



## BREEDING ECOLOGY OF THE MANGROVE WARBLER (*DENDROICA PETECHIA BRYANTI*) AND COMPARATIVE LIFE HISTORY OF THE YELLOW WARBLER SUBSPECIES COMPLEX

JAVIER SALGADO-ORTIZ,<sup>1,3</sup> PETER P. MARRA,<sup>2</sup> T. SCOTT SILLETT,<sup>2</sup> AND RALEIGH J. ROBERTSON<sup>1</sup>

<sup>1</sup>Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada; and <sup>2</sup>Smithsonian Migratory Bird Center, National Zoological Park, P.O. Box 37012 MRC 5503, Washington, D.C. 20012, USA

**ABSTRACT.**—It is widely accepted that tropical birds differ from temperate species in life-history traits and social behaviors, yet baseline ecological data are lacking for most tropical species and comparative studies often fail to control for phylogenetic influences. Within the Americas, the Yellow Warbler (*Dendroica petechia*) is ideal for such comparisons because its subspecies encompass a range of life-history strategies; the subspecies include long-distance migrants, temperate–tropical migrants, and tropical residents. We collected baseline data on the breeding ecology of Mangrove Warblers (*D. p. bryanti*) from southern Mexico (2001–2003) and compared their life-history traits with those of temperate and other tropical subspecies using existing data. Mangrove Warblers actively defended territories year-round during both nonbreeding and breeding seasons. The timing of breeding varied by year, and clutch size averaged  $2.9 \pm 0.5$  [SD] eggs, with both a median and a mode of 3 eggs. Annual estimates of nesting success ranged from 18% to 33%, and nest depredation was the primary cause of nest failure. Annual survival was significantly higher for males (0.65) than for females (0.52) and, given our data, did not vary by age or year. On the basis of a comparative analysis of life-history data from published studies on the Yellow Warbler subspecies complex, we found that most life-history traits differed between tropical and temperate latitudes. Specifically, compared with temperate Yellow Warblers, Mangrove Warblers exhibited longer breeding seasons, smaller clutch sizes, longer incubation and nestling periods, lower nesting success, higher rates of nest depredation, and higher annual adult survival rates. Received 18 January 2007, accepted 17 July 2007.

Key words: breeding ecology, cost of migration, *Dendroica petechia*, latitudinal variation, life history, Mangrove Warbler, Yellow Warbler.

### Ecología Reproductiva de *Dendroica petechia bryanti* y Comparación de los Rasgos de Historia de Vida de las Subespecies del Complejo de *Dendroica petechia*

**RESUMEN.**—Las diferencias en los rasgos de historia de vida entre especies de aves tropicales y de zonas templadas es una noción ampliamente aceptada. No obstante, se carece de información biológica para la mayoría de especies de aves tropicales y los estudios comparativos con especies de zonas templadas frecuentemente omiten controlar las influencias filogenéticas. En el continente americano, *Dendroica petechia* es una especie ideal para comparaciones de este tipo ya que cuenta con subespecies migratorias que se reproducen en las zonas templadas y con poblaciones tropicales residentes. Estudiamos la biología reproductiva de la subespecie tropical *D. p. bryanti* del sur de México por tres años (2001–2003), y comparamos los rasgos de historia de vida con los de poblaciones de Norte América y de otras subespecies tropicales. Encontramos que *D. p. bryanti* defiende territorios durante todo el año, que el inicio de la reproducción varió entre años y que el tamaño promedio de la nidada fue de  $2.9 \pm 0.5$  (DE) huevos, con una mediana y moda de tres. Los estimados anuales del éxito de anidación estuvieron entre el 18% y el 33%, y la depredación fue la principal causa del fracaso de los nidos. La supervivencia anual fue mayor en los machos (0.65) que en las hembras (0.52) y no varió entre edades o años. Con base en un análisis comparativo de datos obtenidos de estudios publicados sobre el complejo de subespecies de *D. petechia*, encontramos que la mayoría de rasgos de las historias de vida difieren entre poblaciones de latitudes tropicales y templadas. Específicamente, en comparación con las poblaciones de Norte América, *D. p. bryanti* presentó un periodo reproductivo más largo, un tamaño menor de nidada, periodos más largos de incubación y empollamiento, mayor éxito reproductivo, mayor tasa de depredación de nidos, y mayor supervivencia de los adultos.

<sup>3</sup>Present address: Laboratorio de Ornitología, Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, México. E-mail: javo\_salgado@yahoo.com.mx

THE YELLOW WARBLER (*Dendroica petechia*) has one of the largest breeding distributions of any New World passerine, and its 43 recognized subspecies exhibit considerable geographic variation in plumage, morphology, and life history (Bent 1963, Browning 1994, American Ornithologists' Union 1998, Lowther et al. 1999). The subspecies complex is classified into three groups: (1) the migratory Northern (*aestiva*) group, with nine subspecies distributed throughout North America; (2) the resident Golden (*petechia*) group, which comprises 18 subspecies distributed mainly in the Caribbean islands; and (3) the resident Mangrove (*erithachorides*) group, with 16 subspecies found in mangroves on both Pacific and Atlantic coasts of Central America and northern South America (Dunn and Garret 1997, Lowther et al. 1999). The *aestiva* group has been studied intensively on topics including geographic variation, reproductive biology, vocal behavior, responses to brood parasitism, foraging ecology, and winter territoriality (see Lowther et al. 1999).

