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

Tara R. Robinson,[1,2,3] W. Douglas Robinson,[1,2,3] and E. Ceinwen Edwards[2]

[1]*Department of Ecology, Ethology, and Evolution, University of Illinois, Champaign, Illinois 61820, USA; and*
[2]*Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Republic of Panama*

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 ($\geq 27\%$). 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.*

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 (Sieving 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 nestling 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 stinging

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.

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

[3] Present address: Department of Zoology and Wildlife Science, Auburn University, 331 Funchess Hall, Auburn, Alabama 36849, USA. E-mail: trrobins@acesag.auburn.edu
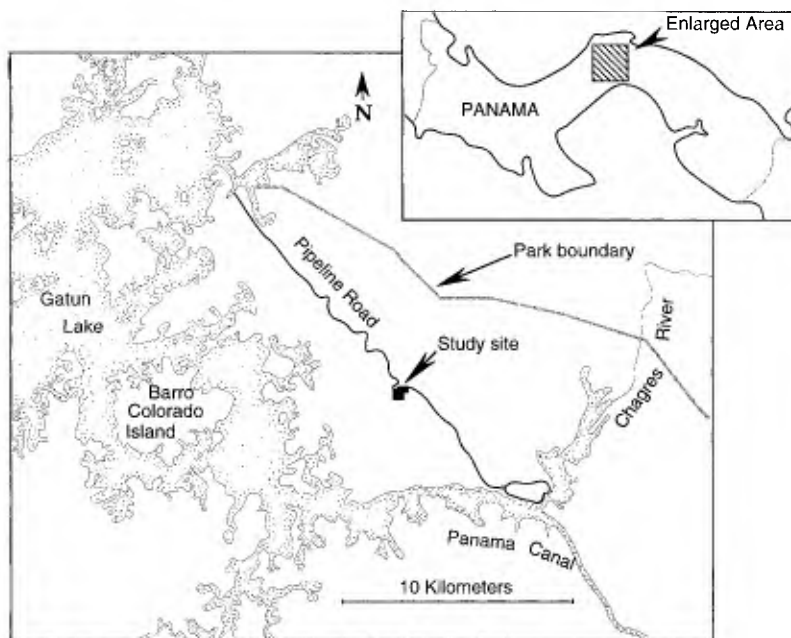
FIG. 1. Location of the 100-ha study site in relation to the Panama Canal and Barro Colorado Island, Panama. All land north of the canal, east of Gatun Lake, and south and west of the boundary indicated lies within Soberania National Park.

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 Soberania 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*, *Sorocea affinis*, *Alseis blackiana*, *Cupania sylvatica*, *Protium panamense*, *Poulsenia armata*, and *Oenocarpus mapora* 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-
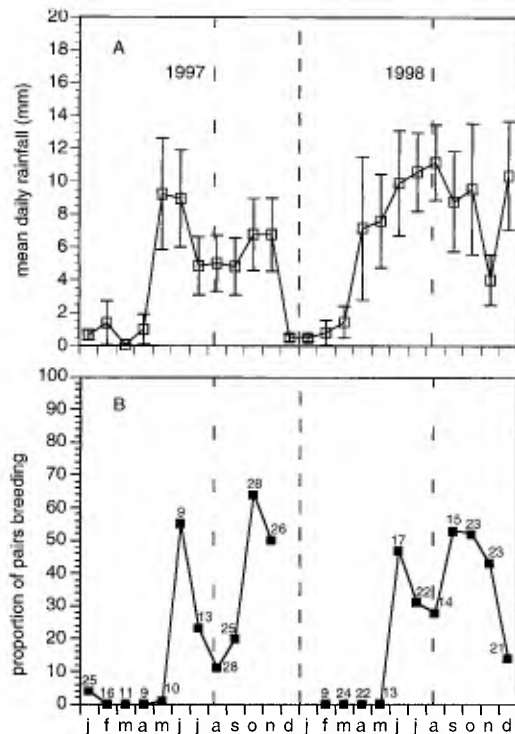
FIG. 2.   (A) Daily rainfall ($\bar{x} \pm$ SE) per month from Barro Colorado Island, Panama (Smithsonian Tropical Research Institute-Terrestrial Environmental Science Program unpubl. data). (B) Proportion of Song Wren pairs on the Limbo plot with eggs per month. Number of territories searched per month is indicated. Break indicates period when no sampling occurred. Close-set dashed lines indicate break between years; wide-set dashed lines indicate early versus late wet season.

tween the day the first egg was laid (or the day the nest was found if after laying) and the day of fledging. For failed nests, we used the midpoint between the last and penultimate nest checks as the day of failure. We compared survival rates using CONTRAST (Hines and Sauer 1989), which incorporates variance and covariance estimates and computes a χ^2 statistic from the resulting contrast matrix (Sauer and Williams 1984). To compare seasonal differences in nest survival, we divided the rainy season into early and late periods. We used mid-August as the dividing point between the early and late periods because of the decrease in the proportion of pairs breeding during that month (Fig. 2).

