

## THE EFFECTS OF FOOD, NEST PREDATION AND WEATHER ON THE TIMING OF BREEDING IN TROPICAL HOUSE WRENS<sup>1</sup>

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**Abstract.** I tested three hypotheses that could explain variation in the timing of breeding in populations of House Wrens (*Troglodytes aedon*) at four sites in Costa Rica. The sites were located at 200–1,500 m elevation on both sides and on top of the central mountain range, and had climates differing in temperature, the severity of the dry season, and total rainfall. For the first hypothesis, that breeding is timed to coincide with peaks in food availability, I monitored the monthly abundance of arthropod prey and wren clutch initiations at the four sites. Cross-correlation analysis showed that at three sites, wrens initiated clutches several months prior to when prey levels were high. Indeed, breeding began when prey levels were at their annual low. At the fourth site, prey levels varied little throughout the year and House Wrens nested nearly year round. These results indicate that sufficient food to produce eggs or feed nestlings may have been available throughout the year. Breeding appeared to be timed so that juvenile dispersal and molt occurred when food was most plentiful. The second hypothesis, that breeding is timed to avoid seasons when nest predation is high, was not supported because the rate of nest predation did not vary temporally. The third hypothesis, that breeding is timed to avoid climatic events that can increase the physiological costs of reproduction, was not supported at the three lower elevation sites. Clutch initiation at the highest site, however, did not commence until the early dry season wind and mist subsided. The termination of breeding was not correlated with climatic changes at any of the sites. Thus reproduction in tropical House Wrens seems generally to be timed to facilitate post-breeding activities, not activities associated with nesting itself.

**Key words:** *Climate; house wren; Neotropics; nest predation; prey availability; timing of breeding; Troglodytes aedon.*

**Resumen.** Probé tres hipótesis que podrían explicar la variación en tiempo de reproducción en poblaciones del soterrey (*Troglodytes aedon*) en cuatro sitios dentro de Costa Rica. Los sitios están localizados a elevaciones entre 200 y 1,500 m.s.n.m. a ambos lados y en la cima de la cordillera central. En los cuatro sitios el clima difiere en temperatura, severidad de la estación seca, y precipitación total. La primera hipótesis es que la época de reproducción está regulada por los picos en abundancia de alimentos, y para comprobarla evalué la abundancia mensual de artrópodos usados como presa y registré el inicio de la nidada de soterreyes en los cuatro sitios. Análisis de correlación cruzada mostraron que en tres de los cuatro sitios, los soterreyes iniciaron las nidadas varios meses antes del pico de abundancia de presas. De hecho, la reproducción se inició cuando la abundancia de presa se encontraban en el mínimo anual. En el cuarto sitio, la abundancia de presas varió muy poco a lo largo del año y los soterreyes anidaron durante casi todo el año. Estos resultados indican que debió haber suficiente alimento para producir huevos y alimentar crías durante todo el año. La reproducción pareció estar regulada de manera que la dispersión de juveniles y la muda ocurrieran cuando la abundancia de alimento se encontraba en su máximo. La segunda hipótesis, que el tiempo de reproducción está determinado de manera de evitar épocas cuando la depredación de nidos es alta, no fue apoyada debido a que la tasa de depredación de nidos no varió temporalmente. La tercera hipótesis, que el tiempo de reproducción está determinado para evitar eventos climatológicos que puedan incrementar los costos fisiológicos de reproducción no fue apoyada por los datos obtenidos en los tres sitios de menor elevación. Sin embargo, en el sitio más elevado, la iniciación de los nidos no se inició sino hasta que disminuyeron el viento y la garúa característicos de la primera fase de la estación seca. La terminación de la reproducción no estuvo correlacionada con cambios climáticos en ninguno de los sitios. Por lo tanto, el tiempo de la reproducción en los soterreyes parece estar determinada para facilitar las actividades post-reproductivas, más que con respecto a las actividades asociadas con la nidada misma.

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*Palabras clave:* Soterrey; *Troglodytes aedon*; tiempo de reproducción; disponibilidad de presas; depredación de nidos; clima; Neotrópicos.

## INTRODUCTION

Although temperate birds apparently time their breeding to coincide with annual peaks in food availability (Lack 1954, Perrins 1970, Ewald and Rohwer 1982, Martin 1987), the factors that influence the timing of breeding in tropical birds are less well understood. Food is probably important, especially in habitats with sharply defined dry and wet seasons (Boag and Grant 1984, Poulin et al. 1992). In tropical habitats with less pronounced dry and wet seasons, food may still be important in determining when birds breed (Skutch 1950, Ward 1969, Fogden 1972, Gradwohl and Greenberg 1982), although other factors such as nest predation (Morton 1971, Dyrz 1983) and climate (Skutch 1950, Tye 1991) could play a role as well. Here I address these issues with observations on four populations of House Wrens, *Troglodytes aedon*, in Costa Rica. House Wren populations nesting in boxes are easy to monitor, and the timing and duration of breeding vary between the study sites, providing a useful system in which to compare hypotheses about breeding in tropical birds.