By contrast, little research has been conducted on either the *petechia* or the *erithachorides* group, despite their extensive distribution. Thus far, ecological data exist largely as anecdotal information in the literature (e.g., Bent 1963, Wiley 1985). We are aware of only three studies that provide information on the breeding biology of tropical Yellow Warblers. Snow (1966) and Barrantes (1998) studied Mangrove Warbler subspecies in the Galápagos Islands (*D. p. aureola*) and Costa Rica (*D. p. xanthotera*), respectively. Prather and Cruz (1995) studied a population of Cuban Yellow Warblers (*D. p. gundlachi*) in Florida. These three studies, however, are largely descriptive or based on few nests.

We studied the breeding ecology of a population of Mangrove Warblers (*D. p. bryanti*) in southern Mexico. Here, we provide the first detailed data on population structure, timing of breeding, clutch size, length of incubation and nestling periods, frequency of renesting and double brooding, reproductive success, and parental care and the first statistically rigorous estimates of annual survivorship. In addition, we compare life-history traits of tropical populations of *D. petechia* with those of temperate migrant conspecifics.

## METHODS

**Study site and species.**—The Mangrove Warbler is a common breeder in the southern half of Baja California and south from Sonora to Chiapas in the Pacific. On the Gulf coast of Mexico it is found from south Tamaulipas southward, except on Cozumel Island, where resident birds belong to the *petechia* group (Howell and Webb 1995, Dunn and Garret 1997). Mangrove Warblers are distinguished from northern types by their larger overall size and shorter primary projection. Males have complete dark-chestnut hoods and narrower chestnut streaking below (Stiles and Skutch 1989, Howell and Webb 1995).

Our research was conducted from 2001 to 2003 at Celestún Biosphere Reserve (20°51'N; 90°23'W) on the Yucatan Peninsula, Mexico, 90 km west of Mérida. The climate in the area is classified as "tropical semiarid." Mean daily temperature is 28°C, and mean rainfall is 750 mm year<sup>-1</sup> (1952–1997). Maximum monthly precipitation occurs in September (mean = 170 mm), and the minimum occurs in March (mean = 5.2 mm), with a pronounced dry season extending from December to May (Secretaría de Medio Ambiente y Recursos Naturales [SEMARNAT] 2000).

**Data collection and analysis.**—All data were collected on six 10- to 15-ha plots established within larger tracts (40–100 ha) of Black Mangrove (*Avicennia germinans*) forest located along the southern portion of the reserve. Red Mangrove (*Rhizophora mangle*) is also commonly found in the area but is confined to deeper waters along the shore of the estuary (SEMARNAT 2000). All six plots were marked with an alpha-numeric grid system at 25-m intervals to facilitate territory mapping, estimation of bird density, and nest searching. Plots were ~1 km apart, and canopy height ranged from 4 to 10 m (Salgado-Ortiz 2006).

On each plot, we captured Mangrove Warblers using song playbacks accompanied by a decoy to lure individuals into mist nets. Captured birds received a unique combination of three color leg bands and were sexed and aged as either second-year (SY) or after-second-year (ASY) individuals (Stiles and Skutch 1989, Howell and Webb 1995). Birds not captured were identified by plumage patterns when possible. In contrast to ASY males, SY males have chestnut spots only around the head rather than a complete chestnut hood and have fewer streaks on the breast. Adult (ASY) females typically have bright yellow plumage with rusty chestnut color extending to the forehead, whereas SY individuals have pale yellow-gray plumage and little or no rusty patch on the forehead. Territories of Mangrove Warblers were determined by mapping locations of color-banded individuals and recording locations of counter-singing males, foraging sites, territorial disputes, and active nests. Bird density was calculated as the total number of adults (pairs) per 10 ha. Age structure was determined by calculating the proportion of ASY to SY individuals defending territories.

We found and monitored nests of color-banded warblers on our study plots. Nests were found by following nest-building females, parents carrying food items, or individuals giving alarm calls, or by carefully scanning vegetation within territories. To determine clutch size, length of incubation and nestling periods, and final nest fate, nests were checked every second or third day. Nests found with complete clutches or with nestlings were visited every two days until hatching or fledging, and dates of clutch initiation or hatching were determined by back-dating (Manolis et al. 2000). To quantify parental care, we observed nests and recorded the number of trips parents made to determine food-delivery rates and whether these varied between females and males. Nest observations lasted 1 h and were conducted when nestlings were between five and seven days of age. After a nest fledged or failed, we continued observing pairs to determine whether additional nests were attempted. We defined "nesting attempt" as a female initiating egg laying and "double brooding" as initiation of egg laying after successfully fledging young from a previous nest within the same season. Parametric statistics were used for analysis of variables related to breeding ecology when data met model assumptions. When errors were not normally distributed or variances were not equal between test groups, we used nonparametric statistics. We report means  $\pm$  SE for all variables unless otherwise specified.

Daily nest survival probabilities were estimated using the Mayfield method (Mayfield 1961, 1975), to allow comparison with other studies of *D. petechia*. We used CONTRAST (Hines and Sauer 1989) to test for differences in nest success at Celestún between years. We determined the proportions of nests failing because of predation, brood parasitism, and other causes. A nest was considered depredated if either eggs or nestlings disappeared between nest checks or if the nest or its contents were damaged or destroyed.

