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TEMPORAL AND SPATIAL PATTERNS IN DAILY MASS GAIN OF MAGNOLIA WARBLERS DURING MIGRATORY STOPOVER

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ABSTRACT.—Whether or not migrants gain mass at a stopover site is an index of site quality. Previous studies have examined mass gain of recaptured birds, and of short-term stopovers by regressing mass at first capture on hour of day. I developed an extension of the latter method using multiple regression to examine the effects on mass gain of hour of day, date, and year. I then used the method to compare the quality of three stopover sites at Long Point, Ontario, for Magnolia Warblers (*Dendroica magnolia*). At the peak of fall migration, warblers at all three sites gained sufficient mass for a net gain over 24 h, but they gained mass at only two of three sites during spring. Mass gain varied significantly over the course of the day, by date in the season, and among years. The earliest spring migrants lost mass at all sites, but rate of mass gain increased as the season progressed. Similar information for many more species and stopover sites might aid in habitat conservation for migrants. *Received 24 July 1998, accepted 23 April 1999.*

MIGRANTS REQUIRE high-quality stopover sites to recover from a flight and to refuel for the next stage of migration. It is relatively easy to identify important stopover sites for waterfowl and shorebirds that have specific habitat preferences and concentrate at relatively few sites (Myers et al. 1987). For broad-front migrants such as songbirds, however, we know very little about the characteristics that affect the quality of stopover sites and how such characteristics might differ among species. In addition, almost nothing is known about temporal variation in site quality (but see Moore and Yong 1991).

The most straightforward means of assessing quality of a given stopover site for broad-front migrants is to determine whether individuals spending time there normally gain body mass. This measure is an index not only of food abundance, but of its availability (reflecting, for example, typical levels of harassment by predators). Many authors have analyzed mass change of banded birds recaptured later in the same migration season (e.g. Mueller and Berger 1966, Moore and Kerlinger 1987, Loria and Moore 1990, Yong and Moore 1997), but recaptured individuals frequently are leaner and lighter at first capture than are conspecifics that are captured only once (Winker et al. 1992, Woodrey and Moore 1997). Thus, mass change in these birds may not be typical of the much larger numbers of birds that stop for only one day. Moreover, recaptured birds often lose mass on the day after first capture before regaining mass (Mueller and Berger 1966, Loria and Moore 1990). Whatever the cause of this phenomenon (see Mueller and Berger 1966, Yong and Moore 1997), the result is that average mass change among recaptured individuals may differ from that of other migrants.

Analyzing mass at first capture is a means of assessing daily mass change in individuals with short stopover times, making use of the much greater sample sizes of birds captured only a single time (Mueller and Berger 1966, Collins and Bradley 1971, King 1976, Winker et al. 1992). Assumptions are that birds arrive at the stopover site at or before dawn and that time of capture is independent of a bird's mass at dawn; therefore, a gain in average mass of birds trapped over the course of a day represents the average mass gain of all individuals in the area.

Here, I present an extension of the "first-capture analysis" using data for Magnolia Warblers (*Dendroica magnolia*) and illustrate its potential use by comparing quality of three sites at Long Point, Ontario. Although geographically quite close together, the three sites differ in habitat and especially in temperature regime, so one might expect differences in their quality for refuelling of migrants. In addition

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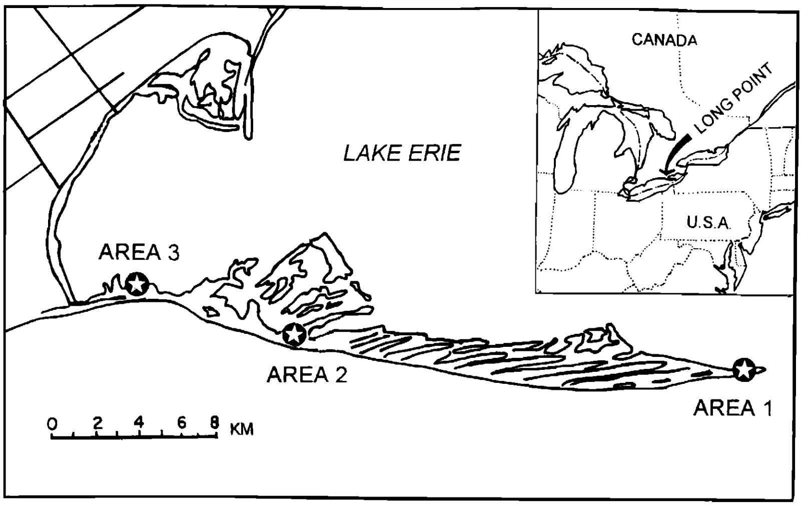

