North American migration is that birds fly in a northward direction in the spring and a southward direction in the fall. However, this general direction of migration does not necessarily coincide with the direction of non-migratory flight at stopover sites. For instance, do birds maintain their directional heading, do they navigate away from oceanic waters, or are their movements purely random? Based upon the general direction of migration, our hypothesis was that migratory birds at a stopover site would fly in a northward direction in the spring and a southward direction in the fall, and therefore, birds would be captured on the south side of mist nets in the spring and on the north side of mist nets in the fall. In this study, we examined the directional movement of migrants at a stopover site with regard to birds captured only once, recaptured birds, and several individual species. Additionally, we addressed the relationship between age and the migrants' directional movement at a stopover site.

## METHODS

Our field site was Appledore Island, Maine (42°58'N, 70°36'W), a 33.6 ha island in the Gulf of Maine (Fig. 1). 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. This stopover site is well vegetated with a mix of shrubs and low trees surrounding the area where the nets are placed. More information on the field site was given in Morris et al. (1994). Vegetation was generally similar on both sides of a single net, although dominant shrubs varied among nets.

Birds were captured in mist nets (12 x 2.6 m, 30 mm mesh). Up to ten nets were used; however, fewer nets were opened in poor conditions and/or on mornings with an expectedly high capture rate. During heavy rains or high winds, the mist nets were closed. The nets were generally open throughout the day from sunrise to sunset and were checked approximately every thirty minutes. Each net was determined to be either north-south or east-west by compass. Nets were designated north-south if the direction of capture were on a north-south axis, while east-west designation was used if capture were on an east-west axis. Five nets were designated north-south and five were designated east-west. The direction of capture was determined by the side of the net from which the bird was removed. Birds caught on one side of a net were assumed to be flying in the opposite direction of capture. For instance, a bird caught on the south side of a net was presumed to be flying north. Birds were removed from nets, the net location and direction of capture were recorded, and birds were brought to a central banding station where they were banded with U.S. Fish and Wildlife Service bands. For each captured bird, we recorded the day and time of capture, the net and direction, age, sex, lengths of the wing and tarsus, fat class, and mass. Age and sex determination were based on criteria in Pyle et al. (1987). Age determination in the spring is harder than in the fall because skull pneumatization cannot be used in age determination, but previous work on Appledore suggests that plumage characteristics could be used fairly accurately for age determination (Morris and Bradley 2000). The same information was recorded for birds that were recaptured (i.e., caught at least one day following initial capture). Captured birds were then released outside the banding station.

We used capture data from fall 1993 to fall 1997, including data from both spring and fall seasons. Spring data were collected in May and June, while fall data were collected in August, September, and early October. For most analyses, we pooled data across years to reduce the

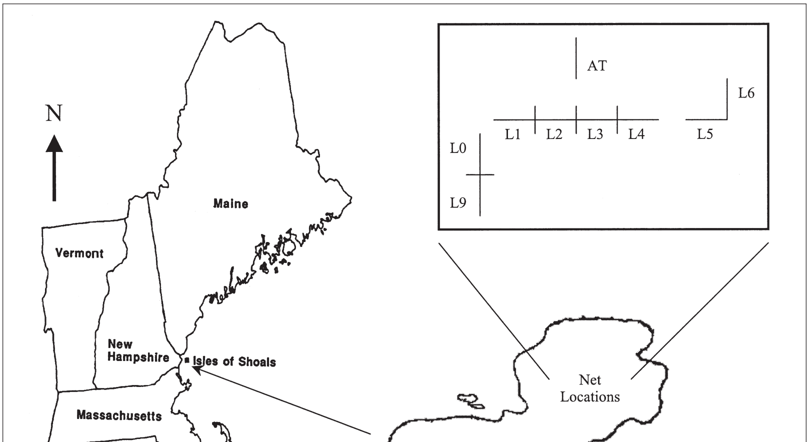

Figure 1. Location of the study site, Appledore Island, Maine. Nine of the ten nets used in this study were located in the northern portion of the island while the tenth net was located adjacent to the pond in the southern portion of the island.