Cormack-Jolly-Seber (CJS) models (Pollock et al. 1990, Lebreton et al. 1992) were used to estimate age- and sex-specific annual survival probabilities. Survivorship data were based on resighting of color-marked territorial individuals present on our study plots in each year. We made an additional visit to our plots in 2004 to obtain data on the number of color-banded individuals still defending territories. Candidate CJS models were chosen prior to data analysis. To eliminate nonterritorial individuals, only birds resighted within a week of initial capture were included in data analyses. All marked individuals that remained at our study plots each year were detected during our routine field work; therefore, resighting probabilities in all CJS models were fixed at 1. We constructed CJS models in MARK (White and Burnham 1999) using a sine link function. Model-selection methods based on second-order Akaike's information criterion ( $AIC_c$ ) were used to rank candidate models (Burnham and Anderson 1998). Goodness-of-fit of our global model was verified with RELEASE (Burnham et al. 1987) implemented in MARK.

## RESULTS

**Population structure and density.**—Territory occupancy and density of Mangrove Warblers remained relatively stable within and between years. In total, 135 males and 104 females were banded across all plots and years combined. Of these, 119 males (88%) and 83 females (80%) were ASY, and 16 males (12%) and 21 females (20%) were SY. After mapping territories of banded individuals, we determined that in any year, the proportion of banded individuals within study plots ranged from 70% to 100% for males and from 50% to 80% for females. Density averaged  $10.6 \pm 0.7$  pairs per 10 ha (range:  $8.3 \pm 0.7$  to  $13.2 \pm 0.5$ ), with territories ranging in size from 0.45 to 1.20 ha (mean =  $0.77 \pm 0.06$ ). Densities did not change between nonbreeding and breeding seasons. Age ratios of territorial individuals remained stable over the three breeding seasons (Table 1). Most males (83%) were monogamous, but bigamy also occurred (Table 1). On average,  $7.7 \pm 2.0\%$  of males were unmated per year, with most unmated individuals being SY (Table 1). We found no evidence of unmated females.

**Timing of breeding.**—Most Mangrove Warbler clutches were initiated in May, with the earliest recorded on 20 April 2003 and the latest on 19 June 2001 (first attempts only), a period spanning 60 days. Mean date of first egg-laying within first nesting attempts was  $18 \text{ May} \pm 0.9$  days ( $n = 161$ ). Breeding started significantly later in 2001 (mean date =  $25 \text{ May} \pm 1.7$ , range: 14 May to 19 June,  $n = 42$ ) than

in 2002 (date =  $13 \text{ May} \pm 1.3$ , range: 26 April to 12 June;  $n = 65$ ) and 2003 (date =  $17 \text{ May} \pm 1.4$ , range: 20 April to 16 June;  $n = 57$ ) (analysis of variance [ANOVA]:  $F = 18.54$ ,  $df = 2$  and  $156$ ,  $P < 0.0001$ ). Most replacement nests were initiated in June, but third and later attempts were initiated as late as the second half of July, which resulted in a breeding season of three and a half months (mid-April to the end of July).

**Clutch size, nesting attempts, and length of incubation period.**—Clutch size for first nest attempts averaged  $2.90 \pm 0.04$  (range: 2–4;  $n = 160$  nests), with both a median and a mode of 3. Four-egg clutches were uncommon (5.2%). Mangrove Warblers typically laid one egg per day, but females sometimes skipped one day after laying the first egg. Clutch size did not vary between years for either first clutches ( $\chi^2 = 2.57$ ,  $df = 2$ ,  $P = 0.27$ ) or all clutches combined ( $\chi^2 = 1.44$ ,  $df = 2$ ,  $P = 0.48$ ). The number of nesting attempts by individually marked females ( $n = 162$ ) ranged from 1 to 5 per season, with an average of  $1.80 \pm 0.05$  and a median of 2 for the three years combined. The average number of nesting attempts varied by year (Kruskal-Wallis  $H = 8.20$ ,  $df = 2$ ,  $P = 0.02$ ), with more replacement nests found in 2002 ( $2.00 \pm 0.08$ , range: 1–5) than in either 2001 ( $1.40 \pm 0.07$ , range: 1–3) or 2003 ( $1.51 \pm 0.07$ , range: 1–4). Fourth and fifth nesting attempts were, however, rare (7% in 2002,  $n = 131$  nests; 2% in 2003,  $n = 92$  nests). An analysis of covariance [ANCOVA] was used to test for seasonal declines in clutch size by using the first three nesting attempts, with clutch size as dependent variable, and year, number of nesting attempts, and their interaction as independent factors. There were no significant differences in clutch size from the first to third attempts among years (ANCOVA:  $F = 1.61$ ,  $df = 8$  and  $265$ ,  $P = 0.12$ ). However, clutch size declined significantly in 2003 (range: 2.91–2.33 eggs; first to third nest), resulting from the interaction of year and number of nesting attempts (ANCOVA: year,  $F = 0.97$ ,  $df = 2$  and  $271$ ,  $P = 0.38$ ; nesting attempt,  $F = 0.22$ ,  $df = 2$  and  $271$ ,  $P = 0.80$ ; year\*nesting attempt,  $F = 2.88$ ,  $df = 4$  and  $269$ ,  $P = 0.02$ ). Females initiated incubation with the laying of the penultimate egg. Mean incubation period was  $13.1 \pm 0.5$  days (range: 12–14 days;  $n = 172$ ) but did not differ within years ( $\chi^2 = 1.04$ ,  $df = 2$ ,  $P = 0.90$ ) or between years ( $\chi^2 = 2.50$ ,  $df = 2$ ,  $P = 0.29$ ) (Table 2).

