Hermit Thrush is the First Observed Dispersal Agent for Pondberry (*Lindera melissifolia*)

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ABSTRACT

We investigated dispersal opportunities for the endangered pondberry, *Lindera melissifolia* (Lauraceae). In 199 hours of observation at 5 fruiting colonies in the Delta National Forest, Sharkey County, Mississippi, we recorded 82 bird species in the vicinity of a colony. Of these, 12 were observed on pondberry plants, and two consumed ripe pondberry fruits. Of these, the northern cardinal, *Cardinalis cardinalis* (Cardinalidae), was a seed predator. The other, hermit thrush, *Catharus guttatus* (Turdidae), was a dispersal agent for the plants. Numbers of fruits declined rapidly after hermit thrushes arrived in October and no fruits remained by January. Winter behavior of hermit thrushes constrains their dispersal of seeds to short distances. Without establishment of additional colonies, pondberry dispersal by birds to unoccupied patches of suitable forest is unlikely.

INTRODUCTION

Pondberry, *Lindera melissifolia* (Walt.) Blume (Lauraceae), is a federally-endangered plant (United States Fish and Wildlife Service 1986). This dioecious, cloning shrub is widely distributed in the southeastern United States from Missouri to North Carolina. Within that wide range, pondberry is restricted to a very few localities (United States Fish and Wildlife Service 1986, 1993; Devall et al. 2001). In some localities the populations occur in a small number of forest patches, but colonies are numerous within individual patches (Morgan 1983). In the Mississippi Alluvial Valley the species is very numerous in the Delta National Forest, Sharkey County, Mississippi, but missing from smaller patches of apparently suitable habitat in Yazoo National Wildlife Refuge and Leroy Percy State Park, both in Washington County, within 20 km.

Pondberry colonies may contain hundreds of individual stems. The fruits of the species are showy red and persist from early autumn to mid-winter. Fruits and/or pedicels may remain on the stems into the following spring after production (Devall et al. 2001). The 6 to 10-mm-long drupes contain a single large seed, greater than 4 mm in diameter (Radford et al. 1968, cf. United States Department of Agriculture, Forest Service 1974). No disperser has been identified for pondberry.

Dispersal of the seeds passively by water or actively by animals is possible. Many plant species that grow near lakes and ponds but not in running water are widely scattered, often over a very large area (Ridley 1930). The local distribution of pondberry fits this description. Although intact pondberry fruits sink after being in water for a short time, seeds with the pulp removed float for a day and sometimes longer (Devall and Schiff, pers. obs.). Flood control projects have radically altered Mississippi Alluvial Valley hydrological cycles (Sharitz 1992, Stanturf et al. 2000) providing little opportunity for water to play a role in pondberry dispersal today.

The combination of showy fruits and persistence on the stems suggests that animals, particularly birds, may be dispersal agents of the plant. No chemical analysis has yet been

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conducted on pondberry fruits. However, unlike many bird-dispersed fruits, those of the congeneric spicebush, *Lindera benzoin* (L.) Blume, are high in fat content (Stiles and White 1986) and low in sugar content (Witmer 1996). Neither pondberry nor spicebush is listed by Miller and Miller (1999) in the standard treatment of wildlife plants in the Southeast.

Birds have been observed to disperse the fruits of 22 species of tropical Lauraceae (Wheelwright 1986) as well as of the spicebush. Ridley (1930) listed northern cardinals *Cardinalis cardinalis* (L.) (Cardinalidae), American robins *Turdus migratorius* L. (Turdidae), red-eyed vireos *Vireo olivaceus* (L.) (Vireonidae), eastern kingbirds *Tyrannus tyrannus* (L.) (Tyrannidae), and hairy woodpeckers *Picoides villosus* (L.) (Picidae) as dispersers of spicebush. Fruits of spicebush are used often by wood thrushes, *Hylocichla mustelina* (Gmelin) (Turdidae), veeries, *Catharus fuscescens* (Stephens) (Turdidae), American robins, hermit thrushes, *Catharus guttatus* (Pallas) (Turdidae), northern flickers, *Colaptes auratus* (L.) (Picidae), eastern kingbirds, northern mockingbirds, *Mimus polyglottos* (L.) (Mimidae), and brown thrashers, *Toxostoma rufum* (L.) (Mimidae), and perhaps others (Martin et al. 1951, in Morgan 1983, Bent 1949, Witmer 1996, Fontenot 1998). Witmer (1996) further noted that cedar waxwings, *Bombycilla cedrorum* Vieillot (Bombycillidae), do not eat these fat-rich fruits.

