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FRUIT ABUNDANCE AND LOCAL DISTRIBUTION OF WINTERING HERMIT THRUSHES (*CATHARUS GUTTATUS*) AND YELLOW-RUMPED WARBLERS (*DENDROICA CORONATA*) IN SOUTH CAROLINA

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ABSTRACT.—We conducted winter censuses of two short-distance migrants, Hermit Thrushes (*Catharus guttatus*) and Yellow-rumped Warblers (*Dendroica coronata*), over seven years in five different habitats to determine whether their local abundances could be predicted by fruit pulp biomass. Sampled habitats were stands of upland and bottomland hardwood, loblolly pine (*Pinus taeda*), longleaf pine (*P. palustris*), and young (<10 years) longleaf pine. Hermit Thrush abundance, which was highest in bottomland hardwood habitats, was positively related to total dry mass of fruit pulp. Those results are consistent with the hypothesis that resource availability affects the local distribution of migrant passerines on their wintering grounds. Our results also indicate that bottomland hardwood habitats in the southeastern United States may be especially important to wintering Hermit Thrushes. Yellow-rumped Warbler abundance was correlated with ripe-fruit pulp dry mass of *Myrica cerifera*, a major source of winter food for that species. However, because *M. cerifera* pulp dry mass was confounded with habitat type, we could not distinguish the relative importance of fruit resources and habitat for Yellow-rumped Warblers. Our results underscore the importance of fruit to wintering birds. However, the overall percentage of variation in winter bird abundance explained by differences in ripe-fruit biomass was modest, indicating that other factors are also important. *Received 12 June 2002, accepted 28 August 2003.*

RESUMEN.—Durante un período de siete años realizamos censos invernales, en cinco ambientes diferentes, de dos migrantes de corta distancia, *Catharus guttatus* y *Dendroica coronata*, para determinar si las abundancias locales pueden ser predichas a partir de la biomasa de pulpa de fruto. Los ambientes muestreados fueron plantaciones de especies de madera dura en sitios altos y bajos (inundables), de *Pinus taeda*, de *P. palustris* y bosques jóvenes (<10 años) de *P. palustris*. La abundancia de *C. guttatus*, la cual fue mayor en las plantaciones de sitios bajos, se relacionó positivamente con la masa seca total de pulpa de fruto. Estos resultados son consistentes con la hipótesis de que la disponibilidad de recursos afecta la distribución local de aves migrantes paserinas en sus áreas de invernada. Nuestros resultados también indican que los ambientes de plantaciones en sitios bajos en el sudeste de Estados Unidos pueden ser especialmente importantes para albergar a individuos de *C. guttatus* durante el invierno. La abundancia de *D. coronata* se correlacionó con la masa seca de pulpa madura de frutos de *Myrica cerifera*, la cual representa una fuente importante de alimento durante el invierno para esta especie. Sin embargo, debido a que la masa seca de pulpa de *M. cerifera* no pudo ser separada del efecto del tipo de hábitat, no pudimos distinguir entre la importancia relativa de los frutos y del hábitat para *D. coronata*. Nuestros resultados enfatizan la importancia de los frutos para las aves invernantes. Sin embargo, el porcentaje total de variación en la abundancia invernal de aves explicado por las diferencias en la biomasa de frutos maduros fue modesto, indicando que otros factores son también importantes.

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THE DISTRIBUTION AND abundance of birds is a central theme in avian biology (MacArthur 1972, Cody 1985, Root 1988, Wiens 1989, Jones 2001). Habitat use, in particular, has drawn attention because of its relevance to conservation and management (Verner et al. 1986, Martin and Finch 1995, Sherry and Holmes 1996, Kilgo et al. 2002). Although most studies have focused on the habitat requirements of breeding birds, recent studies have begun to emphasize nonrandom habitat associations of species, especially long-distance migrants, when they are not breeding (Sherry and Holmes 1996, Marra et al. 1998, Marra 2000, Strong and Sherry 2000, Marra and Holmes 2001). To truly understand such patterns and their ecological consequences, one must first uncover the ecological mechanisms that generate them.

Availability of food is a likely mechanism underlying nonrandom distributions of wintering birds (Fretwell 1972, Jansson et al. 1981, Hutto 1985, Leisler 1990, Newton 1998, Johnson and Sherry 2001). However, winter bird distributions may not always mirror food distribution. Potential reasons include overabundance or rapid fluctuation of food, inability to accurately assess food abundance, high risk of predation, social interactions, and preference for habitats that mirror those used during the breeding season (Hutto 1985, Greenberg 1986, Recer et al. 1987, Rappole et al. 1989, Lindström 1990, Greenberg et al. 1993, Herrera 1998). Those alternative explanations for nonbreeding-season distributions are often difficult to separate. A first step is to focus on a single factor that seems important to determine if it alone can explain habitat use. Here we focus on food abundance.

