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WINTERING YELLOW-RUMPED WARBLERS (*DENDROICA CORONATA*) TRACK MANIPULATED ABUNDANCE OF *MYRICA CERIFERA* FRUITS

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ABSTRACT —Food availability during winter may determine habitat use and limit populations of overwintering birds, yet its importance is difficult to judge because few studies have experimentally tested the response of nonbreeding birds to changes in resource abundance We experimentally examined the link between fruit availability and habitat use by manipulating winter abundance of *Myrica cerifera* L. (Myricaceae) fruits in managed longleaf (*Pinus palustris*) and loblolly (*P. taeda*) pine stands in South Carolina *Myrica cerifera* is a common understory shrub in the southeastern United States and provides lipid-rich fruit in late winter (February and March), when insects and other fruits are scarce. On treatment plots, we covered fruiting *M. cerifera* shrubs with netting in early winter to prevent birds from eating their fruits. In late February, when *M. cerifera* fruit crops were largely depleted elsewhere on our study site, we uncovered the shrubs and documented the response of the bird community to those patches of high fruit availability. Relative to control plots, total bird abundance (excluding the most common species, Yellow-rumped Warbler [*Dendroica coronata*]) and species richness did not change after net removal Yellow-rumped Warblers, however, became significantly more abundant on treatment plots after net removal, which suggests that they track *M cerifera* fruit abundance We suggest that *M cerifera* plays a role in determining the local distribution of wintering Yellow-rumped Warblers at our study site. To put these results into a management context, we also examined the effect of prescribed fire frequencies on *M cerifera* fruit production Across pine stands with different fire regimes, *M. cerifera* fruit abundance increased with the number of years since burning It takes 4–6 years for individuals to recover sufficiently from a burn to produce large quantities of fruit Thus, shorter intervals between burns will reduce winter fruit availability Taken together, these results suggest that within those pine plantations, the local winter distribution of at least one common migratory bird is closely tied to fruit abundance, which in turn is tied to the frequency of prescribed fires. *Received 22 October 2002, accepted 15 September 2003.*

RESUMEN —La disponibilidad de alimentos durante el invierno puede determinar el uso del hábitat y limitar las poblaciones de aves que permanecen en sus áreas de nidificación durante el invierno. Sin embargo, es difícil determinar su importancia debido a que pocos estudios han evaluado experimentalmente la respuesta de aves no reproductivas a cambios en la abundancia de recursos. Nosotros examinamos experimentalmente el vínculo entre la disponibilidad de frutos y el uso del hábitat manipulando la abundancia invernal de frutos de *Myrica cerifera* L. (Myricaceae) en plantaciones bajo manejo de *Pinus palustris* y *P. taeda* en Carolina del Sur. *Myrica cerifera* es un arbusto común del sotobosque en el sudeste de Estados Unidos que provee frutos ricos en lípidos hacia fines del invierno (febrero y marzo), cuando los insectos y otros frutos son escasos A principios del invierno, en las parcelas experimentales, cubrimos con redes los arbustos de *M. cerifera* que presentaron frutos para impedir que las aves los comieran. A fines de febrero, cuando se agotaron casi por completo los frutos de *M. cerifera* en cualquier otro lugar de nuestro sitio de estudio, descubrimos los arbustos y documentamos la respuesta de la comunidad de aves a los parches con alta disponibilidad de frutos. Con relación a las parcelas de control, la abundancia de aves (excluyendo a la especie más común, *Dendroica coronata*) y la riqueza de especies no cambiaron luego de sacar las redes *Dendroica coronata*, sin embargo, se tornó

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significativamente más abundante en las parcelas experimentales luego de sacar las redes, lo que sugiere que rastrea la abundancia de frutos de *M. cerifera*. Sugerimos que *M. cerifera* juega un rol en determinar la distribución invernal local de *Dendroica coronata* en nuestro sitio de estudio Para poner estos resultados en un contexto de manejo, también examinamos el efecto de la frecuencia de quemas planeadas sobre la producción de frutos de *M cerifera* A lo largo de las plantaciones de pino con diferentes regímenes de fuego, la abundancia de frutos de *M. cerifera* incrementó con el número de años desde la quema. Los individuos requieren de 4 a 6 años para recuperarse luego de la quema y producir grandes cantidades de frutos. De este modo, intervalos más cortos entre quemas reducirán la disponibilidad invernal de frutos. Analizados de modo integral, estos resultados sugieren que dentro de estas plantaciones de pino, la distribución local invernal de al menos un ave migratoria común está íntimamente ligada a la abundancia de frutos, la cual a su vez esta ligada a la frecuencia de quemas planeadas

WINTER ECOLOGY OF migratory birds has attracted much attention because nonbreeding season conditions are thought to limit, at least partially, populations of migratory birds (Newton 1988, Robbins et al. 1989, Rappole and McDonald 1994, Sherry and Holmes 1996). At issue are the factors that best predict a bird's ability to survive the winter and reproduce the following spring. Several recent studies strongly support the hypothesis that variation in food abundance determines habitat use and survival of overwintering birds (Lefebvre et al. 1994, Wunderle 1995, Strong and Sherry 2000, Johnson and Sherry 2001, Marra and Holmes 2001). Alternative hypotheses suggest predation (Rappole et al. 1989), social dominance (Greenberg et al. 1993, Marra 2000), and interspecific competition (Greenberg 1986) as mechanisms underlying winter habitat use.

We examined the role of fruit resources in determining the local distribution of overwintering frugivorous birds. A focus on fruits is justified because frugivory is wide spread among nonbreeding, passerine migrants (Willson 1986, Skeate 1987, Blake and Loiselle 1992, Levey and Stiles 1992, Parrish 2000), and because fruit-eating birds appear sensitive to changes in fruit abundance (Rey 1995, Parrish 2000, Moegenburg and Levey 2002). Although temperate fleshy fruit resources are generally thought to be most important during migration (Thompson and Willson 1979, Blake and Hoppes 1986, Willson 1986, Parrish 1997), peak removal of ripe fruit occurs during the winter in the southeastern United States, which suggests its importance to wintering birds (Skeate 1987, McCarty et al. 2002). Fruit may be particularly important to short-distance migrants because they face colder temperatures and fewer daylight hours for foraging than their long-distance counterparts. Moreover, winter fruits provide an easily accessible, energy rich food source when invertebrate resources are scarce.

