The Auk 118(1):191–210, 2001

COMPARISON OF THE REPRODUCTIVE BIOLOGY OF TWO NEOTROPICAL WRENS IN AN UNPREDICTABLE ENVIRONMENT IN NORTHEASTERN COLOMBIA

JORGE A. AHUMADA[1]
Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544-1003, USA

ABSTRACT.—Buff-breasted (*Thryothorus leucotis*) and Rufous-and-white (*T. rufalbus*) wrens living in a dry forest in northeast Colombia (Parque Nacional Natural Tayrona) are faced with a large year-to-year uncertainty in the arrival time of the rainy season, as well as the amount of rain falling in the first six months of the year. Those factors are thought to be important cues used by those species in their reproductive decisions. In this study, I gathered data on several reproductive parameters (clutch size, nesting success, timing of breeding, renesting attempts) for both species during two years of contrasting rainfall patterns. I collected information on the foraging behavior of both species to identify their main food and to study how rainfall affects the dynamics of those resources. Buff-breasted Wrens fed mostly in the understory, gleaning arthropods from upper and lower leaf surfaces, dry branches, and aerial litter. Numbers of arthropods in those microhabitats depend strongly on the amount of rainfall; understory arthropod levels are low during the dry season and increase with the arrival of the rains. Buff-breasted Wrens timed their reproduction with the arrival of the rains in both years, delaying the onset of breeding significantly and continuing to breed during the dry year (1994). Rufous-and-white Wrens spent a large proportion of their time feeding on arthropods in the leaf litter. Number of arthropods in the litter varied little between dry and wet periods. Therefore, Rufous-and-white Wrens had a more constant food environment despite large differences in rainfall within and between the years of the study. That species started breeding earlier in the dry season and extended its breeding longer than Buff-breasted Wrens. My observations suggest that the evolution of the reproductive strategies in those species was mostly through the change of behavioral parameters rather than physiological reproductive parameters such as changes in clutch size, egg size, or number of broods. *Received 14 June 1999, accepted 16 September 2000.*

MANY BIRDS LIVE in environments that are somewhat unpredictable as to when resources are available for growth, maintenance, and reproduction. When should birds breed in an environment that is unpredictable in its favorability for reproduction? The very existence of a distinctive period of the year when most individuals of a bird species breed—a breeding season—suggests that most of the time, the amount of food available to them is just enough to sustain their basic metabolic needs. Because of their high turnover rate of energy per unit of body weight and their inability to allocate large amounts of energy to short and long-term storage and growth, birds are more dependent on food for breeding than other endotherms of similar body size (Martin 1987, Paladino 1989). That imposes constraints on the life-history characteristics that birds can evolve (Walsberg 1983). Thus, when the arrival time of food necessary for reproduction is unpredictable, birds are constrained to breed whenever pulses of resources are above a certain threshold. This translates into a "tracking" strategy in which individuals should be able to detect and process information on the amount of food available to them and time their reproduction accordingly.

Few studies have specifically examined effects of the duration and intensity of resource pulses on timing and duration of the breeding season of birds. That generally requires detailed knowledge of the temporal dynamics of the resources that birds require for reproduction as well as long-term data on breeding phenology. One of the best data sets available for temperate zones comes from a long-term study in the Hubbard-Brook forest (Holmes et al.

---

[1] Present address: Laboratorio de Ecología de Poblaciones, Departamento de Biología, Universidad Javeriana, Bogotá, Colombia and Department of Botany, University of Georgia, Athens, Georgia 30602, USA. E-mail: jorge@dogwood.botany.uga.edu

1986). Most species in that forest depend on pulses of lepidopteran larvae for successful breeding. Between outbreaks, birds usually have a lower reproductive output and success, suggesting that most species depend on brief but intense pulses of food which constrain the time of breeding.

Such long-term study information is largely unavailable for Neotropical birds. There is evidence that suggests that some Neotropical species exhibit a distinct breeding season (see review in Poulin et al. 1992), but examination of community patterns shows that other species breed all year (Skutch 1950, Miller 1963, Snow and Snow 1963, 1964; Gradwohl and Greenberg 1990). Do the latter species rely on resource levels that are more constant through time or that occur in long resource pulses? What types of food resources show this dynamic behavior? Can species that rely on these resources choose to breed in periods when nest predation and other causes of nest loss are low?

There is partial evidence that suggesting that Neotropical birds that utilize foods that are constant through time breed year round (Miller and Miller 1968). Good candidates for those resources are arthropods in bark and rotten wood (Pierpont 1986), arthropods in leaf litter (Levings and Windsor 1990, Poulin et al. 1992), some communities of shrub understory arthropods (Young 1994), or resources associated with human-made habitats. In contrast, most shrub understory arthropods and fruits vary in abundance seasonally (Janzen 1973a, b, 1980; Wolda 1978a, b, 1980, 1990; Levings and Windsor 1990, Poulin et al. 1992, Blake and Loiselle 1992, Heideman 1989, Hilty 1980, Kinnaird 1992, Levey 1988, Loiselle and Blake 1991, Van Schaik et al. 1993).

Thryothorus leucotis and *T. rufalbus* are two species of insectivorous wren, (Buff-breasted and Rufous-and-white wren, respectively) living sympatrically in the northeastern dry forests of Colombia. They constitute a good system for studing how temporal variation in food abundance affects timing and intensity of reproduction because (1) the dry forest they live in has highly unpredictable rainfall not only from year-to-year, but also within a year, which might influence insect and arthropod abundance in their habitat, and (2) the species differ in feeding height and slightly in body size—factors that are known to influence food choice in birds—providing a natural setting to compare how differences in their respective food dynamics affects onset and duration of reproduction. In this study, I gathered information on morphology, foraging behavior, and reproduction of those species and measured variation in abundance of their main food: arthropods that occur on live plant tissue in the understory and in leaf litter. The two years of my study were dramatically different in amount of rainfall and in the date of initiation of the rainy season. This offered me a unique opportunity to study the reproductive strategy of both species when faced with environmental variation in food supply. It also allowed me to gain new insight into some of the proximate mechanisms and ultimate causes that underlie the life history of those species.

METHODS

STUDY AREA

This study was carried out in Parque Nacional Natural Tayrona (henceforth "Tayrona") located on the northeast Caribbean coast of Colombia (Fig. 1). The park consists of a strip of land of 15,000 ha of dry forest and scrub reaching from the coastal plains to the Sierra Nevada of Santa Marta, and rising from sea level to about 400 m. This region of the country receives moderate amounts of rainfall on a yearly basis (<1,500 mm) and is highly seasonal as a result of the seasonal movement of the thermal equator with two dry seasons (December to March and July to August) and two wet seasons (September to November and April to June) (Fig. 2A). Annual average temperature is around 25°C with daily temperatures oscillating between 20 to 31°C (taken from Instituto Nacional de Hidrología, Meteorología y Adecuación de Tierras—HIMAT). That climatic pattern is influenced by the presence of the Sierra Nevada of Santa Marta which can affect the extent of rainfall by condensation of moisture along its northeast slope (Herrmann 1970). This has created an east–west moisture gradient along the park that determines the structure of the vegetation (Herrmann 1970, Hernández-Camacho and Rodríguez-Guerrero 1972). Despite that general annual pattern in rainfall seasonality, the amount of rain in a given year varies dramatically especially in the first half of the year (Fig. 2B). An analysis using Colwell's index (Colwell 1974, Beissinger and Gibbs 1993) shows that predictability of rainfall for Tayrona is low [0.239] when compared to climatic stations within the same region but outside of the influence of the Sierra Nevada de Santa Marta (Ahumada 1995). I installed a rain gauge and a maximum–minimum thermometer in

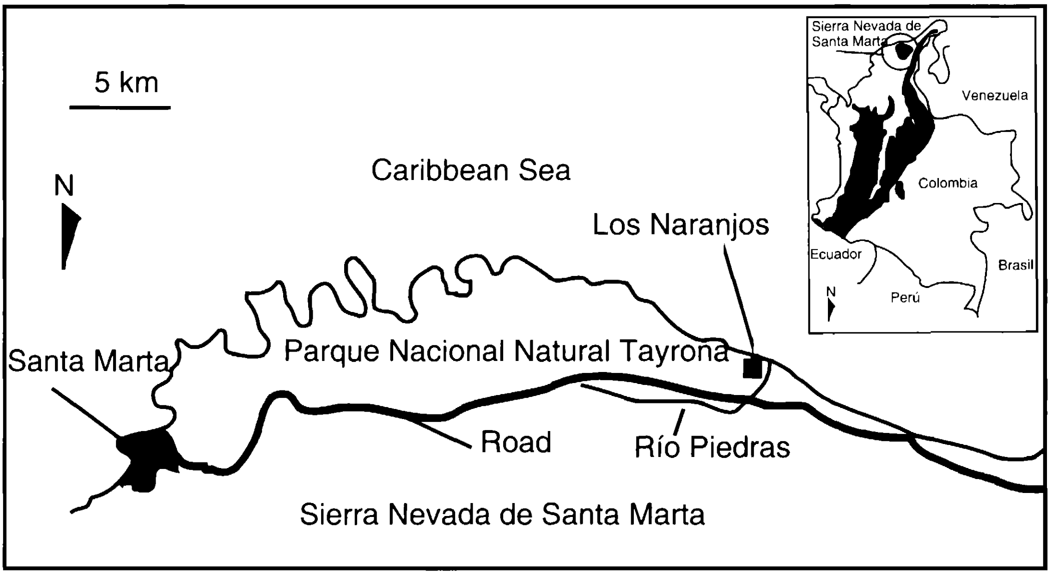

FIG. 1. Geographical location of the study site in northeast Colombia.

the park guard station located at Tayrona and data were collected daily from August 1992 to June 1993. The two years (1993 and 1994) in which reproductive information of the wrens was collected differed in amount of rainfall (Fig. 2C). That difference was particularly pronounced for the first five months of the year; 1993 received 300 mm more rain than 1994. Those months are the most crucial for the breeding of most bird species in the area including the wrens (J. Ahumada pers. obs.). The difference in total rainfall between 1993 and 1994 was on the order of 200 mm. Also, and maybe more significant for the wrens, there were differences in the arrival of the rainy season in both years. In 1993, rains started by day 50 and accumulated much more rapidly in a short period in the third quarter of the year. In 1994, rains started later, and accumulation was more constant throughout the year.

