

COURTSHIP, COPULATION, NESTING BEHAVIOR AND BROOD PARASITISM IN THE VENEZUELAN STRIPE-BACKED WREN¹

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Abstract. Here I report the results of intensive observations of breeding behavior in the Stripe-backed Wren *Campylorhynchus nuchalis* of Venezuela, a polyandrous cooperative breeder. The breeding season in this species begins soon after the first rainfall of the wet season, and its onset is marked by conspicuous courtship of the dominant female by the dominant male and by subordinate males that are not sons of the dominant female. Copulations, of which an estimated nine occur per breeding attempt, take place in plain view and throughout the day but not in close temporal association with courtship. The amount of food provided to nestlings varies greatly among adult group members but is not correlated either to their relatedness to the young or their dominance status. Stripe-backed Wrens defend their nests vigorously, chasing dozens of species away including predators, nest competitors and the Shiny Cowbird, which parasitized at least 16% of nests surveyed in 1990 and 1991 and which appears to reduce severely the reproductive success of large and small groups alike.

Key words: *Campylorhynchus nuchalis*; cooperative breeding; courtship; copulation; brood parasitism.

Resumen. Aquí presento los resultados de observaciones intensas del comportamiento reproductivo del Cucarachero Chocorocoy *Campylorhynchus nuchalis* de Venezuela, un reproductor poliándrico y cooperativo. La estación reproductiva de esta especie comienza poco después de la primeras lluvias de la época lluviosa, y su comienzo es marcado por el cortejo conspicuo hacia la hembra dominante por el macho dominante y por machos subordinados que no son hijos de la hembra dominante. Las copulaciones, de las cuales se estima que ocurren nueve por intento de apareo, acontecen a plena vista y durante todo el día, pero nunca en proximidad temporal con el cortejo. La cantidad de alimento proveído a los pichones varía grandemente entre los adultos de cada grupo, pero no está correlacionada ni con parentesco, ni con nivel de dominancia. Los cucaracheros defienden sus nidos vigorosamente, persiguiendo a docenas de especies inclusive depredadores, competidores, y a los Tordos Mirlos *Molothrus bonariensis*, aves que parasitizan por lo menos el 16% de los nidos vistos en 1990 y 1991, y las cuales parecen reducir severamente el éxito reproductivo de grupos grandes y pequeños por igual.

Palabras claves: *Campylorhynchus nuchalis*; reproducción cooperativa; cortejo; copulación; parásitos de nidos.

INTRODUCTION

Cooperative breeding, in which physiologically mature animals forego breeding and help raise the offspring of others, has now been reported in over 200 species of birds. During the past three decades a wealth of data has accumulated on cooperative species as a result of a large number of long term studies, and we have learned much

about the different forms that helping behavior can take and the circumstances under which it can evolve (see Emlen 1984, Brown 1987, Stacey and Koenig 1990).

In the cooperative Stripe-backed Wren (*Campylorhynchus nuchalis*) of Venezuela, our understanding of helping behavior has improved in recent years not merely from the continued accumulation of demographic data (over 15 years), but also because of the use of new research techniques that have opened new vistas onto breeding behavior. Foremost among these new techniques has been parentage determination by DNA fingerprinting, which revealed shared paternity between dominant and subordinate males (Ra-

¹ Received 8 September 1993. Accepted 7 March 1994.

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benold et al. 1990). These genetic findings led to a detailed investigation of many aspects of breeding behavior through focal samples on breeding females from which emerged a clear view of the polyandrous mating system of this species (Piper and Slater 1993). As a consequence of this recent research, it is now possible to present a comprehensive account of breeding behavior in the Stripe-backed Wren.

In this study I report the discovery of a stereotyped form of courtship, describe copulation, analyze feeding contributions and nest defense by group members according to their status in the group, examine the importance of nest composition on reproductive success and investigate the relationship between rainfall patterns and the timing of breeding in the Stripe-backed Wren. I hope that this report will offer further insights into the evolution of helping behavior by detailing the roles of dominant and subordinate wrens in reproduction and will also serve as a thorough account of breeding behavior in a tropical passerine that will prove useful in comparative studies.

MATERIALS AND METHODS

STUDY AREA

Stripe-backed wrens were studied from April through June of 1990 and 1991 at Hato Masagual, a cattle ranch in the seasonally-inundated lowlands of central Venezuela. This region is a vast palm (*Copernicia tectorum*) savanna that contains occasional stands of leguminous trees in which Stripe-backed Wrens forage, roost and breed. Since 1977, wrens from three clusters of social groups ("populations") on the ranch have been routinely captured with mist nets, marked with colored leg bands and studied (see Rabenold 1990). These three clusters are the Samán Population (25–30 groups observed since 1978), the Guácimo Population (30–40 groups observed since 1985) and the Palma Population (20–30 groups observed since 1987).

BEHAVIORAL ECOLOGY OF THE STRIPE-BACKED WREN

Many aspects of the behavior and ecology of the Stripe-backed Wren have already been described (see Rabenold 1990 for a review), and I will give only a brief sketch here. The Stripe-backed Wren is a medium-sized passerine (25 g) and occurs in cooperative groups of 2–10 individuals (mean group size in 1991 = 3.9 ± 1.8 SD, $n = 59$).

