ORNITOLOGIA NEOTROPICAL 20: 255–263, 2009

BREEDING SEASONALITY OF THE MANGROVE WARBLER (*DENDROICA PETECHIA BRYANTI*) FROM SOUTHERN MEXICO

Javier Salgado-Ortiz[1], Peter P. Marra[2], & Raleigh J. Robertson[1]

[1]Department of Biology, Queen's University, K7L 3N6, Kingston, Ontario, Canada.
E-mail: javo_salgado@yahoo.com.mx

[2]Smithsonian Migratory Bird Center, National Zoological Park, P.O. Box 37012, MRC5503, Washington, D.C. 20012, USA.

Resumen. – Estacionalidad reproductiva del Chipe Manglero (*Dendroica petechia bryanti*) del sur de México. – El complejo taxonómico Dendroica petechia incluye subespecies con poblaciones migratorias Neartico-Neotropicales y poblaciones residentes anuales Neotropicales. Mientras que las poblaciones migratorias han sido ampliamente estudiadas, se conoce muy poco sobre la historia de vida de las poblaciones residentes tropicales. Durante tres años (2001–2003), estudiamos la biología reproductiva de una población residente del Chipe Manglero (*D. p. bryanti*) en la Península de Yucatán, México. Encontramos que la reproducción fue muy estacional con nidadas iniciadas cada año al final del periodo de secas, justamente antes de la llegada de lluvias intensas. La fecha promedio de inicio de puesta de huevos fue Mayo 18, sin embargo hubo variación anual significativa, resultando en un periodo reproductivo con extensión de tres meses y medio (mitad de Abril hasta finales de Julio). La abundancia de artrópodos no estuvo correlacionada con la precipitación pluvial ya que los picos de abundancia de artrópodos ocurrieron al final de la estación seca y disminuyeron con el inicio de las lluvias. La mayor actividad de anidación coincidió con la mayor abundancia de artrópodos en el mes de Mayo. La variación anual en el inicio de la reproducción sugiere que el Chipe Manglero podría rastrear los cambios en la abundancia de alimento para ajustar el tiempo de su reproducción.

Abstract. – The Yellow Warbler (*Dendroica petechia*) taxonomic complex includes long-distance temperate-tropical migrants and year-round tropical resident subspecies. While life history traits of northern migratory populations have been widely studied, little is known from their tropical counterparts. Based on observations obtained during three consecutive years (2001–2003), we provide baseline data on breeding seasonality of the Mangrove Warbler (*D. p. bryanti*) from southern Mexico. Breeding was quite seasonal, with clutches initiating each year during the latest portion of the dry season. The average date of clutch initiation was 18 May, but there was a significant annual variation resulting in a breeding season expanded over a period of three and a half months (mid April to end of July). Percentage of active nests was highest in May coinciding with peaks in food abundance. Arthropod abundance was not correlated with the amount of rainfall as abundance peaks occurred during the last portion of the dry season and dropped with the arrival of the rainy season. Annual variation in nesting and clutch initiation suggests that Mangrove Warblers might track changes in food availability as an environmental clue to adjust their timing of breeding. *Accepted 28 April 2009.*

Key words: Breeding biology, Mangrove Warbler, Yellow Warbler, *Dendroica petechia*, ***Dendroica petechia bryanti***, Yucatan Peninsula.

INTRODUCTION

Life history traits of tropical birds supposedly are characterized by small clutch sizes, high nest depredation rates, long nesting season, extended parental care, permanent pairbonds, and high adult survival (Skutch 1985, Martin 1996, Stutchbury & Morton 2001). However, for most species, data substantiating these assertions are lacking (Stutchbury & Morton 2001). Such information is essential for better understanding the factors that limit and regulate population dynamics, and for explaining differences in the evolution of life history traits between north-temperate and south-tropical birds (Martin 1996).

