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MASS LOSS AND PROBABILITY OF STOPOVER BY MIGRANT WARBLERS DURING SPRING AND FALL MIGRATION

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Abstract.—Although lean migrants are more likely to be recaptured than fatter ones at many stopover sites, the effects of mass loss on the probability of recapture have not been investigated experimentally. During fall mist-netting on Appledore Island, Maine, when two Northern Waterthrushes (*Seiurus noveboracensis*) or American Redstarts (*Setophaga ruticilla*) were captured simultaneously, they were divided randomly into control and experimental categories. In the spring, pairs of American Redstarts or Magnolia Warblers (*Dendroica magnolia*) were treated similarly. Experimental individuals were held without food for up to 6 h before release to investigate the effects of mass loss on the probability of recapture, while control birds were banded and immediately released. Experimental birds significantly decreased in mass during holding. During the fall, experimental individuals were more likely to be recaptured at least 1 d after initial capture than control individuals. However, during the spring, I did not find a difference in recaptures between control and experimental categories, although recapture rates were quite low. These results indicate that mass loss, either directly or as a result of lost foraging time, does lead to extended stopover by migrants during the fall. However, differences in priorities apparently exist between spring and fall migration. During the spring, mass loss may not lead to extended stopovers if migrants have enough energy to continue migration, especially when migrants are close to their final destination.

PÉRDIDA DE MASA CORPORAL Y PROBABILIDAD DE RECAPTURA EN LUGARES DE PARADA POR PARTE DE AVES DURANTE LA MIGRACIÓN EN LA PRIMAVERA Y EL OTOÑO

Sinopsis.—Aunque hay una mayor tendencia a recapturar, en los lugares de paradas durante la migración, a individuos con poca grasa que los que están gordos, el efecto de la pérdida de masa y la probabilidad de recaptura no ha sido investigado experimentalmente. Se dividieron en forma experimental y control dos especies que estaban siendo capturadas en redes simultáneamente durante el otoño en la isla Appledore, Maine. Las especies estudiadas fueron la pizpita (*Seiurus noveboracensis*) y la candelita (*Setophaga ruticilla*). En la primavera se repitió el experimento pero esta vez utilizando a la candelita y a *Dendroica magnolia*. Los individuos experimentales luego de su captura con redes, se mantuvieron cautivos sin comida por 6 h antes de ser liberados; el grupo control fue anillado y liberado inmediatamente. Las aves experimentales perdieron peso considerablemente durante las 6 h. Durante el otoño hubo una mayor tendencia a recapturar a los individuos experimentales. Sin embargo, durante la primavera, no hubo diferencia entre la recaptura de ambos grupos, aunque las tasas de recaptura fueron bajas. Estos resultados indican que la pérdida en masa corporal, ya sea directamente o como resultado de pérdida de tiempo para forrajear, da origen a que los migratorios, durante el otoño, pasen más tiempo en los lugares de parada. Sin embargo, parecen existir diferencias en las prioridades durante el otoño y la primavera. Durante la primavera, la pérdida en masa corporal no necesariamente hace que las aves pasen mayor cantidad de tiempo en los lugares de parada si éstos tienen almacenada suficiente energía para continuar la migración, particularmente cuando éstos se encuentran cercas de su destino final.

Neotropical migrants may spend up to a quarter of the year in transit between breeding and wintering grounds (Keast 1980). However, until recently the biology of migrants during migratory periods has been ne-

glected. Recent studies have focused attention on the importance of stopover habitat (Moore and Kerlinger 1987) and stopover habitat use by migrants (Moore et al. 1990; Moore and Simons 1992; Winker et al. 1992a,b). Stopover sites provide areas between breeding and wintering grounds where migrants can rest, forage, and/or wait for favorable migration conditions. However, it has been difficult to elucidate the factors that affect the probability and duration of stopover by migrants.