We focused our research on fruit of a single species, *Myrica cerifera*. We selected that species because its fruits are abundant in the fall and winter throughout the coastal plain of southeastern North America and are eaten by many bird species (Martin et al. 1951). In addition, *M. cerifera* fruits have been proposed as a "keystone" resource for overwintering birds (McClanahan and Wolfe 1993; see also Place and Stiles 1992, Parrish 1997).

Fruits are ideal for experimental studies because they can be easily seen, counted, and manipulated (Levey 1988, Blake et al. 1990), allowing us to move beyond the traditional approach of correlating bird numbers with habitat characteristics (e.g. Moore et al 1990, Petit et al. 1995, Jones 2001, but see Moore and Yong 1991). We experimentally blocked bird access to fruiting *M. cerifera* shrubs to test for a link between fruit availability and distributions of winter birds in managed stands of loblolly (*Pinus taeda*) and longleaf pine (*P. palustris*). To our knowledge, this study is the first to experimentally test the widely accepted link between resource abundance and the local distribution of overwintering migrants

If fruit resources play an important role in determining distribution patterns of local overwintering birds, then activities that reduce fruit abundance may negatively affect frugivorous birds. Therefore, to place our study in a management framework, we examined how prescribed burns influence the abundance of *M. cerifera* fruits. Managed pine stands throughout portions of the southeastern United States commonly contain populations of *M cerifera* and are burned on a regular basis, typically every

3–5 years. Because *M. cerifera* is often considered a nuisance species by foresters interested in pine production, prescribed burning is often used to control or eliminate it (Haywood et al. 2000). We compared *M. cerifera* fruit abundance among plots burned 0–2 years, 3–4 years, and 5–6 years prior to our study. For this component of our study, the goal was to determine what minimum fire return interval allows *M. cerifera* plants to recover sufficiently to produce fruit.

METHODS

Study site description.—This study was conducted at the Savannah River National Environmental Research Park in South Carolina (33°20′N, 81°40′W), situated between the Piedmont and Coastal Plain. Approximately 72% of the forested landscape at the site is dominated by loblolly and longleaf pine plantations (Workman and McLeod 1990), in which *M. cerifera* is a common understory species Detailed descriptions of the site, its history, and management are provided by Odum (1991) and White and Gaines (2000).

Fruit manipulation experiment.—Six pairs of 1 ha plots (hereafter "fruit plots") were established in mature longleaf and loblolly pine stands with similar burn histories; fruit plots were burned 4–6 years prior to our study. Stands were chosen that appeared to have approximately equal densities of *M. cerifera* shrubs in the understory and that were floristically and structurally similar. Plots within pairs were 75–200 m apart, with the exception of one pair in which plots were 500 m apart Pairs of plots were >500 m apart. Within pairs, treatment and control plots were randomly assigned. On treatment plots, a total of 40% (10–15 individuals per treatment plot) of female *M. cerifera* shrubs were covered with BirdBlock (Easy Gardener, Waco, Texas) netting in early January 2000, which blocked access to most fruits Netting was removed on 23 February 2000, when the majority of *M. cerifera* fruit on the landscape had been depleted elsewhere (McCarty et al 2002) Thus, we were able to increase the amount of fruit available on treatment plots relative to controls.

In each fruit plot, all fruiting *M. cerifera* shrubs were tagged and fruit abundance was estimated on each throughout the experiment. Fruit abundance was visually indexed on the following scale 0 = no fruits, 1 = 1–500 fruits, 2 = 500–2,500 fruits, 3 = 2,500–5,000 fruits, 4 = 5,000–8,000 fruits, 5 = 8,000–11,000 fruits, and 6 = >11,000 fruits Throughout the study, the same person estimated fruit indices To determine accuracy, 20 shrubs were scored and then individual fruits were counted on the same shrubs. We accurately scored fruit abundance on 80% of these shrubs. The total number of *M cerifera* fruit on each plot was calculated by multiplying the number of shrubs bearing fruit in each of the abundance categories by the mean number of fruit in those categories (see Levey 1988) Fruit abundance was estimated weekly before net removal and daily after removal.

Bird surveys were conducted within 3 h after sunrise along two parallel 100 m transects in each fruit plot. Those transects were 50 m apart and 25 m from the plots' edges We walked slowly and sequentially along both transects, stopping at two points (25 and 75 m) for 4 min each Most surveys were between 20 and 22 min (range 17–26 min); we did not limit surveys to a fixed amount of time because we felt it was more important to take the time needed to accurately record number, species, and location of birds than to arrive at the end of a transect at a set time All species seen or heard within the plot were recorded This nonstandard census technique was chosen because most birds were not territorial and because a secondary goal was to collect data on foraging; two points per plot were too restrictive to accomplish the latter We emphasize that our fruit plots were too small to accurately estimate densities of winter birds, which move over a much larger area on a daily basis Thus, we do not attempt to calculate densities, restricting our analyses to counts Because canopy height was similar and tree and understory characteristics were statistically identical (see below), detection distances were consistent among plots. A disadvantage of our technique is that the long time spent in each plot increased the risk of double-counting individuals. When we were unsure whether a bird had been already counted, we did not count it We believe that double counting was rare because our plots were relatively small and birds within them were easily detected and followed Any error resulting from double counting was consistent between treatments and controls

