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

C   K   ,[1,3] D   J. L   ,[1] C   H. G   ,[2] S   F. P   ,[1,4] J   P. M C   ,[1,5] S   S   ,[1,6] R   L. M   [1,6]

[1]*D*&*a*   &*r Z*   , *B* 118525, *U* &   *r F   da, Ga* & *F   da 32611-8525, USA; a d*
[2]*U.S. D*&*a* &   *A c* &*F d S* c*c, S* &*R* &*c S a* *r, B* *C*&*E* &*a F* *r, A*&*N* *Ca* *a 28806, USA*

A   .—We conducted winter censuses of two short-distance migrants, Hermit Thrushes (*Ca a   a* s) and Yellow-rumped Warblers (*D*&*d* *rca c* *r* *a a*), over seven years in five di erent habitats to determine whether their local abundances could be predicted by fruit pulp biomass. Sampled habitats were stands of upland and bo omland hardwood, loblolly pine (*P   a*&*da*), longleaf pine (*P. a   *), and young (<10 years) longleaf pine. Hermit Thrush abundance, which was highest in bo omland hardwood habitats, was positively related to total dry mass of fruit pulp. Those results are consistent with the hypothesis that resource availability a ects the local distribution of migrant passerines on their wintering grounds. Our results also indicate that bo omland 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 *M   ca c*&*r*&*a*, a major source of winter food for that species. However, because *M. c*&*r*&*a* 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 di erences in ripe-fruit biomass was modest, indicating that other factors are also important. *R*&*c*&*d 12 J*&*r 2002, acc*&*d 28 A   2003.*

R   .—Durante un período de siete años realizamos censos invernales, en cinco ambientes diferentes, de dos migrantes de corta distancia, *Ca a   a* y *D*&*d* *rca c* *r* *a a*, 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 *P   a*&*da*, de *a ab*&*de* *r*&*a a*&*r*&*a a b*&*r bu*&*d*&*d d*&*d*&*E* a*&*U* *du*a dancia de *D. c* *r* *a a* se correlacionó con la masa seca de pulpa mad *c*&*r*&*a*, la cual representa una fuente importante de alimento duran especie. Sin embargo, debido a que la masa seca de pulpa de *M. c*&*r*&* del efecto del tipo de hábitat, no pudimos distinguir entre la importar y del hábitat para *D. c* *r* *a a*. Nuestros resultados enfatizan la impor las aves invernantes. Sin embargo, el porcentaje total de variación en de aves explicado por las diferencias en la biomasa de frutos maduros que otros factores son también importantes.

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K   .

a well-developed understory stratum (e.g. *I   * spp.,
P   a bo bo a, *Vacc*   spp.), and a pronounced

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 (*O   a ⚹*) song was played continuously (3 songs min⁻¹; 8-watt speaker, Lenox Casseøe 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.

D   A

F   .—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. c⚹ ⚹a* pulp dry mass. *P⚹ - ⚹c* tests were conducted using Tukey–Kramer pairwise comparisons, with *P*-values adjusted for all possible pairwise comparisons. Analyses of fruiting paøerns were performed using the MIXED procedure in SAS (SAS Institute 1994), which uses a maximum-likelihood technique to estimate model parameters.

H⚹   T   ⚹.—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. *P⚹ - ⚹c* 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).

Y⚹⚹ -   ⚹d Wa b ⚹.—Unlike Hermit Thrushes, which eat many types of fruits in the winter, Yellow-rumped Warblers specialize on *M   ca* fruit (Martin et al. 1951, Hunt and Flaspohler 1998). Thus, our analyses of Yellow-rumped Warbler abundance were limited to *M. c⚹ ⚹a* pulp dry mass. Habitat type was confounded M. cerifera

0.1 ha^{-1} for bo omland 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}).

M   ca c   a fruits were not encountered in any of our bo omland hardwood or upland hardwood study plots. In the remaining habitats (regeneration, longleaf pine, and loblolly pine), *M. c   a* pulp dry mass was marginally a ected by habitat (*F* = 3.08, df = 2 and 33, *P* = 0.06; Fig. 2A) and significantly a ected by time (*F* = 2.98, df = 6 and 33, *P* = 0.02; Fig. 2B). The highest amounts of *M. c   a* 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). .

