

A Review of the Behavior and Ecology of the Northern Parula (*Parula americana*) With Notes From Oklahoma and Texas

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INTRODUCTION

The Northern Parula (*Parula americana*) is one of several migratory wood warbler species (Family Parulidae) that breeds throughout eastern United States and Canada (1), including the eastern 1/2 of Oklahoma and Texas (2-4). In Oklahoma, the Northern Parula appears around March 25 and may remain until late September or early October (5). During the breeding season in west Texas, several individuals (including singing males) had been seen in the Big Bend Park area (Brewster County); however, there was no evidence of nesting (6). Western-most records for Oklahoma include Comanche County (7) and Cimarron County in the Panhandle (3). Wintering areas include central Mexico south to Guatemala and Belize and the islands of the Greater and Lesser Antilles (8, 9). Some southern states, e.g., Texas (2); Louisiana (10) also have supported wintering Northern Parula including a rare occurrence in the Lower Rio Grande Valley of Texas (4).

In this paper, I report the latest findings on the Northern Parula with emphasis on its ecology and behavior, especially studies in Oklahoma and Texas.

BEHAVIOR

The foraging strategy of the Northern Parula is often compared to that of chickadees and titmice (Family Paridae) because it is able to dart in and out of the tips of vegetation (11). This type of foraging movement, with >50% of movements on small limbs, is due to small body size, which enables the Northern Parula to use a foraging niche more effectively than many other warblers, e.g., some *Dendroica* species (12). However, some foraging overlap occurs with unrelated species of birds, such as the Golden-crowned Kinglet (*Regulus satrapa*) and Ruby-crowned Kinglet (*R. calendula*), in areas where their breeding ranges overlap such as northern spruce forests (13). Apparently however, enough differences exist in foraging behavior to prevent common hostile encounters (13). When compared to other warbler species, the Black-throated Green Warbler (*D. virens*) exhibits the most similarities in foraging with the Northern Parula in the spruce forest (12-14). On small coastal Maine islands, Morse (14) found the Northern Parula to be more flexible (or plastic) in foraging movements when no Black-throated Green or Yellow-rumped Warblers (*D. coronata*) were present. This indicates a more submissive behavior of the Northern Parula to species that have similar foraging behaviors, resulting in rare hostile encounters (13). In some cases, however, the Northern Parula may be dominant or at least initiate a successful aggressive attack, such as Morse (15) observed against larger *Dendroica* warblers. In theory, interspecific aggressive encounters are likely to occur with greater frequency during certain stages of the nesting cycle. In southern parts of the breeding range, hostile encounters are probably rare because other birds of similar size and foraging behaviors are absent, e.g., Kinglets and Black-throated Green Warblers; thus parulas tend to be more tip-gleaning specialists (12).

Whenever encounters are observed between individual parulas or with other species, two distinct song types are sung and have been designated type A and type B. The context in which these songs are sung may be comparable to other warbler species in that type A songs are more likely given by males to advertise territories to females (intersexual usage), whereas type B songs are given more at the edge of territories during hostile encounters with other males (intrasexual usage). In the interspecific foraging study by Morse (13), he found that type A songs (accented ending songs) were more frequently sung (10 out of 22 observations) during interspecific encounters, while B songs (unaccented ending songs) were sung in fewer (7 out of 10) encounters. In addition, he recorded a few instances (5 out of 22) where muted or incomplete songs were sung during interspecific encounters. It is difficult to draw conclusions from these results because of the small sample size and the lack of information on the status or breeding

stage of the birds. An individual's status could influence how it responds to interspecifics and conspecifics. For instance, during the early part of the breeding season when territories are newly established, the Northern Parula may appear more aggressive compared to later in the season or nesting cycle, and use of the B song or in some cases muted A and B songs appear more frequently. Bay (16) found that individuals from a Texas population (Walker County) were likely to approach very close to a speaker playing the A song and sing either a normal or muted type B song during early territorial establishment in March. As the breeding season progressed, however, a variety of behavioral responses was noted, including occasional switching between song types or simply responding with only the type A (Table 1). Stowell (17) also performed playback experiments, but was unable to discern any usage difference between the two song types. However, because the status of the birds in her study was not completely known, the exact role of the two song types could not be completely ascertained. As indicated by Highsmith (18), the song types used by most wood-warblers may carry some specific messages, but probably do not represent solitary messages. For instance, A songs used to advertise territories and attract mates may also be used in territorial disputes (countersinging with conspecifics or a researcher's tape recorder), and B songs, while more frequently used to encounter conspecifics in territorial disputes, may also carry messages about individual identity that may be valuable to females.