In addition to species identity and number of individuals, each bird's vertical position (shrub or canopy) was recorded Because the stands had virtually no mid-story, the division between canopy (>5 m height) and shrub layer (<5 m height) was distinct We distinguished between shrub and canopy detections because we believed vertical position within a plot might reflect birds' use of *M cerifera* fruit during the survey (i e birds must be in the shrub layer to feed on *M cerifera* fruit) In addition, we noted all observations of birds feeding on *M. cerifera* fruit within fruit plots. Treatment and control plots within the pair were always surveyed on the same morning but the order in which they were surveyed was alternated Surveys began on 12 January 2000 and ended on 7 March 2000 or when the difference in fruit abundance between control and treatment plots in a particular pair was reduced to ~1,000 fruits, whichever occurred first. All plots were surveyed twice per week from 12 January until 1 February 2000. Because fruit removal was slower than anticipated during the first weeks of the study, we switched to weekly surveys from 1 February

to 23 February 2000 After net removal on 23 February 2000, plots were surveyed daily for the first two days, and every two days thereafter because we anticipated a rapid response to newly available fruit

To describe understory vegetation, one 0 5 ha subplot was established in the center of each fruit plot Within all subplots, understory shrub volume and the diameter (measured at 1 4 m above the ground) of all trees ≥10 cm diameter were measured. Understory shrub volume was measured to 3 m with a density board (Noon 1981). Four density board readings were recorded at the four corners of each subplot (n = 16 per plot). Percentage shrub volume was calculated as the number of 10 × 10 cm squares on the density board that were at least 50% obscured, divided by the total number of squares

Fire frequency.—We compared *M cerifera* fruit abundance on plots (hereafter "fire plots") burned <2 years (n = 6 sites), 3–4 years (n = 6), and 5–6 years (n = 6) prior to our study. Loblolly and longleaf pine stands were selected within those fire-frequency categories that had similar canopy tree basal areas and overall stand characteristics to those of our fruit plots In each, one 20 × 100 m transect was randomly placed and fruit abundance was estimated using the index described previously To compare stand similarity among fire plots and between the fire plots and fruit plots, only tree diameters (measured at 1.4 m above the ground) for all trees ≥10 cm diameter within the 20 x 100 m transect were measured

Data analysis.—We used ANOVAs to compare habitat variables between treatments and controls for fruit plots, and to compare habitat variables between fruit and fire plots. When an overall F value was significant, univariate F-tests were used to examine each habitat variable individually. For the fruit manipulation experiment habitat analyses, mean tree diameter, basal areas, and percentage shrub volume were used for each plot For the fire study, only mean tree diameter and basal areas were compared among time intervals because shrub volume was not measured on those plots When comparing habitat variables between fire and fruit plots, mean tree diameter and basal areas were used. Because plot size differed between fire and fruit plots (2,000 and 2,500 m^2, respectively), average values per 1000 m^2 were used

The program COMDYN (Hines et al. 1999) was used to generate estimators of avian species richness on treatment and control fruit plots before and after net removal. Program COMDYN accommodates heterogeneity in detection probabilities among species and can be used to compare communities at different times or in different areas (Nichols et al. 1998a, b). With the exception of treatment plots after net removal, the heterogeneity model of COMDYN adequately fit all sampling periods (P > 0.05) Despite that lack of fit in one case, the estimators derived generally perform much better than *ad hoc* estimators (Nichols et al. 1998a). We report a jackknife estimate of species richness, derived using a bootstrap approach. Bootstrap variance estimates were calculated using a goodness-of-fit test Species richness was compared between treatments and controls prior to and after removing the netting separately because the number of censuses differed before and after removal.

The effect of "adding" fruit in the treatment plots was examined using a multivariate repeated-measures ANOVA. A significant treatment × time interaction indicates that birds responded differently to treatment and control plots over time. When the treatment × time interaction was significant, univariate F-tests were used to examine the relationship between treatments and controls before and after net removal. Separate repeated-measures ANOVAs were performed for the number of bird detections in the canopy, in shrubs, and for the number of observations of birds feeding on *M. cerifera* fruits. Avian species richness and abundance was examined only in the shrub layer because preliminary analyses showed no patterns for species richness or abundance in the canopy Also treatment effects were examined individually for all species commonly detected (>20 detections; n = 7; Table 1). Only the more abundant species were included to eliminate species with small sample sizes and low statistical power to detect a treatment response (see below). For all repeated-measures ANOVAs, the mean number of detections per plot before net removal was compared to that after net removal. We had two reasons for using mean values. First, plots were visited an unequal numbers of times after net removal because fruit was rapidly depleted on some plots. That resulted in an unbalanced sampling protocol and, consequently, empty cells in the data matrix Those cells violate a requirement of the multivariate, repeated-measures model we used (Abacus Concepts 1989). Second, even if we had visited all plots an equal number of times after net removal, the enormous variation in detections among visits to any given plot would have generated a data matrix with many zeros, thereby violating the assumption of normality The disadvantage of using mean values was a reduction in statistical power, because of loss of degrees of freedom. Thus, for all repeated-measures ANOVAs, the power of the interaction effect was calculated (equation 11.27 in Zar 1984) The relationship between the amount of fruit on control plots and the number of bird detections was examined using the curve-fitting program in SPSS (SPSS 1996).

Because the total amount of fruit on the fire plots did not approach a normal distribution even when transformed, a Kruskal-Wallis one-way analysis of variance was used to compare the total amount of fruit among the three fire-frequency categories. For all other analyses, data not meeting the assumption of normality (Kolmogorov-Smirnov one-sample test) or homogeneity of group variances (Bartlett's F-test,

TABLE 1. The ANOVA results and mean counts ± SE for the common species detected in the canopy, in the shrub layer, and detected foraging on *M cerifera* fruits 1 ha^{-1} before and after net removal.