A primary challenge in testing for a link between food abundance and wintering bird abundance is the difficulty of quantifying food resources in a way that accurately reflects food availability from a bird's perspective. In North America, many migrant passerines consume fruits, seeds, and insects during winter (Martin et al. 1951). Insects are difficult to sample; different methodologies yield different results and are appropriate for different types of insectivores (Cooper and Whitmore 1990, Wolda 1990, Johnson 2000). In contrast, fruits are conspicuously displayed and relatively easy to census and are often consumed by many species (Moermond and Denslow 1985).

Using seven years of data across five habitats, we examined whether local abundances of Hermit Thrushes (*Catharus guttatus*) and Yellow-rumped Warblers (*Dendroica coronata*) are related to fruit abundance. We selected those species because they are common and highly frugivorous and differ markedly in social behavior (and, therefore, may respond differently to variation in fruit abundance). In particular, many Hermit Thrushes defend territories on their wintering grounds (Brown et al. 2000), whereas nonbreeding Yellow-rumped Warblers usually occur in flocks (Hunt and Flaspohler 1998). Hermit Thrushes and Yellow-rumped Warblers also differ in the types of fruits they consume: Hermit Thrushes take a large variety of fruits (Martin et al. 1951), especially those that are lipid-rich (e.g. *Cornus, Lindera, Viburnum*; Whitmer and Van Soest 1998); whereas Yellow-rumped Warblers specialize on *Myrica* spp. fruits (Place and Stiles 1992, Hunt and Flaspohler 1998). A second goal was to test, when possible, whether variation in local abundance of those migrants could also be explained by other general factors, such as habitat type and year.

METHODS

STUDY AREA

The study was conducted from 1996 through 2002 at the U.S. Department of Energy's Savannah River Site, a National Environmental Research Park located in Aiken and Barnwell counties, South Carolina, USA (33°18'N, 81°37'W). The site lies within the Sandhill and upper Coastal Plain physiographic provinces. Forested areas cover >80% of the site (Workman and McLeod 1990). The majority of that area consists of a patchy mosaic of managed longleaf pine (*Pinus palustris*) and loblolly pine (*P. taeda*) stands and, to a lesser extent, upland and bottomland hardwood stands (Odum 1991, White and Gaines 2000).

As part of a long-term study begun in 1994 to address spatiotemporal patterns of fleshy-fruit and hard-mast production, a total of 56 plots, 0.1 ha (50 × 20 m) each, were established in 56 stands of 5 structurally and floristically distinct habitat types. Plots are separated by at least 600 m and are assumed to be independent. Ten plots each were placed in bottomland hardwood, upland hardwood, and stands clearcut in 1993. Thirteen plots each were placed in longleaf pine and loblolly pine stands that were at least 40 years old. Bottomland hardwoods on the site have a nearly continuous canopy layer of trees (e.g. *Nyssa biflora, Magnolia virginiana, Quercus* spp.) and canopy-reaching vines (*Rhus radicans, Smilax* spp.),

a well-developed understory stratum (e.g. *Ilex* spp., *Persea borbonia*, *Vaccinium* spp.), and a pronounced ground layer of *Sphagnum*, woody stems, and herbs (e.g. sedges, *Mitchella repens*, *Arisaema triphyllum*). Upland hardwoods are characterized by a well-developed canopy (e.g. *Quercus* spp., *Carya* spp., *Pinus taeda*) and understory (e.g. *Cornus florida*, *Ilex opaca*, *Vaccinium arboreum*), and a relatively sparse ground layer. Although clearcuts initially consisted of short, second-growth vegetation (e.g. *Phytolacca americana*), by the end of our study they had a "canopy" of densely planted longleaf pine (maximum height = 6 m) and often included a well-developed understory (e.g. *M. cerifera*, *R. copallina*, *Prunus* spp.) and a ground layer (e.g. grasses, sedges, *Vaccinium stamineum*, *R. toxicodendron*, *Opuntia compressa*); hereafter, we will refer to those former clearcuts as "regeneration habitat." Longleaf and loblolly pine habitats have a sparse canopy layer of pines, a few understory shrubs and trees (e.g. *M. cerifera*, *Quercus* spp.), and a sparse ground layer that often includes low-lying vegetation (e.g. *V. stamineum*, *R. toxicodendron*) and vines (e.g. *Vitis rotundifolia*, *Smilax* spp.). Successional development undoubtedly typified regeneration habitats in our study; however, prescribed fires in pine habitats, treefall gaps, and other natural processes contributed some degree of vegetational change in all study plots.