The Northern Parula usually sings while high in trees (\bar{x} =10.9 m of perch height or 73% mean tree height), with B songs sung from perches slightly higher than A songs (12.3 vs. 10.2 m, respectively) (16). During singing activity, most individuals tend to move about frequently while probing in leaves and Spanish moss (in areas where available). In only 10 of 47 (21%) observations in Oklahoma and Texas were males observed stationary while singing, and in most of these cases (73%) the type A song was used

TABLE 1. Behavioral responses of the Northern Parula to playback of its two song types in relation to breeding status and time of the breeding season.

Responses to playback of type A song	Cases N=51	Status/Time of year
1. No response	9	possibly unmated/June
2. Approached and sang normal B songs	11	early territory establish/ March
3. Sang B songs first then switched to sing A songs with some intermediate songs ^a	7	nest construction or incubation/May and June
4. Sang only muted A songs	3	incubation or rearing nestlings/ June
5. Sang only muted B songs	2	unknown/ May and June
6. Sang both muted A and B songs	6	rearing of nestlings or unknown/ May and June
7. Sang only A songs	13	possibly after fledgling period in some cases/ May and June
Response to playback of type B song	Cases N=6	
1. No response	4	unknown/ June
2. Sang only A songs	1	unknown/ June
3. Sang A and B songs	1	unknown/ June

^aintermediate songs- a mixture of the two song types.

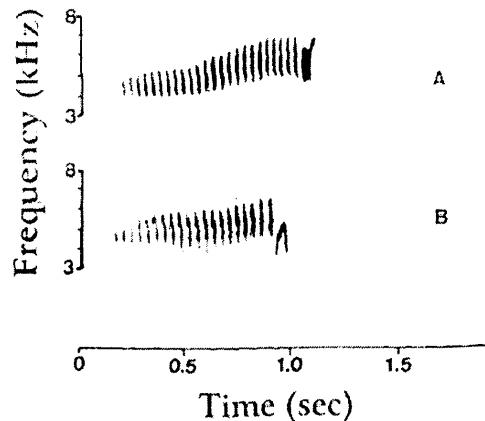


Figure 1. Type A songs of the Northern Parula. (A) Western type A recorded from Walker County, Texas. (B) Eastern type A recorded from Lincoln County, Maine. Note differences in the terminal syllable between eastern and western types (see also 20 in references).

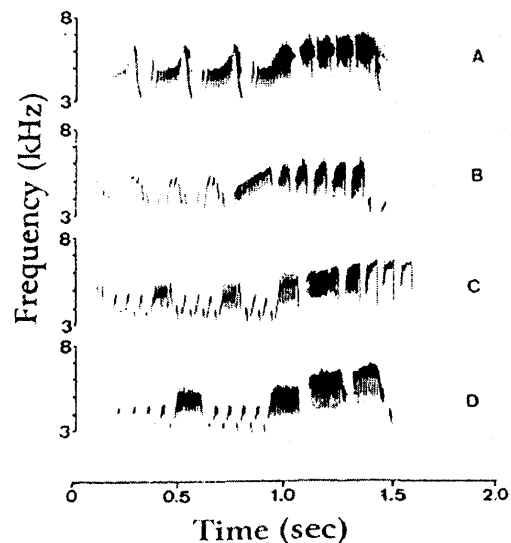


Figure 2. Type B songs of the Northern Parula. (A) Dale County, Alabama. (B) Walker County, Texas. (C) Walker County, Texas. (D) St. Tammany Parish, Louisiana. A and B represent the most frequent pattern used to structure a type B song. C and D represent a type of phrase pattern (notice the repeated chevron-like simple syllables in the middle of the song) found only in birds distributed within the species' western breeding range (from sample songs this includes Texas, Mississippi, and Louisiana (see also 21 and 22 in references).

(16). Apparently, foraging motions or movement during advertisement have little effect on song rate when compared to individuals that sang while stationary. In addition, some individuals appeared to be capable of singing while carrying food (16).

The type A song rate was found to be highest during pre-nesting periods (March) in Texas (\bar{x} = 7.4 songs/min) and then declined slightly as the breeding season progressed (16,17). However, in some cases, males tending young had decreased song rate by only 1 song/min when compared to birds singing during pre-mating periods (16). In comparison, B songs tend to be sung at higher rates (\bar{x} = 8.5 songs/min) during the nesting periods than during pre-nesting periods (16).

Peterson (19) was the first to extensively analyze the type A song both micro- and macro-geographically, revealing a distinct east to west variation in the terminal syllable. Moldenhauer (20) expanded this finding to show that not only do eastern and western populations differ in the terminal note (Fig. 1), but they also differ significantly in temporal, e.g., trill rate, and frequency characteristics. Mapping of the two type A song forms revealed an almost allopatric distribution with some overlap in southwestern Alabama and eastern Kentucky, yet no individual recorded contained any intermediate song type (20).