FIG. 1. Location of Long Point, Ontario (inset), and of banding sites on the point (stars).

to estimating average hourly mass gain for each site and season, I examine temporal variation in mass gain within days, seasons, and among years, a topic that could not be examined with the limited sample sizes available from recapture data.

METHODS

Study site.—The Long Point Bird Observatory operates three banding sites on a 35-km sand spit extending into Lake Erie (Fig. 1). The sites differ in habitat and seasonal temperature. Area 1 (eastern tip of the point) has a sparse scattering of cottonwoods (*Populus deltoides*) and little ground cover or understory on the open dunes. During spring, a pronounced climatic influence of the lake delays plant phenology up to a week or more compared with the mainland. Area 2 is located about 20 km west of Area 1 and also has a savannah-like habitat, but the development of ground cover is better, and the variety of mature tree species is greater. It is adjacent to extensive marshes and is better protected from wind. Area 3 is near the base of the point about 10 km west of Area 2 and consists of a small mixed woodlot adjacent to damp areas dominated by dense shrubs (primarily red osier dogwood [*Cornus stolonifera*]). In spring, Area 3 is typically warmer than the remote stations, and leaf-out is a week or more earlier than at Area 1 (although still retarded compared with inland sites).

At each site, mist nets were set up daily (weather permitting), usually at or before dawn, and nearly always run for at least 6.5 h. The number of net hours did not vary importantly among the years analyzed here, and although net locations were changed occasionally at Area 1 because of shore erosion, the habitat remained the same as described above.

Among the data collected on each bird were fat score, body mass (to nearest 0.1 g, measured with a triple-beam or electronic balance), unflattened wing chord (to nearest mm), age and sex (using plumage characteristics and skulling; Wood 1969, Pyle et al. 1987), and time of weighing (to nearest 10 min). Times were converted to hours since sunrise to account for seasonal changes in sunrise time. Fat was scored as 0 for no fat, "T" for trace of fat (converted arbitrarily to 0.3 for numerical analysis), 1 for little fat (filling no more than 1/3 of furculum), 2 for moderate fat (furculum 1/3 to 2/3 filled), and 3 for heavy fat (furculum nearly filled to overflowing).

Analyses.—All analyses were limited to the spring and fall periods in which 98% of Magnolia Warblers passed through the Long Point study sites (4 May to 7 June and 13 August to 15 October) for the years 1980 to 1996. To test whether a bias occurred in the size of bird caught by time of day, wing length was regressed on hour (time of weighing expressed as hours since sunrise), hour^2, and hour^3 (the higher-order terms testing for nonlinear changes).

The basic model for analysis of hourly mass gain in birds captured once is:

$$\hat{M} = b_0 + b_1 H, \qquad (1)$$

where $\hat{M}$ is the regression estimate of mass, H = hour (since sunrise), and b_0 and b_1 are coefficients estimated by the regression. However, mass is also affected by the overall size of the bird, as indicated by wing length. In southern Ontario, Magnolia Warblers have strongly differential migration in spring (with

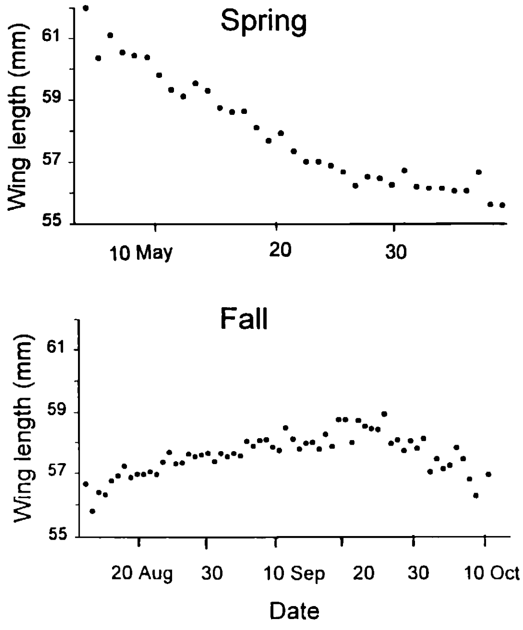

FIG. 2. Mean daily wing length of Magnolia Warblers at Long Point in spring and fall (all sites combined, 1980 to 1996).