Because the plants produce numerous fruits, yet are restricted in their distribution, we suspected that dispersal may be a limiting stage in the life history of pondberry. Limited dispersal may reduce the potential for recovery and expansion of existing populations. Two conservation questions follow from this: What characteristics of the dispersers are responsible for limited distribution of pondberry?, and How can management activities mitigate the limitation of the dispersal? In order to begin to address these questions, the identity of potential dispersers is needed.

Because we suspected avian dispersers, our first objective in this work was to identify the avian species responsible for the dispersal of pondberry. Our second objective was to investigate the possibility that the distribution of the plants may be controlled by the presumed avian dispersal. In this work, we (1) determined species of potential dispersers and (2) observed their behavior in the vicinity of fruiting pondberry colonies. We noted the rate of fruit removal and consumption, and investigated the association between plant distribution and movement patterns of dispersers.

MATERIALS AND METHODS

Study Site

The Delta National Forest, Sharkey County, Mississippi, includes more than 60,000 acres (24,000 ha) of bottomland hardwood forest and is one of the largest single contiguous blocks of forest in the Mississippi Alluvial Valley. The Delta National Forest contains at least 50 colonies of pondberry [Gulf South Research Corporation (GSRC) 2000].

Field Techniques

Based on available data (GSRC 2000), we calculated the distances from individual pondberry colonies to other pondberry colonies. We conducted a nearest neighbor analysis of the colony positions using techniques in Krebs (1999).

Fruiting pondberry colonies were selected from among those on the Delta National Forest. Initially, they were selected because their fruit crops were the highest reported by GSRC (2000). In 2000–2001, five colonies formed the initial observation sites. Three colonies were located in the Red Gum Research Natural Area (Compartment 7). In 2000–2001, however, they had at most only several dozen fruits. The two most important colonies for this study, GSRC 42 and GSRC 43, were within 40 m of each other in Compartment 16. Each of these two colonies had several hundred fruits within it in both years. In 2001–2002, observations were conducted in three colonies. One of the three colonies in Compartment 7 (Colony #2) had more than 100 drupes and was subject of observations in the second year, along with GSRC 42 and GSRC 43.

Fruit depletion rate was measured in each of three cohorts of approximately 100 fruits in each of the two years of the study. Each cohort consisted of a selection of an initial fruiting stem