## FOOD

The food hypothesis suggests that breeding (defined here as the initiation of a clutch of eggs) should be timed so that energetic demands are the highest when food is the most plentiful. Major energetic demands of reproduction may come during egg production (Ewald and Rohwer 1982), chick rearing (Lack 1954), or dispersal of fledglings (Morton 1971). Thus breeding may co-occur with food peaks or breeding may precede food peaks. Many authors assert that tropical birds generally time their reproduction to take advantage of seasonally abundant food (Skutch 1950, Bell 1982, Fogden 1972, Poulin et al. 1992). No study, however, has shown which stage of the reproductive cycle best coincides with food peaks, because most of the evidence is based on community-wide studies which obscure between-species differences in the fine scale tuning of the timing of reproduction (but see Boag and Grant 1984, Grant and Grant 1989).

For tropical House Wrens, the food hypothesis predicts that breeding will (1) coincide with food peaks if egg production is limiting; (2) be about

one month in advance of food peaks if food to feed nestlings is limiting; or (3) be two to five months in advance of food peaks if food for dispersing offspring is important. In some habitats in the humid tropics, food availability may not change appreciably during typical years. In this case, breeding attempts should be well spaced and be initiated throughout the year (Ashmole 1961). On the other hand, breeding should occur seasonally if the food supply undergoes sharp seasonal changes.

## NEST PREDATION

If nest predation varies seasonally, it too can affect the timing of breeding seasons. This effect could be secondary to food availability and merely limit breeding to a portion of the time when food levels are high (Gradwohl and Greenberg 1982, Pienkowski 1984), or it could be strong enough to force birds to nest when food is less abundant (Morton 1971, Dyrz 1983). In the tropics, nest predation may be highest during the late dry season (Sieving 1992) or during the early wet season (Gradwohl and Greenberg 1982). The nest predation hypothesis predicts that breeding seasons are timed to avoid peaks in nest predation. Most breeding should take place after a peak in predation and finish before the next peak.

## CLIMATE

Birds may time their breeding to avoid periods of harsh weather that increase the physiological costs of reproduction. For example, cold weather, wind, or rain could reduce foraging time (Foster 1974) or increase the incubation needs of eggs (Tye 1991). In the tropics, temperature varies little throughout the year and therefore cannot be an important factor. Annual rainy periods could be detrimental to open or ground nesting species by washing out nests, but probably do not affect House Wrens which nest in cavities. In cold, highland communities, the physiological costs of foraging in the rain or wind may be great enough to cause birds to avoid breeding during wet seasons (Skutch 1950, Tye 1991). The climate hypothesis therefore predicts (1) that breeding seasons do not overlap with windy and rainy periods and (2) that year to year variation in the timing of breeding is correlated with variation in the timing of the inclement weather.

TABLE 1. Characteristics of the four study sites.

Site	Elevation	Dry season	Range in monthly mean temperature, °C (month)	Number of nest boxes	Years of data
La Lucha	200 m	short, some showers	30.2 (Jul.)–33.3 (Apr.)	19	late 1990–1992
Monteverde	1,500 m	long, much mist	17.4 (Feb.)–19.6 (Jun.)	65	1989–1991
Upper San Luis	1,150 m	long, some mist	21.6 (Dec.)–24.7 (Apr.)	40	1989–1991
Lower San Luis	800 m	long, dry	insufficient data	20	1990–1991

## METHODS

### STUDY ORGANISM, STUDY SITES AND NEST CHECKS

House Wrens are 10–14 g insectivorous birds that nest in cavities in disturbed habitats throughout much of North, Central, and South America. Tropical House Wrens are permanent residents on their territories, which both members of a pair defend year round. Females lay one egg per day until the completed clutch of three to four eggs is reached. Incubation lasts 14–16 days, and fledging occurs 18 days after hatching. Fledglings remain on their natal territories for about three weeks before dispersing (Freed 1986, Winnett-Murray 1986).

The four study sites are located on or near the Cordillera de Tilarán in Costa Rica (Fig. 1) in habitat predominated by pastures and scattered trees interspersed with forest fragments. During the December–April dry season, northeast trade winds blow Caribbean moisture across the central mountain range, which is oriented northwest to southeast. This causes lowland Caribbean sites to receive some rain, mountaintop sites to receive mist, and Pacific slope sites to be dry (Fig. 1). During the intervening rainy season, all areas receive rain from localized convective heating events. At each site, a field assistant operated a weather station to characterize seasonal changes in temperature and rainfall. In addition, the Monteverde station provided data on daily average wind speed.

I erected nest box trails on each site between 1988 and 1990, attaching boxes to trees or fenceposts in densities that matched existing densities of territorial pairs of wrens based on a census of singing males. In this manner, I prevented an artificial population increase that can result from erecting nest boxes indiscriminately (e.g., Haartman 1971, Hågvar et al. 1990). My field assistants and I monitored nesting activity by visiting the boxes 1–2 times weekly during the subse-

quent 2–3 breeding seasons (Table 1). I assigned clutch initiations (defined as whenever at least one egg was laid in a nest) to months according to when egg laying most likely began. In Monteverde, I visited nests twice weekly during the egg laying period and was able to back-calculate the actual date of clutch initiation by assuming females laid one egg per day.