the larger males preceding females; Francis and Cooke 1986), leading to seasonal patterns in wing length (Fig. 2). A seasonal pattern occurs in fall, too, although less striking (Fig. 2), and fall age ratios at Long Point differ among sites (Dunn and Nol 1980). Therefore, it is important to standardize mass across age/sex groups. Winker et al. (1992) did this by substituting "condition index" (mass × 10,000/wing length^3) as the dependent variable in the simple regression model shown above:

$$\hat{C} = b_0 + b_1H. \quad (2)$$

However, the relationship between mass and wing length differs among age/sex classes of Magnolia Warblers (Fig. 3). Individual lines shown in the figure are slopes from separate regressions for each age/sex class of mass on wing length and fat score (when fat score is set to 0), which is a one-step analysis equivalent to the two-step procedure of Ellegren and Fransson (1992). A combined analysis (adding dummy variables for each age/sex class) showed that slopes for after-second-year (ASY) males and second-year (SY) females differed significantly from the slopes for the other two groups (r^2 of regression = 0.27, n = 2,091, $P < 0.001$; and $P < 0.001$ for partial regression coefficients for ASY males and SY females).

These results indicate that condition indices will underestimate true condition for some age/sex groups and overestimate it for others. Therefore, I used mass as the dependent variable in a multiple regression and added wing length as an independent variable:

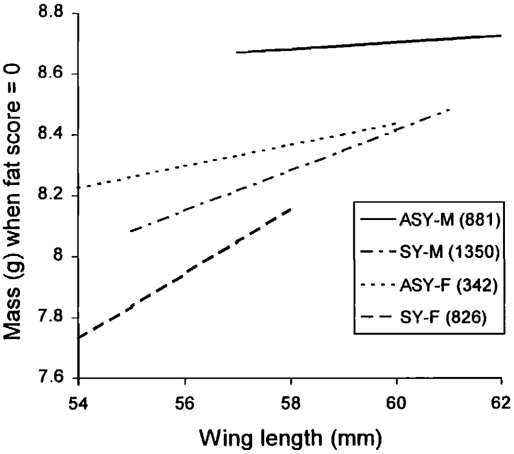

FIG. 3. Fitted lines for mass regressed on wing length and fat score in Magnolia Warblers at Long Point in spring (all sites combined), when fat = 0 (see text). Lines are plotted over the range of wing chords typical for each age/sex group (5th to 95th percentiles). ASY = after second year, SY = second year, F = female, M = male. Sample sizes in parentheses.

$$\hat{M} = b_0 + b_1H + b_2W, \quad (3)$$

where variables are the same as in the previous model, and the new variable W = wing length. Thus, the coefficient b_1 represents the average hourly mass gain for all birds regardless of size. Exploratory analyses showed that the relationship between mass and wing length was linear, so no higher-order wing length terms were required in the model. This regression model is hereafter referred to as the "reduced regression model."

To examine seasonal change in mass gain, I used the following regression model, run stepwise:

$$\hat{M} = b_0 + b_1H + b_2W + b_3D + b_4D^2 + b_5D^3 + b_6(HD) + b_7(HD^2) + b_8(HD^3), \quad (4)$$

where hour was forced to enter and the new variables are D = day, D^2 = day^2, D^3 = day^3, (HD) = hour × day, (HD^2) = hour × day^2, and (HD^3) = hour × day^3. Day was set to 0 for the peak migration date in each season (averaged across all years), so that if hour-day interactions prove significant, the coefficient for hour (b_1) will represent the average hourly change in mass at the peak of the migration. The date terms model date-related changes in mass (higher-order terms modeling nonlinear changes), whereas the interaction terms (HD) indicate whether signifi-

TABLE 1. Hourly mass change of Magnolia Warblers at three sites on Long Point, Ontario, and significance of difference from estimated threshold value for net mass gain over 24 h. Other rows show r^2 and significance levels for regression, and partial r^2 and significance levels for the independent variable hour.