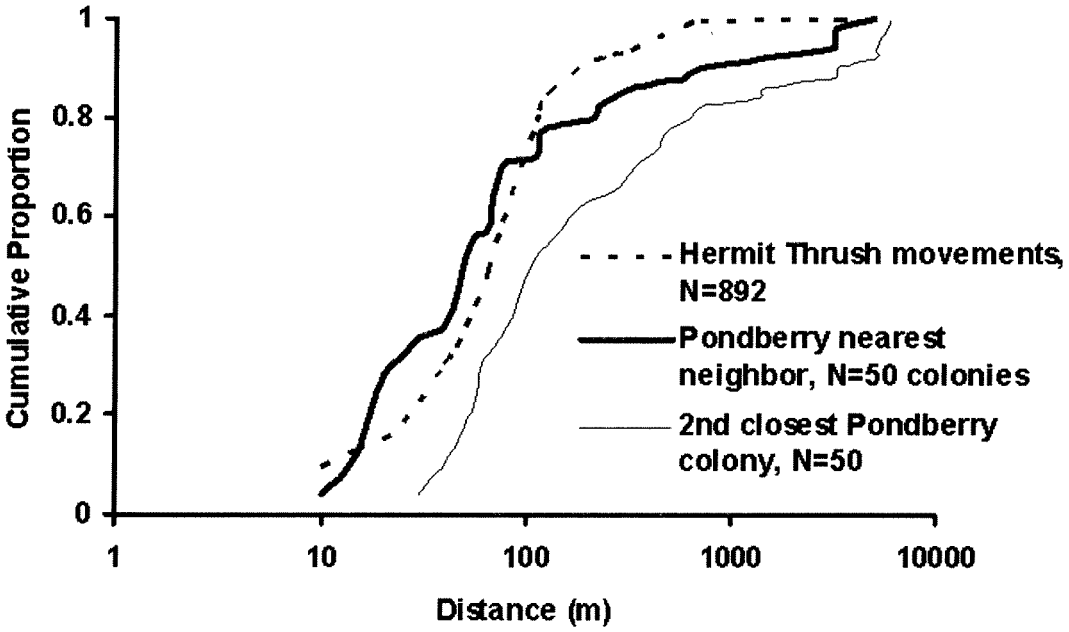

Figure 1. Observed distances to the nearest neighboring colony from pondberry colonies on Delta National Forest and hypothetical dispersal distances for pondberry seeds eaten by Hermit Thrushes. Pondberry colony data taken from GSRC (2000); hermit thrush data simulated from movement data recorded by Brown et al. (2000).

with a substantial crop of drupes to which other nearby stems were added until a total of at least 100 fruits was included. Fruits were counted on these stems once per week from September until no fruits remained. Fruits were recorded as unripe (green), ripe (red), overripe (black and/or shriveled), or gone (empty pedicel remaining). No attempt was made to measure the rate at which unconsumed fruits fell to the ground. The two samples from GSRC 42 were pooled for analysis in the 2000 data because the pattern of fruit depletion was virtually identical.

Bird sampling consisted of 1-hr observation periods by stationary observers wearing camouflage clothing who sat within 15–20 m of the colonies. Observation positions and colonies were visited in random sequence. Observations began in mid-September and continued until no fruits remained in January. Observations were conducted during daylight hours; 82% of 199 hr of observation occurred during the first three and last three hours of daylight. Sampling was conducted twice weekly during the migration period in September and October and once weekly thereafter in 2000–2001, for a total of 75 hr. Because all observations of foraging on pondberry were observed after the migration season in 2000–2001, effort in the second year was once weekly until hermit thrushes were observed, and twice weekly after that time, for a total of 124 hr.

During each observation period, all bird species seen or heard were recorded in one or more of the following categories: a) heard in the sampling period at any distance from the observer (HEARD), b) seen near or over the pondberry colony (SEEN), c) perched on a pondberry plant (ON), or d) observed ingesting a pondberry fruit (EATING).

For a portion of the observation periods in 2000–2001, a small number of ripe pondberry fruits was placed upon a feeding tray adjacent to the colony. No birds visited the feeding trays and no fruits were taken from them during the sessions involving this bait.

Bird occurrence data were summarized as frequency of occurrence of bird species in each category of observation, by type of observation period. Fruit depletion data were summarized as mean proportion of pedicels bearing fruit by week during the sampling period. Foraging observations were summarized as identity of fruit consumer and number of fruits eaten during observation periods.

Table 1. Bird species observed on pondberry plants during 201 hours of observation at fruiting colonies of pondberry, *Lindera melissifolia* (Walt.) Blume, on the Delta National Forest, Mississippi, September 2000–January 2001, and September 2001–January 2002. All species observed in both years. Species sequence reflects the usage of the American Ornithologists' Union (1998)

Scientific and Common Name	Number of Times Observed in 201 Observation Periods		
	Present	On Pondberry	Eating Pondberry
Sphyrapicus varius (L.) Yellow-bellied Sapsucker	194	1	—
Sayornis phoebe (Latham) Eastern Phoebe	61	2	—
Poecile carolinensis (Audubon) Carolina Chickadee	193	2	—
Baeolophus bicolor (L.) Tufted Titmouse	156	6	—
Thryothorus ludovicianus (Latham) Carolina Wren	199	7	—
Troglodytes troglodytes (L.) Winter Wren	24	1	—
Regulus satrapa Lichtenstein Golden-crowned Kinglet	55	2	—
Regulus calendula (L.) Ruby-crowned kinglet	15	3	—
Catharus guttatus (Pallas) Hermit Thrush	72	13	11
Dendroica coronata (L.) Yellow-rumped Warbler	26	3	—
Zonotrichia albicollis (Gmelin) White-throated Sparrow	49	2	—
Cardinalis cardinalis (L.) Northern Cardinal	54	4	2