### ARTHROPOD SAMPLES

For an accurate measure of food available to an insectivore, it is important to know which of the many taxa of arthropods occurring in an area are preferred by the study species, and what microhabitats are most frequently used for foraging (Cooper and Whitmore 1990, Wolda 1990). Consequently, I performed trials on captive House Wrens to learn which arthropods they preferred to eat. A feeding trial consisted of introducing a recently captured (i.e., within 30 min) wren to a flight cage (2.0 × 1.2 × 0.5 m) with a variety of prey items. The prey items represented all taxa of arthropods captured in sweep net passes through wren territories. I assume that the major prey of House Wrens is included among the various arthropod taxa captured in the net. Indeed, I frequently saw House Wrens feed their young the same species that I caught. Using insect pins, I attached 20–30 live prey items representing a variety of taxonomic groups to a butterfly pinning board that could be inserted into the cage. After entering the cage, wrens quickly learned of the presence of the food and foraged actively, ripping the impaled prey from their pins. I set the duration of the trial at 30 min to ensure that starvation did not influence what wrens ate. In addition, I ran a feeding trial on a free ranging wren that had learned to enter my field lab and forage for flies in the window. In this case, I simply set a loaded pinning board on a window sill, waited for the wren to make its morning visit, and scored which prey it took.

Initial observations indicated that tropical

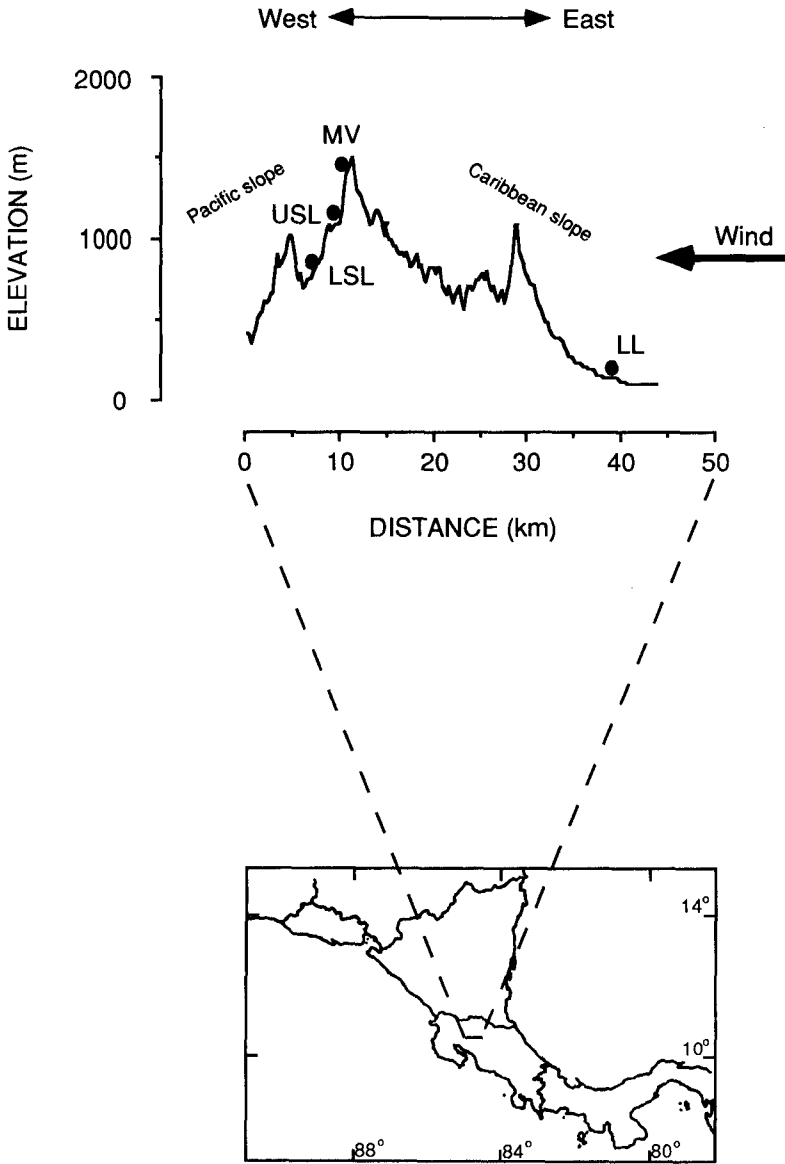


FIGURE 1. Locations of the study sites (Lower San Luis [LSL], Upper San Luis [USL], Monteverde [MV], La Lucha [LL]) along an east-west transect across the Cordillera de Tilarán in northern Costa Rica.

House Wrens forage frequently in pasture grass, as well on dead stumps, logs, and trees. Pasture grass is the easiest to sample, so I collected sweep net samples of pasture arthropods and assumed that arthropod abundance in the other microhabitats was correlated. To assess the importance of this assumption, I estimated the frequency with which House Wrens foraged in grass compared to the other areas where I observed wrens

searching for prey. In Monteverde during the 1991 breeding season, I performed 60 min observations of nests with chicks 6–13 days old. After each feeding visit, I scored whether a parent subsequently flew to (1) pasture grass, (2) a dead stump or log, or (3) a live tree or shrub to forage. I performed one or two observations at each nest, and treat all observation periods as independent.

For the actual arthropod samples, I selected

seven wren territories at each study site from which to take sweep net samples. For convenience, these territories were the seven closest to a dirt road or path extending across each site. There were no obvious habitat heterogeneities at any of the sites that might suggest these sample territories were not representative of their respective sites. To avoid unwanted variation caused by differences in territory quality, I sampled at the same seven territories at each site throughout the study. A sample of a territory consisted of 30 sweeps through pasture grass and vegetation along each of four transects extending in the four cardinal directions away from the nestbox. I sampled each territory in each site once per month from October 1990 through September 1991. To control for the effect of temperature and weather on arthropod abundance, I avoided sampling within two hours of sunrise or sunset or on rainy days.

