

BREEDING BIOLOGY OF FLORIDA PRAIRIE WARBLERS AND CUBAN YELLOW WARBLERS

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ABSTRACT.—We studied the breeding biology of the Florida Prairie Warbler (*Dendroica discolor paludicola*) and the Cuban Yellow Warbler (*D. petechia gundlachi*) in black mangrove (*Avicennia germinans*) habitats in the Florida Keys. A total of 42 Prairie and 20 Yellow warbler nests was located during 1990–1993. The breeding season for both species extended from late April through early July. The two species used a similar range of nest heights and placed their nests in similar locations within the mangroves, but Yellow Warbler nests averaged higher (1.77 m) than Prairie Warbler nests (1.60 m) and were less likely to be placed against mangrove trunks. Incubation periods averaged 12 days for both warblers. Brooding periods averaged 11 days for Prairie Warblers and 12 days for Yellow Warblers. These periods are equivalent to or slightly longer than typical periods for other races of Prairie and Yellow Warblers that breed in North America, and similar to those for races of Yellow Warblers that breed in the West Indies. Mean clutch sizes for Prairie Warblers (2.50, $N = 29$) and for Yellow Warblers (2.50, $N = 16$) are smaller than those for temperate races of these warblers. Fledging success (number of young fledged/number of eggs laid) was higher for the Yellow Warbler (65.0%) than for the Prairie Warbler (45.8%), but the number of young fledged per nest did not differ significantly between the two species. Predation was the major cause of nest failure, accounting for approximately 64% of all egg losses. Received 15 Nov. 1994, accepted 28 Feb. 1995.

Two distinct subspecies of wood warblers (Family Emberizidae, subfamily Parulinae) breed in the mangrove habitats of south Florida. The Florida Prairie Warbler (*Dendroica discolor paludicola*) is a Florida endemic, breeding only in the Florida Keys and along the southern and central Florida coast. The Cuban Yellow Warbler (*D. petechia gundlachi*) was first recorded breeding in the Florida Keys in 1941 (Greene 1942), and it is now resident in the keys and along the south Florida coast (Robertson and Woolfenden 1992). Cuban Yellow Warblers are found elsewhere only in the Bahamas and Cuba (Robertson 1955, Bond 1956).

Both the Florida Prairie Warbler and the Cuban Yellow Warbler have been designated “species of special concern” in Florida due to their limited range and threats to their mangrove habitats such as development, human disturbance, and hurricanes (Kale 1978). In addition, two species of brood-parasites, the Brown-headed Cowbird (*Molothrus ater*) and the Shiny Cowbird (*M. bonariensis*), have recently invaded the south Florida region (Cruz et al. 1989, Cruz et al. unpubl. data) and may affect the breeding success of these warblers in the future. As part of a larger study,

baseline data on the breeding biology of Prairie and Yellow warblers were gathered during spring and summer 1990–1993.

STUDY AREA AND METHODS

Study sites.—This study was carried out in mangrove forests on south Key Largo, Florida, and on several small, mangrove dominated keys in Florida Bay, just offshore from Key Largo. The dominant vegetation in all of the sites was black mangrove (*Avicennia germinans*), comprising between 70% and 100% of the woody vegetation. Other woody plants in some sites included red mangrove (*Rhizophora mangle*), buttonwood (*Conocarpus erecta*), and sea grape (*Coccoloba uvifera*). In some sites, the mangroves occurred in clumps surrounded by open areas subject to tidal fluctuations. Mangroves in these areas rarely exceeded 2.5 m in height. In other sites, the mangroves averaged 3 to 5 m tall and formed a moderately dense woodland with a closed canopy. A sparse understory of the succulent saltwort (*Batis maritima*), grasses (*Monanthochloe littoralis*, *Sporobolus* sp.), and black mangrove aerial roots (pneumatophores) was present in the study sites.

Nest placement.—Nests were located by searching mangrove trees and shrubs and by locating and following warblers that were actively constructing nests. In some cases, nests contents were examined by climbing trees. For each active nest, the substrate in which the nest was placed, the nest height, and the location of the nest were recorded. Data were not recorded on inactive nests because of the similarity between Prairie and Yellow warbler nests; inactive nests could not be attributed to one species with 100% certainty. A two-tailed Mann-Whitney *U*-test was used to determine if there were differences in the nesting heights of Florida Prairie Warblers and Cuban Yellow Warblers.

Timing of breeding.—Each site was searched for new nests every two to three days during June 1990 and 1991, late March to early July 1992, and late April through early August 1993. For each nest, the dates of laying of the first egg, hatching of the young, and fledging of the young were recorded, when these were known.