The Yellow Warbler (*Dendroica petechia*) has one of the largest breeding distributions of any new world passerine (AOU 1998, Lowther *et al.* 1999). The 43 recognized subspecies complex is classified into three groups: 1) the migratory Northern (*aestiva*) group, distributed throughout North America, 2) the resident Golden (*petechia*) group, distributed mainly in the Caribbean islands, and 3) the resident Mangrove (*erithachorides*) group, found in mangroves of both Pacific and Atlantic coasts of Central America and northern South America (Dunn & Garret 1997, Lowther *et al.* 1999). Several aspects of the *aestiva* migratory group, including geographic variation, reproductive biology, vocal behavior, responses to brood parasitism, foraging ecology, and winter territoriality, have been studied extensively (see Lowther *et al.* 1999). In contrast, little research has been conducted on either the *petechia* or *erithachorides* groups despite their extensive distribution. Biological data are largely anecdotal (e.g., Bent 1963, Stiles & Skutch 1989, Howell & Webb 1995), and information on breeding biology is scarce with descriptions of nesting behavior based on a rather small number of nests (<15) found over periods ranging from two to four years (Snow 1966, Prather & Cruz 1995, Barrantes 1998). Only recently, Salgado-Ortiz *et al.* (2008) have provided for the first time detailed data on life history traits (e.g., clutch size, length of incubation and nestling periods, and nesting success) of the Mangrove Warbler subspecies (*D. p. bryanti*) from southern Mexico. In this paper we provide complementary information on breeding seasonality.

METHODS

In Mexico, Mangrove Warbler is a common breeders in the southern half of Baja California and south from Sonora to Chiapas in the Pacific. On the Gulf coast of Mexico the species is found from south Tamaulipas southward except for Cozumel island where resident birds belong to the Golden group (Dunn & Garret 1997; Howell & Webb 1995).

We studied a breeding population of the subspecies (*D. p. bryanti*) in three consecutive years (2001–2003) at Celestún Biosphere Reserve in the Yucatan Peninsula, Mexico. The Reserve is located at the northwestern portion of the Yucatan Peninsula (20°46’–21°06’N, and 90°11’–90°25’W), 90 km west of Mérida, the capital of the state of Yucatan (Fig. 1). The climate in the area is classified as tropical semi-arid with an average annual temperature of 28.5°C and an average annual rainfall of 750 mm with a maximum monthly average in September (170 mm) and minimum in March (5.2 mm) (SEMARNAT 2000). These fluctuations result in a pronounced climatic regime characterized by a dry season extending from December to May and a wet season extending from June to November (SEMARNAT 2000).

All of our observations occurred on six (10–15 ha) plots established randomly within large (40–100 ha) black mangrove forest (*Avicennia germinans*) tracts located along the southern portion of the Celestún estuary (Fig. 1). All six plots were approximately 1 km apart from each other and were marked with an alpha-numeric grid system at 25 m intervals to facilitate territory mapping and nest searching. At each plot, Mangrove Warblers were captured using song playback and a decoy to lure birds into mist nets. All cap-

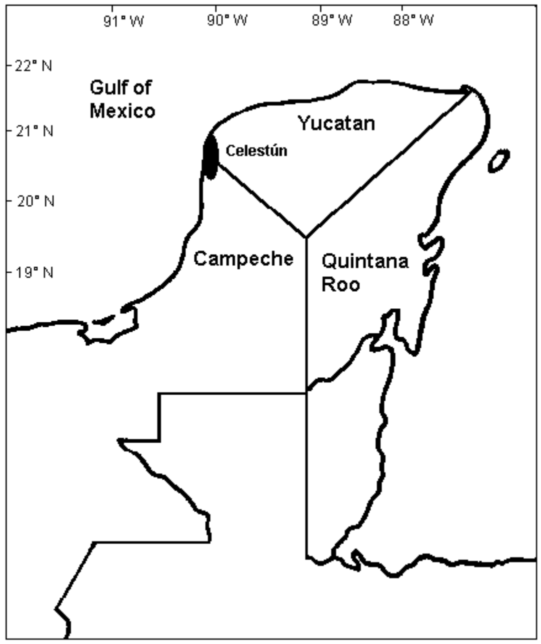

FIG. 1. Location of the Celestún Biosphere Reserve (black oval) in the Yucatan Peninsula, Mexico.

tured birds received a unique combination of three colour bands, and were sexed and aged as either SY (second year) or ASY (after second year) individuals (Stiles & Skutch 1989, Howell & Webb 1995).