My study site is located on Estación "Los Naranjos" (approx. 11°17'N, 73°9'W), a 2 × 5 km strip of forest located on the northeastern coastline of Tayrona (Fig. 1). I established a 25 ha study plot in the eastern side of Los Naranjos bordering the bank of Río Piedras. A 20 × 20 m grid was created by placing 20 cm plastic stakes in the nodes of the grid, which were located with the aid of a hand-held compass and measuring tape. Most data collection was concentrated on this plot, although some information was drawn from a larger area of about 2 km^2 surrounding it. The 25 ha study plot is dominated by secondary (54.5%) and primary forest (12%). The remaining vegetation is composed of a mixture of coastal vegetation, abandoned coconut plantations, and small patches of grass. The understory is thick and composed of vines, spiny palms (*Desmoncus orthacanthos*), and shrubs. Several species of birds inhabit the secondary forest at Los Naranjos and most of them are common. Among the dominant species are Buff-breasted Wrens (*Thryothorus leucotis*), White-bellied Antbirds (*Myrmeciza longipes*), Crimson-backed Tanagers (*Ramphocelus dimidiatus*), and Lance-tailed Manakins (*Chiroxiphia lanceolata*). A more comprehensive and complete list of the birds of the area can be found in Ahumada (1995).

STUDY SPECIES

The focal species of this study belong to the family Troglodytidae (Wrens), genus *Thryothorus* which means "the reed leaper" (Jobling 1991). Most species in the genus are medium sized (11.5 to 15 cm in body length) and are usually found in pairs that defend a territory all year round. Individuals are often inconspicuous and difficult to see while they forage but they are frequently heard. The pair constructs a dome-shaped nest with a side entrance.

The Rufous-and-white Wren (14 to 15 cm, body length) is found throughout the Pacific slope of Central America from south Mexico to Panama and in northeastern South America. It lives in deciduous woodland, gallery forest, and forest borders up to 1,500 m (Hilty and Brown 1986). The song of Rufous-and-white Wrens is very characteristic, consisting of easily localizable pure tones and intermediate-frequency whistles. Males sing the most, although occasionally duets are also heard (J. Ahumada pers. obs.). The only published information about its reproductive biology and behavior comes from occasional observations of Skutch (1960) and a study by

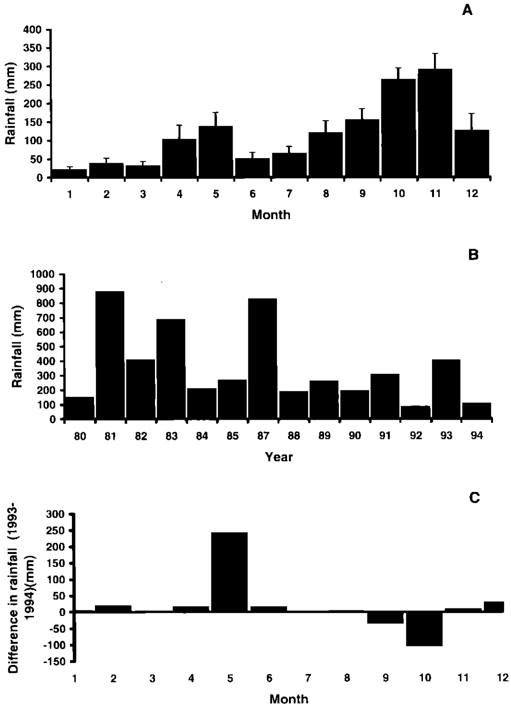

FIG. 2. (A) Monthly average rainfall (standard error in whiskers) from 1980 to 1994 in Parque Tayrona (data obtained from Instituto de Hidrología, Meteorología y Adecuación de Tierras, HIMAT). (B) Year to year variation in rainfall from the first six months of the year from 1980 to 1994 in Parque Tayrona. (C) Difference in monthly rainfall (1993 minus 1994) in Parque Tayrona.

Winnett-Murray (1986). Birds at Monteverde National Park, Costa Rica, breed once a year by constructing an inverted bow-shaped nest and laying a clutch of two to four eggs. As do most wrens in this genus, it lives in pairs that defend a territory all year round. Individuals also construct several dummy nests that are not used for reproduction; some species use these nests as dormitories but their function is not clear in others.

The Buff-breasted Wren (11 to 12 cm) is a smaller and more widespread species. Its range extends from southern Panama into South America east of the Andes to northern Bolivia, central and northern Brazil and Caribbean lowlands, and upper Amazon basins of Colombia and Venezuela. It is usually found in a larger variety of habitats than the Rufous-and-white Wrens; deciduous woodland borders, overgrown clearings, mangroves, Amazonian varzéa, and river borders up to 950 m above sea level. It is also found in several of the Pearl islands in Panama (Rey, Víveros, Puercos, and Cañas) (Ridgely et al. 1989). There is no published information on the reproduction and behavior of this species. Birds live in pairs but also occasionally forage in small groups of four to five individuals, probably family groups (Hilty and Brown 1986; J. Ahumada pers. obs.). As the Rufous-and-white Wrens, they also defend territories and duet frequently (J. Ahumada pers. obs.).

COLLECTION OF FORAGING AND DIET DATA

I collected data on foraging behavior of the wrens mostly during the second field season (March–September 1994) and most intensively during the rainy season. I located individuals or pairs of each species by song and followed them as long as possible. All data were collected by recording information in a microcassette tape recorder. As soon as I spotted a foraging individual, I estimated its height above ground and recorded the type of microhabitat (forest floor, trunk, understory shrub, vine tangle). I only recorded this information the first time that an individual was spotted to assure independence between samples. I then followed the individual continuously, recording the number of capture attempts made and the number of patch changes. I identified a patch change as a short flight of more than 2 to 3 m away from the original foraging position followed by more foraging in the new location. I discarded all focal samples of less than 2 min (maximum 3 min). Although the number of capture attempts has some limitations as an estimator of foraging efficiency, I used it instead of the proportion of successful captures because it was very difficult to observe success or lack thereof directly because of the high speed of those events. I also recorded aggressive interactions in the form of chases whenever they occurred. Because there were only four territories of Rufous-and-white Wrens within the plot, data were also collected from an additional five to six pairs outside it. All the foraging information on Buff-breasted Wrens was collected from pairs whose territories were within the plot (51 pairs).

Detailed analysis of the diet composition of both wrens would have disturbed their reproductive behavior, which was the primary interest of my study. Therefore, to estimate indrectly what the birds were eating, I observed the main substrates they used and then sampled intensively the arthropods in these substrates (next section). I only checked the stomach contents of two Buff-breasted Wrens and three Rufous-and-white Wrens and recorded the items brought to the nest by a pair of Buff-breasted Wrens. Individuals outside of the study plot were mist-netted in February 1993. The method used was after Moody (1970). After capture, a 2–3 mm diameter plastic tube coated with vaseline was introduced in the mouth and forced through the esophagus into the gizzard. Once the tubing was in place, a lukewarm saline solution was injected applying slight pressure to force out the stomach and gut contents via the cloaca or mouth. The gut contents were collected in a plastic cup and preserved in 35% ethyl alcohol for examination in the laboratory.

A pair of Buff-breasted Wrens was observed feeding its nestlings during three consecutive days in May 1993. I observed parents bringing food to the nestlings with binoculars and identified and recorded prey items to order or suborder when possible.

ESTIMATION OF TERRITORY SIZE

With the help of an assistant, I mapped the territories of all pairs of both wren species within the plot. This was done systematically by walking through the plot playing back the recorded song of a pair or individual of each species. I estimated the size and limits of the territory by moving the playback to reference points and observing the behavior of the resident pair and neighboring pairs. Several individuals of both species (12 Buff-breasted and 9 Rufous-and-white wrens) were color-banded so it was possible to confirm the permanent nature of the territories, at least during the study period.

TEMPORAL VARIATION IN ABUNDANCE AND BIOMASS OF ARTHROPODS

I collected information on the abundance of arthropods during two seasons: from September 1992 to June 1993 and from March to August 1994. The type of information collected and the methods used were different in those two seasons. The first field season constituted the sampling of arthropods through 10 months at biweekly intervals. This regular sampling precluded a large sample size during each sampling event (10 stations), but was necessary to look at the relationship between arthropod numbers and rainfall over several months. During the second field season, intensive sampling was done throughout the plot (175 stations) at each sampling event, but only three sampling events were completed at two-month intervals (first dry season, beginning of the wet season, and second dry season). Those were intended mostly to investigate factors that affect the spatial distribution of arthropods in the forest in both the understory and forest litter. Most data in this paper are from the second field season; I refer to data from the first field season when appropriate.

During the first season, I only evaluated the abundance of foliage-dwelling arthropods by performing counts in 10 randomly selected stations within the study plot. The stations were located inside territories of wrens of both species. The counts were done at bimonthly intervals during morning hours with the help of an assistant. The rationale behind the method was to imitate closely the behavior of a wren based on my best knowledge of the substrates that those birds were seen to inspect when foraging. The method attempts to measure numbers of arthropods a wren would find during 15 min in a cylinder 2 m high with a base of 4 m in diameter. This method was preferred over methods like sweep netting, bagging, malaise traps, and light traps because those usually sample flying arthropods, which were rarely pursued by wrens. Some methods fail to give an appropriate measure of the effort required to find a given amount of arthropods per unit of time or volume of forest sampled. The method of standardized counts used here has been used before in avian studies, including previous studies of wrens (Winnett-Murray 1986).