I froze each sample to kill the specimens, sorted the samples to separate known wren prey items, and dried them to constant mass in a 60°C drying oven. I then weighed each sample to  $\pm 1$  mg accuracy with an electronic balance. I assumed that these measures are representative of the availability of food to House Wrens at the times and places the samples were collected. Furthermore, I assumed that the rate at which foraging wrens encountered prey was correlated to this measure of the availability of food on their territories.

#### NEST PREDATION

Because I made more frequent nest visits at Monteverde than the other sites, the information on nest predation is most complete from this site. I therefore limit the analysis to this site. I considered a nest depredated if all eggs or chicks disappeared between successive nest visits. The analysis does not include the few cases ( $< 2\%$  of nest attempts) in which infanticide by other House Wrens was the cause of nest loss (Freed 1986). I compared Mayfield (1975) estimates of daily survivorship of nests in the mid-dry season (from the onset of breeding in February or March through 15 April), late dry season (16 April–15 May), early wet season (16 May–15 June), and mid-wet season (16 June through the end of breeding in August or September).

#### STATISTICAL ANALYSES

I address the food hypothesis with a cross-correlation analysis of monthly food levels and a

measure of monthly reproductive effort (total eggs laid). Cross-correlation, a type of signal analysis based on correlations between two variables that were measured along the same time series, can uncover couplings between biological phenomena that are separated in time (Marmarelis and Marmarelis 1978, Sinclair et al. 1993). The three food hypotheses can thus be distinguished by examining the duration of the lag period corresponding to the greatest positive correlation between food and egg production. Also, in populations of House Wrens where the food supply is strongly seasonal and breeding is tied to food, the cross-correlation should show a sinusoidal pattern of first positive and the negative correlations as the lag period is increased. In populations with less seasonal variation in food, the cross-correlation should show a less regular sinusoidal pattern and weaker correlations overall.

I performed cross-correlation analyses, Kruskal-Wallis, and Pearson correlations with SYSTAT (Wilkinson 1989). I compared estimates of daily nest survivorship using the  $\chi^2$  statistic suggested by Sauer and Williams (1989).

## RESULTS

### THE BREEDING SEASON

The sites varied substantially in when breeding takes place relative to rainy periods (Fig. 2). Breeding began in Lower San Luis a month later than in either Upper San Luis or Monteverde, and continued a month later. In La Lucha, breeding occurred in nearly every month of the year with a lull only during the late wet season months of September and October. In all sites except Lower San Luis, breeding was about equally divided between the dry and wet seasons (Fig. 2). In Monteverde, where adults were individually marked, parents raised one brood in the dry season and then another in the wet season. The pattern of occupancy of the nestboxes indicated that wrens in Upper San Luis and La Lucha probably also raised one clutch in each season. In Lower San Luis, which has the most severe dry season, breeding did not begin until April, just before the beginning of the wet season (Fig. 2). House Wrens there probably also raised two broods, but both would have fledged during the wet season.

### ARTHROPODS

Feeding trials on five birds showed that tropical House Wrens readily take a wide variety of ar-

