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Density-Dependent Mass Gain by Wilson's Warblers During Stopover

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ABSTRACT.—The need restore energetic reserves at stopover sites constrains avian migration ecology. To describe that constraint, we examined relationships among mass gained by Wilson's Warblers (*Wilsonia pusilla*) during stopover, abundance of Wilson's Warblers (i.e. capture rate), and arthropod abundance during autumn migration. We found that amount of mass gained by Wilson's Warblers during stopover declined as a function of their abundance. We found no relationship between mass gained by Wilson's Warblers and arthropod abundance. Abundance of Wilson's Warblers was positively associated with arthropod abundance. These patterns are consistent with the hypothesis that mass gain during stopover is density dependent. They also suggest that Wilson's Warblers respond numerically to abundance of food at that stopover site. This numerical response may override any functional response and thereby account for lack of a relationship between mass change and arthropod abundance.

RESUMEN.—La necesidad de recuperar las reservas energéticas en los lugares de descanso representa una limitante en la ecología de migración de las aves. Para describir dicha limitante examinamos la relación entre el aumento de peso de *Wilsonia pusilla* durante las paradas, su abundancia (i.e. tasa de captura) y la abundancia de artrópodos durante la migración otoñal. Encontramos que el incremento en la masa de *W. pusilla* durante el tiempo de descanso disminuyó en función de su abundancia. No encontramos ninguna relación entre el aumento de peso de *W. pusilla* y la abundancia de artrópodos. La abundancia de *W. pusilla* estuvo positivamente asociada con la abundancia de artrópodos. Estos patrones son consistentes con la hipótesis que plantea que el aumento de peso durante las escalas migratorias es dependiente de la densidad. Los patrones también sugieren que *W. pusilla* responde numéricamente a la abundancia de alimento en este sitio de descanso. Esta respuesta numérica podría anular cualquier respuesta funcional y por lo tanto podría ser responsable por la ausencia de una relación entre el cambio de masa corporal y la abundancia de artrópodos.

Replenishing energy stores at stopover sites may be the most important constraint on long-distance migration in songbirds (Moore et al. 1995). Migrants

have a number of adaptations to cope with that constraint. For example, hyperphagia allows passerines to add 2.4% (median of 31 passerine species) of lean body mass as fat per 24 h, thereby accumulating large amounts of body fat during stopover (mean = 24% of lean body mass in 55 species of passerines; Alerstam and Lindstrom 1990). Given that physiological capacity, it is reasonable to suppose that migrants' ability to refuel is dependent on their ability to find food at stopover sites.

Several studies have found evidence that distribution and energetic condition of insectivorous migrants at stopover sites is influenced by arthropod abundance. Graber and Graber (1983) observed that wood-warblers foraging in forests with high lepidopteran abundance ingested more prey than those foraging in forests of lower prey abundance. Hutto (1985) found that abundance of migrants in southeastern Arizona tracked an index of arthropod abundance. Such studies imply that, to obtain energy for migration, warblers respond both numerically and functionally to availability of food at stopover sites.

Large variation in daily abundance of songbirds at stopover sites is notorious (Dunn and Hussell 1995). It seems likely that this daily flux in abundance might influence patterns in both food abundance and rate at which mass is gained by migrants. Quantitative evaluation of those relationships, however, has been quite limited. The best evidence comes from studies of Moore and Yong (1991), who demonstrated that, on the Gulf Coast, spring migrants recaptured during periods of low migrant abundance gained more mass than those recaptured during periods of high migrant abundance. Their experiments also confirmed that bird predation on arthropods reduced abundance of arthropods in some instances (Moore and Yong 1991), suggesting that competition among migrant birds affected local abundance of prey and rates of mass gain by migrating birds.

To evaluate those relationships at a stopover site in the continental interior, we examined relationships among mass gain by Wilson's Warbler (*Wilsonia pusilla*), abundance of Wilson's Warblers, and abundance of arthropods in the Middle Rio Grande Valley. Wilson's Warbler is the most common long-distance migrant in the Middle Rio Grande Valley and it uses native willow habitat heavily during migration (Kelly et al. 1999, 2000; Yong et al. 1998).