To determine breeding seasonality, intensive nest searching was conducted throughout the study period each year. Nests were found by following females usually during nest building, but also by following parents carrying food items or following individuals giving alarm calls. Nests were also found by carefully scanning vegetation within the territory. After nest failure or after successfully fledging young, we continued following pairs to determine if additional nests were attempted. To determine the relationship of breeding activity with weather, rainfall data for the three years of the study (2001–2003) were obtained from the "Comision Nacional del Agua" (CNA) at the Yucatan state agency. The average distance of the study plots to the nearest weather station was 2.5 km, thus providing a good representation of the local weather conditions experienced at our study sites.

To determine the relationship of breeding activity with food availability, we collected information on the abundance of arthropods from March to July in both 2002 and 2003 using six malaise traps (Darling & Packer 1988). Although this method may not evaluate arthropod abundance directly available to birds, it does reflect the temporal variation in arthropod abundance to which birds are exposed (Copper & Whitmore 1990). One malaise trap was situated at the centre of each study plot and remained at that same site throughout the study period. Insects were collected within a plastic collector head containing 70% ethanol, and samples were collected on a weekly basis and collector heads were refilled with clean ethanol each week. All insect samples were counted and sorted to taxonomic order.

For statistical analysis, we first checked our data for normality. We performed non-parametric Wilcoxon or Kruskal-Wallis tests for statistical differences between group means (with χ^2 indicating probability). T-tests or ANOVA were used when data were normally distributed. Mean ± SD are reported for all measurements unless otherwise specified.

RESULTS

Each year, Mangrove Warbler females initiated nest building during the second half of April. Nest building took an average of 5 ± 0.9 days (n = 200), but building time varied with respect to the age of the female, lasting on average 4.6 ± 0.7 days (n = 170) for ASY females and 5.9 ± 1.0 days (n = 30) for SY females (χ^2_1= 30.53, P < 0.0001). For earlier nests, there was a time lag between 8–15 days from the date of nest completion to the laying of the first egg. The earliest clutch initiation recorded over the three breeding seasons was 23 April and the latest 25 July (Fig. 2). The average date of clutch initiation was May 18 ± 11.4 days (n = 164). Breeding started significantly later in 2001 (mean date = May 25, ± 10 days, n = 42) compared to 2002 (mean date = May 13 ± 12 days, n = 65) and 2003 (mean date = May 17 ± 8 days, n = 57, Fig. 2); (ANOVA, $F_{2\text{-}156}$ = 18.54, P < 0.0001). The duration of the clutch initiation period for first nesting attempts ranged from 37 days in 2001 to 57 in 2003. After failure of first nest attempts, most replacement nests were initiated in June, but third and later attempts were initiated as late as the second half of July, resulting in a breeding season extending over a period of three and a half months (mid April to late July).

Average annual rainfall for the three years of the study was below the historic annual average (750 mm) estimated for the region (2001, 452 mm; 2002, 486 mm; 2003, 514 mm), for an average of 484 ± 31 mm over the three years combined, with no significant differences observed among years (Kruskal Wallis ANOVA, H = 0.055, P = 0.97). Mangrove Warbler breeding started during the latest portion of the dry season before the arrival of heavy rains (Fig. 3). Clutch initiation occurred earlier in 2002, coinciding with higher accumulation of rain (17.8 ± 27.6 mm) during the dry season (Fig. 3), but no statistical differences were observed in comparison to either 2001 (6.7 ± 9.3 mm) or 2003 (7.2 ± 9.9 mm), (H = 0.17, P = 0.91).