impact of weather or other annual variations and to analyze general trends at this site. We also present data comparing direction of movement across the five years of this study. We examined the potential for directional movement among birds that were only captured once and among recaptured birds, both at initial capture and at subsequent recapture. Recaptured birds were analyzed separately because the factors affecting directional flight at a stopover site may be different among birds remaining at a stopover site for an extended time. We also analyzed capture data for five individual species: Common Yellowthroat (*Geothlypis trichas* Linnaeus), Red-eyed Vireo (*Vireo olivaceus* Linnaeus), American Redstart (*Setophaga ruticilla* Linnaeus), Magnolia Warbler (*Dendroica magnolia* Wilson), and Northern Waterthrush (*Seiurus noveboracensis* Gmelin). These species were chosen because they were the most abundantly captured species in both seasons. Furthermore, we analyzed the capture direction for birds captured within the first hour after sunrise. These analyses were used to investigate preferred direction of movement and reduce the effects of the island size, because birds caught later in the day may have reoriented from their preferred direction, rather than taken an over-water flight.

To determine if movement of migrants on the island was random or nonrandom, we performed G-tests with Williams' correction, comparing captures in each direction (north, south, east, and west) with expected values that were calculated based on the total number of birds captured and the number of net hours in each direction. To investigate whether birds were exhibiting a preference for a particular direction between seasons, between years, or among species, we used G-tests with Williams' correction (Winker 1995) comparing directions, i.e., north versus south or east versus west. Pearson chi-square tests were also performed to verify the value determined by the G-test with Williams' correction as suggested by Sokal and Rohlf (1995). Reported p-values reflect sequential Bonferroni correction for multiple comparisons (Beal and Khamis 1991, Rice 1989).

## RESULTS

Between fall 1993 and fall 1997, we captured 20,019 individuals of 119 species during fall and spring migration on Appledore Island, Maine. Although the total number of captures was similar between spring and fall, migrants were much more likely to be recaptured during fall (12.0% of 9845) than during spring (4.4% of 10,174; $G_1 = 369.2$, $p < 0.001$). We present results here on the directional capture data for these passerines.

### All Directions

During both spring and fall, captures of birds that were only encountered once indicated significant nonrandom movements (spring: $G_3 =$

576.5, $p < 0.001$; fall: $G_3 = 555.6$, $p < 0.001$), although the preferred direction varied between the two seasons. The same pattern was observed during each of the five years of this study ($p < 0.001$). During spring, birds were more likely to be moving in a northward direction. During fall, birds were substantially more likely to be moving west than any other direction, although eastward movement was also more likely than expected. These patterns also held for each year of the study, except for the fall of 1993, when the only east-west net was "Apple Tree" and eastward movement was more prevalent than westward movement, although both eastward and westward movement were higher than expected. The same patterns were observed among individuals that were captured within the first hour of sunrise, with significant northward movement during spring ($G_3 = 294.4$, $p < 0.001$) and significant westward movement during fall ($G_3 = 59.8$, $p < 0.001$). These patterns were seen in each year of the study, except fall 1993 when eastward movement was most prevalent.

Among individuals that were later recaptured, initial capture indicated significant nonrandom movement during fall ($G_3 = 63.5$, $p < 0.001$) when westward movement was most common. This pattern held for each year of the study. However, during spring, initial capture of recaptured migrants indicated random movements on the island ($G_3 = 7.6$, n.s.). When only captures within the first hour after sunrise were included in the analyses, movement was nonrandom in both seasons (spring: $G_3 = 2.5$, n.s.; fall: $G_3 = 7.0$, n.s.), although the fall approached significance and westward movement was more frequent than movement in the other three directions. Because of low sample sizes, these analyses for individual years were not included. Subsequent recaptures of previously banded birds indicated significant nonrandom movement in the spring ($G_3 = 46.3$, $p < 0.001$), with the most common direction of movement being eastward, although westward movement was also greater than expected. Eastward movements were substantially higher than expected in the spring of each year of the study, although in 1997 westward movement was more common than eastward movement. Recaptures were also significantly non-random during fall ($G_3 = 80.8$, $p < 0.001$), with the most common direction of movement being westward. Similar significant non-random movements were observed in each fall of the study, with significant westward movement more likely than expected, except in 1995 when movement was random. These patterns were identical when only birds recaptured within the first hour after sunrise were included in the analyses (spring: $G_3 = 15.2$, $p < 0.05$; fall: $G_3 = 14.7$, $p < 0.05$).