FRUIT SAMPLING

Ripe fruits in each study plot were censused in January from 1996 to 2002. We define fruit functionally, as a seed-containing structure with a nutritious outer coating (i.e. pulp) consumed by vertebrates. That definition includes both fleshy fruits and fruits with a hard waxy coating (e.g. *M. cerifera*). Methods for estimating the number of fruit on a given plant depended on the species' life-form and the number of fruiting individuals of that species in a plot. For species with stems not obviously joined underground and with spatially distinguishable canopies, all "individuals" (regardless of potential underground connections) were tagged and the number of fruits on them estimated, except when >10 individuals were encountered in a given plot. In those cases, 10 individuals were chosen at random and the mean number of fruits on them was multiplied by the total number of fruiting conspecifics to estimate fruit abundance of that species in the plot. When possible, all fruits on a given plant were counted. Otherwise, fruits were counted from portions (e.g. branches) of the plant, and those counts were extrapolated to the entire plant. For species whose individuals were not clearly distinguishable (e.g. clones of *Vaccinium stamineum*, *R. toxicodendron*, *Mitchella repens*), the total number of fruits in a 4 × 50 m strip down the center of the plot were counted and multiplied by 5 to estimate total number of fruits of that species in the entire plot. Dry biomass of ripe fruit pulp was determined from off-plot samples of ripe fruits (for each species, 10 fruits from each of 10 fruiting individuals; $n = 100$ species^{-1}). Half of the samples remained intact (i.e. whole fruit samples), and the pulp was removed from the other half (i.e. seed samples). All samples were then placed in a drying oven (55°C) for seven days, and per-fruit ripe-fruit pulp dry mass (grams) was determined from the difference. Dry mass of fruit pulp in each study plot (grams 0.1 ha^{-1}) was used as a quantitative index of fruit biomass in the immediate vicinity within the same habitat. Species with ripe fruits in January at our study site are listed in Table 1.

BIRD SAMPLING

During each January from 1996 to 2002, birds were censused from the center of each study plot. Point

TABLE 1. Plant species producing ripe fleshy fruits in study plots in January and their primary habitats at the Savannah River Site. (Habitat abbreviations: BHW = bottomland hardwood, REG = regeneration, LLE = longleaf pine plantation, LOB = loblolly pine plantation, UHW = upland hardwood.)

Species	Habitat
Arisaema triphyllum	BHW
Calicarpa americana	UHW, BHW
Celtis occidentalis	LLE, UHW, LOB
Cornus florida	UHW, LOB
Euonymous americana	UHW
Ilex coriacea	BHW
I. decidua	BHW
I. glabra	BHW
I. opaca	BHW, UHW, LLE, LOB
I. verticillata	BHW
Lonicera japonica	UHW, REG, BHW, LOB
Mitchella repens	BHW, UHW
Myrica cerifera	REG, LOB, LLE
Nyssa biflora	BHW
Opuntia compressa	REG, LLE, LOB
Persea borbonia	BHW, UHW
Rhus copallina	REG, LLE, UHW, LOB
R. radicans	BHW, UHW
R. toxicodendron	LLE, LOB, REG, UHW
Smilax bona-nox	UHW, LLE
S. glauca	BHW, LOB, REG
S. laurifolia	BHW
S. pumila	UHW
S. rotundifolia	BHW
Solanum carolinense	REG
Vaccinium arboreum	UHW, LLE, REG, LOB, BHW
Viburnum rufidulum	UHW
Vitis rotundifolia	UHW

counts were conducted within 3 h of sunrise or sunset. In general, one plot in each habitat type was censused on a given day and the time of the census (morning vs. evening) was alternated from year to year for a given plot. Our report and analysis includes all Hermit Thrushes and Yellow-rumped Warblers seen or heard within ~60 m in each plot, a distance that allowed consistent detection in all habitats.

Because wintering Hermit Thrushes and Yellow-rumped Warblers have different social systems, slightly different census methodologies were used for each. Because Yellow-rumped Warblers were generally conspicuous, a single 5-min count proved adequate to estimate their abundance. Hermit Thrushes were often not detected in the same 5-min period, even though they were likely present. Thus, immediately after the initial 5-min period, censusing was continued for a second 5 min, during which a recording of an Eastern Screech Owl (*Otus asio*) song was played continuously (3 songs min^{-1}; 8-watt speaker, Lenox Cassette Recorder, model B-371, placed on the ground with sound projecting vertically). That song typically generated an immediate response from Hermit Thrushes, including those that had been detected during the initial 5 min. Because broadcast vocalizations can attract birds from beyond the bounds of the point count's radius (Sliwa and Sherry 1992), our report includes the number of Hermit Thrushes per point count, not per area.

Data Analysis

Fruit.—Repeated-measures ANOVA was used to test for spatial and temporal differences in January measures of total ripe-fruit pulp dry mass. Ripe-fruit pulp dry mass from each study plot was natural-log transformed (ln + 1) to improve normality of residuals. No assumptions were made concerning the potential correlation between pulp dry mass among years in individual sample plots (i.e. within-subject heterogeneity) and an unstructured variance–covariance matrix was imposed. Although statistical power was thereby diminished, the resulting tests were much more appropriate than they would have been if a constant correlation among repeated measures from sample plots (i.e. a compound symmetric variance–covariance matrix, often used in repeated-measures designs) had been assumed. A similar protocol was used to investigate *M. cerifera* pulp dry mass. *Post-hoc* tests were conducted using Tukey–Kramer pairwise comparisons, with *P*-values adjusted for all possible pairwise comparisons. Analyses of fruiting patterns were performed using the MIXED procedure in SAS (SAS Institute 1994), which uses a maximum-likelihood technique to estimate model parameters.