	Spring			Fall		
Model	Area 1	Area 2	Area 3	Area 1	Area 2	Area 3
	Simple regression: Dependent variable = condition index					
Equation 2[a]	0.013	0.052+	0.016+	0.062**	0.046*	0.061***
$r^2_{\text{regression}}$	NS	0.02***	0.002*	0.04***	0.02***	0.03***
	Multiple regression: Dependent variable = mass					
Equation 3 (reduced)	−0.001**	0.054**	0.038**	0.057***	0.061***	0.064***
$r^2_{\text{regression}}$	0.03***	0.11***	0.09***	0.18***	0.17***	0.15***
r^2_{hour}	NS	0.04***	0.02***	0.07***	0.08***	0.07***
Equation 4 (full)	−0.001**	0.065**	0.047***	0.072***	0.053***	0.061***
$r^2_{\text{regression}}$	0.13***	0.16***	0.13***	0.18***	0.18***	0.17***
r^2_{hour}	NS	0.04***	0.03***	0.07***	0.08***	0.07***
Sample size	767	678	3,729	914	2,095	2,063

NS, $P > 0.1$; +, $0.05 < P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

[a] Change in condition index was back-transformed to represent mass change (see Methods).

cant variation occurs in hourly mass change with date in the season. Inclusion of date and wing length terms eliminates the need to consider age and sex variables, which is a desirable outcome not only because aging and sexing are problematic in this species (and many others for which this method could be used), but because of sample-size limitations for separate consideration of age/sex groups. The model shown here was adopted as the standard and hereafter is referred to as the "full regression model."

Variations of the full regression model were used to investigate changes in mass gain according to time of day and among years. Possible nonlinearity in mass gain over the course of the day was investigated by adding the independent variables H^2 (hour^2) and H^3 (hour^3). This model assumed no change in daily pattern of mass gain with date in the season. Annual variation in mass change was investigated separately by adding independent variables to the full regression model for year and interaction between hour and year: i.e. equation 4 with the addition of independent variables *Y80* . . . *Y96* and (*HY80*) . . . (*HY96*), where the dummy variables for the years 1980 to 1996 (*Y80* . . . *Y96*) have the value of 1 for the indicated year and 0 for all other years, and (*HY80*) . . . (*HY96*) = hour × *Y80* . . . hour × *Y96*. This model was not run stepwise because of sample-size restrictions and because coefficients were desired for all year variables regardless of significance.

To compare results with those of other published analyses, condition index was regressed on hour (equation 2), which is equivalent to equation 3 except that the method used to correct body size for wing length differs. Hourly mass change was back-calculated as mass change = b_1(wing length)^3/10,000, where b_1 is the regression coefficient for hour and wing length is the average wing length for all Magnolia Warblers at Long Point (i.e. 57.77 mm).

I conducted *F*-tests to determine whether hourly changes in mass estimated from the regressions were significantly different from the estimated value required for net gain in mass over a 24-h period. The latter threshold was an arbitrary value calculated on the assumption that mass gain continues at the average rate over all hours of daylight, and that overnight mass loss of a nonmigrating bird equals 4.5% of average body mass (Winker et al. 1992). The threshold values used in this test (based on local day length during Magnolia Warbler migration) were 0.026 g/h in spring and 0.031 g/h in fall.

RESULTS

Hour of weighing had a significant effect on mass at Areas 2 and 3 in spring, and at all sites in fall, regardless of the regression model used ($r^2_{\text{regression}}$ for equation 2 and r^2_{hour} for equations 3 and 4; Table 1). Wing length did not change significantly by time of day in either season or at any of the sites, indicating that hourly mass change did not result from capture of different size classes at different times of day. All estimates of hourly mass change from multiple regressions (equations 3 and 4) were significantly greater than the estimated threshold values for net gain over 24 h, except that values for Area 1 in spring fell significantly below the threshold (Table 1).

Estimates of hourly mass change from simple regression of condition index on hour (equation

TABLE 2. Net 24-h mass change in Magnolia Warblers in fall at different geographic locations based on regression of condition index on hour.[a]

Location	Mass change (g)	n	Source
Minnesota	0.06	761	Winker et al. 1992
Maine	0.21	223	Morris et al. 1996
Ontario (Area 1)	0.39	914	This study
Ontario (Area 2)	0.19	2,095	This study
Ontario (Area 3)	0.38	2,063	This study

[a] Equation 2. See Methods for estimation of net daily change in mass.