## North-South Heading

All five of the nets with north-south headings showed the same trends in directional movement. Migrants that were only captured once were significantly more likely to be headed north than south during both spring

Table 1. Directional capture percentages of migrants only captured once and migrants recaptured on Appledore Island, Maine, from 1993 to 1997. We present analyses for all captures as well as for those captures within the first hour after sunrise (see methods).

| | All captures | | | Captures within one hour of sunrise | | |
|---|---|---|---|---|---|---|
| | Spring % (n [a]) [b] | Fall % (n [a]) [b] | G [c] | Spring % (n [a]) [b] | Fall % (n [a]) [b] | G [c] |
| **North-South Heading: Northward direction** | | | | | | |
| Birds captured only once | 64.9 (5841) *** | 54.3 (4030) *** | 113.0 *** | 66.5 (1319) *** | 57.3 (840) *** | 18.6 *** |
| Recaptured birds | | | | | | |
| Initial capture | 55.3 (266) | 51.3 (557) | 1.1 | 61.5 (39) | 53.5 (71) | 0.7 |
| Subsequent capture | 63.4 (194)*** | 49.4 (524) | 11.1 ** | 72.0 (25) | 38.6 (70) | 8.4 * |
| **East-West Heading: Westward direction** | | | | | | |
| Birds captured only once | 52.8 (3886) ** | 55.9 (4632) *** | 8.2 * | 54.4 (553) | 59.4 (742) *** | 3.2 |
| Recaptured birds | | | | | | |
| Initial capture | 43.1 (181) | 55.0 (626) | 7.9 * | 44.4 (27) | 52.6 (78) | 0.5 |
| Subsequent capture | 49.4 (251) | 52.9 (639) | 0.9 | 43.9 (41) | 61.5 (78) | 3.4 |

[a] n is the total number of birds captured in nets with a particular heading, e.g., the combination of all birds captured in north and south directions in nets with a north-south heading.
[b] G-tests with Williams' correction tested between direction of captures within a season.
[c] G-tests with Williams' correction (2-way contingency tables) tested between direction of captures between seasons.
* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

and fall migration (Table 1). We did observe significant differences among years in the proportion of birds moving northward during both the spring and the fall (spring: $G_3 = 42.0$, $p < 0.001$; fall: $G_4 = 69.4$, $p < 0.001$), although each year showed the same trend of more northward movement in each season (except fall in 1996 when southward movement was more prevalent). Although significant movement occurred in the same direction for both seasons, the data indicated a significantly greater proportion of northward movement during spring than fall (Table 1). Among birds that were later recaptured, the direction of initial capture indicated no significant north or south movement during either the spring or the fall (Table 1). However, direction of recaptures showed significant northward movement during spring, while no significant movement in the north-south direction was detected in the fall (Table 1).

When captures within the first hour after sunrise were analyzed, similar results were obtained, with northward heading more frequent in both seasons and a higher percentage of birds moving north in the spring than in the fall among birds that were captured once (Table 1). Likewise, direction of initial capture of recaptured birds was not significantly different between the two directions during either season while subsequent recaptures suggest more northward movement during the spring than the fall (Table 1).

## East-West Heading

Data from migrants only captured once in east-west nets revealed that migrants were significantly more likely to be headed west than east during both spring and fall migration (Table 1). We did not find a significant difference in movement in the east-west heading among years during either the spring or the fall (spring: $G_3 = 7.9$, n.s.; fall: $G_4 = 8.1$, n.s.). While most individual nets demonstrated this pattern, one east-west net, designated Apple Tree (AT), was an exception with 57.0% ($G_1 = 25.1$, $p < 0.001$) of spring captures indicating eastward movement, and 53.7% ($G_1 = 7.3$, $p < 0.01$) of fall captures suggesting eastward movement. Despite the exception with this one net, the westward movement of birds only captured once was greater in the fall than in the spring for all east-west nets. Initial capture data of recaptured birds showed no significant direction of movement during either the spring or the fall (Table 1). Likewise, data on subsequent recaptures indicated that there was not directed movement in the east-west heading in either the spring or the fall (Table 1).

Among birds captured within the first hour of sunrise, significant westward movement occurred among birds only captured once in the fall, and this westward movement was significantly higher than during the spring (Table 1). Recaptured birds did not show significant differences in direction of movement, either at initial capture or subsequent recapture.

