BREEDING ECOLOGY AND NEST-SITE SELECTION OF SONG WRENS IN CENTRAL PANAMA

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ABSTRACT.—We describe nest-site selection and report measures of breeding productivity from a population of Song Wrens (Cyphorhinus phaeocephalus) in central Panama. We studied 31 pairs from 1995 to 1998 and collected data on nest predation from 1996 to 1998. Song Wrens are year-round residents that build breeding nests for reproduction and dormitory nests for roosting. Twenty-five of 50 Song Wren breeding nests produced fledglings (daily nest survival rate = 0.968). Song Wrens usually (78%) placed their breeding nests in ant-defended acacias (Acacia melanoceras). However, nests placed in acacias did not experience lower rates of nest predation than nests placed in sites not defended by ants. The population-wide breeding season was seven months long, but individual pairs often bred within a span of only 2.5 months. Modal clutch size was two (n = 42), but the frequency of three-egg clutches was high (≥ 27%). Pairs that lost eggs or chicks renested more quickly than pairs that fledged young and attempted a second brood. Observed annual production of young was 1.4 fledglings per pair. Compared with other wrens, Song Wrens had a much longer breeding season and longer intervals between broods. The annual productivity of Song Wrens was the lowest recorded for any wren, which may have been due to smaller clutch sizes, long intervals between broods, and the correspondingly low number of nesting attempts per pair per year. Received 8 March 1999, accepted 20 August 1999.

STUDY AREA AND METHODS

Song Wrens inhabit lowland tropical forests from Honduras to western Ecuador. They are medium-sized (25 to 26 g) insectivores that forage exclusively in the leaf litter of the forest floor (Skutch 1940, Stiles and Skutch 1989, Robinson 2000). Groups of two to

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FOR MOST NEOTROPICAL forest birds, basic ecological data such as length and timing of breeding season, rates of nest predation, and renesting intervals are lacking. Such components are essential for estimating the annual production of young (Ricklefs and Bloom 1977) and also may be used for predicting species-specific responses to habitat disturbance (Siev- ing 1992). Once obtained, such data can be used to test hypotheses about the evolution of life-history traits (Ricklefs 1969, Martin 1996).

The purpose of our study was to describe the reproductive ecology of Song Wrens (Cyphorhinus phaeocephalus) in central Panama. We report data on nest-site selection, nest predation, timing and length of the breeding season, clutch size, length of incubation and nesting periods, annual production, and renesting interval. We tested two hypotheses about nest predation. The first hypothesis was that nests placed in ant-defended acacias (Acacia melanoceras) would have lower predation rates than nests placed in sites not defended by ants. Several investigators have suggested that stinging ants should deter nest predators (Skutch 1945, Janzen 1969, Young et al. 1990), but only one study has tested this hypothesis with data from real nests. Joyce (1993) found that nests of Rufous-naped Wrens (Campylorhynchus rufinucha) in ant-defended acacias were more successful than those in sites that were not defended by ants, but no data were reported. Thus, our study is the first to report actual rates of predation from real nests placed in ant-defended acacias. The second hypothesis was the predator search-strategy hypothesis (Watts 1987). Watts proposed that occupied nests should be more difficult for predators to find in the presence of multiple empty nests. Because Song Wrens build and sleep in dormitory nests year-round (see below; Skutch 1940, 1960), we hypothesized that pairs in territories with higher numbers of dormitory nests would suffer less nest predation.
five birds (pairs and their offspring) sleep together in bulky gourd-shaped dormitory nests that are built in understory plants 0.6 to 2.5 m off the ground (Skutch 1940, 1960; Stiles and Skutch 1989). Skutch (1960) observed breeding activity on the Caribbean slope of Costa Rica during February and cited a single breeding record in the "low wet forest of the Canal Zone" in Panama in May (Stone 1918 in Skutch 1960).