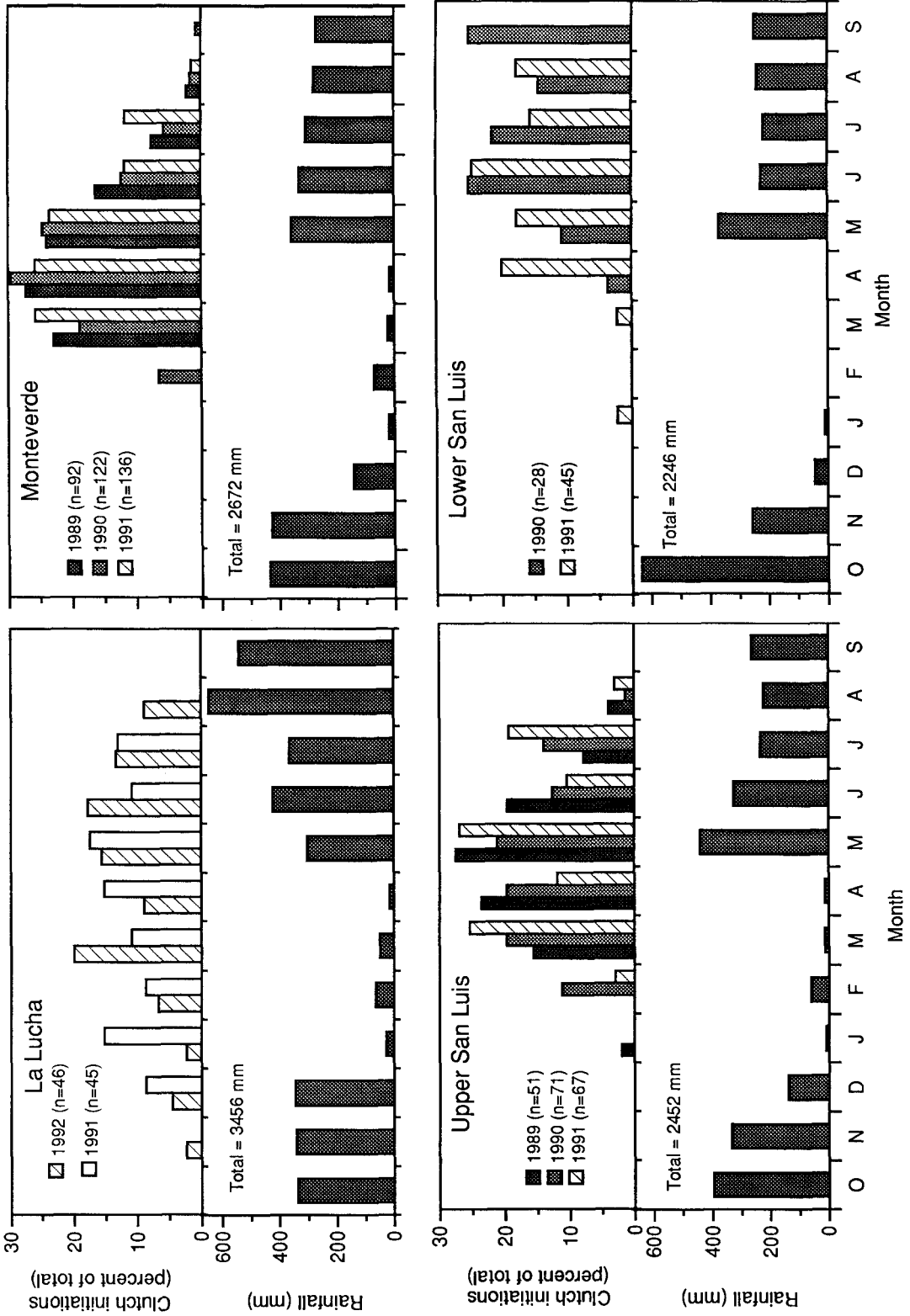


FIGURE 2. Monthly rainfall (1990–1991) and clutch initiations at the four study sites.

TABLE 2. Prey preferences of tropical House Wrens based on the results of feeding trials.

Prey taxa*		Nonprey taxa	
Taxon	No. taken/ no. offered	Taxon	No. taken/ no. offered
Arachnida			
Unidentified spp.	8/8	Hemiptera	
Orthoptera		Lygaeidae	0/7
Acrididae	23/30	Pentatomidae	0/5
Tettigoniidae	17/17	Unidentified spp.	0/3
Gryllidae	1/1	Coleoptera	
Blattidae	1/1	All taxa (including Chrysomelidae, Curculionidae, Staphilinidae)	0/14
Hemiptera			
Miridae	9/11		
Homoptera			
Cicadellidae	11/12		
Lepidoptera			
Unidentified spp.	6/7		
Diptera			
Unidentified sp.	1/1		

\* Individuals in these taxa only are included in the analyses of prey biomass.

thropods, but not all that occurred in the sweep samples (Table 2). In 56 nest observation periods, wrens flew from their nests to forage in pasture grass  $51 \pm 34$  ( $\bar{x} \pm SD$ ) percent of the time, on average. They foraged on stumps and dead logs  $17 \pm 22$  percent of the time, and flew to trees or bushes  $32 \pm 33$  percent of the time. The differences are significant (Kruskal-Wallis test,  $H = 28.19$ ,  $df = 2$ ,  $P = 0.0001$ ). Thus House Wrens, at least in Monteverde, most frequently foraged in the microhabitat I sampled for the prey analysis.

Among arthropods that were potential prey of House Wrens, biomass varied seasonally at all sites except La Lucha (Fig. 3). Biomass was highest in the late wet season when sampling began and lowest in the late dry season. In La Lucha, prey biomass did not vary systematically with seasonal weather changes. Prey biomass during the wet seasons of 1990 and 1991 at both Monteverde and Upper San Luis appeared to differ. After initial increases at the beginning of the 1991 wet season, prey biomass fell and appeared unlikely to attain the high levels of the previous wet season (Fig. 3).

Cross-correlation results show that in all four study areas, food availability and egg production were either uncorrelated or negatively correlated with a zero to two month lag (Fig. 4). In Lower San Luis, breeding may have been correlated with

food availability 3–5 months hence. In the other three sites, even this correlation was absent. For Monteverde and Upper San Luis, this may be due to the low increase in prey biomass in the 1991 wet season.

Lower San Luis shows the most regular sinusoidal relation of the four sites (Fig. 4). This indicates that both breeding and prey biomass levels show regular seasonal patterns of increase and decrease, at least for the 12 months sampled. This is in sharpest contrast with La Lucha, where prey biomass fluctuated erratically during the year and the breeding season was very long (Fig. 3). This caused there to be little pattern in the cross-correlation for La Lucha (Fig. 4). Although cross-correlation alone tells us nothing about cause and effect, the differences between these two sites suggest that food and breeding may be more tightly coupled in Lower San Luis.

#### NEST PREDATION

Nest predation rates were remarkably constant throughout the breeding season at Monteverde (Table 3). The rate of nest predation did not differ among the four periods measured ( $\chi^2 = 3.30$ ,  $df = 3$ ,  $P = 0.35$ ).