Hermit Thrushes.—We used repeated-measures ANCOVA to simultaneously test the effects of habitat, year, fruit-pulp dry mass, and all two-way interactions on Hermit Thrush abundance. The three-way interaction among habitat, year, and pulp dry mass was not included because the sample sizes that would have been used to infer differences among slopes relating Hermit Thrush abundance with pulp dry mass for each habitat–year combination were small. January measures of ripe-fruit pulp dry mass of all fruit-producing species were used because Hermit Thrush eat all or most of the winter-fruiting species at our site (Martin et al.1951, Skeate 1987, Jones and Donovan 1996). Hermit Thrush abundance was natural-log transformed (ln + 1) to improve normality of residuals. Ripe-fruit pulp dry mass was natural-log transformed (ln + 1) to linearize the relationship. Because of potential site fidelity of individual Hermit Thrushes among years, no assumptions were made about Hermit Thrush abundance among years in individual sample plots (i.e. within-subject heterogeneity), and thus an unstructured variance–covariance matrix was imposed. *Post-hoc* tests involved Tukey–Kramer pairwise comparisons with *P*-values adjusted for all possible pairwise comparisons. All Hermit Thrush analyses were performed using the MIXED procedure in SAS (SAS Institute 1994).

Yellow-rumped Warblers.—Unlike Hermit Thrushes, which eat many types of fruits in the winter, Yellow-rumped Warblers specialize on *Myrica* fruit (Martin et al. 1951, Hunt and Flaspohler 1998). Thus, our analyses of Yellow-rumped Warbler abundance were limited to *M. cerifera* pulp dry mass. Habitat type was confounded with *M. cerifera* pulp dry mass (i.e. some habitats had consistently more *M. cerifera* biomass than others; see below), so the ANCOVA model used for Hermit Thrushes was inappropriate for Yellow-rumped Warblers. Because the residuals from parametric linear regressions were non-normally distributed, Spearman rank correlations were used to correlate warbler abundance with *M. cerifera* pulp dry mass on three levels: (1) across all five habitats, (2) across only habitats that contained *M. cerifera* at least occasionally (regeneration, loblolly, and longleaf), and (3) within each habitat that contained *M. cerifera* at least occasionally. Warbler abundances from separate years within plots were assumed to be uncorrelated and were treated as independent samples. Analyses were performed using the statistical package SPSS (SPSS 2001).

Results

Fruit

January measures of total ripe-fruit pulp dry mass varied both spatially ($F = 8.49$, df = 4 and 51, $P < 0.0001$) and temporally ($F = 6.32$, df = 6 and 51, $P < 0.0001$), and the spatial patterns were not consistent through time ($F = 3.99$, df = 24 and 51, $P < 0.0001$; Fig. 1). Total pulp dry mass was often, but not always, highest in hardwood habitats (99.93 ± 29.00 [SE] and 34.72 ± 8.95 g

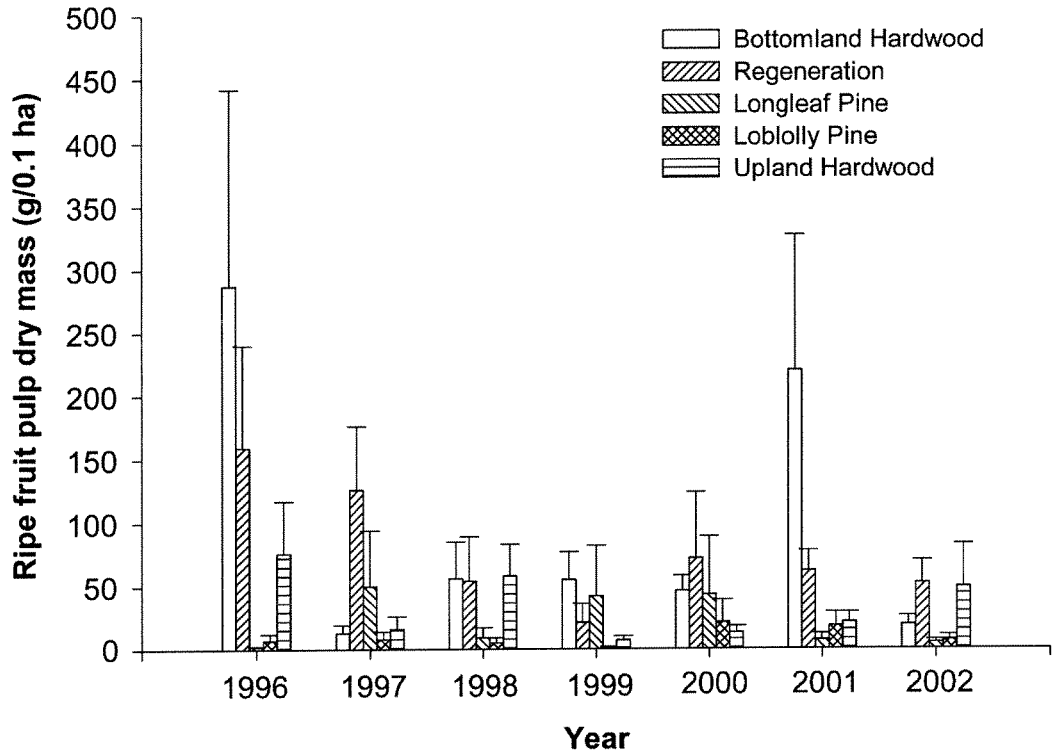

FIG. 1. Mean total ripe-fruit pulp dry mass (grams 0.1 ha^{-1} ± SE) from January fruit censuses in five habitat types and seven years (1996–2002) at the Savannah River Site, Aiken and Barnwell counties, South Carolina. Pulp dry mass estimates for each species were used to calculate total pulp dry mass in each sample plot. Sample sizes in each year were 10 plots apiece in bottomland hardwood, regeneration, and upland hardwood habitats, and 13 plots apiece in longleaf pine and loblolly pine habitats.