We studied Song Wrens from April 1995 to November 1997 and from February to December 1998 in Soberanía National Park, Panama Province, Panama (Fig. 1). The park is a 22,000-ha moist tropical forest (Holdridge 1967). All of our observations occurred in a 100-ha study plot within the forest interior near the Rio Limbo (9°09'N, 79°44'W). The plot is more than 3.5 km from any nonforest edge. The forest of the plot is characterized by a closed canopy; the lower understory is dominated by Oxandra longipetala, Quassia amara, Sorocca affinis, Alcis blackiana, Cupania sylvestica, Protium panamense, Poulsenia armata, and Oenocarpus bataua with minimal ground cover (R. Condit unpubl. data). Central Panama experiences a pronounced dry season from mid-December until mid- to late April (Windsor 1990). The Limbo plot receives an average of 2.6 m of rain yearly (Karr 1971).

Throughout 1997 and 1998, we searched a total of 31 territories for nests. The number of territories searched and pairs monitored varied from month to month (see Results) depending on available time and personnel. However, a core set of nine territories was searched for nests every month in 1997 and 1998 except December 1997 to January 1998. We found a total of 440 nests; 50 were breeding nests, 206 were dormitory nests, and 184 were of uncertain use status. We mapped the location of each nest found and recorded the plant species or morphotype (palm, sapling, or shrub) of the nest tree, nest height, diameter at breast height (dbh) of nest tree, compass direction of nest entrance, and status (active or abandoned). A nest was considered active if the nest entrance and chamber were open. We captured 298 Song Wrens (mostly in mist nets) and individually color marked all breeding pairs and their offspring.

From the onset of the rainy season in May, we visited territories weekly to determine when breeding was initiated. We searched for new nests and checked all active nests in each territory for evidence of breeding activity (eggs or chicks). Once breeding was confirmed, we visited the nest every three days until the nest failed or the young fledged (i.e. left the nest). To minimize the likelihood that monitoring would lead predators to the nests (Götmark 1992), we were careful not to create an obvious trail directly to the nest.

We calculated daily nest survival using methods in Mayfield (1961, 1975) and Hensler and Nichols (1981). Exposure days were based on the interval be-
FIG. 2. (A) Daily rainfall (± SE) per month from Barro Colorado Island, Panama (Smithsonian Tropical Research Institute-Terrestrial Environmental Science Program unpubl. data). Mean daily rainfall on the Limbo plot (April to August 1998; J. Nesbitt unpubl. data) did not differ from that on Barro Colorado Island for the same time period (F = 0.686, df = 1 and 216, P = 0.408).

To facilitate comparisons of annual productivity among species, we calculated production of young in two ways. First, we averaged the number of young fledged per pair per year (1995 to 1998), yielding 91 pair-years of data on reproductive success. Second, we estimated annual production of young (fledglings per pair of adults) using the methods of Ricklefs and Bloom (1977). This allowed us to compare productivity of other wren species with published values in Ricklefs and Bloom (1977).

We performed nonparametric tests whenever data were nonnormal or sample sizes were very uneven. We report x ± SD for all measurements unless otherwise indicated. P-values are quoted as an exact probability value where such values were available, and P < 0.05 was considered significant in all cases. All tests were two-tailed except x² tests, for which one-tailed tests are the convention.

RESULTS

Dormitory nests.—Song Wrens slept year-round in dormitory nests (n = 206) that were composed of rootlets, fungal rhizomorphs, strips of dead palm fronds, small twigs, and occasionally green vegetation such as fern fronds and decaying vegetable matter. Dormitory nests usually were lined with leaf skeletons and did not contain a well-defined cup. We observed construction of new nests during every month of the year except March. In addition, we saw birds carry fresh nest material (dead leaves and leaf skeletons) to completed nests, presumably to maintain and refurbish them. Males and females gathered and added materials to nests. When independent offspring were present, they also helped build new nests and refurbish old ones.