2) were similar to those from the full and reduced regressions, except for a much reduced estimate for Area 3 in spring; however, less variation was ascribed to hour, and the P-value for the difference from threshold values was lower (Table 1). Results from this regression yielded estimates of 24-h gain that were as high or higher than those from two other studies of Magnolia Warbler that used the same method of analysis (Table 2).

Mass gain over the course of a day in fall was linear at Areas 2 and 3 and close to linear at Area 1 (Fig. 4). In spring, birds did not gain much mass until several hours after sunrise, but gains then increased significantly at Areas 2 and 3. Except at Area 1 in spring, gains continued throughout the day. (Note that other results presented here did not consider nonlinear mass gain throughout the day.) Rate of mass gain increased throughout the spring season at Areas 2 and 3 and at Area 3 in fall ($P < 0.05$; Fig. 5), whereas the spring increase at Area 1 was not significant ($P = 0.06$). Fall mass gain at Area 2 declined significantly early in the season and then leveled off.

A special analysis that included year variables (see Methods), revealed significant annual variation both in mass and in hourly mass gain (Fig. 6). There was no correlation in annual values for hourly mass gain among sites, either within or between seasons. However, annual hourly mass gain was negatively correlated with average mass at dawn ($r = -0.81$, $P < 0.001$, $n = 96$ combinations of year, site, and season). Some extreme values were from years with low sample sizes and few days on which Magnolia Warblers were banded, but correlations weighted by sample size or number of banding days remained strongly negative.

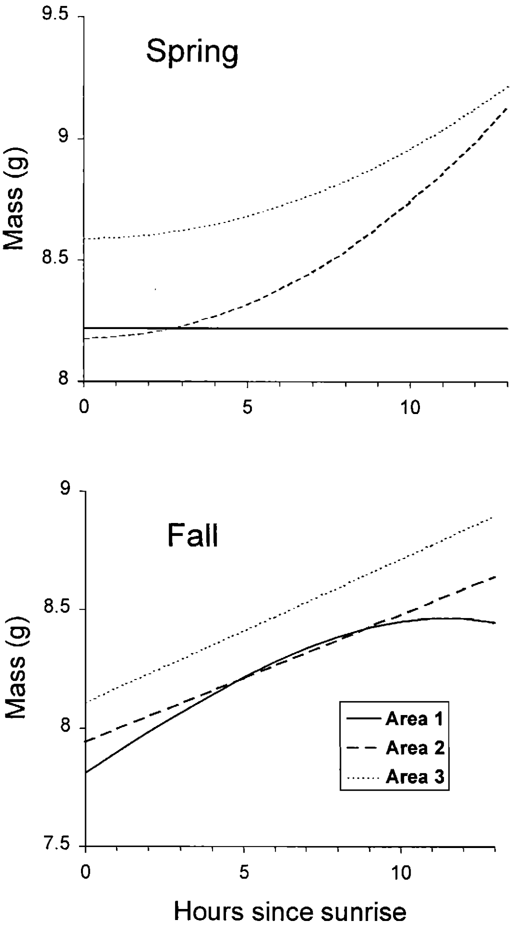

FIG. 4. Hourly mass according to time of day for Magnolia Warblers at the peak of migration. Estimated from stepwise full regression with addition of higher-order terms for hour.

DISCUSSION

Analysis methods.—One of the assumptions of the analysis is that birds arrive at or before dawn. This assumption often is true (Moore et al. 1995), but for locations such as the Gulf Coast in spring, where birds may continue to arrive all day (Aborn and Moore 1997), the method of analyzing first captures is not suitable. The other important assumption is that hour of capture is independent of mass at dawn. In this study, wing length did not vary with hours since sunrise, indicating that birds of all size classes were captured with equal probability throughout the day. However, lean birds have been shown to forage more actively