Table 2. Directional capture percentages of the five most abundantly captured species on Appledore Island, Maine, for all north-south and east-west nets during spring and fall. Data are presented for those birds that were only captured once.

| | All captures | | | Captures within one hour of sunrise | | |
|---|---|---|---|---|---|---|
| Species | Spring % (n [a]) [b] | Fall % (n [a]) [b] | G [c] | Spring % (n [a]) [b] | Fall % (n [a]) [b] | G [c] |
| | North-South Heading: Northward direction | | | | | |
| Red-eyed Vireo | 61.1 (265) *** | 53.6 (420) | 3.8 | 77.3 (22) * | 77.1 (35) * | 0.0 |
| Magnolia Warbler | 70.4 (595) *** | 61.2 (85) | 2.9 | 69.4 (147) *** | 71.4 (14) | 0.0 |
| American Redstart | 69.9 (389) *** | 48.6 (294) | 31.8 *** | 79.8 (109) *** | 50.9 (55) | 14.1** |
| Northern Waterthrush | 70.8 (106) *** | 50.9 (344) | 13.3 *** | 71.4 (28) * | 57.6 (92) | 1.7 |
| Common Yellowthroat | 64.1 (1447) *** | 58.5 (388) ** | 0.0 | 60.7 (374) *** | 52.5 (118) | 2.4 |
| | East-West Heading: Westward direction | | | | | |
| Red-eyed Vireo | 43.4 (304) | 56.9 (436) * | 13.0 ** | 52.9 (17) | 51.0 (51) | 0.0 |
| Magnolia Warbler | 54.4 (410) | 62.0 (100) | 1.9 | 49.1 (55) | 72.7 (11) | 0.0 |
| American Redstart | 54.2 (325) | 51.8 (342) | 0.4 | 66.7 (51) | 60.4 (53) | 0.4 |
| Northern Waterthrush | 42.0 (75) | 55.2 (355) | 0.3 | 68.2 (22) | 59.7 (77) | 0.5 |
| Common Yellowthroat | 51.0 (518) | 51.8 (257) | 0.5 | 50.9 (110) | 49.3 (73) | 0.0 |

[a] n is the total number of birds captured in nets with a particular heading, e.g., the combination of all birds captured in north and south directions in nets with a north-south heading.
[b] G-tests with Williams' correction tested between direction of captures within a season.
[c] G-tests with Williams' correction (2-way contingency tables) tested between direction of captures between seasons.
* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

## Individual Species and Age

Of the 119 species captured, we investigated directions of movement among the five most abundantly captured species: Red-eyed Vireo, Magnolia Warbler, American Redstart, Northern Waterthrush, and Common Yellowthroat. During both the spring and the fall, bird captures indicated non-random movements in all five species. During the spring, northward movement was more frequent than expected in all species except among Red-eyed Vireos, which were most frequently moving eastward ($p < 0.001$ for each species). During the fall, westward movement was more frequent than expected in all species except the Common Yellowthroat, which was most frequently moving northward (COYE: $p < 0.05$, all others: $p < 0.001$). The results for the north-south nets were similar to the results seen for all birds captured on Appledore Island. All five species exhibited highly significant northward movement in the spring (Table 2), although we also observed significant differences among species ($G_4 = 26.9$, $p < 0.001$). In general, these species also exhibited greater northward movement in the fall. While we did observe significant differences among species in the proportion of birds moving north during fall ($G_4 = 28.7$, $p < 0.001$), northward movement was only significantly more common than expected among Common Yellowthroats. In the east-west nets, most species did not demonstrate preference for either the east or west direction (Table 2), and we did not find differences among species (spring: $G_4 = 8.6$, n.s.; fall: $G_4 = 7.0$, n.s.). However, the Red-eyed Vireo showed a significant difference between its east-west directional movement during the fall (Table 2).

Among birds captured within the first hour of sunrise, significant northward movement occurred among all five species of birds during the spring (Table 2). Northward movement was only significantly higher than southward movement in one species during the fall, and the difference between the seasons was significant in only one species. Among birds captured in east-west oriented nets in the first hour after sunrise, birds did not demonstrate an increased likelihood of either eastward or westward movement (Table 2).