The average number of arthropods captured per plot at all plots combined was significantly higher in 2003 (2100 ± 871 individuals) compared to 2002 (869 ± 193 individuals) (t-test = -6.0, P < 0.001). However, the number of arthropods within years was not correlated with the amount of rainfall (r_s = -0.19, P = 0.59). Within each year, the average number of arthropods was highest in May (Table 1), but differences among months were significant only in 2003 ($F_{4,17}$ = 8.0, P = 0.002) and not in 2002 ($F_{4,17}$ = 1.9, P = 0.17). Between years, the average number of arthropods for each month was not significantly different for March and April, but did vary significantly for May, June, and July, with higher numbers for these months in 2003 compared to 2002 (Table 1). Overall, the lower abundance of arthropods in 2002 coincided with drier conditions over the two months (March–April) prior to breeding (1.0 mm of rain for 2002 and 26 mm for 2003; Fig. 4). A similar trend occurred over the breeding period (May–July in 2002; 36.6 ± 23 mm and 70.8 ± 62 mm; in 2003; Fig. 4), although differences were not statistically significant (H = 0.43, P = 0.51). The percentage of clutches initiated in April averaged 8% (range 7–18%), 82% for May (range 77–89 %), and 10% for June (range 4–19%). The percentage of clutches for each month was correlated with monthly differences in num-

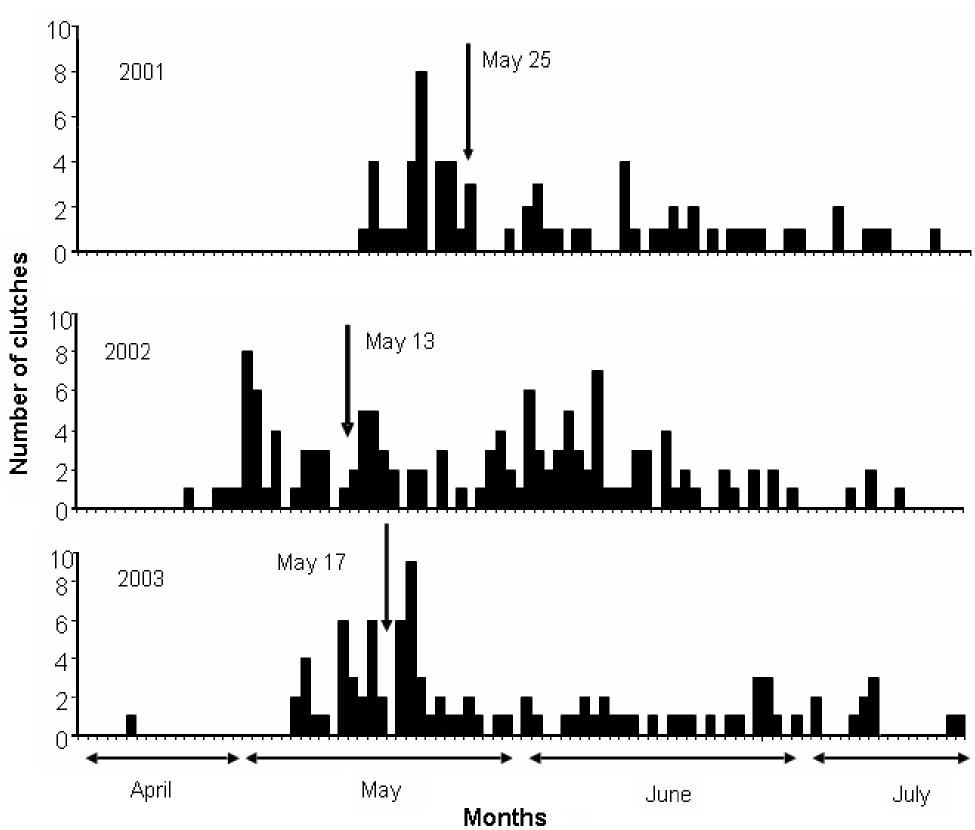

FIG. 2. Clutch initiation (all nesting attempts) of Mangrove Warblers (2001–2003) at Celestún Biosphere Reserve, Yucatan, Mexico. Arrows indicate the average date of clutch initiation for each year.

ber of arthropods ($r_s = 0.82$, $P = 0.003$; Fig. 4).