#### CLIMATE

In general, no obvious climatological events coincided with the beginning or end of the breeding

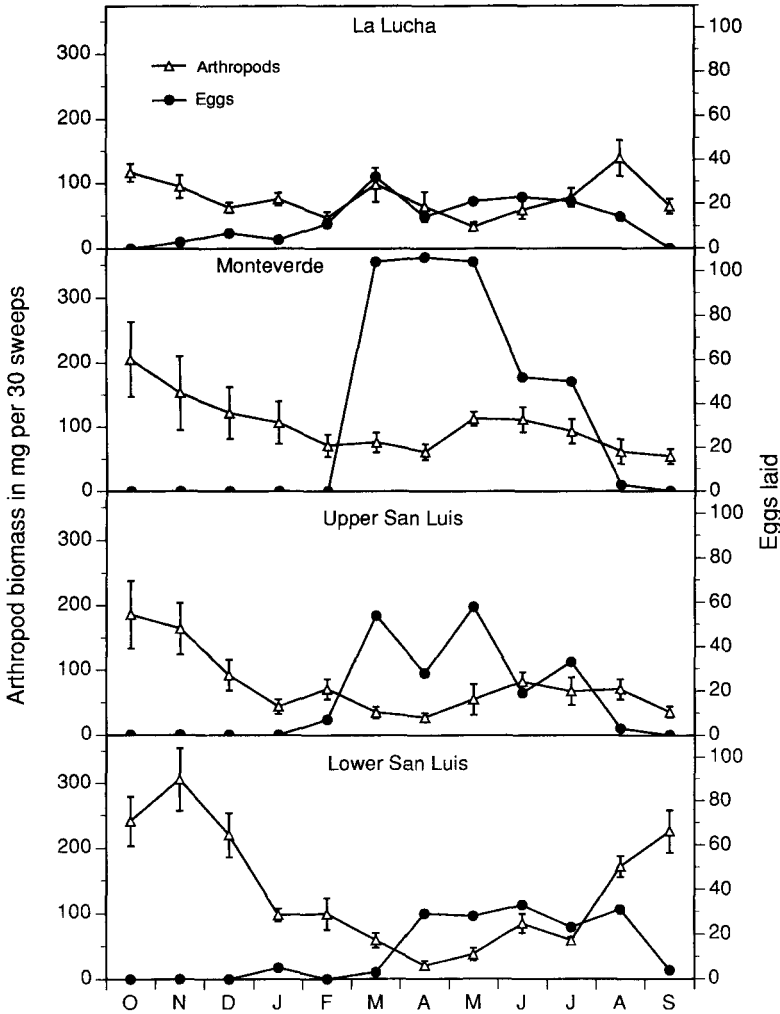


FIGURE 3. Seasonal changes in the biomass of arthropods preyed upon by House Wrens and reproductive output of House Wrens (in terms of total number of eggs laid), 1990–1991. Error bars represent the standard error of the biomass means.

season at most of the sites (Fig. 2). In Monteverde, the highest site, wrens apparently do not begin nesting until the mists of the early dry season subside. A fine scale comparison between three-day rainfall totals (virtually all in the form of mist) and clutch initiations shows that nesting began in February only during the year with the least rainfall in that month (Fig. 5). When nesting began in March, it did so once rainfall began to decline (Fig. 5). Because February is also one of the coldest months of the year in Monteverde (Table 1, Buskirk and Buskirk 1976), House

Wrens may breed during this month only if there is little precipitation. Daily average wind speed and precipitation (both log transformed) were positively correlated during the January through April dry period ( $r = 0.31, P < 0.01$ ), indicating that House Wrens also avoided nesting during the windiest periods. The behavior of the wrens further supports the contention that climate influences the onset of breeding. In the early breeding season, I observed nest building activity only on relatively calm, sunny days. Wrens temporarily abandoned their uncompleted nests if wet



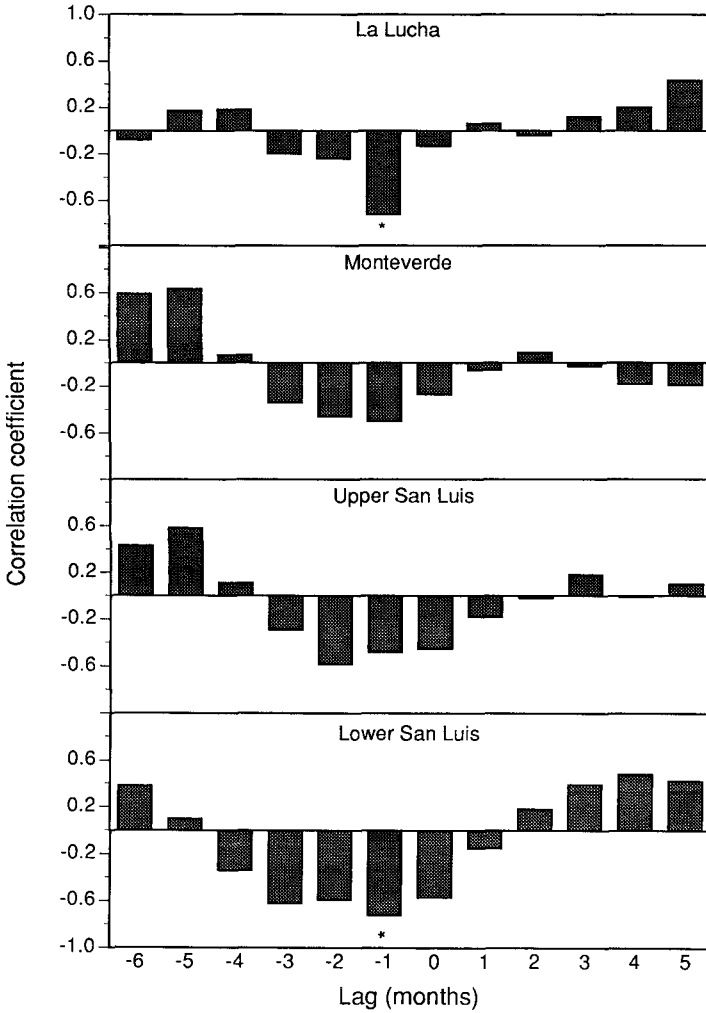


FIGURE 4. Cross-correlation analysis of the arthropod biomass and reproductive output data in Figure 3. Positive lag refers to correlations between breeding and future arthropod biomass, and negative lag refers to correlations between breeding and previous arthropod biomass. (\* $P < 0.05$ ; not corrected for multiple tests.)