I searched for arthropods on upper and lower leaf surfaces, in rolled-up dry leaves, on the surface of dead and living twigs, and on the surface of flowers and fruits. I also counted live arthropods that were hanging from or standing in silk (e.g. spiders). Whenever I encountered an arthropod, I recorded the following information: taxonomic order, substrate where it was found (see above), life stage (adult or larvae), and size. Only the length of the body (head-tip to abdomen-tip) was used to estimate size. I classified arthropods in five different size classes: 1 (2–5 mm), 2 (6–10 mm), 3 (11–15 mm), 4 (16–20 mm), and 5 (>20 mm). Ants, isopods, dead arthropods, and arthropods with aposematic coloration were excluded from the counts. I considered more than five individuals of the same arthropod species aggregated in a given substrate as a "cluster." For clusters, I recorded the same information as for individual arthropods. However, clusters were considered separately in the data analysis.

The arthropod counts made during the first field season did not take into account litter-dwelling arthropods, which were found to be extremely important for the diet of Rufous-and-white Wrens. Therefore, during the second field season (March through August 1994) the methodology was modified, both to include litter-dwelling arthropods and to increase number of sampling stations for both types of arthropods as explained before. Litter arthropods were sampled by collecting samples of litter at 175 stations (corresponding to previously placed plastic stakes) distributed in a regular lattice 40 m apart in the study plot. At each station, two samples of leaf litter were collected by placing a wooden box (33 × 28 cm) upside-down over the ground and sliding a piece of plywood underneath, trapping the litter in the box. The exact location of the box was determined by throwing it at random within a 2 m radius of the location of the plastic stake. The litter of both samples at each station was combined and placed in a ziplock bag. A total of 20 to 25 stations were sampled in a day and their litter contents were taken to the lab to separate the arthropods the same day. Litter samples were emptied into metal trays and the arthropods were separated by hand and collected in plastic bottles containing 75% ethyl alcohol. Arthropods smaller than 1 mm, ants, isopods, and arthropods with aposematic colorations were excluded from the counts because these are rarely consumed by insectivorous birds. Information on the size class, taxonomic order, and life stage was gathered for each individual arthropod found in the sample. The whole plot was sampled three times during the season: first dry season (March), first rainy season (May), and second dry season (August). Each sampling effort took about 10–12 days. In March, only 135 stations were sampled because of the following. The first litter samples were collected and, once bagged, sprayed with insecticide to kill the arthropods and to facilitate their separation from the litter in the laboratory. However, it took me and my assistants much more time to separate arthropods from insecticide-sprayed samples than from insecticide-free samples. In the latter, the arthropods were detected easily while trying to escape from the metal tray whereas in the former, we missed many arthropods because of their immobility. Therefore, I abandoned insecticide use and discarded the data from insecticide-sprayed samples.

Counts of foliage-dwelling arthropods were simultaneously done with the collection of litter samples at each station. The methods followed were the same as used in the first field season, with the exception of the duration of each count. Due to the large number of stations sampled and the need to sample the plot in no more than 10 to 15 days, counts were reduced from 15 to 10 min in each station. To make comparisons among field seasons, the number of arthropods found in each station during the first field season was expressed as an average per minute and then multiplied by 10. Because I collected information on the size of each arthropod counted, it was easy to calculate arthropod biomass by using published within-order regression equations of dry biomass and body length (Rogers et al. 1977, Sample et al. 1993). I used the median size class as an estimate of the length of an arthropod: class 1 (3 mm), 2 (8 mm), 3 (13 mm), 4 (18 mm), and 5 (25 mm). If the regression equation for a given order was lacking, the following general regression for all insects was applied (Rogers et al. 1976):

$$W = 0.0305L^{2.62}$$

where W is the weight of the insect in milligrams and L its body length in millimeters.

To make temporal comparisons in abundance and biomass for both foliage and litter-dwelling arthropods, it was necessary to determine the degree of spatial autocorrelation for the data. Because the counts and litter samples were taken at regular 40 m intervals, the degree of spatial association had to be determined before considering each sampling point as independent (Legendre 1993). Details of how the degree of spatial autocorrelation was calculated and the main results are presented in Appendix 1.

REPRODUCTIVE BIOLOGY

I searched intensively for nests of both species from August 1992 to July 1993 and March–August 1994. My searches for Buff-breasted Wren nests were mostly restricted to the study plot. However, due to their lower density, I surveyed a large area for Rufous-and-white Wren nests (about 2 km). I observed the behavior of individual pairs of both species to determine their reproductive activity. This was relatively easy to do because members of a pair usually perform their activities together, so the prolonged absence of one them (mostly the female) usually meant that there was nesting activity of some kind (incubation, nestling feeding). I then carried out an intensive search for the nest. Pairs that I observed building nests were followed later to check if they had eggs.

Once I found an active nest, I checked number of eggs every two days or as frequently as possible. With the help of an assistant, I visited nests that were higher than 2–3 m using an aluminum ladder that could be extended up to 12 m secured by ropes. In the 1994 season, I measured the widths and lengths of eggs from several clutches of both species to the nearest 0.1 mm. I observed and recorded when eggs, nestlings, or fledglings disappeared or when additional eggs were added by parasites. Sometimes it was easy to determine causes of nest failure (infertile eggs, signs of predators, brood parasites). A nest was considered successful if at least one nestling was fledged. Based on nests that were followed in their entirety, I estimated the length of the incubation and nestling periods to be 14–15 days for each species. I used that information to estimate the starting dates of clutches that were found in the laying or nestling stage.

RESULTS

DIET

Both species of wrens are typical foliage gleaners that spend most of their time looking for arthropods in the undersides and tops of understory shrub leaves and tangles, in rolled-up dry leaves, on the surface of branches and in leaves in the litter (see Ahumada 1995 for details on microhabitat use). Inspection of those substrates showed that they harbored mostly spiders, coleopterans, orthopterans, homopterans, and to a lesser extent lepidopteran larvae (leaf surfaces: 32% spiders, 18% coleopterans, 13% homopterans, 10% orthopterans, 4% lep. larvae, 23% others; undersides of leaves: 59% spiders, 19% coleopterans, 9% homopterans, 4% lepidopteran larvae, 11% others; rolled-up

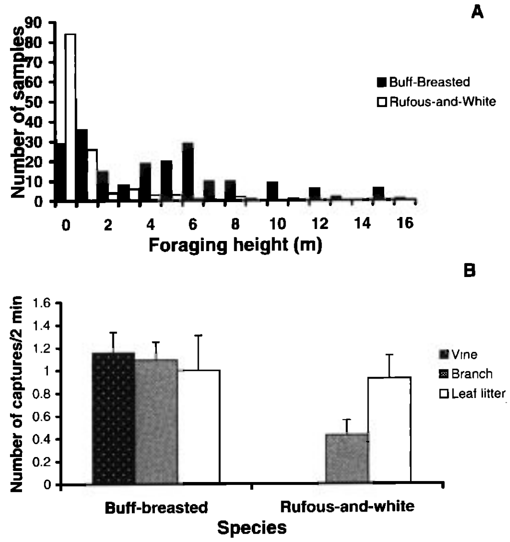

FIG. 3. (A) Distribution of foraging heights for both species of wrens. (B) Average number of capture attempts per 2 min observation bouts (standard errors in whiskers) for both species of wrens in three different microhabitats.

dry leaves: 43% spiders, 20% orthopterans, 20% coleopterans, 2% lepidopteran larvae, 15% others; leaf-litter: 33% spiders, 16% coleopterans, 19% pseudoscorpionids, 9% orthopterans, 23% others). Those results indicate that those taxa were probably the most important in the wren's diet, although pseudoscorpionids seemed also important for Rufous-and-white Wrens (see below and Ahumada 1995).

Despite partial digestion, the stomach contents confirmed this. The stomach contents of two Buff-breasted Wrens and three Rufous-and-white Wrens showed remains of orthopterans, spiders, and coleopterans. Additionally, observations of a pair of Buff-breasted Wrens that brought food to a nest by stopping in a nearby branch first, show that most of the items consisted of spiders (13/30), lepidoptera larvae (7/30) coleopterans (4/30), adult butterfly (1/30), hemipterans (2/30), orthopteran (1/30), and small dragonflies (2/30).

FORAGING BEHAVIOR

The two species clearly differed in their foraging height (Fig. 3A). Buff-breasted Wrens foraged between 0 and 18 m, peaking slightly at 1 and 6 m. Rufous-and-white Wrens had a smaller vertical foraging range (0 to 8 m) with 65% of the samples occurring on the ground. That vertical segregation also resulted in Buff-breasted Wrens foraging in more microhabitats than Rufous-and-white Wrens. A comparison of the total number of capture attempts for both species showed that there was no difference between the species (Sign Test, $Z = 1.23$, $P = 0.21$, $n = 139$). However, when capture attempts are divided according to microhabitat for each species (Fig. 3B), it is clear that Buff-breasted Wrens were equally good at capturing arthropods (or at least attempting to capture them) in all the microhabitats they forage in, whereas Rufous-and-white Wrens were equally good to Buff-breasted Wrens only in the forest floor (Mann-Whitney tests: Understory branch—Buff-breasted vs. Rufous-and-white, $Z = -2.78$, $P < 0.001$, $n = 53$; Floor, $Z = -0.75$, $P = 0.44$, $n = 46$).

While observing both species, I noted that all aggressive interactions were directed at Rufous-and-white Wrens which were always displaced. Out of a total of 10 aggressions, 7 occurred while they were foraging above 1 m in height in either a understory branch ($n = 5$) or vine tangle ($n = 2$). In five cases, Buff-breasted Wrens aggressively chased Rufous-and-white Wrens and in two cases White-bellied Antbirds chased Rufous-and-white Wrens.

TERRITORY SIZE AND DENSITY

From those observations in habitat use of both species, one would expect that the two dimensional projections of Rufous-and-white Wren territories have to be larger than those of Buff-breasted Wrens because their main foraging microhabitat (the forest floor) is basically two dimensional in nature. On the other hand, the territory of a Buff-breasted Wren encloses a volume of forest ranging from 0 to about 15 m. Indeed, a comparison of the size of the two dimensional projections of the territories of both species showed a difference in about an order of magnitude (Fig. 4). There was also an order of magnitude difference in the density of both species in the plot. Whereas Buff-breasted Wrens were very common (51 pairs, density = 4 individuals/ha), Rufous-and-white Wrens were rare (5 pairs, density = 0.4 individuals/ha).