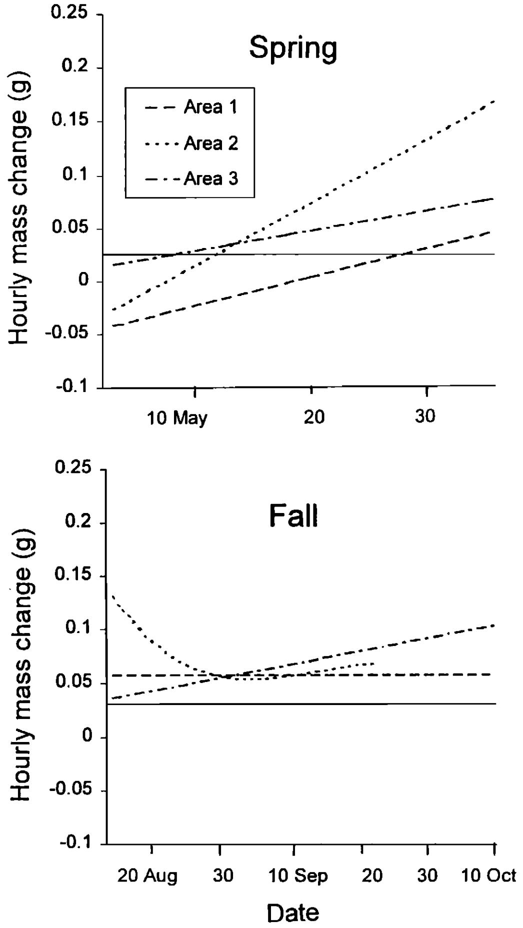

FIG. 5. Hourly mass change for Magnolia Warblers according to date in the season, estimated from the full regression (coverage at Area 2 ceases before fall migration is complete). Solid horizontal line indicates estimated threshold for 24-h net gain.

than heavy individuals (Loria and Moore 1990, Yong and Moore 1993), and if heavy birds drop out of the sample as the day progresses, then mass gain from first captures will be underestimated. Without controlled experiments, it will be impossible to determine whether time of capture is wholly independent of mass at dawn. Indirect evidence suggests that the assumptions are met, however, in that estimates of mass gain from first capture (Mueller and Berger 1966, Winker et al. 1992, Morris et al. 1996, this paper) fall into the same range as values determined from studies of recaptured individuals (Mueller and Berger 1966, Loria and Moore 1990, Lindström 1991, Winker et al. 1992, Morris et al. 1996, Yong and Moore 1997).

The reduced multiple regression (equation 3) is equivalent to the simple regression of condition index on hour (equation 2), except that the method of correcting mass for body size differs. Although results from the two models were similar in most cases, the reduced regression detected clearer effects of hour (Table 1; compare partial r^2 for equation 3 with the regression r^2 for equation 2) and is recommended as a better method (as well as simplifying the analysis). The full regression model (equation 4, including date effects), did not alter estimates of hourly mass gain very much compared with those from the reduced regression (equation 3). The reduced regression model does not specifically estimate mass gain at the peak of migration, but because sample sizes are normally largest at that time, estimates should be similar to those from the full regression unless sampling is skewed toward early or late migration dates. An advantage of using the reduced regression is that sample size for analysis of one site can be as low as 40 (20 cases per independent variable; Tabachnick and Fidele 1989), whereas 160 is the recommended minimum for the full regression (twice that if the stepwise option is used). Nonetheless, the number of birds captured on a given date will vary among sites and years not only as a result of variation in effort, but also in weather patterns that cause more or fewer birds to cease migration at a particular site. Taking date effects into account should help reduce variance in estimates of mass gain and allow appropriate comparison of sites with different sampling schedules, while also allowing study of seasonal change in mass gain. Thus, the full regression model is preferable when sample sizes allow. Whatever analysis method is used, several years of data should be included to even out effects of annual variation in mass gain (Morris et al. 1996; Fig. 6), and hour of day should be converted to hours since sunrise (see Methods).