0.1 ha^{-1} for bottomland hardwood and upland hardwood habitats, respectively) and lowest in pine plantation habitats (22.95 ± 10.34 SE and 10.02 ± 3.45 g 0.1 ha^{-1} for longleaf and loblolly pine habitats, respectively). In addition, regeneration habitats contained more total pulp dry mass earlier (e.g. 1996, 159.13 ± 81.61 g 0.1 ha^{-1}; 1997, 126.26 ± 50.33 g 0.1 ha^{-1}) than later in the study (means <75 g 0.1 ha^{-1}).

Myrica cerifera fruits were not encountered in any of our bottomland hardwood or upland hardwood study plots. In the remaining habitats (regeneration, longleaf pine, and loblolly pine), *M. cerifera* pulp dry mass was marginally affected by habitat ($F = 3.08$, df = 2 and 33, $P = 0.06$; Fig. 2A) and significantly affected by time ($F = 2.98$, df = 6 and 33, $P = 0.02$; Fig. 2B). The highest amounts of *M. cerifera* pulp dry mass were found in regeneration habitats (7.23 ± 2.64 g 0.1 ha^{-1}) and more was present later in the study (e.g. 10.22 ± 5.17 g 0.1 ha^{-1} in 2001, and 6.2 ± 2.61 g 0.1 ha^{-1} in 2002) than earlier (means < 0.65 g 0.1 ha^{-1} from 1996 through 1998).

HERMIT THRUSHES

Variation in Hermit Thrush abundance was largely explained by ripe-fruit pulp dry mass ($F = 8.26$, df = 1 and 51, $P = 0.006$), habitat type ($F = 3.89$, df = 4 and 51, $P = 0.008$), and the interaction between habitat type and year ($F = 2.17$, df = 24 and 51, $P = 0.01$). More specifically, pulp dry mass was positively correlated with Hermit Thrush abundance (Fig. 3); its parameter estimate was positive (0.10 ± 0.05) and significantly different from zero ($t = 2.14$, df = 51, $P = 0.037$). Twice as many Hermit Thrushes were detected in bottomland hardwood stands compared to any other habitat; no differences in Hermit Thrush abundance were detected among all

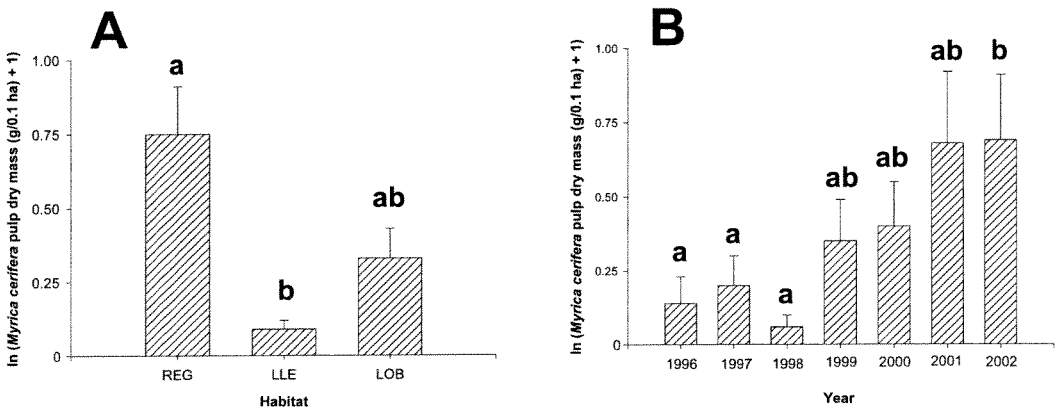

FIG. 2. Mean ripe-fruit pulp dry mass (natural-log transformed; grams 0.1 ha^{-1} ± SE) of *M. cerifera* from January fruit censuses across (A) habitats (REG = regeneration, $n = 70$; LLE = longleaf pine plantation, $n = 91$; LOB = loblolly pine plantation, $n = 91$) and (B) years ($n = 36$ plots per year). Yearly means were calculated using data solely from regeneration, longleaf pine, and loblolly pine habitats. Different letters correspond to significant ($P < 0.05$) differences in *M. cerifera* pulp dry mass from Tukey pairwise comparisons from a model examining the effects of habitat, year, and the habitat × year interaction on *M. cerifera* pulp dry mass (natural-log transformed).