Dormitory nests were placed in at least nine species of understory trees: Oxandra longipetala, Poulsenia armata, Psychotria sp., Bactris sp., Cas-
Table 1. Types of trees used by Song Wrens for dormitory nests and breeding nests.

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Dormitory</th>
<th>Breeding</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acacia melanoceras</td>
<td>24</td>
<td>39</td>
</tr>
<tr>
<td>Bactris sp.</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Poulsenia armata</td>
<td>18</td>
<td>5</td>
</tr>
<tr>
<td>Sapling</td>
<td>151</td>
<td>3</td>
</tr>
<tr>
<td>Shrub</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>Palm</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Totals</td>
<td>206</td>
<td>50</td>
</tr>
</tbody>
</table>

* Defended by stinging ants.

tilla elástica, Rhinoria sp., Gustavia sp., Acacia melanoceras, and Asphodila sp. Acacia melanoceras is defended by stinging ants (Pseudomyrmex satánicas), and Poulsenia armata and Bactris have spines. The remaining species of trees lacked physical or insect defenses and therefore were identified only to morphotype (i.e. sapling, shrub, or palm) for subsequent analyses. Trees used for dormitory nests averaged 19.6 ± 12.2 mm in dbh (n = 182), and nest height averaged 2.1 ± 0.7 m above ground (range 0.95 to 6.0 m, n = 204). The compass orientation of nest entrances was random (Raleigh test, Z = 0.0943, n = 206, P > 0.05). Most territories had more than one active dormitory nest in use at any one time (x = 2.8 ± 0.9, range 2 to 5, n = 29 territories, 1998 data). However, the number of dormitory nests was not correlated with group size (r = 0.233, P > 0.05).

Breeding nests.—Like dormitory nests, breeding nests were bulky and gourd-shaped, but they differed from dormitory nests in having a distinctive “L” shape and a well-defined nest cup that was built below the nest entrance. Materials used in breeding nests were similar to those used in dormitory nests. The lining of breeding nests sometimes included small contour feathers of unidentified bird species. We observed construction of five new breeding nests in May and June. Most often, breeding nests (n = 45) were already built before the breeding season began.

All breeding nests (n = 50) were built in understory trees. Fewer tree species were used for breeding nests than for dormitory nests, however, and most of the breeding nests were placed in ant-defended acacias (G = 9.86, P < 0.005; Table 1). Nest trees averaged 28.4 ± 18.7 mm in dbh (n = 48), and nest height averaged 2.97 ± 1.9 m (range 1.1 to 12.1 m, n = 50). The compass orientation of nest entrances was randomly distributed (Raleigh test, Z = 0.257, n = 50, P > 0.05).

Comparison of breeding and dormitory nests.—Trees with breeding nests were larger in dbh than those with dormitory nests (Mann-Whitney U = 6,220, n₁ = 48, n₂ = 182, P = 0.001), and breeding nests were placed higher in trees than were dormitory nests (U = 7,304, n₁ = 50, n₂ = 204, P = 0.001). In addition, breeding nests were built in ant-defended trees more often than were dormitory nests (78% vs. 11%, respectively; x² = 95.34, df = 1, P < 0.001; Table 1).

Nesting success.—Twenty-five of the 50 breeding nests were successful (i.e. fledged at least one young; Table 2). The overall daily nest survival was 0.968. Daily nest survival was higher in 1996 than in 1997 and 1998 (Table 2); however, the sample size for 1996 was insufficient for statistical comparison. Daily nest survival differed significantly between 1997 and 1998 (χ² = 57.80, df = 1, P < 0.001; Table 2). For all years combined, daily nest survival was

Table 2. Comparison of nesting success of Song Wrens among and within years, between seasons, and whether nest trees were defended by ants. Success is a simple percentage of nests known to have fledged at least one young. Daily nest survival (s) was calculated using the methods of Mayfield (1961, 1975).