**Timing of hatching, length of nestling period, and timing of fledging.**—The average date of hatching (first nests attempts) was  $30 \text{ May} \pm 11$  days (range: 8 May to 29 June). Hatching of clutches typically concluded within 24 h, which suggests hatching synchrony. Mangrove Warbler nestlings fledged, on average,  $11.0 \pm 0.9$  days after hatching (range: 9–13 days;  $n = 73$  nests), with no differences associated with brood size (Kruskal-Wallis  $H = 3.30$ ,  $df = 2$ ,  $P = 0.20$ ). Duration of the nestling period was significantly shorter in 2003 than in either 2001 or 2002 (ANOVA:  $F = 9.1$ ,  $df = 2$  and  $69$ ,  $P = 0.0003$ ; Table 2). Mean number of young fledged per successful nest was  $2.00 \pm 0.06$  for all years combined (range: 1–3;  $n = 73$  nests), with no differences between years (Table 2). The average date of fledgling for first nest attempts was  $12 \text{ June} \pm 13$  days, with the earliest fledglings observed on 20 May 2002. Mangrove Warblers fledged young as late as 30 July.

**Parental care.**—Parental investment varied by sex and by the number of young fledged. Males were observed feeding incubating females in 21 (38%) of 55 nests. Incubation feeding ranged from one to three times per hour (mean =  $1.33 \pm 0.58$  visits  $h^{-1}$ ). In all but 2 of the 32 nests observed to quantify parental care, both sexes fed nestlings. Feeding visits by males (mean =  $8.14 \pm 0.97$  feeding visits  $h^{-1}$ ,

TABLE 1. Population structure of Mangrove Warblers at Celestún Biosphere Reserve, Yucatan, Mexico, February–May, 2001–2003, from all study plots combined (five in 2001 and six in 2002–2003). Numbers in parentheses indicate percentage of the population.

	2001	2002	2003
Males ( $n$ )	75	87	80
ASY	63 (84)	84 (96)	73 (91)
Monogamous	61 (81)	71 (82)	69 (86)
Bigamous	11 (15)	9 (10)	4 (5)
Unmated	3 (4)	7 (8)	7 (9)
Females ( $n$ )	82	88	75
ASY	49 (60)	64 (73)	60 (80)

TABLE 2. Reproductive effort and nesting success of Mangrove Warblers at Celestún Biosphere Reserve, Yucatan, Mexico, 2001–2003. Variance is given as mean ± SE.

	2001	2002	2003	All years
Number of active nests	62	129	92	283
Total eggs laid	186	362	266	814
Mean eggs laid per female	3.80 ± 0.19	5.30 ± 0.28	4.60 ± 0.29	4.60 ± 0.16
Mean incubation period (days)	13.10 ± 0.14	13.10 ± 0.08	13.20 ± 0.09	13.10 ± 0.06
Mean nestling period (days)	11.40 ± 0.17	11.10 ± 0.12	10.50 ± 0.17	11.00 ± 0.10
Nesting success <sup>a</sup>	0.310 ± 0.005	0.180 ± 0.005	0.330 ± 0.004	0.260 ± 0.003
Mean number of fledglings (successful nests)	2.20 ± 0.53	1.90 ± 0.54	1.90 ± 0.58	2.00 ± 0.50

<sup>a</sup>Mayfield estimates of nesting success are based on the complete nesting period (26 days, including laying–incubation and nestling stages).

range: 2–17) and females (mean = 10.35 ± 1.01 visits h<sup>-1</sup>, range: 3–18) were not significantly different (paired *t*-test: *t* = -1.60, *df* = 23, *P* = 0.12). After leaving the nest, fledglings remained on natal territories for an average of 27.4 ± 4.7 days (range: 20–32; *n* = 5). Both parents provided care to fledglings, but this varied depending on the number fledged. Only males provided parental care when one offspring fledged (*n* = 10), whereas both parents provided care when two or three offspring fledged (*n* = 25).

**Nesting success, double brooding, and causes of nest failure.**—For all years combined, the Mayfield estimate of daily survival probability for Mangrove Warbler nests was 0.950 ± 0.003 (range: 0.936–0.960). Annual estimates of nesting success ranged from 18% to 33%, being significantly lower in 2002 than in either 2001 ( $\chi^2 = 8.22$ , *df* = 1, *P* = 0.004) or 2003 ( $\chi^2 = 12.34$ , *df* = 1, *P* = 0.0004; Table 2). Over the three years of our study, 61% of females failed in all nesting attempts and, thus, fledged no young (range: 53–68%; *n* = 162 females). Only 5.5% of the females (9 of 162) initiated a second brood; two were successful. The primary cause of nest failure was depredation, which accounted for the loss of 64% of all active nests. Nest parasitism by Bronzed Cowbirds (*Molothrus aeneus*) was the second most frequent cause of nest failure, affecting 8.5% of all active nests over the three years (Table 3). Minor causes of nest failure included infertility (*n* = 5) and weather (*n* = 1).

**Adult survival.**—The best-fit model for annual survival in Mangrove Warblers included an effect of sex but no effect of age or year (Table 4). Sex-specific survival (based on the sum of AIC<sub>c</sub> weights; models 1 and 2; Table 4) was 20.4× more likely than age-specific survival (models 5 and 8) and 8.7× more likely than the models combining age and sex (models 4 and 7; Table 4). In the best-fit model, females

(0.52 ± 0.04) had lower estimated survival than males (0.65 ± 0.03), and this pattern was consistent across all four years.