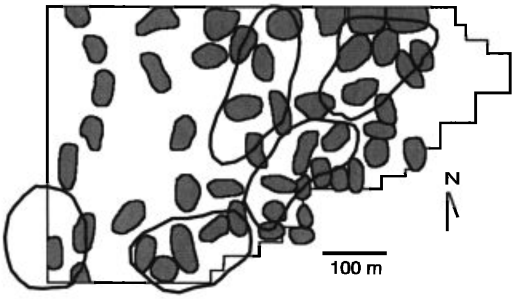

FIG. 4. Comparison of the two-dimensional projections of territories of both species of wrens in the study plot. Small-filled territories are from Buff-breasted Wrens. Large-transparent territories are from Rufous-and-white Wrens.

TEMPORAL VARIATION IN ARTHROPOD ABUNDANCE AND BIOMASS

Forest understory.—Biweekly counts of understory arthropods showed a positive correlation with rainfall from September 1992 to June 1993 ($r = 0.259$, $P = 0.03$, $n = 18$). During most of the dry season (January–April), arthropod numbers were low and then steadily increased with the arrival of the rains in May and June.

In 1994, number of stations sampled was increased (from 10 to 175) at the cost of decreasing the interval between successive samples. However, the pattern was similar to that of 1992–1993; arthropod numbers in the understory increased with the arrival of the rainy season and then decreased as the rains subsided in August (Fig. 5) (Wilcoxon matched pairs test: $Z_{\text{March-May}} = 4.550$, $P < 0.001$, $Z_{\text{May-August}} = 7.521$, $P < 0.001$). Average biomass of arthropods showed a substantial decrease during the second dry season when compared to the first dry season and rainy season (t-test: $t_{\text{March-August}} = 1.54$, $P < 0.05$; $t_{\text{May-August}} = 7.6$, $P < 0.05$). There was no difference in the biomass of arthropods between the first dry season and the wet season (t-test: $t_{\text{March-May}} = -0.17$, $P = 0.86$).

Leaf litter.—In contrast to understory arthropods, litter-dwelling ones were relatively invariant in both numbers and biomass. Despite the large change in rainfall from March to May and from May to August, there was no significant difference in number of litter arthropods among the three different seasons (Fig. 5). Biomass, however, was significantly lower during the second dry season by ~ 3 g in average (t-

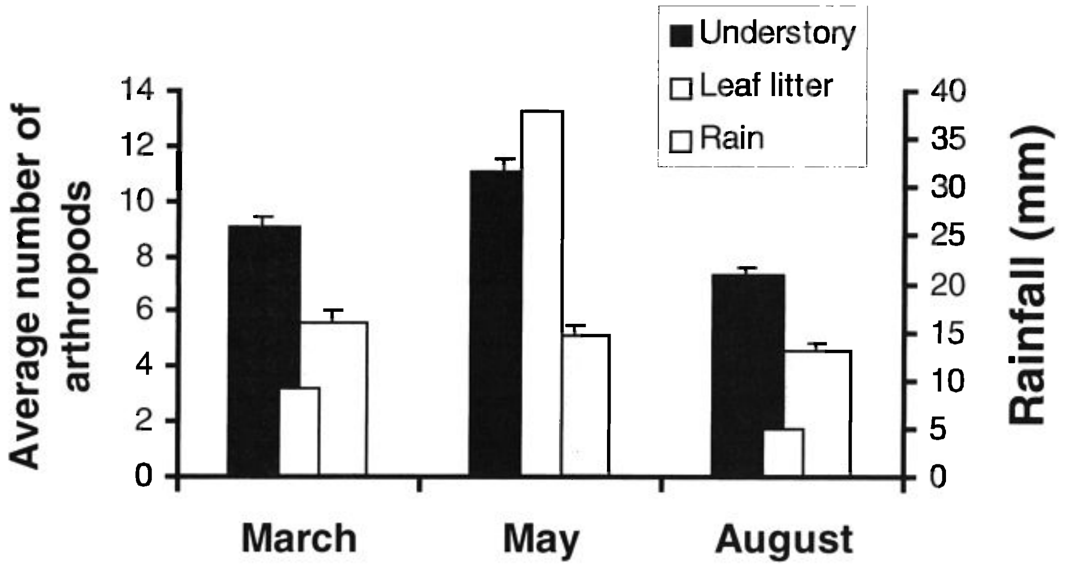

FIG. 5. Variation in the average number of arthropods found during 175, 10 min counts per month in the understory and 175 superficial litter samples (0.18 m^2) per month (whiskers denote standard errors) in three different months in 1994: March (first dry season of the year), May (first wet season of the year), and August (second dry season of the year). White bars denote the amount of rainfall within 45 days previous to the first day of each sampling period. The number of arthropods per sample in the understory was significantly higher in May (Wilcoxon matched pairs test, see text).

test: $t_{\text{May–August}} = 2.5$, $P = 0.01$, $t_{\text{March–August}} = 1.76$, $P = 0.02$) (see Ahumada 1995).

COMPOSITION OF THE ARTHROPOD COMMUNITY

Forest Understory.—A total of 4,813 arthropods was found by inspecting the forest understory during the 1994 field season. More than half of the arthropods were spiders, followed by coleopterans, orthopterans, and homopterans (Appendix 2). Biomass of spiders also constituted the largest proportion (72.7%) followed by orthopterans (6.9%) and coleopterans (4.7%) (see Appendix 2).

Some, but not all taxa (7 of 12) showed changes in absolute numbers through time. Appendix 3 shows the results of pairwise comparisons between the numbers of different taxa for different sampling regimes (dry, wet, and dry season). Only spiders and homopterans showed an increase in numbers during the wet season (May) compared to the dry periods before and after the rains (March, August). Pairwise comparisons of the biomass of different taxa through time showed similar trends compared to absolute numbers of arthropods. Spiders were significatively smaller (same number but smaller biomass) at the beginning of the second dry season (August). Other taxa such as coleopterans, orthopterans, and phasmids showed similar trends to spiders. The data show a pattern in which groups that increased in number during the rainy season demonstrated a decrease in average biomass either after (Araneae) or before (Homoptera) the rains. For other groups, changes in numbers were consistent with changes in biomass; when their numbers were high, so was their biomass, and vice versa. Half of the taxa showed no change in abundance or biomass through time. Surprisingly, lepidopteran larvae were among that group.

Leaf litter.—A total of 2,420 arthropods were found in 485 leaf-litter samples collected in 1994. Again, spiders were the predominant taxon followed by pseudoscorpionids, coleopterans, and orthopterans (Appendix 4). Diplopods were predominant in biomass owing to the their large size, but spiders still constituted 27.8% of the total biomass, followed by coleopterans, dictyopterans, and scorpionids.

Seven out of the 15 taxa showed a significant change in abundance through the sampling period. However, only one taxon, Pseudoscorpionida, showed a significant increase during the rainy season in May which persisted through August (Appendix 5). Interestingly, spiders, which were the most abundant taxon, showed no change in abundance through time. In general, leaf-litter taxa were more invariant through time in both relative numbers and biomass compared to arthropod taxa in the understory. Some taxa that were highly variable in the understory (Araneae, Orthoptera, Heteroptera) showed no change in the leaf-litter.

REPRODUCTIVE BIOLOGY

Both species of wrens construct globular nests made of small sticks, plant fibers, dry leaves, and feathers. The nest has the shape of an inverted elbow with the bending point over a branch or vine supporting the entire weight of the nest and the entrance pointing downwards. Both male and female participate in nest construction. Rufous-and-white Wren nests were larger than those of Buff-breasted Wrens, measuring 50 to 60 cm from the entrance to the edge of the incubating chamber (about 30 to 40 cm for Buff-breasted Wrens).

The two species showed differences in their preferred nesting heights and the general location of their nests. Buff-breasted Wrens usually nested lower in the forest with over 50% of the nests placed between 1 to 2 m ($n = 28$). They also nested in a variety of substrates including shrubs, vine tangles, and spiny vine palms. Rufous-and-white Wrens nested higher (up to 10 m) and constructed most of their nests hanging from *Desmoncus* spiny palm vines and occasionally (2/12) on the top of small understory trees.

Buff-breasted Wrens constructed additional dormitory nests that were never used for reproduction. Those nests were smaller and shallower than breeding nests and several of them could be found within each of the territories of Buff-breasted Wrens. I confirmed their use as dormitories by observing Buff-breasted Wren individuals entering them at dusk. In contrast, I never observed such behavior in Rufous-and-white Wrens. They did have two to three nests at a given time and they reused old nests by replacing old twigs, repairing holes, and renew-

TABLE 1. Summary of reproductive parameters for both species of wrens in two different years: wet (1993) and dry (1994). Mean clutch start date is given in Julian date ± SD. BB = Buff-breasted Wrens, RW = Rufous-and-white Wrens. * = significant at $P < 0.05$.

Species	Year	No. of nests	Mean clutch start date	Proportion successful	Loss to predation	Loss to parasites	Loss to other
BB	1993	16	105 ± 38.7	0.31	0.54	0.27	0.18
	1994	29	156 ± 32.7*	0.38	0.55	0.28	0.17
RW	1993	9	115 ± 32.9	0.33	0.50	0.33	0.16
	1994	7	129 ± 16.4	1	0	0	0

ing the lining of the incubating chamber. Once I observed a pair of Rufous-and-white Wrens constructing a nest for two weeks while simultaneously repairing and old nest that had several holes. A week later the female laid eggs in the old nest while leaving the new nest intact.

Females of both species lay one egg per day to complete a clutch of 2 to 3 eggs (Buff-breasted Wrens: 2.8 ± 0.38, $n = 23$; Rufous-and-white Wrens: 2.7 ± 0.45, $n = 11$). Eggs of Rufous-and-white Wrens were significantly wider and longer than Buff-breasted Wren eggs (Ahumada 1995). The eggs of Rufous-and-white Wrens were uniform ocean blue without speckles, whereas Buff-breasted wren eggs were cream colored, speckled with brown, and blue, especially at the larger end.