We also tried to determine if there were an age-related difference in directional movement at this site. Overall, 80.0% of the spring migrants were young, and 94.1% of the fall migrants were young. We did not find a significant difference in the direction of movement between young and adult birds in either season. Both adult and young birds were equally likely to be heading northward in the spring (adult: 67.2%, $n = 509$; young: 66.7%, $n = 2039$; $G_1 = 0.05$, n.s.) and the fall (adult: 56.2%, $n = 267$; young: 53.7%, $n = 4250$; $G_1 = 0.6$, n.s.). The east-west nets indicated similar patterns among age groups in both seasons. Both adult and young birds were equally likely to be moving westward in the spring (adult: 56.1%, $n = 346$; young: 52.8%, $n = 1393$; $G_1 = 1.2$, n.s.) and in the fall (adult: 58.2%, $n = 304$; young: 55.7%, $n = 4879$; $G_1 = 0.8$, n.s.). Similar results were obtained for the most common species.

## DISCUSSION

### North-South Heading

Based upon the general heading of spring and fall migration for North American migrants, we expected that birds would be moving north during spring and that birds would be moving south during fall. Our data were consistent with this hypothesis for spring migration. Northward movement was substantially more frequent than any other direction of movement in the spring, and nearly two-thirds of the migrants captured in north-south oriented nets in this study appeared to be maintaining their northward directional heading during the spring (Table 1). Additionally, all five species that were studied individually exhibited highly significant northward movement in the spring (Table 2). These results at an island stopover site near the final destination of migrants are very different from the lack of specific directional movements observed by Winker (1995); however, unlike our study site, his stopover site in the Neotropics was inland, not adjacent to a major ecological barrier.

In the fall, our data were not consistent with our hypothesis because we found a significant northward heading by all migrants as well as by the Common Yellowthroat. Therefore, migrants seemed to be flying opposite to the general southward direction. Thus the fall data suggested that other factors play a role in the flight direction of migrants at a stopover site. One possible explanation for our results is that birds that reach the coast of the island during foraging may change direction on the island to avoid overwater flight and thus may not be flying in their preferred direction. Aborn and Moore (1997) found that shape and habitat configuration influenced the movement of Summer Tanagers on the Gulf coast. However, because the northward movement by migrants on Appledore was also observed among migrants captured only within the first hour of sunrise (Table 1), this movement seems unlikely to be an artifact of the island topography. A more plausible explanation for these results is reverse migration. Birds migrating over a body of water may reorient, resulting in flight opposite to the normal migratory direction to find suitable stopover areas (Alerstam 1990, Richardson 1982). Reverse migration is most likely at the end of a flight when migrants' fat reserves are low. Because the Atlantic Ocean, a significant ecological barrier, surrounds the eastern and southern sides of Appledore Island (Figure 1), fall migrants flying southward will only see water ahead of them and must either have enough energy for this barrier crossing or change their orientation, thus resulting in stopover. This movement away from an ecological barrier was consistent with that of Aborn and Moore (1997) on Horn Island, Mississippi. Finally, although both spring and fall capture data revealed significant northward flight directions, the percentage of birds exhibiting the northward heading in the spring was significantly higher than that of the fall (Table 1). Therefore, the general migratory direction (north in the spring and south in the fall) did appear to play a role in the directional flight of migrants at this stopover site. Nevertheless, the presence of the Atlantic Ocean appeared to have a large impact on directional movement at this stopover site.

## East-West Heading

Migratory movements along the east-west axis were more difficult to characterize than movement along the north-south axis. In the spring, many birds in the Atlantic provinces of Canada move in northeast, north-northeast, or even east directions (Richardson 1971). In the fall, radar studies have documented many migrants flying southeast as well as southwest (Richardson 1972, 1978; Williams and Williams 1978). Similar to our analyses of north-south directional capture, both spring and fall migration exhibited the same directional heading on the east-west axis. The data showed significant westward directional movement for both the spring and the fall (Table 1). Among the individual species studied, all five species showed the same pattern of westward movement during the fall, although it was significant only among Red-eyed Vireos (Table 2). This westward movement coincides with the possible effects of the Atlantic Ocean that were seen with the north-south nets. With the Atlantic Ocean serving as an ecological barrier on the eastern side of the island, migrants may have a tendency to fly away from the open ocean and towards the mainland.