DISCUSSION

It has been suggested (Stutchbury & Morton 2001) that a higher stability of climatic conditions in tropical habitats allows for food resources to be available year-round. This assumption predicts that breeding could occur at any time of the year (Tallman & Tallman 1997). However, recent studies indicate a significant heterogeneity in the timing and length of the breeding season of tropical birds, depending on taxa or geographic region (Stutchbury & Morton 2001). In some species, breeding activity has indeed been found to occur throughout the year (Skutch 1950, Miller 1962, Tallman & Tallman 1997), but for most species seasonality in breeding is prevalent (Skutch 1950, Fogden 1972, Cruz & Andrews 1989, Tarroux & McNeil 2003). A general consensus from tropical avian phenology studies is that the onset of breeding is closely connected with the rainy seasons (Snow & Snow 1964, Wunderle 1982, Boag & Grant 1984, Bancroft *et al.* 2000, Ahumada 2001, Tarroux & McNeil 2003). Thus, rainfall may be a primary stimulus for reproductive activity in tropical birds, especially in arid hab-

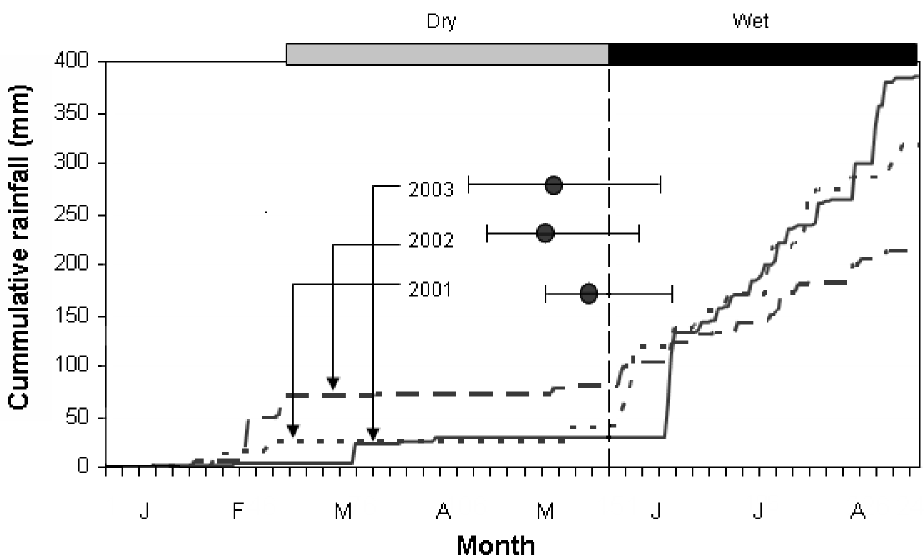

FIG. 3. Cumulative rainfall patterns (January–August) and comparison of the mean date of clutch initiation (black dots) of Mangrove Warblers (2001–2003) at Celestún Biosphere Reserve, Yucatan, Mexico. The lines crossing the dots show the length of clutch initiation for each year considering the first and last clutch.

itats where environmental conditions are unpredictable (see Immelmann 1971). Moreover, reproductive activity is driven indirectly through the effects of rainfall on plant phenology, which in turn influences food supply, rather than by rainfall itself (Poulin *et al.* 1992, Bancroft *et al.* 2000, Ahumada 2001, Tarroux & McNeil 2003).

In this study, we found that Mangrove Warbler breeding was quite seasonal, spanning a period of three and a half months (mid April to end of July). The extension of the breeding season was longer by one month as compared to that of the temperate migrant Yellow Warbler populations (Lowther *et al.* 1999, Salgado-Ortiz *et al.* 2008). Breeding patterns were consistent among years, indicating a predictable breeding seasonality similar to that of temperate zone species (see Immelmann 1971). Rainfall and arthropod abundance were also quite seasonal, with rainfall patterns over the three years being consistent with historical descriptions of the climatic region (SEMARNAT 2000) in which roughly 75% of the rain occurs during the peak of the rainy season from June to September. Rainfall was also present during the dry season (January–May), although in this particular period the precipitation amount was very unpredictable. In concordance with the well defined climatic season at Celestún, Mangrove Warbler's clutches always started during the last portion of the dry season but in the absence of immediate previous rains, suggesting that timing of breeding was not triggered by local rainfall. Moreover, each year females started nest building during the dry season. For earlier nests there was a time lag of up to 15 days between the end of nest construction and the laying of the first egg, suggesting that other complex interactions of environmental factors trigger clutch initiation. Recent evidence indicates that photoperiod and food might be more important factors influencing reproduc-