H   T

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 di erent from zero (= 2.14, df = 51, *P* = 0.037). Twice as many Hermit Thrushes were detected in bo w46iation was
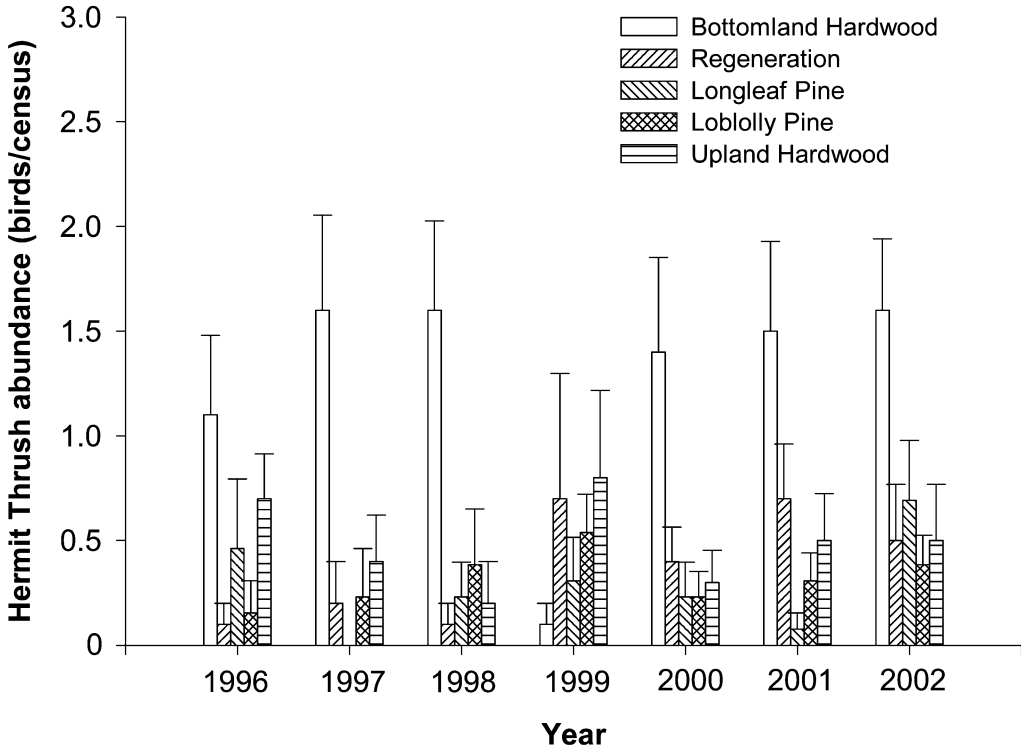
other habitats (✎ - ✎ tests; Fig. 4). The sig-
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F . 5. Yearly means (SE) of Hermit Thrush abundance from censuses in five habitat types. Sample sizes in each year were 10 plots apiece in bottomland hardwood, regeneration, and upland hardwood habitats, and 13 plots apiece in longleaf pine and loblolly pine habitats.

between pulp dry mass and habitat suggests that although habitats di ered 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.

Y   -   W

Combining data across all habitats, Yellow-rumped Warbler abundance was significantly and positively correlated with ripe *M. c& &a* fruit pulp dry mass (Spearman's $_s$ = 0.21, $P <$ 0.0001). That same trend was present when we restricted the analysis to habitats that had *M. c& &a* fruit (i.e. regeneration, longleaf pine, and loblolly pine; Spearman's $_s$ = 0.23, P = 0.0001). Moreover, the relationship was detected separately among two of those three habitats (Fig. 6): regeneration plots (Spearman's $_s$ = 0.25, P = 0.017) and loblolly pine plots (Spearman's $_s$ = 0.21, P = 0.021). However, Yellow-rumped

Warbler abundance was not correlated with *M. c& &a* pulp dry mass in longleaf pine habitats (Spearman's $_s$ = 0.05, P = 0.33). That result is not surprising, given the low average of *M. c& &a* pulp dry mass in longleaf pine habitats at our study site (see Fig. 6). Yellow-rumped Warblers were detected most o en in regeneration habitats (36% of detections). Although *M. c& &a* did not occur in bo omland hardwood or upland hardwood plots, Yellow-rumped Warblers did. Twelve and 11% of Yellow-rumped Warbler detections were in bo omland hardwood and upland hardwood plots, respectively.