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Our analyses were designed to test three predictions. First, if patterns documented by Moore and Yong (1991) apply, then we expected the rate at which Wilson's Warblers gained mass during stopover to be negatively related to their abundance. Second, if Wilson's Warblers were responding numerically to local patterns in food availability (e.g. Hutto 1985), we expected abundance of migrants to be positively associated with arthropod abundance. Third, if Wilson's Warblers' ability to gain mass during stopover depended on food abundance, there should be a positive relationship between mass gain and arthropod abundance.

Methods.—We netted fall migrants and sampled arthropods weekly from the first week of August through the first week of November in 1996 through 1998 in a variety of vegetation types at the Bosque del Apache National Wildlife Refuge (33°48'N, 106°52'W; Kelly et al. 2000, Yong et al. 1998). All birds were marked with a uniquely numbered aluminum band at first capture. Of vegetation types sampled, we only had enough recaptures from willows for analysis ($n = 137$). Consequently, analyses were based on birds that were initially captured or recaptured in willow vegetation.

We used 13×18 cm pieces of yellow cardboard coated with Tanglefoot™ to trap insects. Traps (4 to 13 per week, usually 10 or 13) were attached to the vegetation at 1 m height for a 24 h period each week. Exact sampling location varied among weeks and years, but all traps were located in the same general area (within a 1 km radius). Each arthropod was identified to family.

There are few published accounts of Wilson's Warbler diets, and most of that information has been collected during the breeding season. Raley and Anderson (1990) found that stomach contents of Wilson's Warblers contained higher proportions of Coleoptera, Ephemeroptera, Plecoptera, Diptera, and Hymenoptera compared to composition of arthropod species found in willows at a site in Wyoming. Lepidoptera larva and leafhoppers (Homoptera) also constituted a large proportion of the diet of Wilson's Warblers (Raley and Anderson 1990). Generally, arthropods between 3 and 7 mm in length were over represented in Wilson's Warbler diets. Based on this literature, we used a subset of arthropods sampled from 1996 to 1998 as an index of food availability. We restricted our comparisons to insects (≤ 6 mm) in four taxa that were abundant on our glueboards and documented in the literature to be important components of Wilson's Warbler's diets: Hymenoptera, Coleoptera, Diptera, and Homoptera.

Analyses.—To evaluate our predictions we examined correlations among (1) percentage change in mass of recaptured Wilson's Warblers as an estimate of their mass gain; (2) capture rates ($100 \times$ total number of captures per net hour) of Wilson's Warblers as an estimate of their daily stopover abundance; (3)

number of arthropods captured on sticky traps as an estimate of food availability. The percentage mass gain of each recaptured Wilson's Warbler was matched with the (1) capture rate for the day of recapture and (2) arthropod abundance for that week. To further explore correlations among those variables we also examined partial correlations.

Correlations among those variables could potentially be confounded by numerous other factors, which we examined prior to analyses. Those factors included seasonal changes in capture rate, age, sex, and fat scores of Wilson's Warblers; time interval between capture and recapture; abundance of other wood warblers; and seasonal patterns in arthropod abundance. For example, we used nonlinear regression to model capture rate of Wilson's Warbler by capture date. We then correlated residual capture rate from that regression against number of arthropods captured during a give week. Another example of an analysis that we examined was the relationship between residual capture-rate and mass change adjusted for length of time between initial and last recapture. When adequate data were available, we examined those types of relationships for males, females, hatch-year birds, and after-hatch-year birds. After examining those factors, we concluded that they did not have strong effects on the patterns we report here. That is, we found no evidence that those factors either contribute to or diminish significance of patterns we report. Consequently, we do not discuss those factors further.

Results and discussion.—Of the Wilson's Warblers we recaptured, 41% gained mass ($\bar{x} \pm SD = 0.55 \pm 0.46$ g, $n = 46$) and 52% lost mass (0.39 ± 0.28 g, $n = 58$) between initial and final capture. Overall mass change between initial and final recapture did not differ from zero (0.02 ± 0.58 g, $n = 111$). These patterns indicate that conditions at that stopover site were not always sufficient to allow most birds to gain mass.