The incubation and nestling periods lasted 14 to15 days each for both species. After hatching, both parents bring food to the nestlings, and the fledglings remain six to eight weeks with their parents. Second broods were infrequent; during the second field season, I only observed second broods in one out of 6 Rufous-and-white Wren breeding pairs and in 2 out of 24 breeding Buff-breasted Wren pairs. During 1994, it was possible to estimate the proportion of the population of both species that attempted to breed (laid at least one clutch of eggs). Of 9 pairs of Rufous-and-white Wrens, 6 bred (0.66), and of 51 pairs of Buff-breasted Wrens, 24 bred (0.47).

Nesting failure.—The main causes of nesting failure for both species were predation and brood parasitism (Table 1). Nests that were preyed upon showed typical signs of disruption, such as holes in the side, deformation and distention of the main entrance, and egg shell remains on the ground. Although the nature of the predators was not confirmed (except for three nests which were taken over by army ants), the signs were unequivocal that predation had occurred.

Brood parasitism by Striped Cuckoos (*Tapera naevia*) and Shiny Cowbirds (*Molothrus bonariensis*) was also a common source of nest failure for both species. Cuckoos were more common in Los Naranjos than cowbirds, and accounted for seven of nine parasitized nests. Cuckoos were sighted and heard mostly at Los Naranjos at the beginning of June in the middle of the rainy season. For the 1994 season, Buff-breasted Wren pairs that bred before the arrival of cuckoos had a higher probability of fledging at least one chick (0.63) than pairs that bred after the arrival of cuckoos (0.22).

Other causes of nest failure included infertile eggs and falling nests. In 1994, these accounted for about 10% of nest failures in Buff-breasted Wrens and a similar proportion for Rufous-and-white Wrens in 1993 (11%). The proportion of successful nests and the contribution to nest failure from predation, brood parasitism, and other causes was relatively similar in Buff-breasted Wrens for both the wet and dry year (Table 1). In contrast, Rufous-and-white Wrens had a much higher nesting success in the dry year compared to the wet year. In 1993, proportion of successful nests and relative contributions of nest failure were similar for both species. All Rufous-and-white Wren nests fledged at least one nestling in 1994.

Timing of nesting and duration of the breeding season.—The species differed significantly in their mean date of clutch initiation for 1994 (Fig. 6). In the previous year, Buff-breasted Wrens started breeding around the third week of April with most of the clutches starting in the first and second weeks of May. However, in 1994 only a few pairs had started to show some reproductive activity by the first week of May and most of the population started laying by

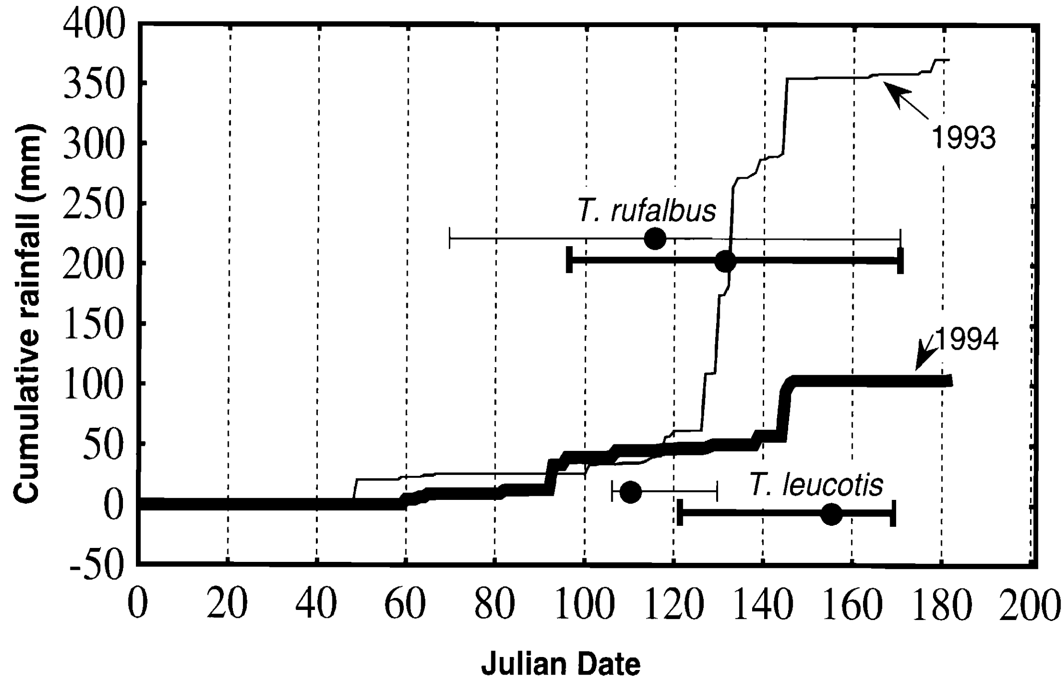

FIG. 6. Comparison of the length of the breeding season and mean date of clutch initiation for both species of wren in the two years of the study. The cumulative rainfall for the first 181 days of each year is plotted in the y-axis (thin line, 1993; thick line, 1994). The thin horizontal bars show the length of the breeding season in 1993 for Rufous-and-white Wrens (RW) and Buff-breasted Wrens (BB). These were determined from the first and last date when a clutch was initiated. The thick horizontal bars show the length of the breeding season for 1994. The dark circles over each bar indicate the mean date of clutch initiation. Date 0 = 1 January.

the end of that month (Mann-Whitney U-test, $Z = -3.51$, $P = 0.00$, $n = 23$). In contrast, Rufous-and-white Wrens started breeding at the beginning of April in both years and were more spread out in their nesting during the season with some pairs breeding even into June (Mann-Whitney U-test, $Z = -0.85$, $P = 0.39$, $n = 13$). Buff-breasted Wrens delayed their reproduction for at least a month in the dry year, whereas Rufous-and-white Wrens behaved similarly in both the dry and wet years (Fig. 6).

DISCUSSION

The results of this study show that differences in rainfall can affect significantly the abundance and biomass of arthropods available for Buff-breasted Wrens in the understory. However, rainfall does not seem to have such a clear effect on the abundance and biomass of arthropods in the leaf litter. Because Buff-breasted Wrens prefer to eat arthropods in the understory and exhibit similar capture rates in different microhabitats, one would expect that individuals experience a high year-to-year variability in food abundance in a place like Tayrona were rainfall is so variable between years. Reproductive activity of the main nest parasite in the area (Striped Cuckoo) and predator activity also seem closely dependent on the arrival of the first rainy season. What is the reproductive strategy shown by Buff-breasted Wrens in face of this environmental variation in food supply and activity of nest parasites and predators? My results indicate that Buff-breasted Wren reproduction is closely tied to arthropod abundance, which in turn seems to be determined by the arrival of the rainy season with a minimum cumulative rainfall of around 50 mm (Fig. 6).

Although I could not compare arthropod abundance between the wet and dry years of my study, the within-year comparison in 1994 clearly suggests that arthropod abundance in the understory and rainfall are closely linked. In both years, Buff-breasted Wrens started breeding only when approximately 50 mm of rainfall had fallen. That amount of rain was attained about 30 days earlier in 1993 than 1994, and Buff-breasted Wrens correspondingly started clutches 50 days earlier on average in 1993. If changes in photoperiod were used as an environmental cue by the birds to start reproducing, one would expect no differences in average clutch initiation date between years. Therefore, it seems reasonable to assume that those birds are being cued by rainfall which in turn is positively correlated with the abundance of their main food source (arthropods in the understory). Clearly, the strategy of Buff-breasted Wrens fits well with a typical tracker where the birds are monitoring closely changes in rainfall, food abundance, or both, and then start their reproduction when a minimum amount in any of these, or both is attained. Additionally, there is an advantage for birds that breed earlier in the season because they have a higher probability of escaping parasitism and predation. Overall, that strategy seems to be working well for the species because there were no differences in overall nesting success between contrasting years of rainfall.

The picture is rather different for Rufous-and-white Wrens. These wrens are shy and furtive birds that feed on arthropods mostly on the ground. My foraging behavior data indicate that this was the only microhabitat where Rufous-and-white Wrens had a capture rate of arthropods similar to that of Buff-breasted Wrens in their foraging microhabitats. Because of their foraging habits, the territories of Rufous-and-white Wrens spanned a larger area and their densities were lower in comparison with Buff-breasted Wrens.

The evolutionary processes that led to this foraging specialization in Rufous-and-white Wrens are not the topic of this paper, but my data in conjunction with observations of the same species in Costa Rica (Winnet-Murray 1986) suggest that present-day competition with Buff-breasted Wrens and other understory insectivores might have an important effect. My observations of the aggressive interactions between the two species support the idea that Rufous-and-white Wrens are being displaced to forage closer to the ground by Buff-breasted Wrens and other understory birds. In all the aggressive encounters that I witnessed, Rufous-and-white Wrens were always attacked and chased away by other species, especially Buff-breasted Wrens. Those chases occurred while Rufous-and-white Wrens were foraging above 1 m in the forest understory. Observations of Rufous-and-white Wrens in Panama and Costa Rica indicate that in these sites, the species seems to feed in the understory more frequently than at Tayrona (Winnet-Murray 1986; T. Robinson pers. comm.). At least in Panama, the density of Buff-breasted Wrens is lower than in Tayrona (S. Gill pers. comm.), which supports the idea that the microhabitat "cornering" exhibited by Rufous-and-white Wrens in Tayrona may be linked to a higher density of Buff-breasted Wrens there.

The abundance of arthropods in the leaf litter did not change significantly between wet and dry seasons as did the abundance of understory arthropods. My data agree with results of other studies (Wolda 1990, Poulin et al. 1992), showing that the litter offers a more constant environment for arthropods compared to the understory, although this is not always the case (T. Robinson pers. comm.). Therefore, Rufous-and-white Wrens seem to be experiencing a much more constant food environment despite year-to-year variations in rainfall. If food abundance is influencing timing of breeding in Rufous-and-white Wrens as it seems to do with Buff-breasted Wrens, one would not expect to see a tracking strategy in those birds, because their food environment seems to be less variable through time. That is directly reflected in the breeding phenology: they had a longer period of breeding (100 days in 1993 and 70 days in 1994) and started breeding earlier in both years compared to Buff-breasted Wrens. Although the first Rufous-and-white Wren nest was detected almost three weeks later in 1994 than in 1993, there was no difference in the average clutch initiation date of the population between these two years. The nesting success of Rufous-and-white Wrens was similar to that of Buff-breasted Wrens in 1993, but no Rufous-and-white Wren nests were predated or parasitized in 1994. That can be attributed to the delay in the rainy season which affected the arrival of nest parasites and predators to the area. Therefore, despite its conservative strategy, the Rufous-and-white Wrens might experience a higher yearly variance in nesting success than Buff-breasted Wrens through year-to-year variation in nest parasitism or predation.