**Latitudinal differences in life-history traits.**—We summarized life-history traits of temperate and tropical populations of Yellow Warblers breeding over a latitudinal gradient from 58°N, in Canada, to ~0°S, in the Galápagos Islands. Average clutch size significantly increased from 2.5–2.8 at tropical latitudes to 3.8–5.1 at north-temperate latitudes (*r*<sub>s</sub> = 0.89, *P* < 0.0001; Table 5). The incubation period decreased from ~13 days at tropical latitudes to ~11 days at temperate latitudes, though this difference was not significant (*r*<sub>s</sub> = -0.42, *P* = 0.26; Table 5). The brooding period significantly declined from ~12 days at tropical latitudes to ~8 days at temperate latitudes (*r*<sub>s</sub> = 0.85, *P* = 0.016; Table 5). Nest success tended to be higher at temperate than at tropical latitudes, but data were lacking for most tropical populations (*r*<sub>s</sub> = 0.44, *P* = 0.17; Table 5). Nest depredation significantly decreased from tropical to temperate latitudes (*r*<sub>s</sub> = 0.82, *P* = 0.007; Table 5). Finally, published CJS estimates of annual survival probabilities of Yellow Warbler populations in the temperate zone are lower than our estimates for Mangrove Warblers (Fig. 1). Annual survival probabilities for Yellow Warblers averaged 0.41 ± 0.04 for females and 0.49 ± 0.04

TABLE 3. Causes of nest failure in Mangrove Warblers at Celestún Biosphere Reserve, Yucatan, Mexico, 2001–2003. Values represent the number of active nests lost during incubation and brooding stages (with percentage of active nests in parentheses).

	2001 ( <i>n</i> = 62)	2002 ( <i>n</i> = 129)	2003 ( <i>n</i> = 92)	2001–2003 ( <i>n</i> = 283)
Incubation				
Depredation	17 (27)	55 (42.6)	24 (26)	96 (34)
Brood parasitism	4 (6.5)	7 (5.4)	13 (14)	24 (8.5)
Infertility	2 (3)	0	3 (3)	5 (2)
Subtotal	23 (37)	62 (48)	40 (43)	125 (44)
Brooding				
Depredation	20 (32)	43 (33)	21 (23)	84 (30)
Weather	0	0	1 (1)	1 (0.3)
Total nests lost	43 (69)	105 (81)	62 (68)	210 (74)

TABLE 4. Models of annual survival probability ( $\phi$ ) for adult Mangrove Warblers at Celestún Biosphere Reserve, Yucatan, Mexico, 2001–2004. Recapture probability (*p*) was fixed at 1.0 in all models (see text). Columns give model notation, number of estimable parameters (*K*), second-order Akaike's information criterion values (AIC<sub>c</sub>), AIC<sub>c</sub> differences ( $\Delta_i$ ), and AIC<sub>c</sub> weights (*w<sub>i</sub>*). Subscripts describe parameterizations of  $\phi$ : "age" = two age classes; "sex" = male or female; "year" = parameter varies annually; no subscript = constant over group and time variables. Subscripts joined by an asterisk indicate a factorial model. The global model ( $\phi_{\text{age*sex*year}}$ ) provided a good fit to the data ( $\chi^2 = 0.29$ , *df* = 6, *P* = 0.99).

Model	<i>K</i>	AIC <sub>c</sub>	$\Delta_i$	<i>w<sub>i</sub></i>
(1) $\phi_{\text{sex}}$	2	473.00	0.00	0.63
(2) $\phi_{\text{sex*year}}$	6	476.13	3.13	0.13
(3) $\phi$	1	476.77	3.77	0.10
(4) $\phi_{\text{age*sex}}$	4	476.99	4.00	0.09
(5) $\phi_{\text{age}}$	2	478.71	5.72	0.04
(6) $\phi_{\text{year}}$	3	480.21	7.22	0.02
(7) $\phi_{\text{age*sex*year}}$	10	483.87	10.88	0.00
(8) $\phi_{\text{age*year}}$	6	485.68	12.68	0.00

TABLE 5. Life-history traits of the Yellow Warbler complex across a temperate-to-tropical latitudinal gradient. Values represent means (with range in parentheses; NA = data not available).