Reproductive biology.—After a nest was located, it was checked every two to three days until it failed or young were successfully fledged. Most nests were located in the nest-building or incubation periods, but a few were located when the young had already hatched. Nest contents were recorded at the time of each check, and the data were used to determine incubation periods, clutch sizes, and nesting successes.

Incubation periods were determined by measuring the time, to the nearest day, from the date of the laying of the last egg to the date of hatching for the last egg to hatch. The period was assumed to include the date of laying but not the date of hatching. Brooding periods were determined by measuring the time, to the nearest day, between the hatching of the last egg and the fledging of the young. The period was assumed to include the date of hatching but not the date of fledging. Only nests in which the exact dates of laying, hatching, and fledging were known, and in which all eggs hatched and all young fledged were analyzed.

Clutch sizes were determined using 29 Prairie Warbler nests and 16 Yellow Warbler nests found before egg laying began, or during the egg laying or early incubation periods. It is possible that eggs were lost from some of these nests before they were found, but this seems unlikely. Loss of individual eggs, rather than the complete clutch, was only noted in one nest out of the 28 found before laying began. All of these nests, therefore, were assumed to hold complete clutches. A two-tailed Students *t*-test was used to determine if there were significant differences in the mean clutch size for Florida Prairie Warblers and Cuban Yellow Warblers.

Hatching and fledging success were determined using the same 29 Prairie Warbler nests and 16 Yellow Warbler nests. Hatching success was defined as the number of young hatched

divided by the number of eggs laid in those nests. Fledging success was defined as the number of young fledged divided by the number of eggs laid. The status of each nest was checked every two to three days until the nest failed or the young fledged. If the nest failed, the date of failure was noted and the area was searched for evidence of the cause of failure. If the nest produced fledglings, the date was noted and the number of young fledged was verified by locating and counting the fledglings. In a few cases some of the fledglings could not be located near the nest. In those cases all of the young in the nest at the time of the previous check were assumed to have fledged. A chi-squared test with continuity correction was used to determine if there were differences in the proportion of young fledged/eggs laid for Prairie Warblers and Yellow Warblers. A two-tailed Student's *t*-test was used to determine if there were differences in the number of young fledged per nest for Prairie and Yellow warblers.

RESULTS

Nest placement.—All Prairie Warbler (42) and Yellow Warbler (20) nests were located in black mangrove trees or shrubs. There was a significant difference in the overall nesting heights of Prairie and Yellow warblers, with Yellow Warbler nests being placed higher on average than Prairie Warbler nests ($P = 0.038$). Prairie and Yellow warblers used essentially the same range of nesting heights, however. Prairie Warbler nests ranged from 0.30 m to 4.62 m above ground level, averaging 1.60 ± 1.02 m above the ground. Yellow Warbler nests averaged 1.77 ± 0.77 m above ground level, ranging from 0.37 m to 4.51 m above the ground.

Of 42 Prairie Warbler nests, 20 (48%) were located in forks formed by two or more twigs, 14 (33%) were located on the top of horizontal or diagonal branches, and eight (19%) were located against trunks. Yellow Warbler nest placement was similar to that of Prairie Warblers, with 12 of 20 (60%) nests located in forks formed by vertical twigs, and 7 of 20 (35%) nests located on horizontal or diagonal branches. Only one Yellow Warbler nest (5%) was found against a trunk.

Timing of breeding.—Egg laying occurred between May 4 and June 25 in 19 Prairie Warbler nests and between May 20 and June 12 in nine Yellow Warbler nests for which the date of laying of the first egg was known. In 1993, one Yellow Warbler nest fledged young on May 17, and one Prairie Warbler nest fledged young on May 23, indicating that some birds began nesting in late April of that year. Hatching of eggs of both species typically occurred between May 18 and June 24. Eggs in one Prairie Warbler nest hatched around July 3, this being the latest recorded date of hatching for either species. Fledging of warblers typically occurred between June 5 and July 5.

Incubation and brooding periods.—The period between the laying of the first egg and the hatching of the last egg to hatch varied between 12 and 18 days (average 14.5) in six Prairie Warbler nests and between 12 and 16 days (average 14) in six Yellow Warbler nests. Neither female

TABLE 1
SUCCESS OF PRAIRIE WARBLER AND YELLOW WARBLER NESTS

Nest data	Species	
	Prairie Warbler	Yellow Warbler
Number of nests	29	16
Average clutch size	2.86	2.50
Number of eggs laid	83	40
Number of eggs hatched	41	29
Number of young fledged	38	26
Hatching success ^a	49.4%	72.5%
Fledging success ^b	45.8%	65.0%
Number of fledglings/nest	1.31	1.62

^a Number of eggs hatched/number of eggs laid.