Although there was significant westward movement during both seasons, westward captures in the fall were significantly higher than westward captures in spring among birds captured once (Table 1). Although the difference between seasons was not significant, the same pattern held for birds captured only within the first hour of sunrise (Table 1). This seasonal difference may be attributed to differences in the general migratory direction. In the fall, many migrants fly southwest (Richardson 1972, 1978), often following the coastline, which could have accounted for the higher percentage of westward movement. In the spring, migrants following the coastline would be flying in a northeasterly direction, and migrants could be using breeding grounds in Maine or eastern Canada that lie east of Appledore Island. However, the observed westward flight may have resulted from reorientation away from an ecological barrier. Thus during both spring and fall, movement on Appledore Island had both seasonally predicted components (north in the spring and west in the fall) as well as showing the effects of an ecological barrier (west in the spring and north in the fall).

An additional complication with nets with an east-west heading is the effect of light conditions that may impact capture rate. However, because the proportion of captures differed between seasons and because the pattern was the same in the first hour after sunrise as it was for the entire day, it was likely that this was not responsible for the observed patterns of movement, although the effects of light conditions on our results remain unknown.

Microhabitat may also be important in movements by migrants. Despite the fact that the capture in east-west nets showed a higher percentage of westward movement by birds, captures in one individual net (net AT) indicated that birds were moving east in that location during both spring and fall migration. The AT, or "Apple Tree," net was named for the large apple tree at net level on the east side of the net. Serving as a source of flowers, nectar, pollen, fruit, and insects, and, therefore, food in both seasons, the apple tree may attract migrants. Therefore, the eastward movement of birds in this specific location, which is opposite to the direction of the other nets, may have reflected the selection of this microhabitat and, thus, movement towards the ecological barrier rather than orientation away from the barrier.

## Recaptures

Migrants with depleted fat reserves have a greater probability of remaining at a stopover site for several days (Bairlein 1992, Biebach et al. 1986, Loria and Moore 1990, Moore and Kerlinger 1987). Furthermore, these birds may be actively choosing among available habitats at a stopover site (Moore et al. 1990, Moore and Simons 1992, Winker 1995, Yong et al. 1998). The extended stay may affect the direction of initial capture because birds foraging throughout the island might be captured in any direction, regardless of the seasonal migratory direction, particularly if migrants are sampling available habitats. Our results are consistent with this suggestion since most tests found no significant directed movements among birds that were later recaptured in either season (Table 1). However, significant northward movement among recaptured migrants may indicate resumption of migration in the spring.

In this study, fewer migrants were recaptured in the spring than in the fall. Previous studies on Appledore Island demonstrated the increased probability of recapture in the fall (Morris et al. 1994). One explanation for these results is that spring migrants may need to arrive at the breeding grounds early to secure optimal territories. In contrast, fall migrants are at the beginning of their migratory journey and may prioritize adequate fat reserves over the early arrival at wintering grounds. Recaptured birds generally did not exhibit movement in a particular direction in either season or directional heading, either at initial capture or at subsequent recapture (Table 1). The lack of specific directed movement of recaptured migrants was in stark contrast to directional movements by most migrants. These results support the possibility that migrants with extended stopovers utilize stopover sites differently than most passage migrants. Movement in all directions by migrants recaptured on Appledore may reflect habitat selection, active foraging, or other site-selection tactics that are unrelated to the location of a stopover site or the direction of migration.

### Age

The greater proportion of young migrants, especially in the fall, is consistent with other coastal studies (Baird and Nisbet 1960, Drury and Keith 1962, Morris et al. 1996, Murray 1966). We found no difference in direction of movement between young and adult birds, either among all captures or among individual species. Thus, at this site, movements appear to be similar among the two age classes.

## ACKNOWLEDGEMENTS

We sincerely appreciate the time and energy of the many people who volunteered to help operate the Appledore Island Migration Banding Station, especially Carol Cushing, Dorothy Fitch, Anthony Hill, David Holmes, Rozzie Holt, Mac McKenna, John Munier, Jonah Shull, Martha Stauffer, Becky Suomala, and Mary Wright. The Shoals Marine Lab has been extremely supportive of the banding station. We are particularly grateful to the SML staff who provided logistical support as well as help at the station when needed. Canisius College supported CEG with travel grants and SRM with departmental research grants and a summer faculty fellowship. We also thank Arthur Clark, Robert Morris, Wang Yong, and an anonymous reviewer who critically reviewed earlier drafts of this manuscript. This is contribution 7 of the Appledore Island Migration Station and contribution 107 of the Shoals Marine Laboratory.

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