Locality <sup>a</sup>	Latitude	Clutch size	Incubation period (days) <sup>b</sup>	Nestling period (days) <sup>c</sup>	Nest success (%) <sup>d</sup>	Nest depredation (%) <sup>e</sup>	<i>N</i>
<b>Temperate</b>							
Churchill <sup>1</sup>	58°40'N	4.7 (4–5)	11.7 (11–13)	8.5 (8–10)	49	36	62
Alaska <sup>2</sup>	58°17'N	5.1 (4–6)	NA	NA	95	5	20
Delta Marsh <sup>3</sup>	50°11'N	4.5 (3–5)	11.3 (10–13)	8.2 (8–10)	48	34	227
Southern Ontario <sup>4</sup>	44°34'N	4.1 (3–5)	11.5 (10–13)	8.8 (8–11)	50	37	109
Iowa <sup>5</sup>	43°00'N	4.0 (3–5)	11.0 (11–12)	9.5 (8–10)	54	NA	41
Wisconsin <sup>6</sup>	43°00'N	3.5 (3–5)	NA	NA	42	29	12
Michigan <sup>7</sup>	42°00'N	3.8 (3–5)	NA	NA	45	NA	20
Rhode Island <sup>8</sup>	41°27'N	4.5 (4–5)	11.3 (10–12)	9.5 (8–10)	51	NA	94
Colorado <sup>9</sup>	37°14'N	3.8 (3–5)	10.5 (8–14)	9.0 (8–9)	52	39.1	66
<b>Tropical</b>							
Key Largo <sup>10</sup>	25°06'N	2.5 (2–4)	13.0 (12–16)	12.0 (10–14)	75	19	16
La Paz <sup>11</sup>	24°08'N	2.8 (2–3)	NA	NA	NA	NA	NA
Celestún <sup>12</sup>	20°46'N	2.8 (2–4)	13.0 (12–14)	11.0 (9–13)	26	64	284
Puerto Rico <sup>13</sup>	18°30'N	2.7 (2–4)	NA	NA	41	NA	107
Costa Rica <sup>14</sup>	10°02'N	2.8 (2–3)	13.0 (13–15)	NA	NA	55	9
Galápagos <sup>15</sup>	0°45'S	2.7 (2–3)	12.0 (NA)	NA	NA	NA	49

<sup>a</sup>References for geographic localities are indicated by superscript numbers: 1 = Briskie 1995, 2 = Rogers 1994, 3 = Goossen and Sealy 1982, 4 = Clark and Robertson 1981, 5 = Schrantz 1943, 6 = Young 1949, 7 = Batts 1961, 8 = Mitra 1999, 9 = Ortega and Ortega 2000, 10 = Prather and Cruz 1995, 11 = Bent 1963, 12 = present study, 13 = Wiley 1985, 14 = Barrantes 1998, and 15 = Snow 1966.

<sup>b</sup>Penultimate egg day to hatch day.

<sup>c</sup>Hatch day to fledged day.

<sup>d</sup>Mayfield estimates of nest success.

<sup>e</sup>Percentage of the total active nests (*N*) reported for each location that failed because of predation.

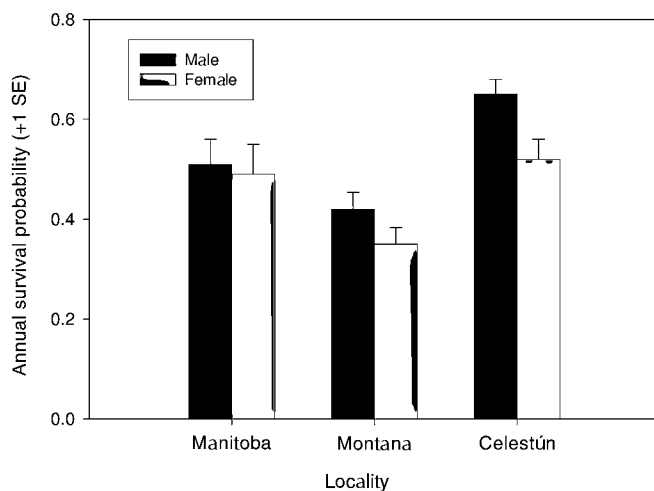


Fig. 1. Apparent survival rate of male and female Yellow and Mangrove warblers calculated by capture–recapture estimates in Manitoba (Mazerolle et al. 2005), Montana (Cilimburg et al. 2002), and Celestún, Mexico (present study).

for males in Montana (Cilimburg et al. 2002) and ranged from 0.41 to 0.62 in Manitoba (Mazerolle et al. 2005).

## DISCUSSION

The life history of Mangrove Warblers at Celestún was similar to that of other tropical passerines (Skutch 1985, Robinson et al. 2000, Stutchbury and Morton 2001) but strikingly different from that of temperate-zone populations of *D. petechia*, particularly those breeding at high latitudes (Table 5). In general, fecundity declines and adult survival increases in Yellow Warblers from temperate to tropical environments. Many hypotheses have been proposed to explain this pattern, including effects of population density, food limitation, nest predation, and fecundity–survival tradeoffs associated with different adult survival rates of tropical, resident populations versus temperate, migratory groups (reviewed by Ricklefs 2000, Russell 2000, Martin 2004). Below, we discuss the behavioral and life-history traits of our study population in comparison with published data from tropical resident bird species and from *D. petechia* over a latitudinal gradient. We also consider the observed variation in life history of Yellow Warblers in the context of environmental differences between temperate and tropical breeding areas.

Mangrove Warblers at Celestún defended territories and maintained permanent pair bonds and stable population density year-round. This pattern fits the descriptions of territorial systems reported for other tropical resident species (Greenberg

and Gradwohl 1986, Morton and Stutchbury 2000). Although the mechanisms of territorial stability are not well understood, it has been suggested that strong competition for limited territories coupled with high adult survival is a likely explanation (Morton et al. 2000). Habitat homogeneity is also considered a potential factor contributing to territorial stability in tropical birds (Greenberg and Gradwohl 1986). These explanations are consistent with the territorial system of the Mangrove Warblers we studied: they inhabit a highly homogeneous habitat, and vacant territories are rapidly occupied by new individuals (J. Salgado-Ortiz et al. unpubl. data).