^b Number of young fledged/number of eggs laid.

Prairie Warblers nor female Yellow Warblers incubated the eggs until the last egg was laid, and both laid one egg per day. The average period of incubation for both Prairie Warbler and Yellow Warbler eggs was 12 days (range 10–15 days).

The period between the hatching of the last egg and the fledging of the young varied from 10 to 14 days in the same 12 warbler nests mentioned above. The brooding period averaged 11 days for Prairie Warblers and 12 days for Yellow Warblers. Only female warblers brooded the young, but both males and females fed nestlings. Adding both incubation and brooding periods together gives an average time of 23 days for nest attentiveness of Prairie Warblers and 24 days of nest attentiveness of Yellow Warblers.

Clutch sizes.—Mean clutch size was 2.86 ± 0.69 eggs for Florida Prairie Warblers and 2.50 ± 0.73 eggs for Cuban Yellow Warblers (Table 1). Of the 29 Prairie Warbler nests in which a full clutch was known or assumed to have been laid, five (17%) contained four eggs, fifteen (52%) contained three eggs, and nine (31%) contained two eggs. Of the 16 Yellow Warbler nests in which a full clutch was known or assumed to have been completed, one (5%) contained four eggs, seven (35%) contained three eggs, seven (35%) contained two eggs, and one (5%) contained only one egg. There were no significant differences in the mean clutch size of the two species ($P = 0.107$).

Nesting success.—In nests in which a full clutch was known or assumed to have been completed, 41 of the 83 eggs (49.4%) laid by Prairie Warblers were successfully hatched, while 29 of the 40 eggs (72.5%) laid by Yellow Warblers were successfully hatched (Table 1). Of the 41 Prairie

Warblers that successfully hatched, 38 (92.7%) were successfully fledged, and of the 29 Yellow Warblers that hatched, 26 (89.7%) were successfully fledged (Table 1). Overall rates of nesting success (number of eggs laid/number of young fledged) were 45.8% for the Florida Prairie Warbler and 65.0% for the Cuban Yellow Warbler (Table 1). In all 13 (45%) of the 29 Prairie Warbler nests and 12 (75%) of the 16 Yellow Warbler nests produced at least one young. The mean number of fledged young per nest was 1.31 for Prairie Warblers and 1.62 for Yellow Warblers. No significant differences were found in the number of young fledged per nest by the two species ($P = 0.258$), but a significantly higher percentage of Yellow Warblers fledged per egg laid ($P = 0.026$).

Predation was the major cause of nest failure for both species. Twenty-seven Prairie Warbler eggs in 10 nests and seven Yellow Warbler eggs in three nests were believed to have been lost to predators during the course of this study. This accounts for 64.3% of the egg losses by Prairie Warblers and 63.6% of the egg losses by Yellow Warblers. A higher percentage of Prairie Warbler eggs (35.9%) than Yellow Warbler eggs (17.5%) were lost to predators. Evidence for egg loss to predators included animal tracks (rat [*Rattus* sp.] and raccoon [*Procyon lotor*]) at the nest site, punctured or crushed eggs in or near the nest, and nests damaged in ways consistent with a predation event. In three cases, eggs disappeared from nests without a trace and were thought to have been lost to snakes. Probable nest predators included rats, raccoons, Red-winged Blackbirds (*Agelaius phoeniceus*) and mangrove water snakes (*Nerodia compressicauda*). Strong et al. 1991 found that the White-crowned Pigeon (*Columba leucocephala*) nesting distribution on the Florida Keys appeared to be limited by the presence of raccoons. Of the 33 keys on which they found evidence of raccoons, only six had nesting White-crowned Pigeons.

Failure of eggs to hatch and, in some cases, subsequent nest abandonment were also significant factors in reduced nesting success of the Prairie Warbler. Ten of 83 (12.1%) Prairie Warbler eggs failed to hatch, whereas only two of 40 (5.0%) Yellow Warbler eggs failed to hatch. Other, less important causes of reduced nesting success included storms that damaged nests, young falling from the nest, and death of hatchlings in the nest. A total of eight eggs or young were lost by Prairie Warblers and five eggs or young were lost by Yellow Warblers due to these circumstances. Cowbirds (*Molothrus* spp.), which could reduce warbler nesting success through brood parasitism, were seen near the area of this study, but no evidence for brood parasitism was found in the study sites.