One factor that influenced Wilson's Warbler's ability to gain mass was their abundance. Percentage mass change among Wilson's Warblers during stopover was significantly negatively related to their abundance ($r = -0.22$, $P = 0.02$, $n = 111$). When partial correlation analysis was used to control for effects of arthropod abundance, this relationship became weaker (partial $r = -0.18$, $P = 0.08$, $n = 94$). The negative relationship between mass gain and capture rate was consistent with the hypothesis that mass gain during stopover was density-dependent in Wilson's Warblers; a similar pattern was reported by Moore and Yong (1991). In their study, White-eyed Vireos (*Vireo griseus*), Kentucky (*Oporornis formosus*), and Tennessee (*Vermivora peregrina*) warblers had greater rates of mass gain when abundance of migrants was low than when abundance of migrants was high. Tests for similar patterns in six other species, however, revealed no significant effect of mi-

TABLE 1. Results of Pearson product-moment correlations of capture rate of Wilson's Warblers and mass gain of Wilson's Warblers with number of arthropods captured on sticky traps. Data were collected in the fall of 1996–1998 in the Bosque del Apache National Wildlife Refuge, New Mexico. Significant correlations are in bold typeface. Sample sizes are in parentheses. When a bonferoni adjustment was used to correct for multiple tests, all correlations remain significant except for that of Hymenoptera with mass gain.

Arthropod family	Mass gain (97)		Capture rate (113)	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Diptera	−0.13	0.21	0.23	0.01
Coleoptera	−0.07	0.48	0.29	<0.01
Hymenoptera	−0.24	0.02	0.40	<0.01
Homoptera	−0.17	0.10	0.04	0.64
Families combined	0.08	0.43	0.38	<0.01

grant density on rate of mass change (Moore and Yong 1991).

We found no correlation between mass gain and total number of arthropods captured on sticky traps (Table 1), and controlling for capture rates with partial-correlation analysis did not alter that result (four families combined, partial $r = 0.03$, $P = 0.78$, $n = 94$). Abundance of Wilson's Warblers, however, was significantly positively correlated with number of Hymenoptera, Diptera, and Coleoptera captured on sticky traps, but unrelated to number of Homoptera captured (Table 1). Of those relationships, all except the one involving number of Coleptera were also significant when using partial-correlation analyses to control for effects of mass change. These positive correlations suggest that Wilson's Warblers were responding numerically to the abundance of food. A similar pattern was reported by Hutto (1985), although in that case the pattern occurred across rather than within vegetation types. A numerical response may help to explain lack of relationship between mass gain in Wilson's Warblers and abundance of arthropods. If enough Wilson's Warblers are attracted at times of high arthropod abundance, then the actual mass gain for each individual (i.e. functional response) might be limited by increased competition for food.

An alternative explanation is that different temporal scales of sampling in these data sets reduced our ability to detect some important patterns. That is, we know the rate of mass gain for Wilson's Warblers fairly precisely for a well-defined time period (capture to recapture time). On the other hand, what we know about arthropod abundance is derived from relatively coarse temporal sampling during a single day of each week. Consequently, if the impor-

tant scale of temporal variation is finer than the scale at which we measured arthropods, it would not be evident in our data.

Where density-dependent mass gain occurs, it could influence migration strategies. For example, most passerines migrate through stopover sites with a pronounced seasonal peak in abundance (Rotenberry and Chandler 1999). Our results imply that migrants passing through during those peak periods would be more likely to encounter depleted food resources and therefore have more difficulty in refueling than those migrating before or after peak migration. If the cost of migrating during peak abundance was greater, in terms of fitness, than benefits derived in terms of other factors (e.g. reduced predation risk or better climate conditions for migration), then we would expect migrants to avoid migration during peak periods, resulting in a more diffuse pattern of passage with no discernable peak period. Depletion of food resources could contribute to early passage of adult Wilson's Warblers relative to hatch-year birds at our stopover sites and the use of inferior habitats by hatch-year birds (Yong et al. 1998).

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