We investigated the possible relationship between pondberry distribution on the Delta National Forest and hermit thrush winter distribution. We used the data from GSRC (2000) for pondberry plant distribution, and the data of Brown et al. (2000) for hermit thrush winter distribution. We conducted our statistical tests using SAS (SAS Institute 1999–2000). Statistical differences were accepted at $P = 0.05$, and power of the comparisons was estimated from the sample data.

RESULTS

Pondberry Nearest Neighbors

The distribution of pondberry colonies on the Delta National Forest reported by GSRC (2000) was highly clumped (index of aggregation corrected for lack of boundary strip = 0.124, $Z = -10.5$, $P = 5 \times 10^{-26}$). Median nearest neighbor distance was 52 m. Mean nearest neighbor distance of the 50 reported colonies was 435 m (Figure 1).

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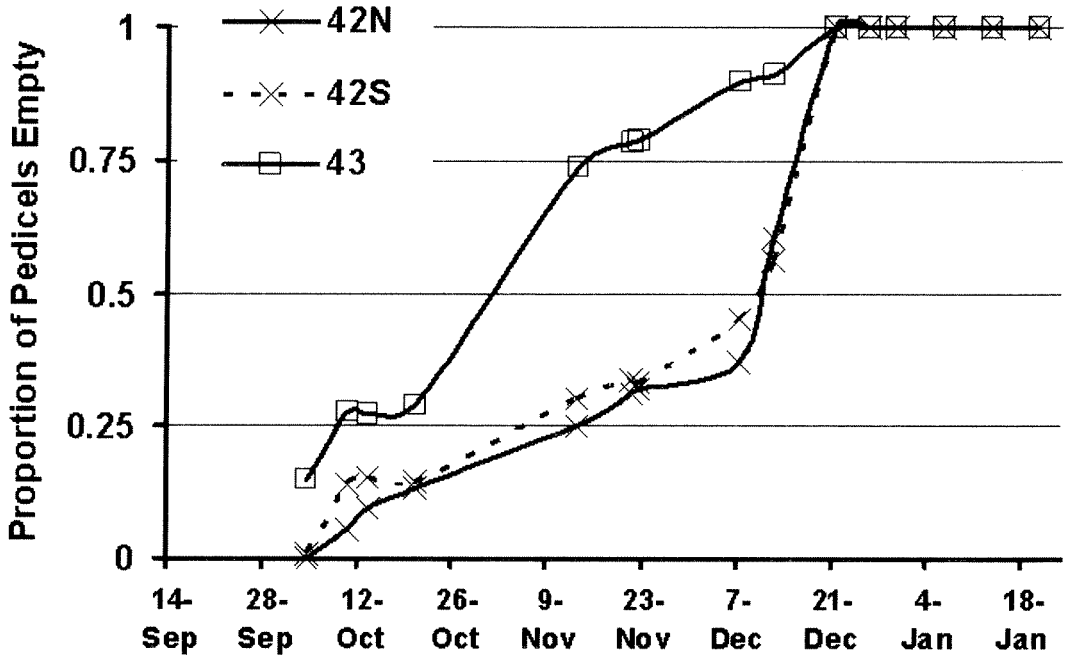
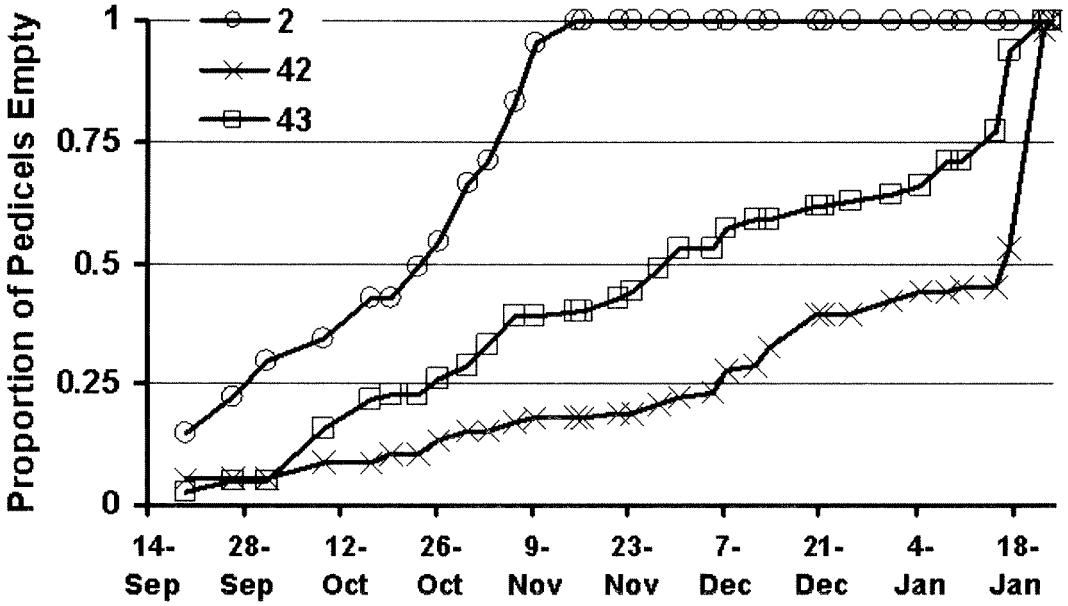
Figure 2. Depletion of fruit crop in intensely sampled cohorts of fruiting pondberry stems on Delta National Forest. a). Proportion of empty pedicels on focal pondberry stems in two fruiting colonies (Colony #42, 2 replicate samples 42N and 42S; Colony #43) in Compartment 16, Delta National Forest, September 2000–January 2001. b). Proportion of empty pedicels on focal pondberry stems in three fruiting colonies, one in Compartment 7 (Colony #2), and two in Compartment 16 (Colony #42 and Colony #43), Delta National Forest, September 2001–January 2002.