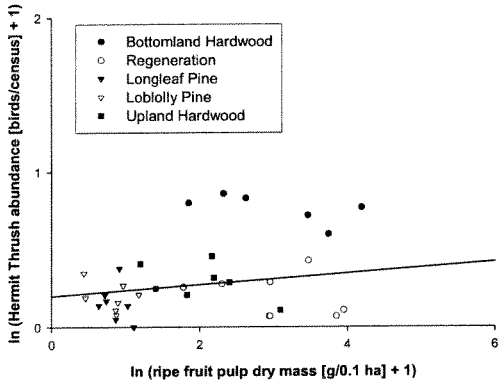

FIG. 3. Relationship (ln–ln) between Hermit Thrush abundance and ripe-fruit pulp dry mass. Data points are yearly means of Hermit Thrush counts and pulp dry mass in each habitat. Line depicts the predicted linear relationship between Hermit Thrush abundance and pulp dry mass from a simple linear-regression model incorporating all data from all bird and fruit censuses ($n = 392$ points), not just the displayed averages.

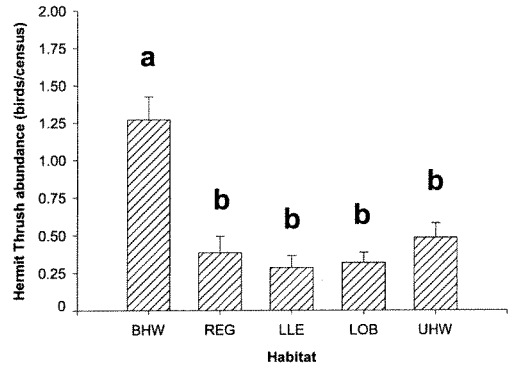

FIG. 4. Mean Hermit Thrush abundance (SE) from censuses in five habitat types (BHW = bottomland hardwood, $n = 70$; REG = regeneration, $n = 70$; LLE = longleaf pine plantation, $n = 91$; LOB = loblolly pine plantation, $n = 91$; UHW = upland hardwood, $n = 70$). Data are pooled across years. Different letters correspond to significant ($P < 0.05$) differences in Hermit Thrush abundance from Tukey pairwise comparisons from a model examining the effects of habitat, year, ripe-fruit pulp dry mass (natural-log transformed; grams 0.1 ha^{-1}), and all two-way interactions on Hermit Thrush abundance (natural-log transformed).

other habitats (*post-hoc* tests; Fig. 4). The significant habitat × year interaction is likely due to a unique pattern observed in 1999 (Fig. 5), when Hermit Thrush abundance in bottomland hardwood stands was lower than in all other years, and Hermit Thrush abundance in all other habitats was higher than in all other years, and higher than that observed in bottomland hardwood stands.

The lack of a significant interaction between pulp dry mass and year suggests that pulp dry mass had the same effect on Hermit Thrush abundance throughout the course of our study. Likewise, the lack of a significant interaction

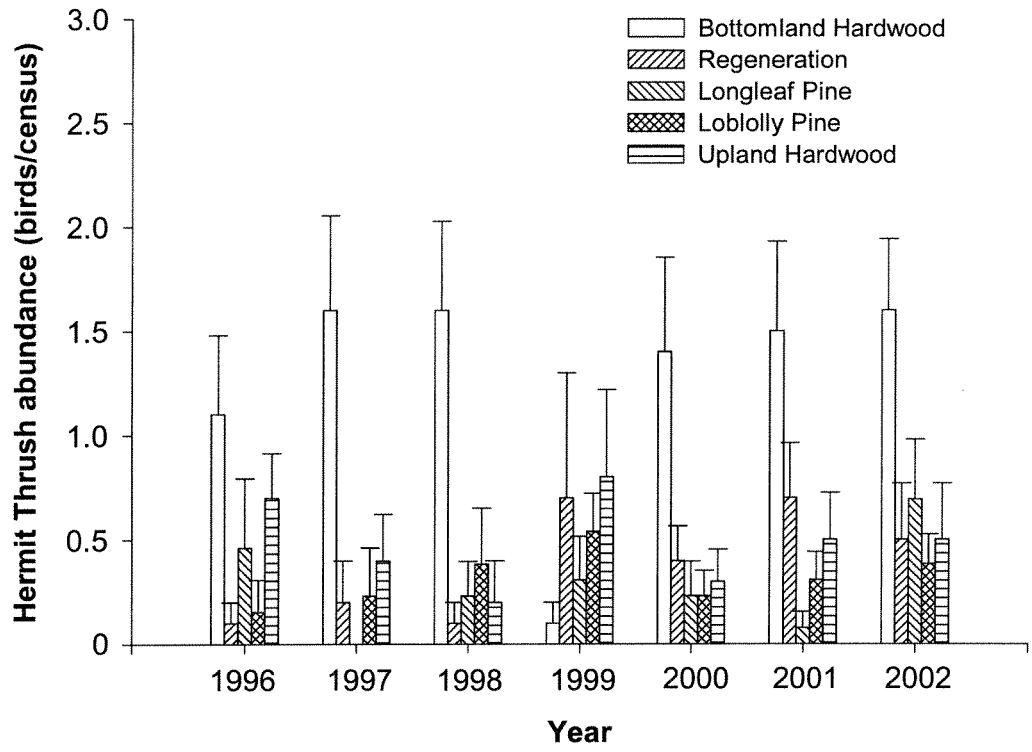

FIG. 5. Yearly means (SE) of Hermit Thrush abundance from censuses in five habitat types. Sample sizes in each year were 10 plots apiece in bottomland hardwood, regeneration, and upland hardwood habitats, and 13 plots apiece in longleaf pine and loblolly pine habitats.