	Canopy						Shrub			
	Before net removal		After net removal				Before net removal		After net removal	
Species	Control (n = 6)	Treatment (n = 6)	Control (n = 6)	Treatment (n = 6)	Treatment F (P)	Time × treatment F (P)	Control (n = 6)	Treatment (n = 6)	Control (n = 6)	Treatment (n = 6)
Tufted Titmouse (*Baeolophus bicolor*)	0.43 ± 0.10	0.23 ± 0 06	0.42 ± 0.10	0.48 ± 0 10	0.65 (0 44)	1.93 (0.20)	0.13 ± 0 09	0.15 ± 0 09	0.18 ± 0.11	0 12 ± 0.12
Carolina Chickadee (*Poecile carolinensis*)	0.35 ± 0.08	0.22 ± 0.05	0.33 ± 0 08	0.46 ± 0 17	0.00 (0 97)	1 55 (0 24)	0.08 ± 0.03	0.12 ± 0 05	0 05 ± 0.03	0 10 ± 0.08
Carolina Wren (*Thryothorus ludovicianus*)	0 00	0.00	0.00	0.00	NA[a]	NA	0.40 ± 0 10	0.27 ± 0.07	0.38 ± 0.11	0 38 ± 0.18
Ruby-crowned Kinglet (*Regulus calendula*)	0.10 ± 0.06	0.18 ± 0 03	0.13 ± 0.03	0.05 ± 0 03	0 00 (1 00)	6.58 (0.03)	1.18 ± 0 05	1.02 ± 0.25	0.29 ± 0.14	0.36 ± 0.19
Yellow-rumped Warbler (*Dendroica coronata*)	3 45 ± 0.79	4.08 ± 1.16	3.00 ± 1 06	2.87 ± 0.46	0 07 (0 80)	0 22 (0.65)	3.45 ± 0.79	4.52 ± 1 69	1 88 ± 0 59	4.60 ± 0.97
Northern Cardinal (*Cardinalis cardinalis*)	0.15 ± 0.07	0.08 ± 0.07	0.05 ± 0.03	0.05 ± 0.03	0 31 (0 59)	0.49 (0.50)	0.33 ± 0.06	0.25 ± 0 18	0 57 ± 0 10	0.22 ± 0 11
Eastern Towhee (*Pipilo erythrophthalmus*)	0.00	0.00	0.00	0 00	NA	NA	0 48 ± 0.23	0.23 ± 0.11	0 50 ± 0.36	0 10 ± 0.08

	Shrub (*continued*)		Forage					
			Before net removal		After net removal			
	Treatment F (P)	Time × treatment F (P)	Control (n = 6)	Treatment (n = 6)	Control (n = 6)	Treatment (n = 6)	Treatment F (P)	Time × treatment F (P)
Tufted Titmouse	0 60 (0.81)	0 18 (0.68)	0.00	0 00	0.00	0 03 ± 0.03	NA	NA
Carolina Chickadee	0 74 (0.41)	0.02 (0.89)	0.00	0.02 ± 0.02	0 00	0 00	0.74 (0.41)	0 02 (0.89)
Carolina Wren	0.21(0.66)	0 47 (0.51)	0.00	0.00	0.00	0 00	NA	NA
Ruby-crowned Kinglet	0 08 (0.79)	0 50 (0.50)	0.15 ± 0.07	0.15 ± 0 07	0.00	0.03 ± 0.03	0.12 (0.74)	0 10 (0 76)
Yellow-rumped Warbler	0.09 (0.77)	3.51 (0.09)	2.20 ± 0.67	2.32 ± 0 89	0 33 ± 0.15	3.50 ± 0.67	6.40 (0.03)	5 31 (0 04)
Northern Cardinal	2.21(0 17)	2.71 (0.13)	0 02 ± 0.02	0 00	0.00	0 02 ± 0.02	0.0 (1 00)	2.00 (0 19)
Eastern Towhee	1.18 (0.30)	0.56 (0.47)	0.00	0.00	0 00	0.00	NA	NA

[a] No detections

TABLE 2. Habitat variables (mean ± SE) measured on control and treatment fruit plots. All values are per 1,000 m²

Variable	Control (n = 6)	Treatment (n = 6)	F	P [a]
Conifer tree diameter (cm)	14 36 ± 0.62	13.81 ± 0 63	0 39	0.55
Deciduous tree diameter (cm)	3 57 ± 1 14	3 7 ± 1 27	0 00	0.96
Conifer tree, basal area (m²)	16 53 ± 1 95	15.74 ± 1 98	0 09	0.78
Deciduous tree, basal area (m²)	0.13 ± 0.06	0.51 ± 0.38	0.69	0.43
Shrub volume (%)				
0–1 m	12 ± 2.0	9 0 ± 2 0	1.47	0.25
1–2 m	16.0 ± 4.0	11.0 ± 3.0	1.11	0.32
2–3 m	15 0 ± 4 0	8.0 ± 2.0	2.51	0.14

[a] Bonferroni adjusted α = 0 007

residual scatter plots) were log (x + 1) transformed (Zar 1984). When analyzing bird count data, an alpha level of 0.10 was used because of small sample sizes and associated low power and because minimizing Type II error is important when making management decisions (Peterman 1990, Smith 1995, Schmiegelow et al. 1997) When analyzing habitat data, an alpha level of 0 05 was used because of larger samples sizes, Bonferroni corrections were used to adjust the alpha level for multiple comparisons.

RESULTS

Fruit manipulation experiment.—Treatment and control fruit plots showed no differences in canopy tree basal areas, mean tree diameter, or in percentage understory shrub volume (F = 0.59, df = 7 and 4, P = 0.74; Table 2). Thus, we attribute any difference between treatments and controls to our experimental manipulation of fruit abundance. Prior to net removal, abundance of available *M. cerifera* fruit decreased similarly on control and treatment plots, from (mean ± SE) 165,729 ± 35,719 fruits ha⁻¹ on 12 January 2000 to 6,854 ± 2,152 fruits ha⁻¹ on 23 February 2000 (Fig. 1). Immediately after net removal, available fruit on treatment plots increased by 51%, whereas available fruit remained virtually unchanged on control plots (Fig. 1). The "added" fruit on treatment plots disappeared rapidly; 89% was consumed within two weeks (Fig. 1).