Because my data come only from two contrasting years of rainfall, I cannot be completely sure that the species would show the same patterns described here in other years with similar conditions, or that this is a general pattern in highly variable environments and other species of birds. However, the differences exhibited by these wrens in their reproductive timing between these two particular years, and the way this was linked to the dynamics of their food resources, is highly suggestive of an underlying pattern that deserves further investigation.

CONSTRAINTS IN THE EVOLUTION OF LIFE HISTORIES IN VARIABLE ENVIRONMENTS

The results of this paper are important for examination within the framework of the evolution of life histories in tropical birds. What are the reproductive strategies that birds can adopt in an environment in which the conditions for successful reproduction fluctuate from one year to the next? What do my results tell about constraints in the evolution of bird reproductive strategies in variable environments?

At the outset of this study, I predicted the reproductive strategies of both wrens based mostly on the existing life-history theory in variable environments (Cohen 1966, MacArthur 1968, Schaffer 1974, Horn 1978, Rubenstein 1982). I expected Buff-breasted Wrens to be very plastic in their reproductive parameters, depending on the amount of food available; to reproduce disproportionately better in good years; and to have a short reproductive period and a high number of broods per year. On the other hand, because of their larger body size, I expected Rufous-and-white Wrens to be less variable in their reproductive output, being able to withstand bad years better than Buff-breasted Wrens and being more conservative in their reproductive output in good years (bet-hedgers). I predicted that Rufous-and-white Wrens would concentrate their reproductive efforts in few broods and would have a long reproductive period.

My results confirmed that Buff-breasted Wrens had a shorter reproductive period than Rufous-and-white Wrens. However, I did not find any evidence for plasticity in reproductive parameters (except onset of breeding), or differences in nesting success or numbers of broods between good and bad years. Rufous-and-white Wrens did have a longer breeding season, and the only reproductive parameter that was less variable than in Buff-breasted Wrens was their timing of reproduction. But they did not have fewer broods and their nesting success changed from one year of my study to the next.

The reason for this discrepancy between my predictions and what the wrens showed lies in the assumption that most of the reproductive parameters that I examined were plastic. This proved not to be the case. The wrens were virtually identical in all the reproductive parameters that I examined: clutch size, number of fledglings produced, incubation time, and nestling time. This is somehow expected because these two species are closely related. However, due to a difference in foraging behavior, the food environment perceived by each species is different, and that has a direct effect on the timing of breeding. Especially in tropical areas, clutch size and other reproductive parameters vary little for many bird species (but see Young 1994), presumably because of high predation pressure (Skutch 1950, Kuleza 1990). Therefore, it is possible that for many tropical birds, the characters that are prone to change are mostly behavioral because reproductive parameters might be under strong stabilizing selection or they might not be as plastic (i.e. do not have enough additive genetic variance) as behavioral characteristics might. That might limit the number of characters or traits available for the evolution of a given reproductive strategy of tropical birds. Because my study was done over a short-term, I could not gather information on other life-history characters of the wrens such as age-specific survival, age at first reproduction, number of reproductive attempts in a lifetime, and dispersal. Clearly, long-term studies on the life histories of tropical birds are needed to further clarify which characters are more constrained to change in response to a variable environment. If those ideas are right, I predict that in cases where no other behavioral choice is available, the timing of reproduction of tropical birds would be very constrained temporally in a similar way exhibited by many temperate bird species.

Previous studies of birds have shown that competition between species can have an effect on community structure (Pierpont 1986), and habitat utilization (Orians and Willson 1964, Greene 1989). This study suggests that competition can have an effect on the reproductive strategy of the species involved. To pursue these ideas further, it is necessary to have a thorough understanding of the natural history of a group of species by simultaneously collecting information on the foraging behavior, the dynamics of their food sources, and their reproductive behavior. A good example of such a study is represented by the long-term research on the Galapagos finches (Grant 1986). The different species of Galapagos finches show no differences in clutch size, incubation time, nesting time, or shape of the nest. Except for the Cactus Finch (*Geospiza scandens*), which bred earlier, all species synchronized their breeding season with the rainy season whenever it arrived. Some individuals of this species could afford to breed earlier because of the availability of pollen and nectar from cacti as a food source during the dry season. The Galapagos Islands are, however, an extremely seasonal environment and the finches do not have many choices as to when to breed. We are in need of similar data sets for tropical birds in a variety of environments with different degrees of seasonality and predictability.

RELATIONSHIP BETWEEN TIMING OF REPRODUCTION AND FORAGING BEHAVIOR IN NEOTROPICAL INSECTIVOROUS BIRDS

Is it possible to make generalizations for predicting the reproductive phenology of a species by knowing its diet? The two wrens that I studied differ in the places they forage and, probably because of its more constant food environment, Rufous-and-white Wrens had a longer breeding season and started reproducing earlier than Buff-breasted Wrens. Can these relationship be extended to other neotropical insectivorous birds?

Plain Xenops (*Xenops minutus*) living in Tayrona, started breeding well before the rains arrived in February and March (J. Ahumada pers. obs.). Those birds feed exclusively on insects and other arthropods that live inside dead branches and hanging vines. White-bellied Antbirds also bred during the dry season and well into the rainy season (August–September) (J. Ahumada pers. obs.). They spend most of their time tossing litter leaves aside looking for fleeing arthropods. The Clay-colored Thrush (*Turdus grayi*) in Panama also spends a substantial amount of time feeding on ground arthropods and breeds in the dry season (Morton 1971).

I propose that insectivores that feed in substrates such as leaf litter, dead wood, or species that follow ants might experience less seasonal variations in their food supply than insectivores that feed on arthropods that inhabit living plant material. That fact allows the first group of insectivores to extend their breeding season and perhaps to breed at times when predation, brood parasitism, or other external causes of nest failure are minimal. To test those ideas further, it is necessary to collect detailed breeding information in a group of closely related species (e.g. within a family or genus) that feed on different types of arthropods with different temporal dynamics. For example, the study of Winnett-Murray (1986) on the behavior of four species of wrens in Costa Rica showed that House Wrens (*Troglodytes aedon*) that lived in open habitats experience a more constant food supply and have a longer breeding period than Gray-breasted Wood Wrens (*Henicorhina leucophrys*) and Rufous-and-white Wrens which are forest species. However, Plain Wrens (*Thryothorus modestus*), which also live in open habitats, showed a similar breeding period compared to the forest wrens. More comparative information of that kind will allow us to untangle the confounded effects of phylogeny and behavior on the reproductive strategies of Neotropical insectivorous birds.

ACKNOWLEDGMENTS

I want to especially thank the supervisors of this study, Henry Horn and Andy Dobson. Their unconditional support and ideas were crucial for its successful development. Francisco Troncoso, Aracelly Caselles, Liz Adriana Serrano, Maritza Jaramillo, Diana P. Molina, and Pablo Stevenson were of invaluable help in the field. Kathy Winnett-Murray, Frank Joyce, and an anonymous reviewer gave invaluable comments to earlier versions of the manuscript. I also want to thank FONDO FEN–COLOMBIA for their logistic support. This study was funded partially by Princeton University in the United States and COLCIENCIAS in Colombia.

LITERATURE CITED

AHUMADA, J. A. 1995. The effects of environmental variation on the reproduction, ecology and behavior of two neotropical wrens. Ph.D. dissertation, Princeton University, Princeton, New Jersey.

BEISSINGER, S. R., AND J. P. GIBBS. 1993. Are variable environments stochastic? A review of methods to quantify environmental predictability. Pages 133–146 *in* Adaptation in Stochastic Environments (J. Yoshimura and C. W. Clark, Eds.). Springer-Verlag, Berlin.

BLAKE, J. G., AND B. A. LOISELLE. 1992. Fruits in diets of Neotropical migrant birds in Costa Rica. Biotropica 24:200–210.

CLIFF, A. D., AND J. K. ORD. 1981. Spatial Processes: Models and Applications. Pion, London.

COHEN, D. 1966. Optimizing reproduction in a variable environment. American Naturalist 126:418–429.

COLWELL, R. K. 1974. Predictability, constancy and contingency. Ecology 55:1148–1153.

GRADWOHL, J., AND R. GREENBERG. 1990. Temporada de reproducción de tres pajaros hormigueros en la Isla de Barro Colorado. Pages 433–440 *in* Ecología de un Bosque Tropical (E. G. J. Leigh, A. S. Rand, and D. M. Windsor, Eds.). Smithsonian Institution Press, Washington, D.C.

GRANT, P. R. 1986. Ecology and Evolution of Darwin's Finches. Princeton University Press, Princeton, New Jersey.

GREENE, E. 1989. Food resources, interspecific aggression, and community organization in a guild of insectivorous birds. Ph.D. dissertation, Princeton University, Princeton, New Jersey.

HEIDEMAN, P. D. 1989. Temporal and spatial variation in the phenology of flowering and fruiting in a tropical rainforest. Journal of Ecology 77: 1059–1079.

HERNÁNDEZ-CAMACHO, J., AND P. RODRÍGUEZ-GUERRERO. 1972. Estudio ecológico de la vegetación del Parque Nacional Natural Tayrona. División de Parques Nacionales y Vida, INDERENA, Colombia.

HERRMANN, R. 1970. Las causas de la sequía climática en la región costanera de Santa Marta Colombia. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 13:479–490.

HILTY, S. L. 1980. Relative abundance of north temperate zone breeding migrants in western Colombia and their impact at fruiting trees. Pages 265–271 *in* Migrant Birds in the Neotropics: Ecology, Behavior, Distribution and Conservation (A. Keast and E. S. Morton, Eds.). Smithsonian Institution Press, Washington, D.C.