between pulp dry mass and habitat suggests that although habitats differed in the number of Hermit Thrushes detected (i.e. an intercept adjustment), each habitat exhibited the same positive increase in Hermit Thrushes with an increase in pulp dry mass.

YELLOW-RUMPED WARBLERS

Combining data across all habitats, Yellow-rumped Warbler abundance was significantly and positively correlated with ripe *M. cerifera* fruit pulp dry mass (Spearman's $r_s = 0.21$, $P < 0.0001$). That same trend was present when we restricted the analysis to habitats that had *M. cerifera* fruit (i.e. regeneration, longleaf pine, and loblolly pine; Spearman's $r_s = 0.23$, $P = 0.0001$). Moreover, the relationship was detected separately among two of those three habitats (Fig. 6): regeneration plots (Spearman's $r_s = 0.25$, $P = 0.017$) and loblolly pine plots (Spearman's $r_s = 0.21$, $P = 0.021$). However, Yellow-rumped Warbler abundance was not correlated with *M. cerifera* pulp dry mass in longleaf pine habitats (Spearman's $r_s = 0.05$, $P = 0.33$). That result is not surprising, given the low average of *M. cerifera* pulp dry mass in longleaf pine habitats at our study site (see Fig. 6). Yellow-rumped Warblers were detected most often in regeneration habitats (36% of detections). Although *M. cerifera* did not occur in bottomland hardwood or upland hardwood plots, Yellow-rumped Warblers did. Twelve and 11% of Yellow-rumped Warbler detections were in bottomland hardwood and upland hardwood plots, respectively.

DISCUSSION

Our results support the hypothesis that local abundance of wintering frugivores is positively and consistently affected by fruit biomass. Although that hypothesis may seem intuitive, factors independent of food (e.g. predators, roosting sites, social interactions, microclimate)

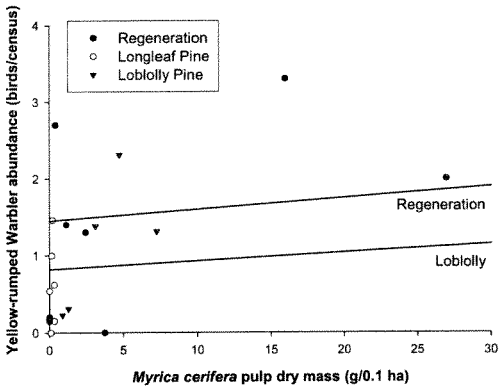

Fig. 6. Relationship between Yellow-rumped Warbler abundance and ripe *M. cerifera* fruit pulp dry mass. Data points are yearly means of Yellow-rumped Warbler counts and *M. cerifera* pulp dry mass in each habitat containing fruiting *M. cerifera*. Lines depict the positive correlations between Yellow-rumped Warbler abundance and *M. cerifera* pulp dry mass and are the result of separate simple linear-regression models incorporating data from all bird and fruit censuses in regeneration and loblolly pine habitats (n = 70 and 91 points, respectively).

may override effects of food in determining habitat use (reviewed in Johnson and Sherry 2001). Despite those potentially confounding factors, the few studies that have attempted to link the abundance of nonbreeding migrants with food availability have generally found a positive association between the two (Hutto 1985, Martin and Karr 1986, Greenberg 1992, Lefebrve et al. 1994, Johnson and Sherry 2001).

Hermit Thrushes

Our results are in general agreement with previous studies that have documented habitat-specific differences in winter migrant abundance (Blake and Loiselle 1992a, Wunderle and Waide 1993, Petit et al. 1995, Wallace et al. 1996, Gram and Faaborg 1997, Murphy et al. 1998, Sykes and Clench 1998, Rappole et al. 2000, Latta and Faaborg 2001, Smith et al. 2001). Some of the differences in local distributions of Hermit Thrushes at our site were clearly linked to fruit biomass. However, much of the variation in Hermit Thrush abundance among habitats was independent of fruit biomass, which suggests that other factors are also important.

Hermit Thrushes were most abundant in bottomland hardwood, a habitat that appears important to wintering Hermit Thrushes at our site. For equal amounts of pulp dry mass, more Hermit Thrushes were found in bottomland hardwood habitats, and the rate at which Hermit Thrush abundance increased with available pulp dry mass was the same in all habitats. Therefore, other attributes of bottomland hardwood habitats (e.g. habitat structure, microclimate, arthropod availability) may also account for higher Hermit Thrush densities. The continued rapid disappearance of bottomland hardwood habitat in the southeastern United States (Rheinhardt and Rheinhardt 2000) may potentially lead to Hermit Thrushes exhibiting different habitat distributions and, perhaps, even population declines. We acknowledge, however, that wintering Hermit Thrushes may be even more dependent on habitat types not included in our study, such as 10- to 40-year-old pine plantations (Brown et al. 2002).