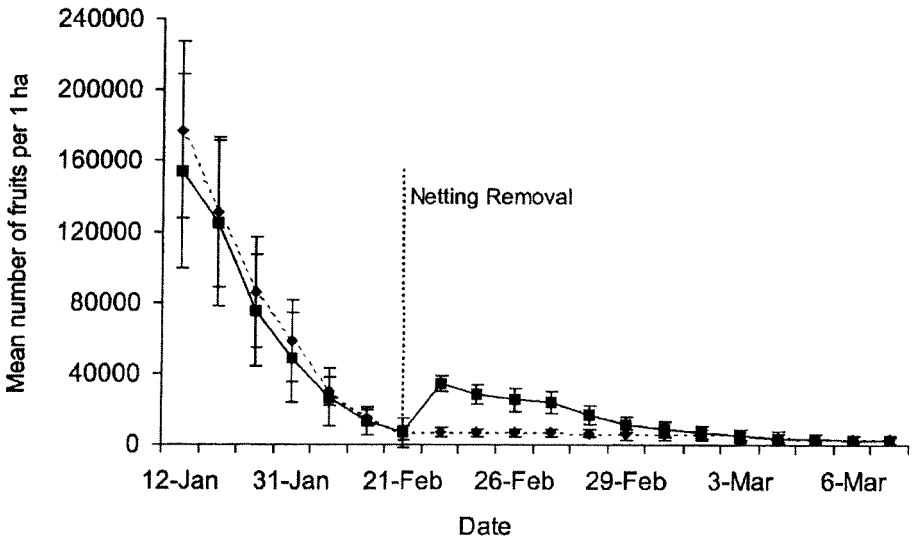

FIG. 1. Mean (± SE) number of available (uncovered) *M cerifera* fruits per hectare on treatment and control plots before and after net removal Dashed line represents control plots and solid line represents treatment plots.

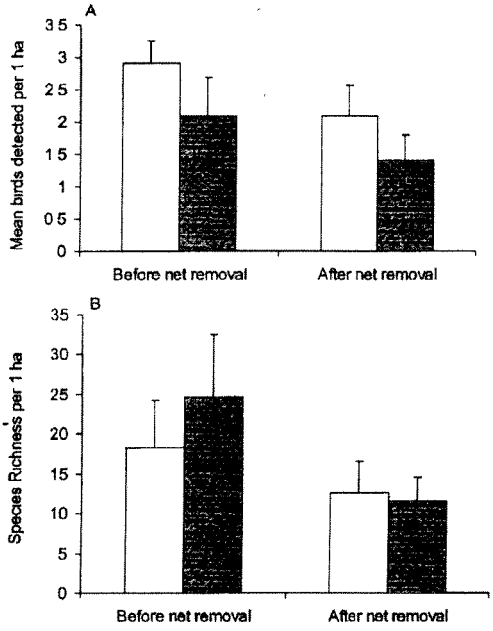

FIG. 2. (A) Mean (± SE) bird detections per hectare (excluding Yellow-rumped Warblers) in the shrub layer pre- and postnet removal, (B) species richness (± SE) in shrub layer before and after net removal.

Community responses.—We first report total bird counts excluding Yellow-rumped Warblers (*Dendroica coronata*) because they numerically dominated the community (48% of total canopy detections, 67% of total shrub detections, and 94% of total foraging detections on *M. cerifera* fruit). The mean number of birds detected in the shrub layer did not demonstrate a time × treatment interaction ($F = 0.03$, df = 1 and 10, $P = 0.86$; Fig. 2A), indicating the lack of a numerical response to the sudden increase in fruit availability when the netting was removed. Likewise, species richness in the shrub layer did not differ between treatments and controls before or after net removal (Fig. 2B); the 95% confidence intervals bounding species richness values for preremoval control (15.00–38.40) overlapped with those for preremoval treatment (12.00–36.88) and those for postremoval control (10.00–24.73) overlapped with those for postremoval treatment (9.00–21.84).

Species responses.—Of the species detected at least 20 times (Table 1), only Yellow-rumped Warblers demonstrated a time × treatment interaction for detections in shrubs ($F = 3.51$, df = 1 and 10, $P = 0.09$), and for the number of foraging observations on *M. cerifera* fruits ($F = 5.31$, df = 1 and 10, $P = 0.04$). However, the time × treatment interaction for detections in the canopy for Yellow-rumped Warblers was not significant ($F = 0.22$, df = 1 and 10, $P = 0.65$; Fig. 3A). Examining those patterns in detail, more Yellow-rumped Warblers were detected in the shrub layer (Fig. 3B) and foraging on *M. cerifera* fruits (Fig. 3C) in treatment plots than in control plots after, but

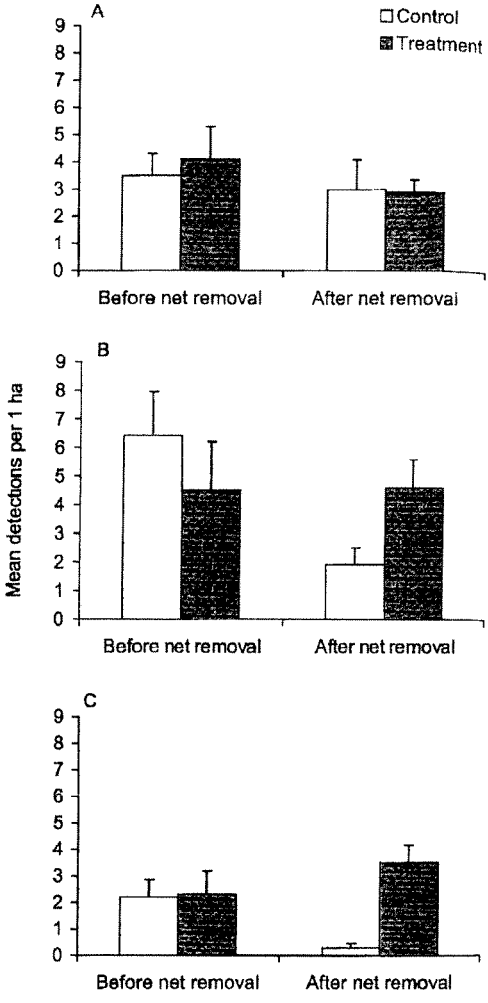

FIG 3 Mean (± SE) detections per hectare of Yellow-rumped Warblers (A) in the canopy, (B) in the shrubs, and (C) observed foraging, on control and treatment plots before and after removal of netting on treatment plots.