According to previously published data, Yellow Warblers exhibit strong territorial behavior in both temperate and tropical habitats. Migratory *D. petechia*, for example, defend territories during the breeding season at temperate latitudes (Lowther et al. 1999) and on their nonbreeding grounds in the tropics (Greenberg and Salgado-Ortiz 1994). Such year-round territorial behavior in both migratory and resident populations suggests that Yellow Warblers are limited by habitat or food throughout their range, though population densities appear to vary with latitude (Table 5). The density of Mangrove Warblers reported here (1.1 pairs ha<sup>-1</sup>) is significantly lower than that estimated for Yellow Warbler populations at various North American localities (range: 3.4–14.5 pairs ha<sup>-1</sup>; Young 1949, Goossen and Sealy 1982, Mitra 1999, Yezerinac et al. 1999). This is consistent with our finding that territory size of Mangrove Warblers is significantly larger (mean = 0.77 ha) than that of Yellow Warblers, in which territory size ranges from 0.043 ha at Delta Marsh, Manitoba (Goossen and Sealy 1982), to 0.20 ha in Rhode Island (Mitra 1999). Lower densities and larger territory sizes in tropical species have been attributed to lower food availability in tropical habitats (Thiollay 1988, Terborgh et al. 1990, Lovette and Holmes 1995).

Breeding-season duration and breeding asynchrony tend to decrease with latitude in Yellow Warblers. The ~3.5-month breeding season (late April through July) at Celestún is similar to that reported for *D. p. gundlachi* in Florida (Prather and Cruz 1995) and shorter than that of breeding populations in Puerto Rico (Wiley 1985), Costa Rica (Barrantes 1998), and the Galápagos (Snow 1966) but longer than that of most populations of *D. petechia* in temperate regions (Lowther et al. 1999). Birds breeding at temperate latitudes may be able to compensate for such seasonal differences because of the significantly longer day-length (Martin 1987). Regardless, the variation in the clutch-initiation period (first clutches only) differs widely between tropical and temperate subspecies. The clutch-initiation period for Mangrove Warblers in our study averaged 47 days, with 50% of clutches initiated within 12 days from the earliest clutch. By contrast, the clutch-initiation period of Yellow Warblers at temperate latitudes ranged from 15 to 34 days, with 50% of the nests initiated within a five-day period (Goossen and Sealy 1982, Briskie 1995). Such a short period of clutch initiation for the migrant subspecies suggests strong selection on the timing of breeding at temperate latitudes, where peaks in food abundance may be critical and the opportunities for reneating are probably lower. High breeding synchrony, which has been reported for many migratory species, also results in synchronous fertility of females and is hypothesized to result in a higher frequency of extrapair copulations in migratory birds (Stutchbury and Morton 1995). The greater variance in the clutch-initiation period of Mangrove Warblers, combined with the fact that they form

permanent pair bonds, predicts a lower frequency of extrapair mating. This, however, remains to be tested in this subspecies.

*Latitudinal differences in clutch size and length of nesting periods.*—Clutch size tends to decline with decreasing latitude and, for most tropical birds, is two eggs (Murray 1985, Skutch 1985, Robinson et al. 2000). Although clutch size was slightly higher for the Mangrove Warblers in our study (median and mode of 3), it is still significantly lower than that reported for migrant Yellow Warblers from all the temperate studies we have summarized (see Table 5). Two primary hypotheses have been proposed as driving the evolution of clutch size in birds: (1) food limitation and (2) nest depredation (for reviews, see Martin 1996, Martin et al. 2000), though neither adequately explains latitudinal differences (Martin et al. 2000). Also critical to consideration of the evolution of clutch size is a complete understanding of adult mortality and the costs and benefits on overall fitness (Martin 1996). For example, if tropical species indeed experience higher survival (Faaborg and Arendt 1995, Johnston et al. 1997, Sandercock et al. 2000; but see Karr et al. 1990), then it follows that tropical birds may invest greater effort in fewer young (Martin 1996). Individual long-distance migrants breeding at temperate latitudes and experiencing higher mortality may be forced to compensate for the lower survival associated with the costs of migration by laying larger clutches (Møller 1984, Russell 2000, Sillett and Holmes 2002, Martin 2004). We argue that the latitudinal differences in demographic parameters we found in the Yellow Warbler subspecies complex are probably associated with multiple factors, some in the local environment on the breeding grounds (including food limitation and nest depredation) and others associated with the costs of migration.

Both incubation and brooding periods decreased with increasing latitude by two to three days in the temperate Yellow Warbler populations compared with the tropical resident Mangrove Warblers in our study. This result supports previous conclusions suggesting that developmental rates tend to be slower in tropical birds and result in longer nesting periods than in related species from temperate areas (e.g., Skutch 1949, Lack 1968, Ricklefs 1976, Martin 1996). Slower developmental rates in tropical species have been attributed to food limitation (Martin 1987, Thiollay 1988), higher nest depredation rates (Martin 1996), and their interaction (Martin 1992). Regardless, incubation and brooding times may also reflect parental tradeoffs between current reproduction and future survival. Rates of egg and nestling development, therefore, are probably influenced by both the local environment and by costs associated with migration (Ardia 2005).