To compare the relationship between breeding seasonality and precipitation, we used rainfall data from a climate station located 7 km away on Barro Colorado Island because a complete time series was available (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). To calculate estimated mean productivity, we used data from 1997 to 1998 because estimates of daily nest survival were best for those years. Productivity was the product of clutch size, nesting success, and number of clutches laid per year and was calculated using seven variables: length of breeding season (days), clutch size, daily nest survival, length of nest cycle (from laying to fledging in days), egg success (proportion of eggs laid that resulted in fledged young), renesting interval after failure, and renesting interval after success.

We performed nonparametric tests whenever data were nonnormal or sample sizes were very uneven. We report $\bar{x} \pm$ 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 χ^2 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.

Substrate	Dormitory	Breeding
Acacia melanoceras[a]	24	39
Bactris sp.	3	3
Poulsenia armata	18	5
Sapling	151	3
Shrub	7	0
Palm	3	0
Totals	206	50

[a] Defended by stinging ants.

tilla elastica, Rhinoria sp., Gustavia sp., Acacia melanoceras, and Asplundia sp. Acacia melanoceras is defended by stinging ants (Pseudomyrmex satanicus), 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 ($\bar{x} = 2.8 \pm 0.9$, 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 $U = 6,220$, $n_1 = 48$, $n_2 = 182$, $P = 0.001$), and breeding nests were placed higher in trees than were dormitory nests ($U = 7,304$, $n_1 = 50$, $n_2 = 204$, $P = 0.001$). In addition, breeding nests were built in ant-defended trees more often than were dormitory nests (78% vs. 11%, respectively; $\chi^2 = 95.34$, 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 ($\chi^2 = 57.80$, 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).

Comparison	Success (%)	s	SD	n
All years, together	50	0.968	0.006	50
Early wet season, all years	42	0.964	0.011	17
Late wet season, all years	55	0.971	0.007	33
1996	80	0.986	0.014	5
1997	67	0.979	0.010	12
1998	40	0.962	0.008	33
Early wet season, 1998	34	0.961	0.013	12
Late wet season, 1998	43	0.963	0.010	21
Ant-defended nest trees, all years	54	0.969	0.007	39
Not ant-defended nest trees, all years	37	0.965	0.013	11

higher late in the wet season than early in the wet season (χ^2 = 9.80, df = 1, P = 0.002; Table 2). A sufficient number of nests was available to compare seasonal differences in nest survival only in 1998, during which time daily nest survival did not differ between early and late nests in the wet season (χ^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 (χ^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 ($\bar{x}$ = 4.5 ± 1.7, n = 10) and the number of nests on territories that failed to produce fledglings owing to nest predation ($\bar{x}$ = 3.7 ± 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 (≥27%) clutches contained three eggs. Among pairs that renested, clutch size did not differ between first ($\bar{x}$ = 2.3 ± 0.48, n = 13) and second ($\bar{x}$ = 2.2 ± 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 ($\bar{x}$ = 24.3 ± 20.4 days, range 13 to 73, n = 8) than pairs that renested after fledging offspring ($\bar{x}$ = 88.5 ± 27.2 days, range 63 to 130, n = 7; t = −5.2, df = 13, P =

0.001). 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 ± 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 ± 1.09; 1996, 1.54 ± 1.17; 1997, 1.3 ± 1.1; 1998, 1.1 ± 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 ± 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-de-

fended 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 Picman (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 capuci-*

nus) depredating Rufous-naped Wren nests in ant acacias in Costa Rica. Although we did not observe nest-destruction 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 sam-

ples 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.

Species	Season length (months)	Clutch size	Daily nest survival	Nest cycle (days)	Egg success[c]	Renesting interval[a]		Young fledged[b]		Source[d]
						r_s	r_f	P	RS	
Temperate										
House Wren (*Troglodytes aedon*)	2.77[e]	5.8	0.9945	34	0.648	10	10	7.54	—	1
Marsh Wren (*Cistothorus palustris*)	4.0	3.4–6.0	0.9232	30	0.21	—	—	—	1.9	2
Bewick's Wren (*Thryomanes bewickii*)	2.5	5.6	—[f]	30	0.51–0.84	—	—	—	4.4	3
Carolina Wren (*Thryothorus ludovicianus*)	4.75	4.8	—[f]	27	0.66	11	9.3	—	2.8	4
Canyon Wren (*Catherpes mexicanus*)	3.0	5.1	—	31	—	—	—	—	—	5
Cactus Wren (*Campylorhynchus brunneicapillus*)	4.09[e]	3.5	0.9752	38	0.478	6	5	6.80	—	1
Neotropical										
Rufous-naped Wren (*Campylorhynchus rufinucha*)	4.25	4	—[g]	37	—	—	—	—	—	6
Song Wren (*Cyphorhinus phaeocephalus*)	7.0	2.16	0.9680	34	0.325	88.5	24.3	2.25	1.4	7

[a] r_s = renesting interval after success (days); r_f = renesting interval after failure (days).
[b] 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.
[c] Proportion of eggs laid that result in fledged young.
[d] 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.
[e] Calculated using equation 2 in Ricklefs and Bloom (1977); other values estimated from dates reported by source or by direct observation.
[f] 25% of nests fledged young.
[g] 36% of nests fledged young.

mated 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.