and windy weather set in after a sunny period. Once fair weather returned, nest building resumed.

DISCUSSION

FOOD AVAILABILITY

Arthropod prey levels at all sites except La Lucha were highest during the wet season and lowest during the dry season as has been reported in other areas of the Neotropics (Janzen 1973, Smythe 1982, Wolda 1982, Poulin et al. 1992). Studies differ with regard to whether the wet sea-

TABLE 3. Seasonal variation in nest predation at Monteverde, 1989–1991.

Season*	Exposure days	Daily survivorship (mean $\pm$ SE)	Nesting success <sup>b</sup>
Mid dry	2,028.5	0.9911 $\pm$ 0.0021	72%
Late dry	2,112.5	0.9939 $\pm$ 0.0017	80%
Early wet	1,951.0	0.9908 $\pm$ 0.0022	72%
Mid wet	1,763.5	0.9887 $\pm$ 0.0025	66%

\* Exact dates are: mid dry, February/March–15 April; late dry, 16 April–15 May; early wet, 16 May–15 June; mid wet, 16 June–August/September.

<sup>b</sup> Probability of a nest successfully fledging young assuming 36 days between when the first egg is laid and fledging.

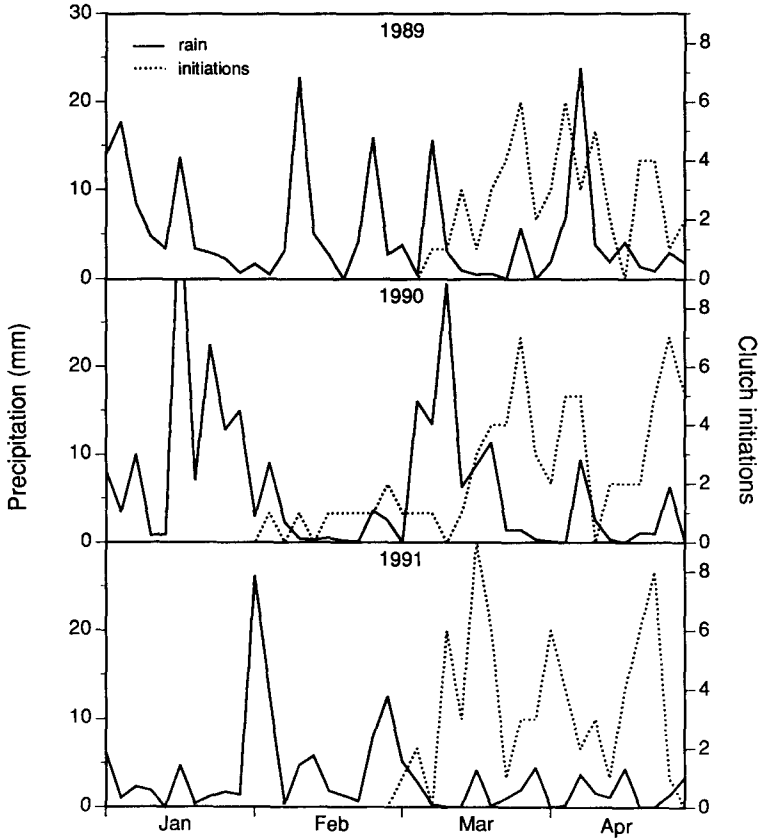


FIGURE 5. Three-day totals of precipitation from wind-blown mist and clutch initiations during the first four months of the dry season at Monteverde.

son peak occurs at the onset of the rains (Buskirk and Buskirk 1976, Janzen 1980, Smythe 1982) or later in the wet season (Janzen 1973, Wolda 1982, this study), but no one has found arthropod numbers or biomass to peak in the dry season. Thus, it is likely that arthropod prey availability in the stumps, logs, shrubs, and trees where I did not sample showed the same general pattern of being lowest in the dry season. In La Lucha, arthropod biomass did not seem to vary systematically with any season. Other surveys have shown that certain taxonomic groups of arthropods may fail to show seasonal changes in populations (Smythe 1982, Wolda 1982), but entire faunas generally do show seasonal changes. However, most published studies are from areas with greater seasonal differences in rainfall than La Lucha.

Tests of the food hypothesis gave mixed results. On the one hand, the general prediction

that the length of the breeding season should be associated with the seasonality of food availability was borne out in the data. La Lucha had fairly stable food levels and breeding occurred there in every month except September and October. The other three sites experienced pronounced seasonal changes in food levels and breeding was restricted to 5–6 months of the year.