Energetic condition appears to influence the likelihood that a migrant will stay at a stopover site. A number of studies have shown that lean migrants are more likely to stay at stopover sites than heavier ones (Biebach 1985, Biebach et al. 1986, Ellegren 1991, Kuenzi et al. 1991, Loria and Moore 1990, Moore and Kerlinger 1987). Furthermore, migrants appear to use stopover sites to increase the energy reserves needed for migration (Biebach et al. 1986, Moore 1991, Moore and Kerlinger 1987, Morris et al. 1994, Safriel and Lavee 1988, Winker et al. 1992c). Studies have also shown that migrants may compensate for low energy reserves by exhibiting foraging behavior plasticity at stopover sites (Loria and Moore 1990, Moore 1991). Although these studies suggest that decreases in body condition may affect the probability of extended stopover, the role of body condition in determining the likelihood of extended stopover has not been investigated experimentally. In this study, I attempt to determine if mass loss affects the likelihood of recapture by migrant warblers during spring and fall migration. Specifically, I hypothesize that individuals that are held, thereby both prevented from foraging and forced to lose mass, will be more likely to be recaptured and will have longer stopovers than individuals banded and immediately released.

MATERIALS AND METHODS

I mist-netted migrants during spring and fall migration from 1990–1992 on Appledore Island, Maine (42°58'N, 70°36'W), a 33.6-ha island in the Gulf of Maine. For further information on the field site see Morris et al. (1994). Mist nets were checked approximately every 30 min throughout the day and all birds captured were taken to a central location for banding. In the fall, whenever I captured two American Redstarts (*Setophaga ruticilla*; AMRE) or two Northern Waterthrushes (*Seiurus noveboracensis*; NOWA) simultaneously, I randomly divided them into control and experimental groups. In the spring, American Redstarts and Magnolia Warblers (*Dendroica magnolia*; MAWA) were handled similarly. This paired design allowed birds to experience similar weather conditions, predation pressure, food availability, and competition from other migrants. All birds were banded and the following information recorded: age, sex, unflattened wing chord, tarsus, fat class (0–4), and mass. I excluded from this study all American Redstarts (spring: $n = 4$; fall: $n = 5$) and Magnolia Warblers ($n = 6$) weighing less than 7.5 g and all Northern Waterthrushes weighing less than 15.0 g ($n = 8$). These limits were set to prevent experimental birds from losing too much mass and thereby decreasing to or below fat-free mass (Connell et al. 1960; Rogers and Odum 1964, 1966).

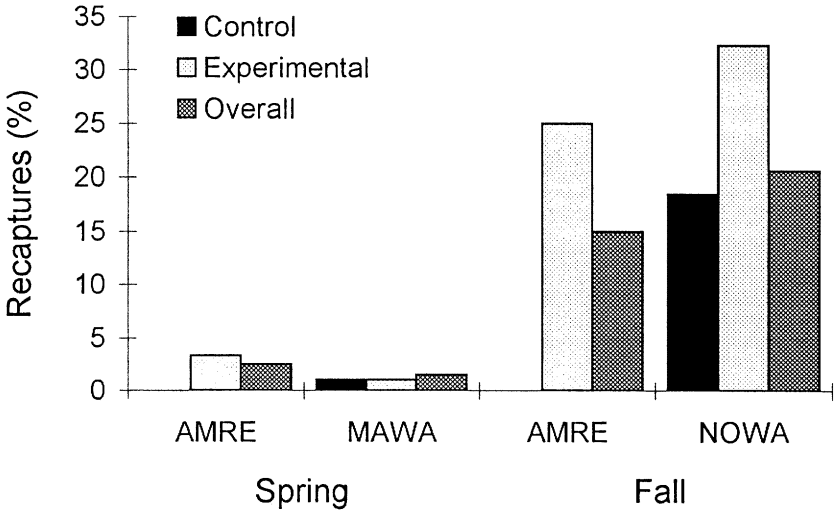


FIGURE 1. Proportion of individuals recaptured at least 1 d after initial capture on Appledore Island, Maine (Sample sizes for each experimental group are as follows: spring AMRE: $n = 60$; MAWA: $n = 98$; fall AMRE: $n = 36$; and NOWA: $n = 65$). Overall recaptures for all non-experimental individuals are given for each species from 1990 to 1992 for comparison (spring AMRE: $n = 404$; MAWA: $n = 800$; fall AMRE: $n = 341$; and NOWA: $n = 515$). No control American Redstarts were recaptured in either season.