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Success (%)</th>
<th>s</th>
<th>SD</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>All years, together</td>
<td>50</td>
<td>0.968</td>
<td>0.006</td>
<td>50</td>
</tr>
<tr>
<td>Early wet season, all years</td>
<td>42</td>
<td>0.964</td>
<td>0.011</td>
<td>17</td>
</tr>
<tr>
<td>Late wet season, all years</td>
<td>55</td>
<td>0.971</td>
<td>0.007</td>
<td>33</td>
</tr>
<tr>
<td>1996</td>
<td>80</td>
<td>0.986</td>
<td>0.014</td>
<td>5</td>
</tr>
<tr>
<td>1997</td>
<td>67</td>
<td>0.979</td>
<td>0.010</td>
<td>12</td>
</tr>
<tr>
<td>1998</td>
<td>40</td>
<td>0.962</td>
<td>0.008</td>
<td>33</td>
</tr>
<tr>
<td>Early wet season, 1998</td>
<td>34</td>
<td>0.961</td>
<td>0.013</td>
<td>12</td>
</tr>
<tr>
<td>Late wet season, 1998</td>
<td>43</td>
<td>0.963</td>
<td>0.010</td>
<td>21</td>
</tr>
<tr>
<td>Ant-defended nest trees, all years</td>
<td>54</td>
<td>0.969</td>
<td>0.007</td>
<td>39</td>
</tr>
<tr>
<td>Not ant-defended nest trees, all years</td>
<td>37</td>
<td>0.965</td>
<td>0.013</td>
<td>11</td>
</tr>
</tbody>
</table>
breeding season, we hypothesized that pairs probably was killed while away from the nest young 10) and the number 

\[ n = (x = 4.5 \pm 1.7, P = 0.16) \] 

did not differ between early and late nests in the wet season \( (x^2 = 0.31, df = 1, P = 0.579; \) Table 2). Neither nest height \( (t = 1.43, df = 48, P = 0.16) \) nor dbh of nest trees \( (t = 1.50, df = 46, P = 0.14) \) differed between successful and unsuccessful nests.

To test the hypothesis that ant-defended sites were safer than sites that were not defended by ants, we compared daily nest survival between the two site types. Although ant-defended sites were marginally more successful than non ant-defended sites, this difference was not significant \( (x^2 = 0.941, df = 1, P = 0.33; \) Table 2). Because few breeding nests were placed in non-acacia sites, however, our test had low power (Hensler and Nichols 1981). Nevertheless, the observed difference of only 0.004 was very small and probably was not biologically relevant. By our calculations, demonstrating a difference in daily survival as small as 0.004 with 95% confidence would have required a sample size of more than 500 nests.

Because each territory had at least two nests (one breeding and one dormitory) during the breeding season, we hypothesized that pairs with more nests in their territories would have lower rates of nest predation (i.e. the predator search-strategy hypothesis; Watts 1987). Only data from 1998 were used to test this hypothesis because data were most complete for that year. We found no significant difference in the number of nests on territories that fledged young \( (x = 4.5 \pm 1.7, n = 10) \) and the number of nests on territories that failed to produce fledglings owing to nest predation \( (x = 3.7 \pm 1.8, n = 14; t = -1.07, df = 22, P = 0.29) \), although the trend was in the predicted direction.

Causes of nesting failure.—Nest predation was the major cause of nesting attempts that failed (22 of 25 failures). Nest predation was characterized by complete loss of the clutch or brood. Eggs were abandoned on two occasions. In one case, the breeding male disappeared during incubation, and in the other case, the female probably was killed while away from the nest (the eggs contained viable embryos). One nest failed owing to accidental destruction of the eggs by an observer. Song Wrens also suffered partial loss of nest contents that resulted from failure of eggs to hatch \( (n = 4) \) and mortality of nestlings \( (n = 4) \), the latter presumably from starvation. Neither of the two unhatched eggs that were recovered contained an embryo.