DISCUSSION

The breeding biology of Florida Prairie Warblers and Cuban Yellow Warblers are very similar in most aspects. Both species also showed a

high degree of resource overlap and occasionally occurred in overlapping territories (Prather and Cruz, unpubl. data). These results are not surprising because the two species are closely related and occur in the same habitats.

Nest placement.—Both Florida Prairie Warblers and Cuban Yellow Warblers seem to prefer to nest in black mangroves, which comprised approximately 90% of the woody vegetation in our study sites. In other Florida habitats, where the composition of the vegetation differs, they have been recorded nesting in other substrates (Stevenson and Anderson 1994). Harrison (1981) found Prairie Warblers in wax myrtle (*Myrica cerifera*) bushes on Sanibel Island, and Bent (1953) reported that Prairie Warbler nests have been found in red mangroves. Cuban Yellow Warblers have also been reported nesting in red mangroves in Florida (Greene 1942, Sprunt 1954). In Puerto Rico, in areas where black mangroves were the predominant woody vegetation, 55 of 57 Yellow Warbler nests found by Wiley (1982) were placed in black mangroves.

The differences in nesting height and nest placement by Prairie and Yellow warblers in black mangroves seem to represent species preferences rather than real differences in nest site selection. A study of multiple habitat variables, including substrate height, mean vegetation height, and mean percentage canopy cover in plots around warbler nest sites revealed no significant differences in nest site selection between the Florida Prairie Warbler and the Cuban Yellow Warbler (Prather and Cruz, unpubl. data). Furthermore, comparison of habitat variables in nest plots with the same variables in randomly placed plots suggested both species chose nest sites randomly with respect to the habitat (Prather and Cruz, unpubl. data).

Timing of breeding.—Florida Prairie Warblers and Cuban Yellow Warblers may become territorial and begin singing as early as mid-January in south Florida (W. Hoffmann, pers. comm.). Active Prairie Warbler nests have been recorded as early as March 29 (Howell 1932) and as late as September 2 (Atherton and Atherton 1987). Despite being in the study areas in early April 1992 and late April 1993, we found no active warbler nests before the beginning of May. Two nests containing young were found in mid-May 1993, however, indicating a few birds began laying eggs in late April of that year. No warbler nests containing eggs were located after mid-June, but two Prairie Warbler nests fledged young in July. Historically, 18 sets of Florida Prairie Warbler eggs were collected during May and June (Stevenson and Anderson 1994), and many observers have reported finding active Prairie Warbler nests during this period (Howell 1932, Sprunt 1954, Harrison 1981, Stevenson and Anderson 1994). Greene (1942) found a Yellow Warbler nest with one egg on June

26, 1941. Therefore, most Prairie and Yellow warblers in Florida appear to breed between late April and early July.

A three month breeding season would give both species enough time to raise two broods. Only one such instance was noted, however. In at least two other cases, one involving Prairie Warblers and one involving Yellow Warblers, a pair renested after an initial nest failure. Northern Prairie Warblers that successfully raised a first brood have been found to have second broods about 21% of the time (Nolan 1978). It is not known if Cuban Yellow Warblers have second broods, but some other Yellow Warbler races do (Bent 1953).

It is as yet unknown what factors affect the timing of breeding in Florida. One possibility is that migratory insectivorous birds that winter in Florida may depress the resource availability in mangroves enough to prevent breeding while they are present, primarily September to May (National Audubon Society Records, Lane 1992). Another possibility is that the timing of breeding is affected by the seasonal rainfall patterns. In Puerto Rico, Yellow Warblers typically breed in mangrove habitats between March and August (Wiley 1982; Nakamura and Cruz, unpubl. data), but the breeding season varies from year to year in response to increases in insect abundance caused by rains. Brief early summer rains in April and May often cause a flush of mosquitoes and probably other insects in the Florida Keys (pers. obs.). On the other hand, heavy rains later in the summer damaged or destroyed at least five warbler nests that were subsequently abandoned, and Yellow Warblers have been known to abandon nests during heavy rains in Puerto Rico (T. Nakamura, pers. comm.).