TABLE 1. Average number of arthropods (± SD) captured per month in malaise traps (all study plots combined) for both 2002 and 2003 at mangroves of Celestún Biosphere Reserve, Yucatan, México. The "*P*" values result from t-test comparisons for each month between years.

Month	2002	2003	P
March	927 ± 41	983 ± 172	n.s.
April	821 ± 83	1802 ± 913	n.s.
May	1030 ± 196	3053 ± 316	$P < 0.001$
June	773 ± 238	2273 ± 501	$P = 0.002$
July	739 ± 213	1649 ± 90	$P = 0.01$

tive activities of tropical birds, especially in seasonally predictable environments (Wikelski *et al.* 2000, Hau *et al.* 2000). Hau *et al.* (2000) demonstrated that food is a very important proximate factor regulating seasonal breeding of tropical Spotted Antbirds (*Hylophylax naevioides*) in Panama. On the other hand, Wikelski *et al.* (2000) found that changes in reproductive activity in the same species correlated strongly with changes in tropical photoperiod and weakly with light intensity and rainfall, but were unrelated to mean temperature. The conclusion from both studies was that tropical birds use changes in food availability as a short-term cue for fine tuning reproductive activities, while photoperiod acts as the long-term factor used to anticipate seasonal changes. In our study, variability in the mean dates of clutch initiation between years and the delay in egg-laying after nest completion suggests that Mangrove Warblers may be tracking changes in arthropod numbers to fine tune initiation of breeding.

In most tropical seasonal environments, arthropod abundance is lower during the dry season and higher during the wet season (Janzen 1973, Poulin *et al.* 1992). We found the opposite pattern in our mangrove study area, where arthropod abundance was highest during the late portion of the dry season and dropped right after the arrival of the rains. Lefebvre *et al.* (1994) noted a similar trend in mangroves of Venezuela. Such differences suggest either that the severity of the dry season is less limiting in mangroves than in other seasonal tropical habitats, or that arthropod numbers in this habitat are influenced by environmental factors other than rain. In support of the first assumption, Janzen (1973) found in Costa Rica that in areas with mild dry seasons, the number and species of insects is higher during the dry season. Mangrove Warblers clearly timed their breeding to coincide with peaks in food abundance, and these were not explained by rainfall. The number of arthropods began to increase just prior to clutch initiation and was highest during the time with the highest percentage of active nests, providing support for the role of food availability in the initiation of breeding (Lack 1954, Perrins 1970). A similar relationship was found for other tropical birds breeding in mangroves of Venezuela (Lefebvre *et al.* 1994) and may explain as well the timing of breeding of Mangrove Warbler in the Galápagos in the absence of rain (Snow 1966).

Our results support the concept that seasonality of breeding is a widespread pattern in tropical birds (Skutch 1950, Fogden 1972, Poulin *et al.* 1992, Bancroft *et al.* 2000, but see Stutchbury and Morton 2001). Nonetheless, whether rainfall or food by itself is the primary factor driving the onset of breeding deserves further investigation. Our study was not aimed to determine the direct effects of environmental factors on the timing of breeding of Mangrove Warbler, thus conclusions can only be validated with further experimental studies. Although both rainfall and food have been put forth as key factors governing the onset of breeding activities in tropical birds, other factors, such as photoperiod, appear to play also a significant role. To gain a better understanding of life history traits of tropical birds, more baseline reproductive and