Timing of reproduction and length of breeding season.—Breeding was closely related to the seasonal occurrence of rainfall. Song Wrens initiated breeding in June within one month of the onset of the rainy season. The proportion of pairs breeding per month had a distinctly bimodal pattern (Fig. 2). In 1997, mean daily rainfall showed a similar bimodal pattern, but this pattern of rainfall was absent in 1998 (Fig. 2). Maximum breeding activity occurred in June and October, when 55 to 66% of pairs initiated clutches. However, Song Wrens initiated clutches in every month of the rainy season. In addition, many pairs made no attempt to breed until September or October. Breeding ceased within one month of the onset of the dry season in December. Thus, the observed breeding season was seven months long each year.

Clutch size.—Mean clutch size was 2.16 ± 0.43 \( (n = 42) \); clutch size was one in 1 nest, two in 33 nests, and three in 8 nests. Each of five pairs for which no nest was found were observed with three fledglings. Thus, at least 13 \( (\geq 27\%) \) clutches contained three eggs. Among pairs that renested, clutch size did not differ between first \( (x = 2.3 \pm 0.48, n = 13) \) and second \( (x = 2.2 \pm 0.43, n = 13; paired t = 0.562, df = 12, P = 0.58) \) nesting attempts.

Incubation and nestling periods.—As reported for other wren species (Skutch 1976), only the female incubated. During incubation and brooding, the breeding male and other family members (when present) roosted in a separate dormitory nest. The only female that we observed during the laying period laid two eggs on consecutive days and began incubation on the day the second egg was laid. The mean incubation period was 20.5 ± 0.7 days \( (n = 2) \), and the mean nestling period was 13.5 ± 0.75 days \( (n = 8) \).

Interval between nesting attempts.—The interval between nesting attempts varied with the fate of the first nest. Pairs whose first nests failed renested sooner \( (x = 24.3 \pm 20.4 \) days, range 13 to 73, \( n = 8) \) than pairs that renested after fledging offspring \( (x = 88.5 \pm 27.2 \) days, range 63 to 130, \( n = 7; t = -5.2, df = 13, P = \)
The interval between nesting attempts did not differ with respect to timing of the initiation of the first nest ($t = 0.978$, $df = 13$, $P = 0.35$). In 1998, the average number of nesting attempts per pair was $2.14 \pm 0.6$ (range 1 to 3, $n = 14$ pairs). Most Song Wren pairs were single brooded ($n = 86$); i.e. once the pair fledged one brood, they did not initiate another clutch during that breeding season. Occasionally, Song Wrens were double brooded ($n = 10$) and rarely triple brooded ($n = 1$).

**Annual production of young.**—The average number of young fledged per pair varied little among years (1995, $1.7 \pm 1.09$; 1996, $1.54 \pm 1.17$; 1997, $1.3 \pm 1.1$; 1998, $1.1 \pm 1.28$). The mean number of young fledged per pair was $1.4 \pm SE$ of 0.03 for the four years combined. The estimated average number of Song Wren young fledged per pair per season using the methods of Ricklefs and Bloom (1977) was $2.25 \pm 0.03$ in 1997 and 1998.

**Discussion**

The average level of productivity attained by Song Wrens was influenced by high nesting success, an unusually large number of 3-egg clutches, and a long breeding season. Most individual pairs attempted to raise only one brood per year, however, despite the prolonged nesting season.

One-third of the Song Wren pairs in our population fledged young, a level of nesting success consistent with that reported for passerines in Costa Rica and Ecuador (Ricklefs 1969, Ricklefs and Bloom 1977). The average daily survival rate of Song Wrens (0.968) was higher than that reported for open-cup nesting Western Slaty Antshrikes (*Thamnophilus atrinucha*) in Panama (0.913; Roper 1996) and for 10 other open-cup nesters (0.945) in Panama (Robinson *et al.* 2000). Robinson *et al.* (2000) found that species that build enclosed nests were more successful (daily survival 0.967 and 0.984, $n = 2$ species) than those that build open cup nests. The enclosed nests of Song Wrens had a similar rate of success.