Incubation and brooding periods.—The data indicate that the duration of incubation and brooding is similar for the Florida Prairie Warbler and Cuban Yellow Warbler. The periods are slightly longer than reported periods for races of the Prairie and Yellow warblers that breed at higher latitudes but similar to those reported for other races of the Yellow Warbler in the West Indies. Nolan (1978) found an incubation period ranging from 10.5 to 14.5 days (average 12 days) and a brooding period ranging from 8 to 11 days (average 9.5 days) for Northern Prairie Warblers in Indiana. Schrantz (1943) reported an average incubation period of 11 days (range 10–12 days) and an average brooding period of 9.5 days (range 8–10 days) for the Eastern Yellow Warbler (*D. p. petechia*) in Iowa. Incubation and brooding periods for races of the Yellow Warbler that breed on St. Lucia and Puerto Rico average about 11–12 days each (T. Nakamura, pers. comm.).

Clutch sizes.—Few clutch sizes for Florida Prairie Warbler nests have been reported in the literature, and those that can be considered to be

complete clutches all contained three eggs (Howell 1932, Harrison 1981). To our knowledge, no other clutch sizes for Cuban Yellow Warbler nests have been published. However, clutch size information exists for two other West Indian subspecies, *D. p. cruciana* of Puerto Rico and *D. p. babad* of St. Lucia, revealing that clutch sizes were similar to the sizes found in this study. In Puerto Rico, Wiley (1982) found an average clutch size of 2.6 ± 0.49 eggs ($N = 15$ nests), Nunez-García (1988) found an average clutch size of 2.2 ± 0.10 eggs ($N = 36$ nests), and Nakamura and Cruz (unpubl. data) found an average clutch size of 2.1 ± 0.56 eggs ($N = 10$). In St. Lucia, Nakamura and Cruz (unpubl. data) found an average clutch size of 2.3 ± 0.61 ($N = 32$) for the Yellow Warbler. Clutch sizes for other species of *Dendroica* warblers from the West Indies, such as Adelaide's Warbler (*D. Adelaidae*), Olive-capped Warbler (*D. pityophila*), Vitelline Warbler (*D. vitellena*), Plumbeous Warbler (*D. plumbea*), and Arrow-headed Warbler (*D. pharetra*) typically range from two to four eggs (Bond 1936; Curson et. al 1994; Nakamura and Cruz, unpubl. data).

The general trend toward smaller clutch sizes for birds breeding in the tropics than for those breeding in temperate zones (Cody 1966), including warblers (Morse 1989), is shown by both Prairie and Yellow warblers. In Indiana, the mean clutch size for nests of the Northern Prairie Warbler that were not affected by brood-parasitism or predation (188 nests) was 3.89 ± 0.50 (Nolan 1978). Of those, 139 (74%) contained four eggs. In Kentucky, 14 Prairie Warbler clutches averaged 3.5 ± 0.14 eggs (Mengel 1965). In Illinois, 33 unparasitized nests of the Eastern Yellow Warbler (*D. p. aestiva*) contained an average of 4.0 eggs (Graber et al. 1983), and 41 nests in Iowa contained an average of 4.1 eggs (Schrantz 1943). In Manitoba, the mean clutch size was 4.5 eggs ($N = 1005$) (Sealey 1992). The mean clutch size for the Florida Prairie Warbler is about one egg fewer than its northern counterpart and that for the Cuban Yellow Warbler appears to be about 1.5 fewer than that for its northern relatives. It is interesting to note that the Florida Prairie Warbler, which is probably derived from temperate stock (Nolan 1978, Robertson 1955), has a slightly higher mean clutch size than the Cuban Yellow Warbler which invaded Florida from the West Indies.

Nesting success.—Overall hatching success was higher for Yellow Warblers than for Prairie Warblers (Table 1). This difference was, in part, due to predation which accounted for about 64% of both Prairie and Yellow warbler egg losses. It also appears, however, that Prairie Warblers are more likely to have infertile or inviable eggs. Two complete Prairie Warbler clutches (total 5 eggs) failed to hatch and were subsequently abandoned. Four other clutches had one egg fail to hatch, and one had two

eggs fail to hatch. Only one Yellow Warbler egg in each of two nests failed to hatch.

Once a nestling hatched from the egg, it was very likely to survive to fledging (Table 1). There are no clear reasons for this, but it may be that most of the nests that were likely to be found by predators or damaged during storms failed during incubation. Yellow Warblers showed higher hatching and fledging success than did Prairie Warblers because a lower percentage of Yellow Warbler eggs failed to hatch and Yellow Warblers were less likely to abandon a nest. Despite this, no significant differences occurred in the number of young fledged per nest by the two species. This may be due to a slightly, but not significantly, larger mean clutch size for the Prairie Warbler.

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