Compared with temperate-zone birds, tropical species are also thought to have higher frequencies of reneating because of higher nest-depredation rates and, because of longer breeding seasons, more opportunities for multiple brooding (for review, see Martin 1996). Mangrove Warblers in the present study reneated multiple times, and double brooding was documented in two of the three years of the study, though it was rare (5%). Unfortunately, reneating in northern populations of Yellow Warblers has not been reported in the available literature and double brooding was only rarely reported (Goossen and Sealy 1982, Lowther et al. 1999), so latitudinal comparisons are problematic. Nevertheless, time constraints may limit migrant Yellow Warblers to one brood per year and fewer reneating attempts after failure, though both are reported in other species of

migratory warblers (e.g., Holmes et al. 1992). In Mangrove Warblers, longer breeding seasons may allow more renesting opportunities and, in good years, more successful double brooding. In addition to a longer breeding period, the higher rates of nest depredation experienced by Mangrove Warblers may have resulted in high rates of renesting (Skutch 1985, Martin 1996).

**Nesting success.**—Overall, nesting success for Mangrove Warblers in the present study (from incubation to fledging) was similar to that reported for other tropical passerine birds (Skutch 1985, Robinson et al. 2000) and lower than estimates reported for northern temperate populations of Yellow Warblers. Comparisons of nesting success with other populations of Mangrove Warblers are difficult to interpret because they are based on small within-year sample sizes. Additional studies at other tropical localities to assess intraspecific differences in nesting success are needed. Nevertheless, as in other studies with tropical species (Robinson et al. 2000; but see Stutchbury and Morton 2001), our primary cause of nest failure was depredation (65% of all active nests). Barrantes (1998) estimated a nest-depredation rate of 67% for a population of Mangrove Warblers in Costa Rica ( $n=9$ ). By contrast, available estimates of nest depredation in temperate Yellow Warblers range from 30% to 40% (Table 5). In both the tropics and temperate regions, rates of nest depredation are likely influenced more by local environmental conditions, such as predator abundance and behavior, than by costs associated with migration. If, however, the length of the incubation and nestling periods changes the probability of depredation or the investment by parents in nest defense, the propensity for adults to abandon the nest will also change. In this case, rates of nest depredation may still be linked to tradeoffs associated with future survival (Ardia 2005).

**Annual adult survival.**—Adult survival is generally thought to be higher in tropical than in temperate species (Faaborg and Arendt 1995, Johnston et al. 1997, Woodworth et al. 1999, Sandercock et al. 2000; but see Karr et al. 1990), and our survivorship data for the Mangrove–Yellow warbler complex are consistent with these patterns (Fig. 1). Apparent annual survival of both male and female Mangrove Warblers breeding in Mexico is higher than that of male and female migratory Yellow Warblers breeding in Montana (Cilimburg et al. 2002) and Manitoba (Mazerolle et al. 2005). Similarly, using the avian-demographic-query interface available online from the Institute of Bird Populations (see Acknowledgments), survival rates from constant-effort mist netting for the Yellow Warbler average 51% across its entire North American range. No other estimates of apparent survival are available, but estimates based on return rates from studies in southern Ontario (Yezerinac and Weatherhead 1997) and Rhode Island (Mitra 1999) are considerably lower than our apparent survival estimates.

Our estimates of apparent survival were based on the number of banded individuals resighted or recaptured exclusively within study plots. As with all survival analyses of small banded birds, we cannot separate emigration from mortality. In fact, we believe that our estimates of apparent survival are probably conservative, because we resighted seven males that were originally banded on our sites as far as 3–4 km away from the original capture site. If an extensive search had been conducted in the areas adjacent to the original banding sites, our survival estimates would likely have increased (Cilimburg et al. 2002).

The present study provides important baseline data for how the breeding ecology and survival of a passerine bird vary across a

tropical-to-temperate latitudinal gradient. Specifically, compared with the migratory subspecies of the Yellow Warbler breeding at temperate latitudes, the tropical resident Mangrove Warbler exhibited (1) longer breeding seasons, (2) smaller clutch sizes, (3) longer incubation and nestling periods, (4) lower nesting success, (5) higher rates of nest depredation, and (6) higher annual adult survival rates. Many of the life-history traits we measured in Mangrove Warblers are more similar to those of other tropical species than to conspecific subspecies of the Yellow Warbler complex. We suggest that these life-history traits and strategies are likely shaped both by local limiting factors in tropical and temperate regions and by the costs associated with migration. Further research on intraspecific variation across latitudinal gradients will help us understand not only how life-history traits evolve in response to factors such as length of breeding season and food supply, but also how species might respond to local climatic variables and to novel factors such as rapid climate change.

#### ACKNOWLEDGMENTS

We thank authorities at Celestún Biosphere Reserve and Ducks Unlimited of Mexico (DUMAC) for permits and logistical support. Special thanks to D. A. Parra, D. Bacab, E. Medrano, L. Carrillo, A. Stevens, and E. M. Figueroa, who were instrumental in the field. We thank H. Delfín and J. Vargas-Soriano from Universidad Autónoma de Yucatán and Universidad Autónoma de Campeche for logistical support. We also thank D. McDonald, S. G. Sealy, an anonymous reviewer, and F. Villaseñor Gómez for insightful comments. The study was supported by scholarships provided by CONACYT-Mexico and grants from Queen's University, the Natural Sciences and Engineering Research Council of Canada, the Smithsonian Institution Fellowship Program, and the Frank M. Chapman Memorial Fund (American Museum of Natural History). Our research was approved by the Animal Care Council at Queen's University. The avian-demographic-query interface mentioned in the text is available from the Institute of Bird Populations at [www.birdpop.org/](http://www.birdpop.org/).

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Associate Editor: D. B. McDonald