An additional factor that could contribute to high nesting success in Song Wrens is the type of site selected for breeding. Song Wrens placed their nests almost exclusively in ant-defended acacias. Congeneric Musician Wrens (*C. aradus*) in Peru also placed their nests in ant-defended trees (*Triplaris* sp.; S. Russo pers. comm.). Why should these two species select ant-defended trees as breeding sites? Skutch (1945) and Janzen (1969) hypothesized that ant-defended acacias provide protection from nest predators. In Panama, Song Wren nests in ant-defended trees were slightly (but not significantly) more successful than sites that were not defended by ants. This slight difference in nest predation is surprising given the strong preference exhibited by Song Wrens for acacias as nest sites. Possibly, Song Wrens selected ant acacias for reasons other than ant defense (see below).

Another possible explanation for the relatively high rate of nesting success of Song Wrens is the predator search-strategy hypothesis. Watts (1987) proposed that if predators use a search strategy similar to that of other foragers, then multiple empty nests within a territory should decrease the probability that a predator locates an active breeding nest. Watts tested this hypothesis by placing artificial eggs in real nests of Northern Cardinals (*Cardinalis cardinalis*). Because cardinal nests are durable, multiple nests accumulate in territories over time. Watts demonstrated that artificial clutches of cardinals survived better in areas with more empty nests than in areas with only one other nest. Leonard and Pieman (1987) found a similar pattern for real nests of Marsh Wrens (*Cistothorus palustris*), the males of which build and maintain multiple nests in their territories. In Song Wrens, we found no difference between the number of nests in territories that successfully fledged young and the number of nests in territories where the breeding attempt failed owing to predation.

Very little is known about the types of predators that destroy Song Wren nests. The one predation event that we observed of a nest in an ant acacia was by a snake (*Pseastes* sp.). The predator search-strategy hypothesis assumes that predators search visually. If the important predators of Song Wren nests are nocturnal or hunt via other cues (such as olfaction), then we might not observe a positive relationship between the number of nests in a territory and predation rate. We suspect, however, that some predation occurs during the day because some nests were ripped apart in a manner suggesting that monkeys were responsible. Joyce (1990) observed white-faced monkeys (*Cebus capuc-
nus) depredating Rufous-naped Wren nests in ant acacias in Costa Rica. Although we did not observe nest-destroy events, white-faced monkeys were common at our site and could have been responsible for the nest damage that we observed.

We did not test explicitly for the influence of vegetation structure on nesting success. Ant acacias generally were well separated from the surrounding vegetation and had little or no physical contact with nearby plants (T. Robinson pers. obs.). Furthermore, Song Wren nest trees that were not defended by ants often were solitary saplings with few low branches and straight, slender trunks. The low number of contacts with the surrounding vegetation may be important in reducing the probability that smaller arboreal predators will access the nest tree. Roper (1996) found a positive relationship between nest failure and the number of contacts between the nest tree and the surrounding vegetation. He suggested that Robinson’s mouse opossum (Marmosa robinsoni) was a major nest predator at his study site <5 km from our Limbo plot (Roper 1996). Mouse opossums move from tree to tree by using vines and branch contacts (G. Adler pers. comm.), and it may be that Song Wrens prefer to nest in acacias simply because these trees tend to be solitary.