D

Our results support the hypothesis that local abundance of wintering frugivores is positively and consistently a ected by fruit biomass. Although that hypothesis may seem intuitive, factors independent of food (e.g. predators, roosting sites, social interactions, microclimate)
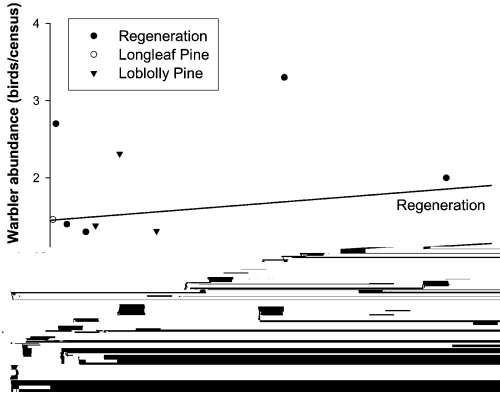
Fig. 6. Relationship between Yellow-rumped Warbler abundance and ripe *M. c& &a* fruit pulp dry mass. Data points are yearly means of Yellow-rumped Warbler counts and *M. c& &a* pulp dry mass in each habitat containing fruiting *M. c& &a*. Lines depict the posit1 Tf26 Twp7.1prdwiM-cerifeW

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

H   T

Our results are in general agreement with previous studies that have documented habitat-specific di erences 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, La a and Faaborg 2001, Smith et al. 2001). Some of the di erences 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

bo omland 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 bo om-land hardwood habitats, and the rate at which Hermit Thrush abundance increased with available pulp dry mass was the same in all habitats. Therefore, other a ributes of bo om-land hardwood habitats (e.g. habitat structure, microclimate, arthropod availability) may also account for higher Hermit Thrush densities. The continued rapid disappearance of bo omland hardwood habitat in the southeastern United States (Rheinhardt and Rheinhardt 2000) may potentially lead to Hermit Thrushes exhibiting di erent 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, consist-ing primarily of territorial individuals, but also containing "floaters" (subordinate, nonterritorial birds). Floaters also occur among wintering pop-ulations of Wood Thrushes (*H   ae c a   & a*) and several warbler species (Rappole et al. 1989, Winker et al. 1990, Marra et al. 1993, Stutchbury 1994, La a and Faaborg 2001). Because we did not a empt to distinguish between territorial and nonterritorial individuals, we cannot infer e ects of habitat type and ripe-fruit pulp dry mass on territoriality (e.g. food resource–territory size relationships; see Dill 1978, Hixon 1980). In ad-dition, Hermit Thrushes arrive and establish ter-ritories in late October at our study site (C. Kwit pers. obs.), a time when pulp dry mass is deter-mined by a slightly di erent set of fruit-produc-ing 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.

Y   -   W

In general, Yellow-rumped Warbler abun-dance was correlated with *M. c& &a* pulp

dry mass. However, definitive support for the hypothesis that local distributions of Yellow-rumped Warblers are determined solely by ripe *M. c a* fruit pulp dry mass is weak. Because no *M. c a* fruits were found in some habitats and other habitats consistently had high amounts of *M. c a* fruit, we were unable to conclusively distinguish e ects 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. c a* fruit abundance. Indeed, when we held habitat type constant by analyzing among plot variation in habitats where *M. c a* was most abundant, we found positive correlations between Yellow-rumped Warbler abundance and *M. c a* fruit pulp dry mass.

R , H A ,
I F M B

Determining whether food resources influence the local distribution pa erns of winter migrants is inherently di cult because resource abundance is o en 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. c a* fruit and what aspects of bo omland 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 e ective habitat management, it is necessary to establish causation via experimental manipulation of fruit abundance. Few experimental manipulations of fruit abundance have been a empted. In the Amazon estuary, removal of *E a ac a* (Palmae) fruits in 1.8-e. For eT* uch

comments and helpful insights, and D. Brown and P. Stou er made valuable comments that greatly enhanced the manuscript.

L   C

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