not before, net removal (shrub layer, after net removal: univariate $F = 5.69$, df = 1 and 10, $P = 0.04$; shrub layer, before net removal: univariate $F = 0.69$, df = 1 and 10, $P = 0.43$; foraging, after net removal: univariate $F = 21.23$, df = 1 and 10, $P = 0.001$, foraging, before net removal: univariate $F = 0.01$, df = 1 and 10, $P = 0.91$; Fig. 3). Those results demonstrate a short-term numeric response by Yellow-rumped Warblers to increases in *M. cerifera* fruit abundance. Moreover, Yellow-rumped Warblers responded rapidly; newly exposed fruit was completely consumed on some plots within two days of net removal.

We next examine the relationship on control plots between naturally occurring fruit abundance and our three metrics of Yellow-rumped Warbler counts. Because those relationships were obviously nonlinear (Fig. 4), we fitted curves of several types We report here the best fits (see Table 3 for complete analysis). The number of Yellow-rumped Warblers in the canopy was inversely related to *M. cerifera* fruit abundance, although the relationship was marginally significant (Table 3). That pattern suggests that Yellow-rumped Warblers moved into the canopy in areas where *M. cerifera* fruits were scarce and into the understory where fruits were abundant. Indeed, Yellow-rumped Warbler abundance in the shrub layer showed a strong positive (quadratic) relationship with fruit abundance. In addition, the number of Yellow-rumped Warblers detected foraging on *M. cerifera* fruits was positively related to fruit abundance (Table 3).

Fire and fruit abundance.—The multivariate ANOVA comparing conifer and deciduous tree diameter and basal areas between fire and fruit plots was significant ($F = 5.15$, df = 4 and 24, $P = 0.004$). Univariate tests indicated that only conifer basal areas differed between fruit and fire plots (compare mean values in Tables 2 and 4; univariate ANOVA: $F = 14.28$, df = 1 and 27, $P = 0.001$).

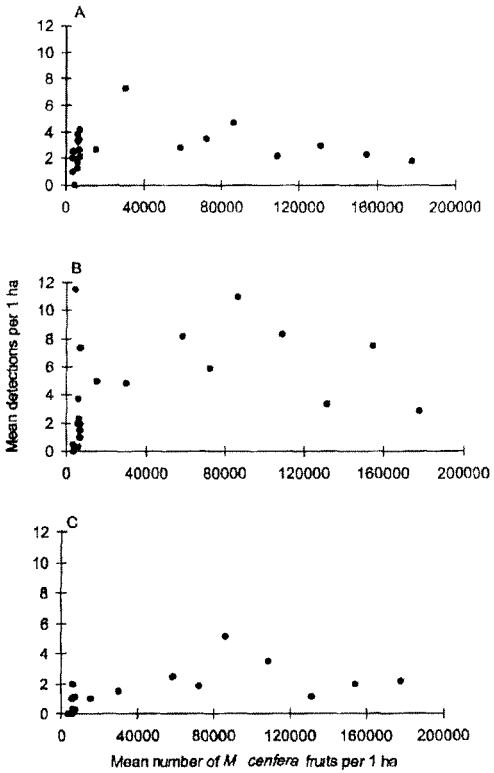

FIG 4. Relationships between mean (± SE) number of available *M cerifera* fruits per hectare and mean detections of Yellow-rumped Warblers per hectare (A) in the canopy, (B) in the shrubs, and (C) observed foraging on control plots.

Among fire plots, conifer and deciduous tree diameter and basal areas differed significantly (Table 4; multivariate ANOVA: $F = 3.49$, df = 8 and 22, $P = 0.01$). Univariate F-tests indicate that only deciduous basal areas differed significantly among fire treatments (Table 4). Because deciduous trees are a minor component (<8%) of the

TABLE 3. The SPSS curve-fit estimations for number of Yellow-rumped Warblers detected in the canopy, in the shrub layer, and foraging on *M. cerifera* fruits versus the amount of *M. cerifera* fruit on control plots

	Canopy				Shrub				Foraging			
Curve	r^2	df	F	P	r^2	df	F	P	r^2	df	F	P
Linear	0.00	19	0.02	0 90	0 13	19	2.80	0.11	0.37	19	11.32	0 00
Log	0.06	19	1.26	0.28	0 25	19	6.37	0.02	0.56	19	23 67	0.00
Inverse	0.17	19	3.95	0.06	0.29	19	7 65	0 01	0.54	19	21 92	0.00
Quadratic	0.19	18	2.05	0.16	0.36	18	5.12	0.02	0.64	18	15.56	0.00
Cubic	0.31	17	2.55	0.09	0.37	17	3.29	0.05	0 65	17	10.73	0.00

TABLE 4. Habitat variables (mean ± SE) measured in plots burned 0–2, 3–4, and 5–6 years prior to this study All values are per 1,000 m².