LITERATURE CITED

CHARNOV, E. L., AND J. R. KREBS. 1974. On clutch size and fitness. Ibis 116:217–219.

GÖTMARK, F. 1992. The effects of investigator disturbance on nesting birds. Current Ornithology 9: 63–104.

HAGGERTY, T. M., AND E. S. MORTON. 1995. Carolina Wren (*Thryothorus ludovicianus*). *In* The birds of North America, no. 188 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

HENSLER, G. L., AND J. D. NICHOLS. 1981. The Mayfield method of estimating nest success: A model, estimators and simulation results. Wilson Bulletin 93:42–53.

HINES, J. E., AND J. R. SAUER. 1989. Program CONTRAST: A general program for the analysis of

several survival or recovery rate estimates. United States Fish and Wildlife Service Technical Report No. 24.

HOLDRIDGE, L. R. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica.

JANZEN, D. H. 1969. Birds and the ant × acacia interaction in Central America, with notes on birds and other myrmecophytes. Condor 71: 240–256.

JONES, S. L., AND J. S. DIENI. 1996. Canyon Wren (*Catherpes mexicanus*). *In* The birds of North America, no. 197 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

JOYCE, F. J. 1990. Nesting associations of birds, ants, and wasps. Ph.D. dissertation, Cornell University, Ithaca, New York.

JOYCE, F. J. 1993. Nesting success of Rufous-naped Wrens (*Campylorhynchus rufinucha*) is greater near wasp nests. Behavioral Ecology and Sociobiology 32:71–77.

KARR, J. R. 1971. Structure of avian communities in selected Panama and Illinois habitats. Ecological Monographs 41:207–233.

KENNEDY, E. D., AND D. W. WHITE. 1997. Bewick's Wren (*Thryomanes bewickii*). *In* The birds of North America, no. 315 (A Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

KROODSMA, D. E., AND J. VERNER. 1997. Marsh Wren (*Cistothorus palustris*). *In* The birds of North America, no. 308 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

LEONARD, M. L., AND J. PICMAN. 1987. The adaptive significance of multiple nest building by male Marsh Wrens. Animal Behaviour 35:271–277.

LEVINGS, S. C., AND D. M. WINDSOR. 1982. Seasonal and annual variation in litter arthropod populations. Pages 355–387 *in* The ecology of a tropical forest: Seasonal rhythms and long-term changes (E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor, Eds.). Smithsonian Institution Press, Washington, D.C.

MARTIN, T. E. 1996. Life history evolution in tropical and south temperate birds: What do we really know? Journal of Avian Biology 27:1–10.

MAYFIELD, H. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255–261.

MAYFIELD, H. 1975. Suggestions for calculating nesting success. Wilson Bulletin 87:456–466.

RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1–48.

RICKLEFS, R. E., AND G. BLOOM. 1977. Components of avian breeding productivity. Auk 94:86–96.

ROBINSON, T. R. 2000. Factors affecting natal dispersal by Song Wrens (*Cyphorhinus phaeocephalus*): Ecological constraints and demography. Ph.D. dissertation, University of Illinois, Urbana.

ROBINSON, W. D., T. R. ROBINSON, S. K. ROBINSON, AND J. D. BRAWN. 2000. Nesting success of understory forest birds in lowland Panama. Journal of Avian Biology 31: in press.

ROPER, J. J. 1996. Nest predation and its importance for a Neotropical bird, the Western Slaty Antshrike (*Thamnophilus atrinucha*): The problem, experiments, and simulations. Ph.D. dissertation, University of Pennsylvania, Philadelphia.

SAUER, J. R., AND B. K. WILLIAMS. 1984. Generalized procedures for testing hypotheses about survival or recovery rates. Journal of Wildlife Management 53:137–142.

SIEVING, K. E. 1992. Nest predation and differential insular extinction among selected forest birds in central Panama. Ecology 73:2310–2328.

SKUTCH, A. F. 1940. Social and sleeping habits of Central American wrens. Auk 57:293–312.

SKUTCH, A. F. 1945. The most hospitable tree. Science Monthly 60:5–17.

SKUTCH, A. F. 1960. Life histories of Central American birds. Pacific Coast Avifauna No. 34.

SKUTCH, A. F. 1976. Parent birds and their young. University of Texas Press, Austin.

STILES, F. G., AND A. F. SKUTCH. 1989. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, New York.

WATTS, B. D. 1987. Old nest accumulation as a possible protection mechanism against search-strategy predators. Animal Behaviour 35:1566–1568.

WINDSOR, D. M. 1990. Climate and moisture variability in a tropical forest: Long-term records from Barro Colorado Island, Panama. Smithsonian Contributions to Earth Sciences No. 29.

YOUNG, B. E., M. KASPARI, AND T. E. MARTIN. 1990. Species-specific nest site selection by birds in ant-acacia trees. Biotropica 22:310–315.

Associate Editor: B. A. Loiselle