Control birds were released immediately after banding. Experimental birds were held in individual chambers ($10 \times 12.5 \times 23$ cm) of a darkened wooden holding box without food or water for up to 6 h ($\bar{x} = 5.4$ h, range = 3–6 h) after banding. I reweighed experimental individuals immediately prior to release. No birds captured after 1300 h were held and all birds were released by 1600 h to allow time for foraging before sunset. Birds did use this time to forage as evidenced by mass increases by same day recaptures of experimental individuals (Spring AMRE: $n = 2$, $\bar{x} = 0.28 \pm 0.43$ g; MAWA: $n = 11$, $\bar{x} = 0.30 \pm 0.17$ g; fall AMRE: $n = 2$, $\bar{x} = 0.24 \pm 0.09$ g; NOWA: $n = 1$, mass increase = 0.38 g).

I performed paired t -tests (normality verified; one-sided alternative hypotheses) to determine mass loss by experimental birds. I compared the number of individuals recaptured at least 1 d after initial banding between experimental and control groups using Fisher's exact tests (two-sided alternative hypotheses). Because stopover lengths are not normally distributed (see Fig. 2), Mann-Whitney U -tests were performed to test for differences in stopover length between the two experimental groups (two-sided alternative hypotheses). All significant P -values reflect sequential Bonferroni corrections for multiple tests (Rice 1989, Beal and Khamis 1991).

TABLE 1. Initial mass (g, $\bar{x} \pm 1$ SD) and number of individuals recaptured of control and experimental migrants and mass loss (g) by experimental migrants on Appledore Island, Maine, from 1990 to 1992. Because of the paired design, n is the same for all three categories.

Species	Season	n	Control		Experimental ^a		Loss ^b $\bar{x} \pm 1$ SD
			Mass	Recap- tures	Mass	Recap- tures	
American Redstart	Spring	60	8.6 \pm 0.6	0	8.6 \pm 0.6	2	0.6 \pm 0.1
Magnolia Warbler	Spring	98	8.6 \pm 0.5	1	8.5 \pm 0.5	1	0.6 \pm 0.1
American Redstart	Fall	36	8.4 \pm 0.9	0	8.5 \pm 0.7	9	0.6 \pm 0.2
Northern Waterthrush	Fall	65	17.7 \pm 1.4	12	18.0 \pm 1.9	21	1.0 \pm 0.3

^a Individuals held for up to 6 h before release.

^b Mass loss by experimental individuals during holding.

RESULTS

Experimental and control birds did not differ significantly in initial mass during spring (AMRE: $t = 0.3$, $df = 118$, $P = 0.75$; MAWA: $t = 0.5$, $df = 194$, $P = 0.60$) or fall migration (AMRE: $t = 0.7$, $df = 70$, $P = 0.50$; NOWA: $t = 1.0$, $df = 128$, $P = 0.33$; Table 1). Experimental birds of all species significantly decreased in mass during holdover (spring AMRE: $t = 34.3$, $df = 58$, $P < 0.001$; MAWA: $t = 49.1$, $df = 97$, $P < 0.001$; fall AMRE: $t = 17.6$, $df = 35$, $P < 0.001$; NOWA: $t = 29.3$, $df = 64$, $P < 0.001$; Table 1). During the fall, experimental birds of both species were more likely to be recaptured than control birds (AMRE: $\chi^2 = 11.1$, $df = 1$, $P < 0.01$; NOWA: $\chi^2 = 3.3$, $df = 1$; $P < 0.05$; Fig. 1). However, in the spring, I found no difference in recaptures between control and experimental birds (AMRE: $\chi^2 = 2.0$, $df = 1$, $P > 0.05$; NOWA: $\chi^2 = 0.0$, $df = 1$; $P > 0.05$; Fig. 1). I did not find a significant difference in stopover length between experimental and control Northern Waterthrushes during the fall ($U = 117.5$, $P = 0.75$; Fig. 2). The small numbers of individuals recaptured did not allow comparison of stopover lengths among Magnolia Warblers or among American Redstarts in either season, nor did sample sizes allow comparisons of changes in mass by individuals recaptured between the two groups in any species.