HILTY, S. L., AND W. L. BROWN. 1986. A Guide to the Birds of Colombia. Princeton University Press, Princeton, New Jersey.

HOLMES, R. T., T. W. SHERRY, AND F. W. STURGES. 1986. Bird community dynamics in a temperate deciduous forest: Long-term trends at Hubbard Brook. Ecological Monographs 56:201–220.

HORN, H. S. 1978. Optimal tactics of reproduction and life-history. Pages 411–429 *in* Behavioural Ecology: An Evolutionary Approach. (J. R. Krebs and N. B. Davies, Eds.). Sinauer Associates, Sunderland, Massachusetts.

JANZEN, D. H. 1973a. Sweep samples of tropical foliage insects: Description of study sites, with data on species abundances and size distributions. Ecology 54:659–686.

JANZEN, D. H. 1973b. Sweep samples of tropical foliage insects: Effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology 54:687–708.

JANZEN, D. H. 1980. Heterogeneity of potential food abundance for tropical small land birds. Pages 545–552 *in* Migrant Birds in the Neotropics: Ecology, Behavior, Distribution and Conservation (A. Keast and E. S. Morton, Eds.). Smithsonian Institution Press, Washington, D.C.

JOBLING, J. A. 1991. A Dictionary of Scientific Bird Names. Oxford University Press, Oxford.

KINNAIRD, M. F. 1992. Phenology of flowering and fruiting of an east African riverine forest ecosystem. Biotropica 24:187–194.

KULEZA, G. 1990. An analysis of clutch size in New World passerine birds. Ibis 132:407–422.

LEGENDRE, P. 1993. Spatial autocorrelation: Trouble or new paradigm? Ecology 74:1659–1673.

LEVEY, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. Ecological Monographs 58:251–269.

LEVINGS, S. C., AND D. M. WINDSOR. 1990. Fluctuaciones de las poblaciones de artrópodos de hojarasca. Pages 443–451 *in* Ecología de un Bosque Tropical (E. G. J. Leigh, A. S. Rand, and D. M. Windsor, Eds.). Smithsonian Institution Press, Washington, D.C.

LOISELLE, B. A., AND J. G. BLAKE. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. Ecology 72:180–193.

MACARTHUR, R. 1968. Selection for life tables in periodic environments. American Naturalist 102: 381–383.

MARTIN, T. E. 1987. Food as a limiting on breeding birds: A life history perspective. Annual Review of Ecology and Systematics 18:453–487.

MILLER, A. H. 1963. Seasonal activity and ecology of the avifauna of an American equatorial cloud forest. University of California Publications in Zoology 66:1–74.

MILLER, A. H., AND V. D. MILLER. 1968. The behavioral ecology and breeding biology of the Andean sparrow (*Zonotrichia capensis*). Caldasia 10: 83–154.

MOODY, D. T. 1970. A method for obtaining food samples from insectivorous birds. Auk 87:579.

MORAN, P. A. P. 1950. Notes on continuous stochastic phenomena. Biometrika 37:17–23.

Morton, M. L. 1971. Nest predation affecting the breeding season of the Clay-colored Robin, a tropical song bird. Science 171:920–921.

Orians, G. H., and M. F. Willson. 1964. Interspecific territories of birds. Ecology 45:735–745.

Paladino, F. V. 1989. Constraints of bioenergetics on avian population dynamics. Physiological Zoology 62:410–428.

Pierpont, N. 1986. Interspecific aggression and the ecology of woodcreepers (Aves: Dendrocolaptidae). Ph.D. dissertation, Princeton University, Princeton, New Jersey.

Poulin, B., G. Lefebvre, and R. McNeil. 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. Ecology 73: 2295–2309.

Ridgely, R., G. Tudor, and W. L. Brown. 1989. The Birds of South America, vol. 1. University of Texas Press, Austin.

Rogers, L. E., W. T. Hinds, and R. L. Buschbom. 1976. A general weight vs. length relationship for insects. Annals of the Entomological Society of America 69:387–389.

Rubenstein, D. 1982. Risk, uncertainty and evolutionary strategies. Pages 91–110 *in* Current Problems in Sociobiology (C. King's College Sociobiology Group, Eds.). Cambridge University Press, Cambridge, United Kingdom.

Sample, B. E., R. J. Cooper, R. D. Greer, and R. C. Whitmore. 1993. Estimation of insect biomass by length and width. American Midland Naturalist 129:234–240.

Schaffer, W. M. 1974. Optimal reproductive effort in fluctuating enviroments. American Naturalist 108:783–790.

Skutch, A. F. 1950. The nesting seasons of Central American birds in relation to climate and food availability. Ibis 92:185–222.

Skutch, A. F. 1960. Life Histories of Central American Birds, vol. 2. Pacific Coast Avifauna no. 34.

Snow, D. W., and B. K. Snow. 1963. Breeding and annual cycle of three Trinidad thrushes. Wilson Bulletin 75:27–41.

Snow, D. W., and B. K. Snow. 1964. Breeding seasons and annual cycles of Trinidad land-birds. Zoologica 49:1–39.

Van Schaik, C., J. W. Terborgh, and S. J. Wright. 1993. The phenology of tropical forests: Adaptive significance and consequences for primary consumers. Annual Review of Ecology and Systematics 24:353–377.

Walsberg, G. 1983. Avian ecological energetics. Pages 161–220 *in* Avian Biology, vol. 7 (D. S. Farner and J. R. King, Eds.). Academic Press, New York.

Winnett-Murray, K. 1986. Variation in the behavior and food supply of four neotropical wrens. Ph.D. dissertation, University of Florida, Gainesville.

Wolda, H. 1978a. Fluctuations in abundance of tropical insects. American Naturalist 112:1017–1045.

Wolda, H. 1978b. Seasonal fluctuations in rainfall, food and abundance of tropical insects. Journal of Animal Ecology 47:369–381.

Wolda, H. 1980. Seasonality of tropical insects. Journal of Animal Ecology 49:277–290.

Wolda, H. 1990. Estacionalidad de los Homópteros de la Isla de Barro Colorado. Pages 403–415 *in* Ecología de un Bosque Tropical (E. G. J. Leigh, A. S. Rand, and D. M. Windsor, Eds.). Smithsonian Institution Press, Washington, D.C.

Young, B. 1994. The effects of food, nest predation and weather on the timing of breeding in tropical House Wrens. Condor 96:341–353.

Associate Editor: T. Martin

Appendix 1. I calculated the spatial autocorrelation among arthropod sampling points within the plot using Moran's index (*I*) (Moran 1950):

$$I = \frac{N \sum_{i=1}^{N} \sum_{j=1}^{N} (x_i - \bar{x})(x_j - \bar{x})}{\sum L_i \sum_{i=1}^{N} (x_i - \bar{x})^2}$$

where N is the number of data points in the lattice, $\bar{x}$ is the mean for all data points, x_i and x_j are the values of two points that are contiguous (at the appropriate lag) and ΣL_i is the sum of the number of links between elements that are contiguous in the lattice (Cliff and Ord 1981).

For regular, unweighted lattices, I behaves similarly to ρ (a correlation coefficient) varying between -1 and 1 (Cliff and Ord 1981). A value of -1 indicates negative spatial autocorrelation (spiked surfaces), a value near 1 indicates positive spatial autocorrelation (smooth surfaces), and a value near 0 indicates no spatial autocorrelation (data points are independent from each other). With large sample sizes, I is distributed normally so it is easy to test its departure from 0 statistically (ibid). The expected value of I for large sample sizes is:

$$E(I) = -\frac{1}{(N - 1)}$$

and its expected variance is:

$$E(I^2) = \frac{4AN^2 - 8N(A + D) + 12A^2}{4A^2(N^2 - 1)}$$

where $A = 1/2\ \Sigma\ L_i$ and $D = 1/2\ \Sigma\ L_i(L_i - 1)$ I calculated I not only for the raw data but also for the difference between the numbers or biomass of arthropods in two months for the three pairwise comparisons: March–May, March–August, and May–August. This difference was further tested for departure from 0 (Wilcoxon matched pairs test) to see if there was any change in numbers or biomass of arthro-

Table A1. Results from the spatial autocorrelation analysis for the arthropod data collected in 1994. Autocorrelation coefficients (I) were calculated for the difference in either number or biomass of arthropods between two months in the understory and the leaf litter and at two spatial lags: nearest neighbor (40 m) and second nearest neighbor (80 m). The differences between March and May and between March and August have a different expected value because of the smaller number of litter stations sampled in March (see the Methods section for details).

		I (biomass)		I (numbers)	
Microhabitat	Difference between	lag 40 m	lag 80 m	lag 40 m	lag 80 m
Understory	March & May[1]	0.0380	−0.0289	−0.0585	−0.0099
	March & August[1]	−0.0318	0.0086	−0.0133	0.0644*
	May & August[1]	0.0620	−0.0249	0.0078	0.0301
Leaf-litter	March & May[2]	−0.0419	−0.0092	0.0734	−0.0704*
	May & August[2]	0.0099	−0.0976*	0.0526	−0.0305
	March & August[1]	0.0443	0.0268	−0.0323	0.0458

[1] $E(I) = -0.0057$, $\sigma(I) = 0.0399$, N = 175.
[2] $E(I) = -0.0074$, $\sigma(I) = 0.0458$, N = 135.
* Significant at $\alpha = 0.05$.

pods from month to month. A program in C was written to perform the necessary calculations. I was calculated at two spatial lags: nearest neighbor (40 m) and second nearest neighbor (80 m). Significant departures of I from 0 were checked using tables of the normal distribution. Additionally, I constructed semivariograms for all data sets to gain insight on the degree of spatial autocorrelation at larger spatial lags (Cliff and Ord 1981).

There was no indication of spatial autocorrelation at the nearest neighbor and second nearest neighbor in any of the three months sampled neither for un-

Appendix 2. Total number (first row in each cell) and biomass (second row) of arthropods from different taxa found in 525, 10-min understory counts. Data are broken-up for each of three sampling periods: March (dry season), May (beginning of the wet season), and August 1994 (end of the wet season). Percentages of the total for each column are shown in parentheses. Biomass is expressed as milligrams of dry weight.