The breeding activity of most understory birds in central Panama peaks in the first four months of the wet season (Robinson et al. 2000). Song Wren breeding activity had two peaks, one during the first month of the breeding season and the other four to five months after breeding commenced (Fig. 2). During the rainy seasons of 1995 to 1997, precipitation patterns also were bimodal, with peaks in June and October. The bimodal pattern of rainfall was less pronounced during 1998, yet Song Wrens maintained the bimodal pattern of breeding activity. Perhaps peaks in breeding mirror peaks in insect abundance. Levings and Windsor (1982) found that populations of litter arthropods increased in abundance immediately following the start of the rainy season. Total abundance of litter arthropods remained high throughout the rainy season, but abundance did not closely track changes in rainfall (Levings and Windsor 1982). However, some insect taxa (e.g. roaches and crickets) showed bimodal patterns in abundance. Stomach samples from Song Wrens at a site less than 5 km from the Limbo plot showed that roaches and orthopterans formed a significant portion of the diet (B. Poulin unpubl. data). Although it is not clear what is responsible for the bimodal pattern in breeding activity observed in Song Wrens, the generally high abundance of food resources throughout the rainy season may be responsible for sustaining the long breeding season exhibited by Song Wrens.

Comparisons with other ecologically and phylogenetically similar species provide the best opportunity to understand the evolution of life-history traits (Martin 1996). Unfortunately, reasonably complete information on the components of breeding productivity is available for only three species of wrens, two of which inhabit temperate latitudes (Table 3). As expected, breeding-season length is shorter in temperate areas. The breeding season of Song Wrens is 1.7 to 2.5 times longer than that of temperate species and 1.6 times longer than that of Rufous-naped Wrens, the only tropical wren available for comparison (Table 3). However, the population-wide breeding season of Song Wrens differs substantially from that of individual pairs. The breeding season for a “typical” single-brooded pair is 2.5 months long. Not all Song Wren pairs in our study population breed synchronously. Because individual pairs do not make repeated breeding attempts throughout the rainy season, the breeding season of individual pairs is approximately 4.5 months shorter than the population-wide measure.

The relatively short breeding season of individual pairs, small clutch sizes, and long time intervals between broods appear to be the main factors that limit productivity of Song Wrens compared with other species of tropical and temperate wrens. Nesting success was not lower than that documented for temperate wrens and was higher than that for another tropical wren. Egg success was relatively low but was not the lowest observed among wrens (Table 3). Yet, the observed annual productivity for Song Wrens in Panama was the lowest for the four wren species for which data were available (Table 3). For the two additional wren species for which average productivity has been estimated (Ricklefs and Bloom 1977), both values were more than three times higher than that estimated for Song Wrens. Why did esti-
Table 3. Components of breeding productivity for six temperate and two Neotropical wren species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Season length (months)</th>
<th>Clutch size</th>
<th>Daily nest survival</th>
<th>Nest cycle (days)</th>
<th>Egg success&lt;sup&gt;c&lt;/sup&gt;</th>
<th>Renesting interval&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Young fledged&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Source&lt;sup&gt;d&lt;/sup&gt;</th>
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<tbody>
<tr>
<td><strong>Temperate</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>House Wren (Troglodytes aedon)</td>
<td>2.77&lt;sup&gt;x&lt;/sup&gt;</td>
<td>5.8</td>
<td>0.9945</td>
<td>34</td>
<td>0.648</td>
<td>10</td>
<td>10</td>
<td>7.54</td>
</tr>
<tr>
<td>Marsh Wren (Cistothorus palustris)</td>
<td>4.0</td>
<td>3.4–6.0</td>
<td>0.9232</td>
<td>30</td>
<td>0.21</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Bewick’s Wren (Thryomanes bewickii)</td>
<td>2.5</td>
<td>5.6</td>
<td>—</td>
<td>30</td>
<td>0.51–0.84</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Carolina Wren (Thryothorus ludovicianus)</td>
<td>4.75</td>
<td>4.8</td>
<td>—&lt;sup&gt;f&lt;/sup&gt;</td>
<td>27</td>
<td>0.66</td>
<td>11</td>
<td>9.3</td>
<td>—</td>
</tr>
<tr>
<td>Canyon Wren (Catherpes mexicanus)</td>
<td>3.0</td>
<td>5.1</td>
<td>—</td>
<td>31</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Cactus Wren (Campylorhynchus brunneicapillus)</td>
<td>4.09&lt;sup&gt;e&lt;/sup&gt;</td>
<td>3.5</td>
<td>0.9752</td>
<td>38</td>
<td>0.478</td>
<td>6</td>
<td>5</td>
<td>6.80</td>
</tr>
<tr>
<td><strong>Neotropical</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rufous-naped Wren (Campylorhynchus rufinucha)</td>
<td>4.25</td>
<td>4</td>
<td>—&lt;sup&gt;f&lt;/sup&gt;</td>
<td>37</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Song Wren (Cypselorhynchus technecapillus)</td>
<td>7.0</td>
<td>2.16</td>
<td>0.9680</td>
<td>34</td>
<td>0.325</td>
<td>88.5</td>
<td>24.3</td>
<td>2.25</td>
</tr>
</tbody>
</table>