Type B songs are much more complex than A songs, usually in the number of different syllables used to form it (3.8 vs. 2.0, respectively). Bay (21) sampled several songs (N=263) from individuals across the breeding range and discovered at least 39 different syllable variants distributed among three syllable types: simple, complex, and trill. The way in which these syllables were used in creating a B song forms a phrase pattern, i.e., repeated syllables of one or more types, of which at least nine types were discovered (22). These phrase patterns appear to vary on an east to west distribution axis (like the terminal note in the A song) with many western songs containing phrase patterns not discovered in the songs of eastern birds (21,22) (Fig. 2). Apparently, males are capable of recognizing the A song of their own population. For instance, western singers respond more to the western type A and eastern singers respond more to the eastern type A (23). Nothing is known regarding behavioral responses to variations in the B song.

Based on the divergence in song biology as

well as morphological comparisons of eastern and western birds, Moldenhauer (20) recommended that subspecific status be given to the two song populations, with western style singers classified as *P. americana ludoviciana* and the eastern singers designated as *P. americana americana*. Subspecific designation for the Northern Parula has previously been introduced by others (2,24,25), and includes several unrecognized designations such as the southeastern or southern race (*P. americana americana*), the northeastern or northern race (*P. americana pusilla*), and the western race (*P. americana ludoviciana*).

ECOLOGY

A nesting preference for epiphytic growth, such as old man's beard (*Usnea* spp.) or Spanish moss (*Tillandsia usneoides*), may restrict the largest populations of the Northern Parula to wet, swampy, bottomland types of habitat. However, in areas where epiphyte growth is minimal or absent, the Northern Parula may use other materials for nesting. For instance, Burleigh (26) reported that in the Georgia Piedmont, where Spanish moss is lacking, nests are constructed using a moss-like lichen that covers hemlock (*Tsuga canadensis*). Bull (27) also mentioned the use of hemlock as a nesting substrate, with the nests constructed of old leaves or pine needles or sometimes constructed in clumps of drift grass caught in the branches of trees. Nice (28) reported of a nest in Washington County, Oklahoma, that was constructed of box elder (*Acer negundo*) blossoms, supported externally by spider webs and internally by sycamore (*Platanus occidentalis*) seed down. Perhaps the species adaptability for nesting substrate in areas without epiphytic growth is best illustrated by one particular pair whose nest was found inside a piece of burlap caught in a tree in the mountains of West Virginia (1). In Oklahoma, the Northern Parula has been found defending territories in Pontotoc and Murray Counties, in areas where no epiphytic growth was evident. However, no evidence of nesting or breeding activity could be ascertained (Bay, unpublished field notes).

Nests composed of the fruticose lichen *Usnea* are usually constructed by hollowing an interior in a clump of the lichen and adding very little lining (1,29). Graber and Graber (30) reported that nests constructed in Michigan were composed of 17.5-30.0 cm strands of *Usnea*, situated so that the main entrance faced the trunk of the tree. A nest constructed of *Usnea* was discovered by Carter (31) in McCurtain County, Oklahoma, and was situated about 2.4 m from the ground in a dogwood tree (*Cornus florida*). This nest (part of the Collection of Recent Vertebrates at East Central University, Ada, Ok.) was examined and found to be 7cm deep with a diameter of 6.5 cm. The entire nest was basically shaped from the *Usnea*, which extended down 8.2 cm. from its attachment to the tree branch. Another Oklahoma nest was discovered by Jim Norman and Jeri McMahan (communicated to Jack Tyler in a note dated May 22, 1991) below Lake Tenkiller dam (Sequoyah County), was determined to be about 7.5 m above ground in a sycamore tree. Apparently the position of the nest made examination difficult, so the nest material was never determined. I was able to examine a photograph of the nest (taken by Jeri McMahan), and it appears to have been pendant (saclike) and supported by two branches from above.

The nest of the Northern Parula is often a challenge to locate, and this difficulty may increase depending on the time of the breeding cycle. The nest discovered by Carter (31) was easily found due to the adults making repeated trips to feed their young; otherwise because of its concealment in *Usnea*, the nest was invisible (Carter, personal communication). In fact, nests in Spanish moss discovered by myself, were detected because of feeding adults. In spite of the potential difficulty in finding nests, it is ironic that the success of some individuals, with 18 and 71 nests found (1 and 32, respectively) has not led to a more complete account on the life history and nesting ecology of the Northern Parula being published. Harrison (1) noted that at least in *Usnea*, nests could be discovered by looking for a tennis ball shape in the bottom of the lichen. My own generalization from field experience is that nests constructed in Spanish moss could be more well concealed when compared to nests constructed in *Usnea* and thus difficult to locate even after a determined search. I know of no reported findings of Northern Parula nests in Spanish moss during the nest construction phase nor during incubation. Only nests discovered as early in the breeding cycle as possible, i.e., during nest construction, egg-laying, or incubation, give the most reliable estimates of nest success (33).