Taxon	All months combined	March n = 175	May n = 175	August n = 175
Araneae	2,667 (55.4)	857 (54.0)	1,082 (55.9)	728 (56.6)
	35,736 (72.7)	14,527 (74.1)	16,909 (78.7)	4,299 (53.4)
Coleoptera	752 (15.6)	243 (15.3)	303 (15.6)	206 (16.0)
	2,325 (4.7)	619 (3.2)	1,043 (4.8)	663 (8.2)
Orthoptera	424 (8.8)	149 (9.4)	191 (9.9)	84 (6.5)
	3,401 (6.9)	1,375 (6.7)	1,055 (4.9)	971 (12.1)
Hemiptera				
Homoptera	346 (7.2)	88 (5.5)	153 (7.9)	105 (8.2)
	452 (0.9)	84 (0.4)	137 (0.6)	231 (2.9)
Heteroptera	107 (2.2)	46 (2.9)	31 (1.6)	30 (2.3)
	1,495 (3.0)	770 (3.9)	346 (1.6)	379 (4.7)
Lepidoptera				
larvae	143 (3.0)	43 (2.7)	51 (2.6)	49 (3.8)
	501 (1.0)	133 (0.7)	182 (0.8)	186 (2.4)
adults	43 (0.9)	11 (0.7)	16 (0.8)	16 (1.2)
	358 (0.7)	68 (0.4)	125 (0.6)	165 (2.0)
Diptera	92 (1.9)	31 (2.0)	32 (1.7)	29 (2.3)
	123 (0.2)	45 (0.2)	23 (0.1)	55 (0.6)
Dictyoptera	43 (0.9)	19 (1.2)	17 (0.9)	7 (0.5)
	1,324 (2.7)	652 (3.3)	463 (2.1)	209 (2.6)
Phasmida	25 (0.5)	11 (0.7)	13 (0.7)	1 (0.1)
	2,025 (4.1)	984 (5.0)	1,034 (4.8)	7 (0.1)
Dermaptera	8 (0.2)	4 (0.3)	3 (0.2)	1 (0.1)
	17 (0.4)	2 (0.0)	8 (0.1)	7 (0.1)
Other	163 (3.4)	87 (5.5)	45 (2.3)	34 (2.6)
	1,432 (2.9)	371 (1.9)	190 (0.9)	871 (10.8)
Total	4,813	1,589	1,937	1,287
	49,135	19,607	21,485	8,050

derstory arthropods nor litter arthropods (Table A1) in numbers or biomass. Although the spatial autocorrelation for a few grids showed a significant departure from 0, the strength of the signal is so small (<0.1) that it can be ignored. Semivariograms indicated that this lack of spatial autocorrelation at the first and second lags was consistent at larger spatial lags. Therefore, comparisons between months were carried out assuming independence of samples.

APPENDIX 3. Results of pairwise comparisons (Wilcoxon matched pairs test) between numbers (first row in each taxon) and biomass (second row) of understory arthropods from different taxa between the three different sampling periods: March (first dry season), May (beginning of rainy season), August (second dry season). Comparisons were done between March and May and May and August (last two columns). Months labeled with "=" within each row do not differ significantly. A month labeled with "+" or "−" has a significantly higher or lower value compared with other months in the same row.

Taxon	March	May	August	$Z_{\text{Mar-May}}$	$Z_{\text{May-Aug}}$
Araneae	=	+	=	4.12*	6.01*
	=	=	−	0.15	6.91*
Coleoptera	=	=	−	1.87	3.18*
	=	=	−	0.97	3.51*
Orthoptera	=	=	−	1.47	4.97*
	=	=	−	1.21	2.72*
Hemiptera					
Homoptera	=	+	=	3.52*	2.37*
	−	=	=	2.38*	0.46
Heteroptera	+	=	=	2.36*	0.46
	+	=	=	2.36*	0.17
Lepidoptera					
larvae	=	=	=	1.03	0.48
	=	=	=	1.93	0.12
adults	=	=	=	0.64	0.16
	=	=	=	0.63	0.20
Diptera	=	=	=	0.05	0.16
	=	=	=	0.31	0.00
Dictyoptera	=	=	=	0.25	1.77
	=	=	=	0.74	1.56
Phasmida	=	=	−	0.39	2.82*
	=	=	−	0.22	2.94*
Dermaptera	=	=	=	0.36	0.80
	=	=	=	0.50	0.00
Other	+	=	=	2.28*	1.47
	+	=	=	2.03*	1.76

* = Significant at the $P < 0.05$ level.

APPENDIX 4. Total number (first row in each cell) and biomass (second row) of arthropods from different taxa found in 485 leaf-litter samples. Data are shown for each of three sampling periods: March (dry season), May (beginning of the wet season), and August 1994 (end of the wet season). Percentages of the total for each column are shown in parentheses. Biomass is expressed as milligrams of dry weight.

Taxon	All months combined	March *n* = 135	May *n* = 175	August *n* = 175
Araneae	791 (32.7)	228 (31.5)	270 (29.9)	293 (36.9)
	3,213 (27.8)	1,582 (46.7)	626 (13.1)	1,005 (29.6)
Coleoptera	385 (15.9)	112 (15.5)	160 (17.7)	113 (14.2)
	1,141 (9.9)	240 (7.1)	437 (9.2)	464 (13.7)
Pseudoscorpionida	470 (19.4)	103 (14.2)	195 (21.6)	172 (21.7)
	432 (3.7)	224 (6.6)	94 (2.0)	115 (3.4)
Orthoptera	226 (9.3)	59 (8.1)	94 (10.4)	73 (9.2)
	521 (4.5)	200 (5.9)	184 (3.9)	137 (4.0)
Dictyoptera	88 (3.6)	39 (5.4)	34 (3.8)	15 (1.9)
	838 (7.2)	201 (5.9)	509 (10.7)	128 (3.8)
Lepidoptera				
adults	3 (0.1)	1 (0.1)	2 (0.2)	0 (0.0)
	21 (0.2)	0.4 (0.0)	20 (0.4)	0 (0.0)
larvae	27 (1.1)	11 (1.5)	11 (1.2)	5 (0.6)
	14 (0.1)	0.7 (0.0)	13 (0.2)	0.3 (0.0)
Protura	58 (2.4)	37 (5.1)	12 (1.3)	9 (1.1)
	49 (0.4)	22 (0.6)	7 (0.1)	21 (0.6)
Hemiptera				
Homoptera	16 (0.7)	13 (1.8)	1 (0.1)	2 (0.3)
	17 (0.1)	11 (0.3)	6 (0.1)	0.8 (0.0)
Heteroptera	99 (4.1)	30 (4.1)	34 (3.8)	35 (4.4)
	207 (1.8)	92 (2.7)	49 (1.0)	66 (1.9)
Diptera	21 (0.9)	2 (0.3)	14 (1.6)	5 (0.6)
	6 (0.1)	1 (0.0)	1 (0.0)	4 (0.1)
Scorpionida	13 (0.5)	3 (0.4)	6 (0.7)	4 (0.5)
	816 (7.1)	170 (5.0)	360 (7.6)	287 (8.4)
Thysanura	78 (3.2)	11 (1.5)	22 (2.4)	45 (5.7)
	500 (4.3)	29 (0.9)	30 (0.6)	441 (13.0)
Chilopoda	15 (0.6)	11 (1.5)	4 (0.4)	0 (0.0)
	113 (1.0)	7 (0.2)	106 (2.2)	0 (0.0)
Diplopoda	60 (2.5)	35 (4.8)	20 (2.2)	5 (0.6)
	3,357 (29.0)	591 (17.4)	2,114 (44.6)	652 (19.2)
Other	70 (2.9)	29 (4.0)	24 (2.7)	27 (2.1)
	285 (2.5)	18 (0.5)	189 (4.0)	78 (2.3)
Total	2,420	724	903	793
	11,532	3,388	4,744	3,399

APPENDIX 5. Results of pairwise comparisons (Wilcoxon matched pairs test) between numbers (first row in each taxon) and biomass (second row) of litter arthropods per station of a given taxon between the three different sampling periods: March (first dry season), May (beginning of rainy season), August (second dry season). Comparisons were done between March and May and May and August (last two columns). Months labeled with "=" within each row do not differ significantly. A month labeled with "+" or "−" has a significantly higher or lower value compared with other months in the same row.

Taxon	March	May	August	$Z_{\text{Mar–May}}$	$Z_{\text{May–Aug}}$
Araneae	=	=	=	0.71	0.88
	=	=	=	0.28	0.58
Coleoptera	=	=	−	1.61	2.48*
	=	+	=	2.83*	2.35*
Pseudoscorpionida	−	=	=	2.14*	0.61
	+	=	=	2.09*	1.02
Orthoptera	=	=	=	0.50	0.93
	=	=	=	0.01	1.70
Dictyoptera	=	=	−	1.43	2.02*
	=	=	−	0.78	2.85*
Lepidoptera[1]	=	=	=	0.16	1.25
	=	=	=	0.92	1.88
Protura	+	=	=	2.71*	0.59
	+	=	=	2.35*	0.02
Hemiptera					
Homoptera	+	=	=	2.53*	0.53
	+	=	=	2.04*	0.00
Heteroptera	=	=	=	1.24	0.75
	=	=	=	0.53	0.47
Diptera	=	=	=	1.00	1.12
	=	=	=	0.00	0.84
Scorpionida	=	=	=	0.63	0.56
	=	=	=	0.84	0.50
Thysanura	=	=	+	0.35	1.98*
	=	=	+	0.18	2.53*
Chilopoda	=	=	=	1.53	1.82
	=	=	=	0.50	1.82
Diplopoda	=	=	−	1.61	2.42*
	=	=	−	0.56	2.11*
Other	=	=	=	0.75	0.75
	=	=	=	0.15	1.15

* = Significant at the $P < 0.05$ level.

[1] This includes only larvae. There were not enough adults to carry out the analysis.