a)


42N
42S
43
Proportion of Pedicels Empty
1
0.75
0.5
0.25
0
14-Sep
28-Sep
12-Oct
26-Oct
9-Nov
23-Nov
7-Dec
21-Dec
4-Jan
18-Jan

b)


2
42
43
Proportion of Pedicels Empty
1
0.75
0.5
0.25
0
14-Sep
28-Sep
12-Oct
26-Oct
9-Nov
23-Nov
7-Dec
21-Dec
4-Jan
18-Jan

Birds Observed

Eighty-two bird species were encountered during pondberry observation periods. Twelve species were observed on pondberry plants (Table 1). Four of these are considered to be frugivores (Hamel 1992): yellow-bellied sapsucker *Sphyrapicus varius* (L.) (Picidae), eastern phoebe *Sayornis phoebe* (Latham) (Tyrannidae), hermit thrush, and yellow-rumped warbler *Dendroica coronata* (L.) (Parulidae). Four species were present in the vicinity of the observed colony during more than 75 percent of the observation periods: yellow-bellied sapsucker, Carolina chickadee *Poecile carolinensis* (Audubon) (Paridae), tufted titmouse *Baeolophus bicolor* (L.) (Paridae), and Carolina wren *Thryothorus ludovicianus* (Latham) (Troglodytidae).

The hermit thrush and northern cardinal were observed eating pondberry fruits. Hermit thrushes were first observed on 20 October during 2000 and 26 October during 2001. They first ate the fruits on 6 November during 2001 and 21 November during 2000. Northern cardinals were observed throughout both sampling periods and first observed eating a pondberry seed on 12 December 2000.

Fate of Fruits

All fruits under observation were red on or very shortly after 4 October. No fruits remained in the target colonies on 2 January 2001, and on 18 January 2002. The pattern of disappearance of the fruits differed between years and among colonies (Figure 2). Half of the drupes had disappeared from the censused cohorts in the colonies under observation by 18 November 2000 (±20 days SE) and by 10 December 2001 (±25 days SE).