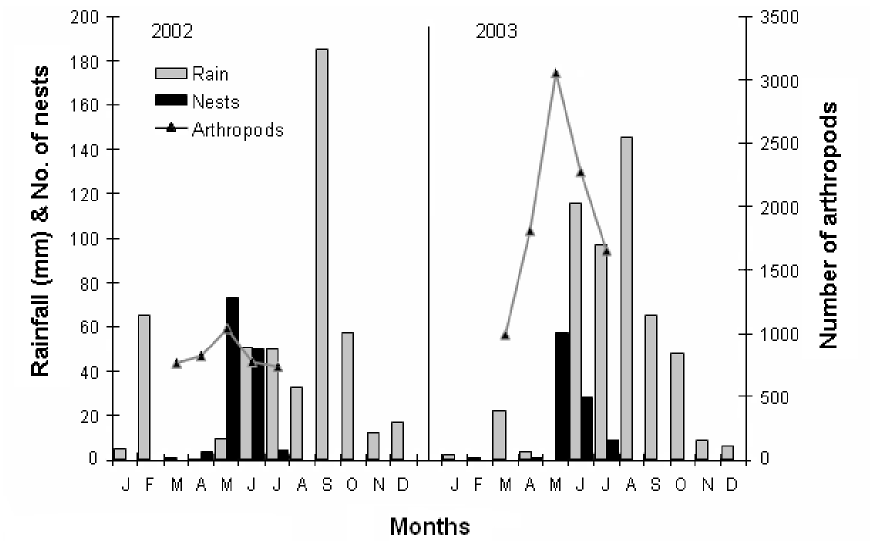

FIG. 4. Relationship of monthly rainfall with the number of arthropods and number of active nests in both 2002 and 2003 at Celestún Biosphere Reserve, Yucatan, Mexico.

demographic studies from additional tropical species and from different geographic locations are needed. The Yellow Warbler complex, with both tropical resident and long-distance migrant subspecies, provides an ideal system for further comparisons of the evolution of life history variation.

ACKNOWLEDGMENTS

We thank the authorities at Celestún Biosphere Reserve and Ducks Unlimited of Mexico (DUMAC) for permits and logistical support. Special thanks go to David Alonso Parra, David Bacab, Esteban Medrano, Luis Carrillo, Andrew Stevens, and Elsa Figueroa for their valuable field assistance. The study was supported financially by CONACYT-Mexico, and grants from Queen's University and the Smithsonian Institution Fellowship Program. We also thank Fernando Villaseñor, Leonardo Chapa Jorge Vega, André Weller, and an anonymous reviewer for their comments to the manuscript.

REFERENCES

Ahumada, J. A. 2001. Comparison of the reproductive biology of two Neotropical wrens in an unpredictable environment in northeastern Colombia. Auk 118: 191–210.

American Ornithologists' Union. 1998. Check-list of North American birds. 7th ed. American Ornithologists' Union, Washington, D.C.

Bancroft, G. T., R. Bowman, & R. J. Sawicki. 2000. Rainfall, fruiting phenology, and the nesting season of White-crowned Pigeons in the upper Florida Keys. Auk 117: 416–426.

Barrantes, G. 1998. Biología y comportamiento de *Dendroica petechia xanthotera* (Aves: Parulidae). Brenesia 49–50: 61–69.

Bent, A. C. 1963. Life histories of North American wood warblers. Dover Publication Inc., New York, New York.

Boag, P. R., & P. R. Grant. 1984. Darwin's finches (*Geospiza*) on Isla Daphne Major, Galapagos: breeding and feeding ecology in a climatically variable environment. Ecol. Monogr. 54: 463–489.