DISCUSSION

Similarities in the initial mass of control and experimental groups suggest that the initial condition of migrants is not responsible for observed differences in recaptures between the two groups during fall migration. Instead, it is likely that mass loss, directly and/or due to foraging time lost during holding, resulted in the higher recaptures of experimental individuals in the fall. Numerous studies have shown that lean migrants are more likely to stay at stopover sites than fat birds (Biebach 1985, Biebach et al. 1986, Ellegren 1991, Kuenzi et al. 1991, Loria and Moore 1990, Moore and Kerlinger 1987). However, the present data are the first

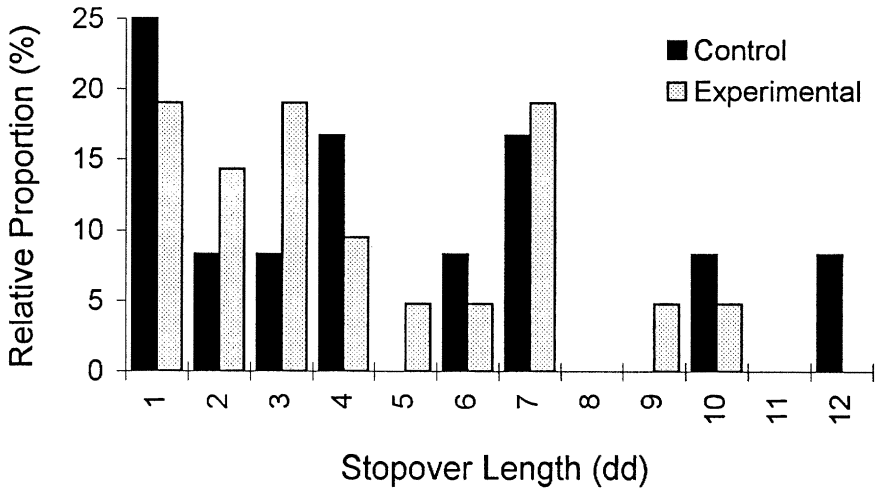


FIGURE 2. Minimum stopover lengths (in days) of experimental and control Northern Waterthrushes on Appledore Island, Maine, during fall migration (Control group: $n = 12$, Experimental group: $n = 21$).

to confirm experimentally that an increased probability of extended stopover results from mass loss.

Results presented here indicate that mass loss by American Redstarts and Northern Waterthrushes increases the likelihood of recapture at a stopover site during fall migration. Migrants presumably would need to compensate for the mass lost during holding and/or the lost foraging time before continuing fall migration. Extended stopovers of more than one day could be used to increase mass in preparation for migratory flights. On Appledore Island, lean non-experimental migrant Northern Waterthrushes captured in the fall are more likely to be recaptured than fatter ones (Morris, unpublished data). These results are similar to those from numerous studies of Palearctic migrants during the fall (Bairlein 1985, Biebach 1985, Biebach et al. 1986, Ellegren 1991). During fall migration in Minnesota, Swainson's Thrushes (*Catharus ustulatus*) that were recaptured were leaner than those captured only once; however, Northern Waterthrushes did not exhibit the same pattern (Winker et al. 1992b). Furthermore, among non-experimental individuals of both American Redstarts and Northern Waterthrushes, lean birds are gaining more mass than heavier ones during fall stopovers on Appledore Island (Morris, unpublished data).

During spring migration, similar mass losses did not result in an increased frequency of recaptures among experimental individuals in this study. I found no difference in recaptures between control and experimental groups of either American Redstarts or Magnolia Warblers during spring migration (Fig. 1), although the frequency of recaptures was quite low in both species. While some studies have shown that initial body con-

dition is negatively correlated with likelihood of recapture during spring migration (Kuenzi et al. 1991, Loria and Moore 1990, Moore and Kerlinger 1987, Moore and Simons 1992), evidence of such a relationship is lacking from Appledore Island (Morris, unpublished data) and other studies (Safriel and Lavee 1988).

Observed seasonal differences in the relationship between initial condition and likelihood of recapture suggest that stopovers may be used differently between the two seasons. Earlier work on migrant warblers documented fewer and shorter stopovers during spring than fall migration on Appledore Island (Morris et al. 1994). Results presented here are similar, with substantially more recaptures of migrants in the fall than in the spring (Fig. 1). Additionally, the results of this study suggest that although mass loss will lead to an increased frequency of recapture in the fall, no such relationship exists in the spring. Francis and Cooke (1986) suggest that migrants may experience significant advantages by arriving at breeding grounds early, regardless of condition. The low recapture rate of both control and experimental birds and the lack of a difference between these two groups during spring migration support this prediction. Furthermore, the higher overall recapture rate and increased recapture rate of experimental individuals in the fall suggest that during fall migration a greater premium is placed on adequate fat stores.

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