Hermit thrushes ate 14 pondberry fruits during six observation periods in 2000–2001, and 13 drupes during five observation periods in 2001–2002. In each case, the birds were observed to pluck and swallow entire fruits. One hermit thrush was observed to regurgitate a possum haw, *Ilex decidua* Walter (Aquifoliaceae), seed near a pondberry colony during one of the observation periods in 2000–2001. The minimum distance from the spot of regurgitation to the nearest fruiting possum haw plant was 37 m. This distance is an empirical estimate of the minimum distance a hermit thrush might move between the consumption of a pondberry and the regurgitation of the seed. During 2001–2002, hermit thrushes regurgitated two pondberry seeds within a colony during an observation period. Both seeds were collected and both germinated, producing healthy seedlings.

Northern cardinal males ate six pondberry fruits during two observation periods in 2000–2001. These birds were observed to pluck, crush and swallow the seeds; to cut in half the fruits still on the plant and swallow the cut portion of seed; and to discard the pulp of the fruit while eating the seed.

Most hermit thrushes maintain small winter territories (0.55 ± 0.03 ha, $n = 34$; Brown et al. 2000). Brown et al. (2000) noted that 14% of the birds they followed, the floaters, occupied larger home ranges (5.8 ± 1.1 ha, $n = 7$). Brown et al. (2000) obtained 1,322 locations of 50 radio-tracked birds; locations were made an average of 45 min apart. Among these the average distance between consecutive locations for 34 territorial birds was 55 ± 1.6 m, and that distance for seven floaters was 121 ± 25 m. Two distances between consecutive locations of floaters exceeded 1,000 m.

The distribution of nearest neighbor distances of pondberry colonies on the Delta National Forest is very similar to the hypothesized distribution of seed dispersal resulting from hermit thrush movements ($r = 0.97$, $n = 26$, $P < 0.001$, Power of the test > 0.99; Figure 1); 70% of observed colonies are within 75 m of their nearest neighbor.

DISCUSSION

Of the large number of winter birds of bottomland forests that occurs in the vicinity of pondberry plants bearing ripe fruit, only two species were observed to consume pondberry fruits in this study. One is a permanent resident species in the area and the other a winter resident (Turcotte and Watts 1999).

Hermit thrushes swallowed entire fruits, and are considered to be seed dispersers (Jones and Donovan 1996). Thus, the hermit thrush is a "gulper" (Levey 1987). Levey (1987) noted that gulpers are likely to disperse seeds farther than are other frugivores (mashers) because they are less likely to drop seeds while consuming the fruits.

Northern cardinals are seed predators of pondberry, based on the direct crushing and consumption of pondberry seeds. Northern cardinals are numerous in winter in the Mississippi Alluvial Valley. Their distribution is ubiquitous. They may be able to consume the entire crop of fruits from small patches completely.

A composite distribution of movements of 41 hermit thrushes based on Brown et al. (2000) provides a hypothesis of potential dispersal distances of pondberry seeds (Figure 1). If a thrush regurgitates a seed approximately 45 min after ingestion, the probability of seed dispersal of less than 100 m is 0.7 (Figure 1). While time to regurgitation is likely less than 45 min (Levey 1987), the time required for a thrush to fly the distances observed by Brown et al. (2000) is much smaller.

These observations suggest that dispersal of pondberry may be carried out, at least in part, by hermit thrushes. Because the birds move relatively short distances during the winter, they are unlikely to carry seeds across open spaces between forest patches (Brown et al. 2000). The observations of Stiles and White (1986) that thrushes are unlikely to leave the forest understory reinforce this notion. Thus, a conservation strategy for pondberry may require the establishment of experimental populations at locations remote from existing colonies.

Our study was designed to assess the potential of birds as dispersers of pondberry seeds. Other, mammalian consumers are potential dispersers as well. These include raccoon, *Procyon lotor* (L.) (Procyonidae), black bear, *Ursus americanus* Pallas (Ursidae), and Virginia opossum, *Didelphis marsupialis* (L.) (Didelphidae). Black bears are presently very rare on the Delta National Forest; the other two species are common there. The potential contribution of these animals to the dispersal of pondberry is unknown.

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