For simplicity's sake, the full regression model did not include H^2 and H^3, even though a special analysis detected significant nonlinearity in mass change over the course of the day. The full regression model therefore generated estimates for mass change that represented an av-

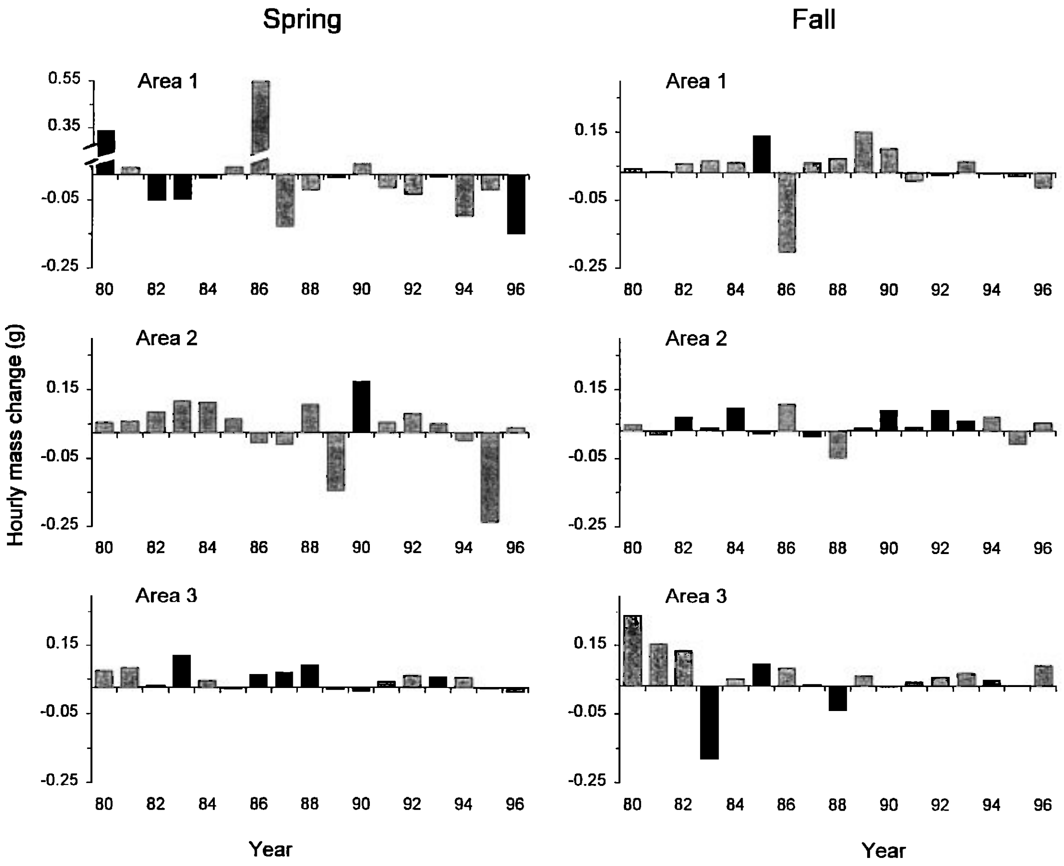

FIG. 6. Hourly mass change at the peak of migration by year. Estimated from full regression with addition of year variables. Black bars indicate values significantly different from estimated threshold value required for net mass gain over 24 h (threshold indicated by the X-axis).

erage over the course of the whole day (weighted toward the hours with the largest sample sizes). A possible alternative would be to include higher-order hour terms and present results for a particular hour of the day (e.g. 4 h after sunrise, when sample sizes are generally high).

Future results should be presented as hourly rates of mass change, even if other values are also presented (e.g. daylight gains [Woodrey and Moore 1997] or net mass change over 24 h [Winker et al. 1992]). Calculation of net mass gain requires assumptions about the nature, degree, and uniformity of overnight mass loss. The figure used here of 4.5% of body mass lost per night is somewhat arbitrary and doubtless varies with temperature, hours of darkness, body mass, and other factors. Moreover, little is known about the actual number of daylight hours passerine migrants spend in active feeding (although results presented here suggest continued mass gain throughout the day). Hourly rate of change is estimated with fewer assumptions than is daily net gain, and daily values can readily be calculated from them if desired.