TABLE 2. Nesting heights of the Northern Parula.

Height (m) \bar{x}	Range	Number of Nests	Location	Substrate	Reference
2.8	2.6-3.0	4	Michigan	<i>Usnea</i>	30
2.4	—	1	Oklahoma	<i>Usnea</i>	31
12.1	—	1	Minnesota	<i>Usnea</i>	29
3.0	—	1	New Jersey	<i>Usnea</i>	49
2.8	0.3-6.0	33	New Jersey	<i>Usnea</i>	46
6.0	—	1	Connecticut	<i>Usnea</i>	50
7.5	1.2-12.1	18	Maine	<i>Usnea</i>	1
— ^a	1.5-15.3	71	Maine	<i>Usnea</i>	32
2.4	—	1	Oklahoma	<i>Usnea</i>	51
8.3	3.0 +13.6	2	Texas	<i>Tillandsia</i>	— ^b
11.8	—	1	Georgia	<i>Tillandsia</i>	— ^b
7.8	—	1	Quebec	<i>Usnea</i>	47
12.1	—	1	Quebec	<i>Usnea</i>	48

^aCould not be determined from published data

^bBay, unpublished data

Apparently, nesting height is highly variable (Table 2), ranging from as low as 0.3 m above the ground to as high as 16.3 m. Two nests that I discovered, one in Walker County, Texas, and the other in Jenkins County, Georgia, were situated very high (\bar{x} =12.7 m) and were very well concealed in a small clump of Spanish moss dangling at the end of a small branch (unpublished field data). The position of these two particular nests made them difficult, if not impossible, to examine. Bent (35) reported that most nests discovered in southern Massachusetts were usually below 3.6 m than above, although some nests were at least 6.0 m above the ground.

Other aspects of nesting biology, such as breeding displays/behavior and number of broods, have never been fully studied, and therefore remain a mystery. In addition, information about nestling food habits and foraging ecology is very scant. Graber and Graber (30) reported lepidoptera larvae and occasional winged insects of unknown species being fed to nestlings in Michigan, but gave no details as to feeding frequency by adults. Lepidoptera larvae were the most frequently identifiable item in the bills of adults foraging in Texas (Bay, unpublished data) during the height of the breeding season. In Magnolia State Park (Jenkins County), Georgia, a female was observed at her nest a total of 27 times in 1 h of observation (\bar{x} =2.14 min between visits). The male was seen and heard singing in nearby trees and occasionally in the nest tree, and was observed carrying food to the nest on one occasion. Types of food material delivered to the nestlings could not be ascertained (Bay, unpublished data). Wetmore (35) analyzed the stomachs of wintering Northern Parula in Puerto Rico and found 98% animal matter. This included spiders (29.5%) Lantern flies (Fulgoridae) (19.9%), a variety of beetles (Coccinellidae, Chrysomelidae, Tenebrionidae, Scarabaeidae and Curculionidae) (22.5%), ants and wasps (Hymenoptera) (3.5%), and other flies (Diptera) (1.2%).

Breeding populations of the Northern Parula appear to be stable (36) or increasing (37) according to results analyzed from Breeding Bird Survey data from the east-southeastern United States. On wintering grounds such as Puerto Rico, some researchers reported a decline in the number of Northern Parulas (38,39) whereas others suggest that it may be the most common wintering warbler (40). A study in southwestern Puerto Rico by Stacier (41) found the Northern Parula to be the most abundant warbler species in the winter community, with individuals exhibiting a strong site fidelity. The latter finding suggests that any habitat destruction in wintering areas could displace individuals that are philopatric and reduce their chances for survival. Contrasting results by Faaborg and Arendt (42) suggest that Northern Parulas do not exhibit much site fidelity, which is likely to contribute to population variation from year to year. The reasons for the discrepancy between studies is

not clear, but Stacier (41) suggested that sample size, habitat, and research methodology may be partially responsible. If populations are truly declining on wintering grounds, perhaps factors other than winter habitat destruction may be the cause, because the Northern Parula appears able to use a variety of habitat types, e.g., coastal scrub and coffee plantations (43-45), and may be even less specific in microhabitat selection (41).

The specific effects of habitat fragmentation on Northern Parula populations with regard to the breeding grounds have not been fully addressed at the local level. What extent parasitism by the Brown-headed Cowbird (*Molothrus ater*) and nest predators have on nesting success in areas with extensive forest fragmentation is poorly understood at best. Moreover, much of what has been reported about nesting success and life history traits is severely outdated (e.g., 30,46-48) or incomplete. More study is needed to compare nesting success and habitat selection in areas with and without epiphytic growth, and in forested habitats of varying size and isolation, to fully assess population stability and recruitment.

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