The behavioral ecology of Hermit Thrushes on their wintering grounds has been relatively well studied. Brown et al. (2000) documented a hierarchical social system in Louisiana, consisting primarily of territorial individuals, but also containing "floaters" (subordinate, nonterritorial birds). Floaters also occur among wintering populations of Wood Thrushes (*Hylocichla mustelina*) and several warbler species (Rappole et al. 1989, Winker et al. 1990, Marra et al. 1993, Stutchbury 1994, Latta and Faaborg 2001). Because we did not attempt to distinguish between territorial and nonterritorial individuals, we cannot infer effects of habitat type and ripe-fruit pulp dry mass on territoriality (e.g. food resource–territory size relationships; see Dill 1978, Hixon 1980). In addition, Hermit Thrushes arrive and establish territories in late October at our study site (C. Kwit pers. obs.), a time when pulp dry mass is determined by a slightly different set of fruit-producing species than in January. Nonetheless, total fruit pulp dry mass in October predicted Hermit Thrush abundance in January in an essentially identical way as January ripe pulp dry mass (C. Kwit unpubl. data). That result provides further evidence for the importance of fruit to wintering Hermit Thrushes.

Yellow-rumped Warblers

In general, Yellow-rumped Warbler abundance was correlated with *M. cerifera* pulp

dry mass. However, definitive support for the hypothesis that local distributions of Yellow-rumped Warblers are determined solely by ripe *M. cerifera* fruit pulp dry mass is weak. Because no *M. cerifera* fruits were found in some habitats and other habitats consistently had high amounts of *M. cerifera* fruit, we were unable to conclusively distinguish effects of habitat type from fruit availability. That does not mean, however, that Yellow-rumped Warblers do not respond to spatial and temporal variation in *M. cerifera* fruit abundance. Indeed, when we held habitat type constant by analyzing among plot variation in habitats where *M. cerifera* was most abundant, we found positive correlations between Yellow-rumped Warbler abundance and *M. cerifera* fruit pulp dry mass.

Resources, Habitat Associations, and the Importance of Fruit to Migratory Birds

Determining whether food resources influence the local distribution patterns of winter migrants is inherently difficult because resource abundance is often confounded with other variables. Our study highlights the importance of long-term studies and replicated designs in tackling this issue. In particular, the spatial and temporal variation in winter fruit production at our site allowed us to examine the general relationship between Hermit Thrush and fruit abundance while controlling for other factors potentially associated with habitat. That approach would not have been possible with only one year of data or a small number of study plots. Even so, we remained unable to explain much of the variation. Further inferences about mechanisms underlying the winter distribution of migrants will require additional sampling from wider geographic scales.

Understanding the mechanisms that determine the local distribution of migratory birds is important from a habitat-management perspective. Although habitat associations exhibited by birds are sometimes suggestive of abundant resources, other factors in the habitat (e.g. vegetation structure, social interactions) may be equally or more important (Van Horne 1983, Marra and Holmes 2001). Thus, development of management plans requires more information than typically gathered in studies such as ours. In our case, for example, it remains uncertain whether Yellow-rumped Warblers use regeneration habitats because of plentiful *M. cerifera* fruit and what aspects of bottomland hardwood habitats Hermit Thrushes use in addition to fruit.

Our results are consistent with other evidence suggesting that fruits are an important dietary component of migratory passerines. Many migrants are known to consume fruit during migration (Willson 1986, Parrish 1997) and on their wintering grounds (Greenberg 1981, Skeate 1987, Blake and Loiselle 1992b, Levey and Stiles 1992, McCarty et al. 2002). Also, frugivorous migrants seem to prefer areas of high fruit abundance during migration (Blake and Hoppes 1986, Hoppes 1987, Suthers et al. 2000). We emphasize, however, that all such evidence for the importance of fruits to migrants is correlative. For effective habitat management, it is necessary to establish causation via experimental manipulation of fruit abundance. Few experimental manipulations of fruit abundance have been attempted. In the Amazon estuary, removal of *Euterpe oleracea* (Palmae) fruits in 1.8-ha plots resulted in a reduction of fruit-eating species diversity (Moegenburg and Levey 2003). At an island stopover site in Rhode Island, manipulation of *M. pensylvanica* fruit abundance in 30 × 30 m plots during fall migration affected bird abundance (Parrish 2000). Finally, at our site, Yellow-rumped Warbler density increased immediately in 1-ha plots after removal of nets that had prevented *M. cerifera* fruit consumption (K. Borgmann unpubl. data). Those results, combined with results of correlative studies and natural or seminatural alterations in food abundance (Rey 1995, Johnson and Sherry 2001), provide strong evidence for the importance of food in determining local distributions of migratory birds during the nonbreeding season.

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