Copper, R. J., & R. C. Whitmore. 1990. Arthropod sampling methods in ornithology. Stud. Avian

Biol. 13: 29–37.
Cruz, A., & R. W. Andrews. 1989. Observations on the breeding biology of passerines in a seasonally flooded savanna in Venezuela. Wilson Bull. 101: 62–76.
Darling, D. C., & L. Packer. 1988. Effectiveness of malaise traps in collecting Hymenoptera: the influence of trap design, mesh size, and location. Can. Entomol. 120: 787–796.
Dunn, J. L., & K. L. Garrett. 1997. A field guide to warblers of North America. Houghton Mifflin Co., Boston, Massachussetts.
Fogden, M. P. L. 1972. The seasonality and population dynamics of Equatorial forest birds in Sarawak. Ibis 114: 307–343.
Hau, M., M. Wikelski, & J. C. Wingfield. 2000. Visual and nutritional food cues fine-tune timing of reproduction in a Neotropical rainforest bird. J. Exp. Zool. 286: 494–504.
Howell, S. N. G., & S. Webb. 1995. A guide to the birds of Mexico and northern Central America. Oxford Univ. Press, London, UK.
Immelmann, K. 1971. Ecological aspects of periodic reproduction. J. Avian Biol. 1: 341–389.
Janzen, D. H. 1973. Sweep samples of tropical foliage insects: effects of season, vegetation types, elevation, time of day, and insularity. Ecology 54: 687–708.
Lack, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, London, UK.
Lefebvre, G. B., B. Poulin, & R. McNeil. 1994. Temporal dynamics of mangrove bird communities in Venezuela with special reference to migrant warblers. Auk 11: 405–415.
Lowther, P. E., C. Celada, N. K. Klein, C. C. Rimmer, & D. A. Spector. 1999. Yellow Warbler (*Dendroica petechia*). *In* Poole, A. & F. Gill (eds.). The Birds of North America, no. 454. The Academy of Natural Sciences, Philadelphia, Pennsylvania and American Ornithologistsí Union, Washington, D.C.
Martin, T. E. 1996. Life history evolution in tropical and south temperate birds: what do we really know? J. Avian Biol. 27: 263–272.
Miller, A. H. 1962. Bimodal occurrence of breeding in an Equatorial sparrow. Proc. Natl. Acad. Sci. U. S. A. 48: 396–400.
Perrins, C. M. 1970. The timing of birds' breeding seasons. Ibis 112: 242–255.
Poulin, B., G. Lefebvre, & R. McNeil. 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. Ecology 73: 2295–2309.
Prather, J. W., & A. Cruz. 1995. Breeding biology of Florida Prairie Warblers and Cuban Yellow Warblers. Wilson Bull. 107: 475–484.
Salgado-Ortiz, J., P. P. Marra, T. S. Sillet, & R. J. Robertson. 2008. The breeding biology of the Mangrove Warbler (*Dendroica petechia bryanti*) and comparative life history ecology of the Yellow Warbler subspecies complex. Auk 125: 402–410.
SEMARNAT. 2000. Plan de manejo, Reserva de la Biosfera de Celestún, México. Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT), México, D.F., México.
Skutch, A. F. 1950. The nesting season of Central American birds in relation to climate and food supply. Ibis 92: 185–222.
Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. Ornithol. Monogr. 36: 575–594.
Snow, D. W., & B. K. Snow. 1964. Breeding seasons and annual cycles of Trinidad land-birds. Zoologica 49: 1–39.
Snow, D. W. 1966. Annual cycle of the Yellow Warbler in the Galapagos. Bird Banding 37: 44–49.
Stiles, F. G., & A. F. Skutch. 1989. A guide to the birds of Costa Rica. Cornell Univ. Press, Ithaca, New York, New York.
Stutchbury, B. J. M., & E. S. Morton. 2001. Behavioural ecology of tropical birds. Academic Press, New York, New York.
Tallman, D. A., & E. J. Tallman. 1997. Timing of breeding by antbirds (Formicariidae) in a seasonal environment in Amazonian Ecuador. Ornithol. Monogr. 48: 783–789.
Tarroux, A., & R. McNeil. 2003. Influence of rain on the breeding and molting phenology of birds in a thorn woodland of northeastern Venezuela. Ornitol. Neotrop. 14: 371–380.
Wikelski, M., M. Hau, & J. C. Wingfield. 2000. Seasonality of reproduction in a Neotropical rainforest bird. Ecology 81: 2458–2472.
Wunderle, J. M., Jr. 1982. The timing of the breeding season in the Bananaquit (*Coereba flaveola*) on the island of Grenada, W. I. Biotropica 14: 124–131.