	Years since burning				
Variable	0–2 years (n = 6)	3–4 years (n = 6)	5–6 years (n = 5)[a]	F	P[b]
Conifer tree diameter (cm)	12.93 ± 0.67	15 39 ± 0.90	16.67 ± 1 62	3.5	0 06
Deciduous tree diameter (cm)	5.45 ± 1 80	8.63 ± 0.41	6 66 ± 0.43	2.1	0.17
Conifer tree, basal area (m²)	23.58 ± 2.28	20.64 ± 0.75	22.48 ± 1.57	0 54	0 59
Deciduous tree, basal area (m²)	0.10 ± 0.05	1 19 ± 0.50	0.39 ± 0.12	8.1	0 005

[a] One plot omitted from analysis because of logging
[b] Bonferroni adjusted α = 0 0125

total basal areas for each plot, their overall effect on forest structure is minimal.

The mean amount of *M. cerifera* fruit increased dramatically with the number of years since burning (Kruskal-Wallis test statistic = 7.16, df = 2, P = 0.028; Fig. 5). Fruit abundance on plots burned 0–2 and 3–4 years prior to this study was very low compared to plots burned 5–6 years prior (0–2 years: 6,333 ± 4,697 per 2,000 m²; 3–4 years: 8,375 ± 4,700 per 2,000 m²; 5–6 years: 39,308 ± 9,577 per 2,000 m²; Fig. 5).

DISCUSSION

Fruit manipulation experiment.—Our study provides the first experimental evidence that food resources play a major role in determining local spatial and temporal distribution of a wintering migratory bird, the Yellow-rumped Warbler. After increasing the amount of available fruit in treatment plots, the number of warblers detected in the shrub layer and observed foraging on *M. cerifera* fruit quickly increased relative to controls. In addition, Yellow-rumped Warblers discovered and completely consumed the newly available fruit in as little as two days on some plots. Further evidence that Yellow-rumped Warblers key in on fruit abundance is provided by their apparent response to natural variation in the abundance of *M. cerifera* fruit On control plots, warbler abundance and foraging activity were highest when fruit abundance was high and declined fairly precipitously once fruit abundance fell below ~90,000 fruits ha⁻¹ (Fig. 4B, C)

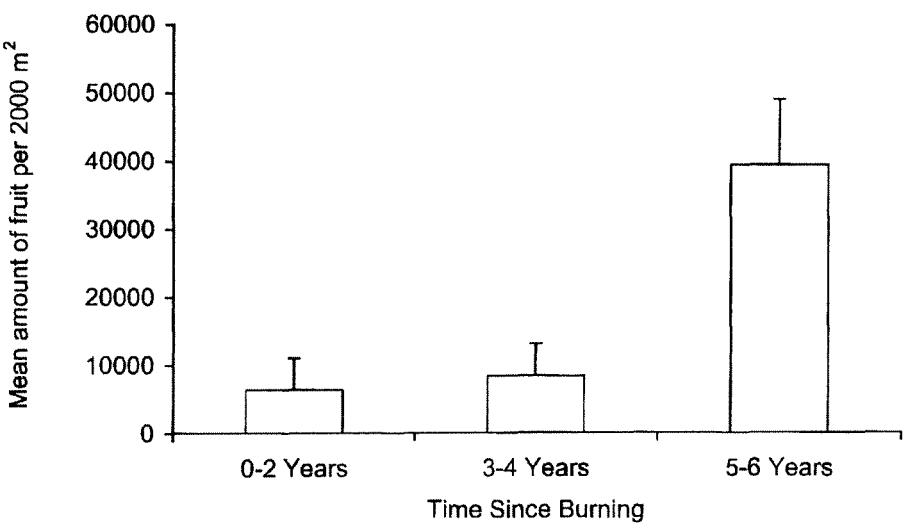

FIG 5. Mean (± SE) number of *M cerifera* fruits per 2,000 m² on plots burned 0–2 years, 3–4 years, and 5–6 years prior to our study.

These results confirm the well-known association between Yellow-rumped Warblers and *Myrica* spp (Wilz and Gimpa 1978, Terrill and Ohmart 1984, Place and Stiles 1992, Hunt and Flaspohler 1998, Parrish 2000). Our goal was not to reconfirm that association but rather to experimentally test its mechanistic basis. In particular, our experimental approach allows us to rule out alternative hypotheses (e.g. that warblers are attracted to the dense and presumably protective foliage of *M. cerifera*). Taken together, the numerical and behavioral responses of wintering Yellow-rumped Warblers to manipulations of *M. cerifera* fruit abundance suggest that they can track local fruit abundance across space and time.

How generally is the distribution of fruit-eating birds affected by variation in fruit abundance? We first summarize evidence that fruit abundance affects the distribution of fruit-eating birds at different scales and in different places. We then focus on our study site and discuss the potential importance of *M. cerifera* to species other than Yellow-rumped Warblers.

Numerous studies across a wide range of scales have concluded that fruit-eating birds are most abundant when and where fruit is most abundant (Martin 1985, Blake and Hoppes 1986, Martin and Karr 1986, Levey 1988, Blake and Loiselle 1991, Loiselle and Blake 1991, Stouffer and Bierregaard 1993, Kinnaird et al. 1996, Suthers et al. 2000, Malizia 2001). Two explanations for that pattern seem most plausible. Either (1) birds respond to variation in fruit abundance (Levey and Stiles 1992) or (2) plants respond to variation in bird abundance (i.e. fruiting is timed to correspond with peak periods of seed disperser abundance, Fuentes 1992, Noma and Yumoto 1997). Experimental evidence from four communities strongly supports the hypothesis that birds respond to variation in fruit abundance. In addition to our study, Parrish (2000) found that Yellow-rumped Warblers responded to small-scale manipulations (30 × 30 m plots) of *Myrica* spp. fruit abundance during migration. Likewise, Moegenburg and Levey (2002) reduced fruit abundance in the Brazilian Amazon on 1.8 ha plots and found reductions in visits and in species diversity of fruit-eating birds. Finally, Rey (1995) showed that nonbreeding birds in Spain responded to olive harvests in an agricultural setting. Although not truly experimental (harvest treatments were not randomly assigned), his evidence for resource tracking by birds is convincing because of concordant patterns of bird and fruit abundance across a large spatial scale.

