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RUFOUS-AND-WHITE WRENS KILL HOUSE WREN NESTLINGS DURING A FOOD SHORTAGE[1]

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Birds of several species have been reported to kill immature birds of other species in contexts other than predation. Contexts include: (1) takeover of specialized nesting sites such as cavities (e.g., Kendeigh 1941, Pinkowski 1977), (2) brood parasitism (reviewed by Payne 1977), and (3) elimination of potential competitors for food (suggested by Picman 1977, 1980 for Long-billed Marsh Wrens [*Cistothorus palustris*]; Belles-Isles and Picman 1986 for temperate House Wrens [*Troglodytes aedon*]). The latter context is problematical because it cannot be inferred without evidence of actual or potential food limitation. In this note I document interspecific infanticide of tropical House Wrens by Rufous-and-White Wrens (*Thryothorus rufalbus*). The infanticide appears to be based on competition for food since nestlings were killed only during an 8-week food shortage within a 4-year period.

The infanticide was detected during a study of House Wrens conducted between 1982 and 1985 near the rural village of La Laguna, Republic of Panama (approximately 25 km northeast of Panama City). Six attacks occurred between 23 May and 14 July 1983; three were observed and three have been inferred (Table 1). On 23 and 24 May, a Rufous-and-White Wren was perched at the entrance of a nest box containing three House Wren nestlings (3 days old on 23 May). The box was mounted on a 1.25 cm diameter pole at a height of 1.6 m. The intruder thrust its head and beak rapidly and repeatedly into the nest and threw out one nestling on the first day. This nestling, as well as one of the remaining nestlings, had lacerations on the head and abdomen and puncture wounds on the abdomen. Thereafter one nestling was missing each day for two days. Parental House Wrens returning to the nest were driven away by the intruder during both days of observation. In a second case, on 9 July, an observer frightened a Rufous-and-White Wren from its perched position at the entrance of the nest box shortly after it commenced thrusting its head repeatedly inside the box. This nest contained six nestlings 10 days old. No mortality or injury resulted from this interrupted attack, and there was no evidence of repeated visits (i.e., no nestling loss or injury) for 3 days, after which a snake ate the nestlings. This second nest was located 3 km from the first, suggesting that two different Rufous-and-White Wrens were responsible for these incidents. In a third case, on 19 June, a Rufous-and-White Wren repeatedly pecked a House Wren fledgling for 15 sec in a family group of recent fledglings and parents. The fledgling escaped and was observed 5 days later. This incident took place approximately 100 m from the first incident. The House Wren breeding season extended through October of 1983 (approximate length 24 weeks), but no further direct interactions between the two wrens were observed.

Three additional nest losses (one partial) between late May and mid-July of 1983 may have been caused by Rufous-and-White Wrens because of similar patterns of lacerations and puncture wounds on the bodies of dead or dying nestlings (Table 1). One nestling had a severely broken tibiotarsus as well. Rufous-and-White Wrens were seen or heard within 25 m of these nests on the day of detection of infanticide. The nests were located at least 1 km apart and between 200 to 1,300 m from the nests mentioned above, suggesting that the Rufous-and-White Wrens seen in the vicinity of these nests were different individuals.

Some alternative causes of the infanticide can be eliminated. Predators were probably not responsible for the killings because the dead or dying nestlings were not eaten. Infanticide by other House Wrens, associated with takeovers of mates or territories during each

TABLE 1. Infanticide of House Wrens by Rufous-and-White Wrens during 1983.

Date	No. birds killed	Evidence
Observed attacks		
23–24 May	3	Nestlings wounded and thrown out of nest.
19 June	0	Fledgling pecked repeatedly.
9 July	0	Nestlings pecked in nest (attacker frightened by observer).
Inferred attacks		
27–28 May	5	Wounded and dead nestlings on ground and in nest, Rufous-and-White Wren in area in all three cases.
14–15 June	4	
14 July	1	

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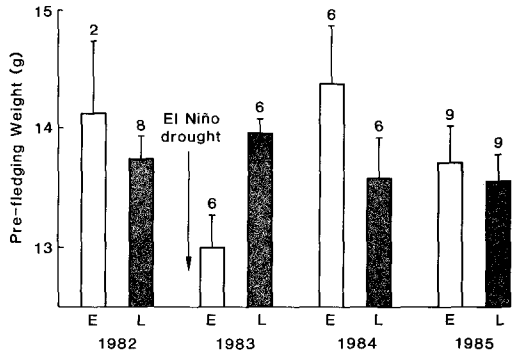

FIGURE 1. Mean prefledging weights of nestlings (13 days old) during early (E, May through early-July) and later (L, mid-July through early September) portions of the breeding season between 1982 and 1985. Thin lines indicate one SE; sample sizes indicate number of broods. With the exception of 1982, all means within years are based on consecutive broods of normal size (three or four nestlings) of the same pairs (too few broods were available during September and October to include in the analysis). For years 1983 to 1985, weights were analyzed using a repeated-measures ANOVA with effects of year, pair (nested within year), portion of season, and appropriate interactions. There were no effects of year and portion of season ($P = 0.62$, 0.99, respectively), but the interaction between year and portion of season was highly significant ($P < 0.01$), as a result of differences in 1983 compared with other years ($P = 0.004$). The early portion of 1983 differed from early portions of all other years and from the later portion of 1983 (all $P < 0.05$), and was also the only time when starvation was evident based on patterns of nestling begging (see text).