On the other hand, the cross-correlation analysis shows that breeding begins several months prior to food peaks. A significant portion of the breeding seasons in Monteverde and Upper San Luis occurred during the second half of the dry season when prey levels were lower than at any other time of the study. Prey levels appeared highest in the latter half of the wet season, well after breeding had ended. Because of this observation that breeding occurs during the leanest time of year, it appears that tropical House Wrens in a wide range of habitats may always be able

to find enough food to produce eggs or feed nestlings. The finding that a tropical insectivore breeds during the dry season is not unprecedented; many insectivores in New Guinea breed during the dry season (Bell 1982).

Why does breeding occur during the dry/wet season transition if this precedes the food peak? There are two advantages of having finished breeding by this time. In many tropical birds, molting, another energetically costly activity, occurs during the late wet season (Poulin et al. 1992). In Monteverde, House Wrens molt in the late wet season months of September and October (unpubl. data), and House Wrens at other sites probably also molt at this time. Second, the late rainy season is when juveniles are dispersing and searching for territories to occupy. With prey levels high during this period, juveniles may survive better than they would if the dispersal phase occurred at any other time of year (Morton 1971). For example, if wrens nested in the late wet season, juveniles would have to disperse during the dry season when prey is least abundant. Thus, given that wrens can successfully reproduce long before food levels peak, they are able to exploit the peak for other activities. This appears to be the case in Lower San Luis where reproductive output was correlated with food levels 3–5 months later.

In Lower San Luis as in the other sites, House Wrens appear to begin breeding when prey levels are low. However, breeding in Lower San Luis began later in the dry season and persisted later into the wet season than at the other sites. Thus, most wrens were feeding nestlings when food levels were rising. The sinusoidal pattern of the cross-correlation between reproductive output and food levels at this site also indicates that food and reproduction may be linked at this site. The tighter correlation between breeding and food levels in habitats with a long, unbroken dry season also occurs at other neotropical sites (Poulin et al. 1992).

Prey levels did not rise as sharply during the first half of the 1991 wet season in Monteverde or Upper San Luis as would have been predicted by the 1990 late wet season levels. It may be that 1991 was an unusual year. In a three year brood manipulation experiment in Monteverde, parents were able to raise broods increased by two chicks equally well as control broods in every year except 1991 (unpubl. data). The environmental cause of the food shortage is unclear,

though, because monthly rainfall in 1991 was close to the 31 year averages for Monteverde (J. Campbell, unpubl. data).

#### NEST PREDATION

Nest predation did not change seasonally at Monteverde. Nest predation is therefore unlikely to be responsible for preventing breeding from starting earlier or from continuing later when food appears to be more available. The breeding season in Monteverde began gradually, with just a few pairs responsible for the early nests. Nest predation was not high in these nests, and late starting pairs certainly were not prevented from nesting earlier by predation.

Without nesting activity between September and January in Monteverde, observations of actual nests give no indication of whether predation would be high at this time. Comparative experiments using artificial nests (e.g., Martin 1988, Sieving 1992) during these months and during the breeding season could indicate whether nest predation ever limits breeding. However, the nest predation data do not suggest seasonal variation. The nest predators I detected included mouse opossums (*Marmosa mexicana*), coatis (*Nasua narica*), and unidentified snakes. All of these taxa appeared to be active year round in Monteverde, such that they would pose threats to nests throughout the year.

#### CLIMATE

Climate seemed to affect breeding only in Monteverde. Here, there was a suggestion that House Wrens wait for a lapse in the mist and accompanying strong winds of the early dry season before beginning to breed. Although prey levels were higher in the first half of the dry season than in the second half, this benefit evidently was outweighed by the costs of attempting to nest during the harsh weather.

Although the rainfall from January through March was small, it nonetheless could have an effect on House Wrens. The precipitation that occurs during this period consists of mist blown nearly horizontally. Much of the mist blows by and is not captured by standard rain gauges such as were used in this study (Vogelmann 1973). Thus, a day with unrelenting wind and mist, which would create difficult conditions for flight, foraging, or incubation by small birds, might only yield 3–5 mm of rain in a gauge.

On the termination of the Monteverde breeding season, no obvious climatic change seemed to cause breeding to terminate. Breeding occurred for at least two months into the wet season. Wet season rains are short bursts of heavy precipitation not accompanied by wind, in contrast to the persistent dry season mists. Also, the temperature is several degrees warmer during the wet season. Thus it may be less physiologically costly for a wren to nest in the wet season than during the early dry season.

Reports of highland tropical birds restricting their breeding to the dry season are from localities that are higher in elevation and therefore colder than Monteverde (Skutch 1950, Tye 1991). Monteverde may be in a transition zone in which wet season breeding still occurs. House Wrens may breed as high as 2,650 m in Costa Rica, and it would be interesting to know if breeding is limited to the dry season at this elevation.

#### WHY DO TROPICAL HOUSE WRENS BREED WHEN THEY DO?

This analysis shows that food may be important in determining when House Wrens breed, but not in the manner traditionally believed. The seasonal patterns of clutch initiations and food availability indicated that, when prey levels vary seasonally, breeding may be timed so that post-reproductive events such as juvenile dispersal and molting, not nesting itself, coincide with periods of elevated food availability. When prey levels do not vary appreciably during the course of a year, breeding occurs nearly year round. Climate, if harsh enough, can interact with food to restrict further the time during which breeding can occur. Whether the roles of food, nest predation, and climate as described here are played out in other tropical systems awaits further study.

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