<sup>a</sup> Renesting interval after success (days); r<sub>f</sub> = renesting interval after failure (days).
<sup>b</sup> Young fledged per pair per season. P = estimated average from equations in Ricklefs and Bloom (1977); RS = observed number of offspring fledged per pair per year.
<sup>c</sup> Proportion of eggs laid that result in fledged young.
<sup>d</sup> 1 = Ricklefs and Bloom 1977; 2 = Ricklefs 1969, Kroodsma and Verner 1997; 3 = Kennedy and White 1997; 4 = Haggerty and Morton 1995; 5 = Jones and Dieni 1995; 6 = Joyce 1993; 7 = this study.
<sup>e</sup> Calculated using equation 2 in Ricklefs and Bloom (1977); other values estimated from dates reported by source or by direct observation.
<sup>f</sup> 25% of nests fledged young.
<sup>x</sup> 36% of nests fledged young.
imated annual productivity of Song Wrens differ so greatly from observed annual productivity (Table 3)? The estimator (Ricklefs and Bloom 1977) used seven measures of breeding productivity averaged over the entire study population, whereas the observed values measured only counts of fledged young. Although the estimate was higher than the observed values, the estimated value was within one standard deviation of the mean of the observed value for every year of the study. Thus, we believe that the estimated value was accurate enough to permit valid comparisons among species.

Data on differences in breeding productivity between tropical and temperate bird species are needed to advance our understanding of the evolution of life-history traits. Although our study cannot provide comprehensive tests, we are able to address a few predictions derived by Martin (1996). If nest predation is the driving force behind the evolution of life-history differences between temperate and tropical birds, then nest-predation rates should be higher for tropical birds (Martin 1996). Moreover, tropical birds should be multibrooded and have short renesting intervals (Martin 1996). Neither of these predictions is supported by our data. Despite small clutch sizes compared with temperate wrens, most Song Wrens raised only one brood per year. If limited food availability is an important influence on reproductive rates of tropical birds, then long intervals between broods should occur, resulting in fewer broods per year (Martin 1996). We did not measure food availability throughout the year, but other data (Levings and Windsor 1982) suggest that food for Song Wrens is equally abundant throughout the nesting season (although food may still be limiting). Experimental food supplementation will be required to determine if food availability limits reproductive rate. Finally, if the tradeoff between adult survival and current reproduction is paramount (Charnov and Krebs 1974), then smaller clutches, long intervals between broods, and prolonged parental care to produce high-quality offspring should result (Martin 1996). Our data on reproductive ecology support this hypothesis. Adult Song Wrens have relatively high survivorship (57 to 76%; Robinson 2000), produce small clutches, and tend to raise only a single brood per year. If the tradeoff between reproduction and survival is true, we would expect to find evidence of high investment in individual offspring. In fact, young Song Wrens typically do not disperse from the natal territory until they are eight months old, which is well past the age (1.5 months) at which they achieve foraging independence (Robinson 2000). Thus, at least for Song Wrens, reproductive rate may indicate a situation in which fewer breeding attempts are made in favor of producing high-quality offspring.

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