year of the study (Freed 1986), was unlikely to be the cause of infanticide in these three nests since the original male and female were present on the day of detection and remained paired thereafter. Infanticide by neighboring House Wrens was unlikely because neighboring pairs were located 80 to 100 m from these nests and breeding pairs were found no closer to neighboring territories during the 8-week period than during other portions of the study. Other species of birds known to perch at the entrance of nest boxes were unlikely to have committed the infanticide. Red-crowned Woodpeckers (*Melanerpes rubricapillus*) perched at the entrance of nest boxes (usually empty), enlarged the entrance hole, and removed all nesting material (usually old nests) during all years of the study. These phenomena were not associated with the cases of infanticide. Striped Cuckoos (*Tapera naevia*) perched at the entrance of nest boxes during other months and years but did not destroy eggs or nestlings in nests at which they were observed. There was no evidence of brood parasitism during the study. In contrast, visits by Rufous-and-White Wrens, the only other species known to visit nest boxes, were observed at active nests only during the same limited period in 1983 during which nestlings with lacerations, puncture wounds, and a broken leg were discovered.

A total of 13 nestlings were killed by observed and inferred interspecific infanticide, accounting for 18% of nestling mortality during this time period (remainder due to predation, starvation, parasites, and infanticide by replacement mates [Freed, unpubl. data]). Attempts of infanticide occurred at 6 out of 46 nests (13%) with successful hatching between 23 May and 14 July. At least five and possibly six different Rufous-and-White Wrens were observed during the attempts or shortly after the discovery of infanticide. The cases were scattered throughout the 140-ha study site, indicating that the phenomenon was general.

There were no instances of similarly wounded or killed nestlings during any other portion of the study. No direct interactions were observed during 1982, 1984, 1985, or after mid-July 1983 even though Rufous-and-White Wrens were present on the study site and existed near at least 40% of the 54 to 56 House Wren nest sites during all years. The only other known event involving both species occurred on 18 February during the dry season of 1985, when a Rufous-and-White Wren put its head inside a nest box containing a few sticks recently inserted by the House Wrens. The absence of additional events was not due to decreased opportunities to observe them since the number of personnel and frequency of inspections of nests and family groups were generally consistent over the 4-year-period.

The early portion of the breeding season for House Wrens in 1983 was unique in that it followed the long and severe dry season in central Panama associated with the 1982 to 1983 El Niño event (Rasmusson and Wallace 1983; Freed, unpubl. data). Data on both nestling weight and behavior indicate that the birds were food-limited during the period when the interspecific infanticide occurred. Normal size broods (three or four nestlings) reared between May and mid-July of 1983 achieved lower prefledging weights than broods of comparable size reared during comparable months in 1982, 1984, and 1985, or during later months (late July through early September) in 1983 (all $P < 0.05$; Fig. 1). Aberrant nestling behavior was coincident with the undernourishment. Audible begging was heard by observers approaching the nest boxes to weigh nestlings between 06:00 to 07:00. Nestlings extended their heads and bodies outside of the cavity entrance while begging loudly for food, and some nestlings even fell out of the nest at least one week before normal fledging. These phenomena were unique to the weeks when Rufous-and-White Wrens killed or attempted to kill nestlings. The comparison of breeding biology within and among years for House Wrens thus suggests that food was in shorter supply (or at least of lesser quality) than usual at the time of infanticide.

Hypotheses to account for the infanticide should explain both the advantage of the infanticide to the Rufous-and-White Wrens and the restriction of the infanticide to a period of 8 weeks during a 4-year study. Several hypotheses can be advanced: competition for nesting sites, elimination of active nests to reduce the attractiveness of the area to predators, and competition for food. The first can be dismissed because Rufous-and-White Wrens do not breed in cavities. The second

cannot be dismissed but is unlikely because both House Wrens and Rufous-and-White Wrens breed over a larger portion of the year than the portion during which interspecific infanticide was evident or apparent (pers. observ., Morton and Farabaugh 1979). The hypothesis of competition for food, however, is supported by the temporal distribution of infanticidal events.

The association between food shortage and infanticidal behavior admits the possibility that the interspecific infanticide was related to competition for food. The association is also consistent with Wien's (1977) assertion that competitive processes may only be expressed during extreme conditions in variable environments. The House Wrens, renesting in the same boxes, did not begin to feed new nestlings for approximately one month after the nesting failure. Rufous-and-White Wrens in the area would therefore have reduced the food demands of House Wrens for that time, possibly making the food available to themselves. Both species were observed to search for insects and spiders on the ground in similar locations, suggesting the potential for competition, but more information on the diversity of prey items and foraging substrates utilized by each species is needed. While this is the first case of interspecific infanticide associated with a food shortage, additional and more detailed observations of interactions between these two species of wrens during another food shortage may establish more firmly the conditional nature and the selective basis of the infanticide.

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SEASONAL CHANGES IN BILL LENGTH IN SUMMERING MOUNTAIN WHITE-CROWNED SPARROWS[1]

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Key words: Bill length; seasonal changes; Zonotrichia leucophrys; *White-crowned Sparrow; montane biology.*

Bill dimensions have served as a primary source of information in a wide range of avian biology studies. Bill length, in particular, has been of value because it is an easily measured, highly heritable, morphological character that is directly correlated with feeding ecology and thus especially responsive to natural selection (Van Valen 1965, Willson 1969, Rothstein 1973, Boag and Grant 1978, Smith and Zach 1979).

It has been known for several decades that bill lengths vary seasonally, being longer in summer by as much as 10%. This effect seems greatest and most predictable in species that exhibit a winter-summer switch in diet from seeds to insects (Clancey 1948; Steinbacher 1952; Davis 1954, 1961; Selander 1958; Selander and Johnston 1967; Johnson 1977).

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