Temporal and spacial variation in mass change.—At all sites on Long Point, the earliest spring migrants either lost mass during the day or gained at too low a rate for a net gain over 24 h, even though net gains occurred later in the season. It is likely that the large seasonal change in spring mass gain primarily is a result of improved feeding conditions (i.e. a greater supply of insects as the season progresses; Hussell and Quinney 1987), but there may be other contributing factors. Fat birds gain less mass than lean ones (Loria and

Moore 1990), and my results showed that annual mass gain was highest when annual arrival masses were lowest; thus, date-related differences in hourly mass gain may be influenced by condition upon arrival. Results in Figure 5 could also be interpreted as showing that birds arriving later in the spring are better foragers or competitors (although the fact that later migrants are probably younger individuals [Francis and Cooke 1986] makes this seem rather unlikely). Lastly, there might be date-related differences among birds in time spent foraging; perhaps early spring migrants (especially males) are more motivated to move on than to completely refuel at stopover sites (Sandberg and Moore 1996).

The three sites at Long Point appear to be areas of net gain for migrating Magnolia Warblers, with the exception of Area 1 in spring. This exception was not unexpected, given the marked retardation in spring phenology at the eastern end of the point, and it indicates that an area is not necessarily good for refuelling just because large numbers of birds are captured there.

Fall mass gain at Long Point compared favorably with the few other sites that have similar data (no comparable data for spring). Birds at the Minnesota site did not lose mass, but gained only about 1% of lean body mass, whereas they gained about 3% at the site in Maine and generally did even better at Long Point. Although vegetation is comparatively sparse on the point, it is likely that the extensive inter-dune wetlands and marshes contribute to high insect productivity there. Without more comparative data, however, it is difficult to judge whether Long Point is truly a high-quality site relative to other sites. Daily mass gains of more than 15% of body mass have been recorded for small passerines (Leberman and Browne 1976, Loria and Moore 1990, Winker et al. 1992), although such high values are normally found only in a few individuals.

In interpreting the quality of specific sites, it should be kept in mind that birds start moving about the local area soon after dawn to find better shelter and feeding opportunities (Moore et al. 1995). Summer Tanagers (*Piranga rubra*) moved only a few hundred meters during stopover (Aborn and Moore 1997), but it is not known how typical this might be of other sites or other species, and "morning flights" are known from some locations (Moore et al. 1995). Analyses of mass gain therefore may include birds that have moved from nearby areas and from unknown distances. This should not bias results as long as no differential movement occurs into or out of the banding area by heavy versus lean individuals, but it means that estimates of mass gain actually reflect quality of a larger area than the immediate banding site. Unless habitat in the vicinity of the site is fairly uniform, few conclusions can be drawn from first-capture analyses about the quality of specific habitat types as opposed to the quality of the surrounding landscape in general.

Given that Long Point is a peninsula, there might be increased chances of movement among the banding sites even though they are a minimum of 10 km apart. Sampling of the same group of birds at Areas 2 and 3 would be particularly likely if birds move off the point throughout the day, such that both sites would sample birds that had spent most of the day elsewhere on the peninsula. Although this probably occurs to some extent, the effect is not obvious: peak hour of capture was about the same at all three sites (3 to 4 h after sunrise), with no sign of additional pulses of birds at Areas 2 or 3 later in the day. Nonetheless, the three sites might be considered together as an indication of the quality of Long Point as a whole. Although Area 1 clearly is less suitable for migrants in spring, it remains unknown how far westward its conditions extend.

Analysis of data for many more species and from many more banding stations should give us a better understanding of the spatial and temporal dynamics of mass gain during migration. Such work has conservation applications in that decisions concerning land stewardship and preservation of habitat should take the needs of migrants into account. Currently, however, we know very little about the relative importance of different stopover areas. For example, even though few migrants stay at a given stopover site for as much as 24 h (Kuenzi et al. 1991, Winker et al. 1992, Morris et al. 1996), fall migrants clearly increase their mass between the northern states and the Gulf Coast. Both Magnolia Warblers (Caldwell et al. 1963) and thrushes (Child 1969) killed by striking towers during fall migration had three times more fat in Florida than at northern sites, and Magnolia Warblers in fall were 10% heavier in

Alabama than at Long Point (Woodrey and Moore 1997, this paper). However, insufficient data exists from sites in between to determine where and when the major portion of mass increase occurs. Conservation planning would benefit from knowing whether migrants gain mass gradually all along their broad-front migration routes or whether sites in relatively narrow geographic zones are of special importance. Moreover, with additional results it may prove possible to compare quality of landscape types, such as unfragmented versus fragmented woodland, or riparian habitat within urban versus rural settings.

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