We suspect that the importance of *M. cerifera* fruits to wintering birds extends beyond what we detected for Yellow-rumped Warblers. During the course of our study, we observed seven other species consuming *M. cerifera* fruits: Downy Woodpecker (*Picoides pubescens*), Red-bellied Woodpecker (*Melanerpes carolinus*), Carolina Chickadee, Northern Cardinal, Ruby-crowned Kinglet, Tufted Titmouse, and Pine Warbler (*D. pinus*). Furthermore, fecal samples from wintering Gray Catbirds (*Dumetella carolinensis*), White-eyed Vireos (*Vireo griseus*), and Ruby-crowned Kinglets at our study site frequently were composed of >90% *M. cerifera* fruit (S. F. Pearson unpubl. data). We emphasize that all those species were much less common than Yellow-rumped Warblers at our study site (Table 1). Hence, low sample sizes and reduced statistical power (power of treatment × time interactions for canopy, shrub, and foraging abundance were ≤0.68 for all species other than the Yellow-rumped Warbler) likely contributed to those species' apparent lack of response to our experimental manipulation of *M. cerifera* fruit abundance. Although those species did not respond to changes in fruit abundance, *M. cerifera* may still be an important resource for them.

Another limitation of our ability to detect responses of other species to changes in *M. cerifera* fruit abundance was the difficulty of detecting rare, short bouts of reliance on the fruit. McCarty et al. (2002) argue that *M. cerifera* at our site is an especially important resource because it produces more fruit biomass than any other species in pine forests, because 98% of the fruit crop is removed during late winter when few other resources are available, and because its fruits are high in saturated fatty acids (Place and Stiles 1992). The importance of *M. cerifera* likely increases in years when other species that produce winter fruit fail to do so (e.g. *Ilex opaca*, *Rhus copallina*) and on days of severe weather In the latter case, birds that normally forage for seeds or insects may find it difficult to do so at a time when their energetic demands would be particularly high. Foraging for fruit is relatively easy because fruits are typically not cryptic, not physically protected, and not difficult to capture (Moermond and Denslow 1985). Even a

few meals of fruit may provide enough calories for a small and otherwise nonfrugivorous bird to survive until conditions improve. Conditions were relatively mild at our site in the period immediately following net removal (daily low temperatures. 6–12°C, high temperatures: 20–25°C), which may have contributed to the lack of response by other species.

Although difficult to document, fruit may be important to many nonbreeding omnivorous birds even when weather is mild. Parrish (1997) noted that *Myrica* fruits were one of the three most commonly consumed species during fall migration in Rhode Island. Perhaps more telling, omnivorous species (>33% fruit in diet) gained significantly more mass at the stopover site than did more insectivorous species (<33% fruit in diet). Parallel experiments with captive birds confirmed that mixed diets of fruits and insects allowed greater gains in body mass than did *ad libitum* diets of solely fruits or insects (Parrish 2000; see also Bairlein 1990).

The lack of a match between fruit abundance and bird abundance for species other than the Yellow-rumped Warbler in our study area may be due to predation (Rappole et al. 1989); social dominance (Greenberg et al. 1993, Marra 2000); interspecific competition (Greenberg 1986); nonterritoriality; availability of alternative resources (other fruits, insects, or seeds); or a combination of these factors. Additionally, some species lack the ability to digest the saturated fatty acids of *M. cerifera* fruits (Place and Stiles 1992), presumably limiting their reliance on those fruits. If such mechanisms are responsible for the distributional patterns of wintering birds, then the relationship between bird and food abundance would be weak or nonexistent.

In summary, we found that *M cerifera* fruits influence the local spatial and temporal distribution of wintering Yellow-rumped Warblers Several lines of evidence suggest winter fruit may be important to less frugivorous species as well. A challenge for future studies is to monitor body condition and survival of individual birds under varying regimes of fruit abundance and weather.

Fire frequency and M. cerifera.—*Myrica cerifera* is often considered a nuisance species in southeastern portions of the United States (Kalmbacher et al. 1993, Haywood et al. 2000). Controlled burns, "mid-story removal" (cutting of mid-story plants), and herbicide applications are common management practices used to control understory shrub populations (Waldrop et al. 1992, Kalmbacher et al. 1993, Glitzenstein et al. 1995, Tucker et al. 1998, Shelton and Cain 2000). Prescribed burns in the southeast typically occur every three to five years but can occur yearly at our site. Johnson and Landers (1978) documented that burns in southeastern pine plantations result in a large and immediate reduction in fruit biomass of *M. cerifera* and other understory species. We found that *M. cerifera* takes two years to reestablish after a fire and takes four to six years to produce substantial amounts of fruit. Thus, an interval of less than four years between prescribed burns will result in reduced availability of an important species of winter fruit in eastern North America (Place and Stiles 1992, McClanahan and Wolfe 1993, Parish 1997, McCarty et al. 2002). Because there were differences in stand structure between the fire and fruit plots, data on fruit production in the former are not necessarily applicable to the latter. However, differences were relatively small.

Our recommendation of longer term fire intervals to promote fruit production in portions of the coastal plain must be balanced with the need for shorter fire intervals to maintain biological diversity in pine savannas (Clewell 1989, Peet and Allard 1993). Frequent fire and mid-story removal benefit a number of rare species (e.g. Red-cockaded Woodpecker [*Picoides borealis*], Provencher et al. 2002; Bachman's Sparrow [*Aimophila aestivalis*], Dunning 1993; and numerous rare vascular plants, Hardin and White 1989) Consequently, the need for frequent fire intervals where site conditions are appropriate for pine savannas should outweigh our recommendation for longer fire intervals to generate fruit for wintering birds.

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