Wren groups defend year-round, all-purpose territories 1–4 ha in size. Territorial vocalizations of wren groups take the form of duets between pairs of opposite sex and occur throughout the year, though more frequently during the wet season when breeding takes place. Two members of each group comprise a dominant pair ("principals"), and the remainder are subordinates ("auxiliaries"), usually young of the dominant pair from previous breeding seasons (69 of 74 subordinates in 1991, 93%). The dominant pair can be distinguished from other group members in their marked tendency to duet during territorial intrusions and their ability to supplant or peck all subordinates (Rabenold 1985). Roosting and raising of young takes place in grass or stick nests 2 m to 10 m above the ground in leguminous trees or in palms; grass nests are built by the wrens themselves, whereas stick nests are usurped from the Plain-fronted Thornbird (*Phacellodomus rufifrons*) that builds them. There is a strong positive correlation between the size of a group and its reproductive success, probably because additional helpers defend the nest from predators (Rabenold 1984). In addition, larger groups are more likely to attempt second or even third broods (Rabenold 1984). The mating system is polyandrous in groups that contain one or more subordinate males unrelated to the dominant female (termed "DF-stepsons") but monogamous in groups containing only those that are sons of the dominant female (termed "DF-sons") because of a strong tendency of incest avoidance in this species (Piper and Slater 1993). Dominant females ("DFs") are mothers of all offspring produced by all social groups, while dominant males ("DMs") sire all offspring in monogamous groups but sire only an average of 85% in polyandrous groups, the remainder being sired by DF-stepsons within the groups (Rabenold et al. 1990).

FOCAL SAMPLING AND NEST WATCHES

I gathered data before, during and after incubation using 2 basic techniques: focal samples on the dominant female and nest watches. During focal sampling, I located the DF in a social group and followed her visually for 15–20 min with binoculars, recording all of her interactions with other group members including duets, allopreening, dominance interactions, courtship (see below) and copulations. Nest watches were done by finding a vantage point (near enough to

the nest that observations could be recorded reliably but far enough away that the wrens behaved normally) and recording all activities of group members, including social interactions, nest building, nest attendance (the number of occasions on which a bird arrived at the nest), nest defense and feeding of young. Sizes of food items brought to nestlings were estimated by comparison with the bill length. Nest watches and focal samples were done on every other day throughout the breeding cycle in 24 groups in 1990 and daily in 13 groups in 1991. I rotated the order in which I carried out nest watches and focal samples so that all groups were visited throughout the periods during which most observations were collected, 06:00–12:00 and 17:00–18:00.

ESTIMATION OF THE FERTILE PERIOD

Precise determination of the fertile periods of female birds (the periods during which copulations with males result in fertilizations; Birkhead and Møller 1992) is impossible in most field studies, primarily because of the difficulties of observing copulations and measuring sperm viability. However, I used data on sperm storage from the literature to make a crude estimate of the fertile period in dominant female Stripe-backed Wrens so that I could compare behaviors during this estimated “fertile period” with those occurring during other phases of the breeding cycle. The estimation of the “fertile period” was based on: (1) the measurement of 18 days for the incubation period, (2) the observation that clutch size was four, (3) the assumption that incubation commenced when the penultimate egg was laid, (4) the assumption that sperm were viable for about eight days (as in the zebra finch *Taeniopygia guttata*; Birkhead and Møller 1992), and (5) the first observation of feeding of the nestlings. Thus, I subtracted 28 and 18 days from the day when feeding of nestlings was first observed to determine the first and last days, respectively, of the estimated 11-day “fertile period” for a dominant female. In the case of groups that raised Shiny Cowbird nestlings, I subtracted 21 and 11 days from the day of first feeding to determine the “fertile period,” because the incubation period for Shiny Cowbird eggs in host nests is 11 rather than 18 days (Cruz et al. 1990).

ANALYSIS OF CONTRIBUTIONS TO FEEDING

I used multiple regression to examine potential correlates of “feeding effort,” the amount of feed-

ing done by each individual relative to others in its group. The index of Bird A’s feeding effort (after Rabenold 1985) was:

$$\text{FEEDING EFFORT} = (F_A)(n)/(F_{GP})$$

where F_A is the number of feedings by Bird A, n is the size of the group to which Bird A belongs, and F_{GP} is the total number of feedings by all group members. This index is convenient because a value of 1.0 indicates that a wren provided exactly its “share” of the feedings (i.e., a proportion of feedings equal to $1/n$ of the total).

Five predictor (independent) variables were examined for possible relationships with feeding effort, the criterion (dependent) variable: age (first-year or older), sex, relationship to the DF (categorized into “offspring” or “not offspring”), relationship to the DM, and coefficient of relatedness (“ r ”) to the young being fed (where $r = 0.5$ for full sibs, 0.25 for half sibs and 0 for unrelated pairs). All five predictor variables were placed in a model and then eliminated by stepwise multiple regression (using the SYSTAT software program: Wilkinson 1990) if they were not significantly related to the criterion (dependent) variable at the 0.05 level. Afterwards, I eliminated from the model one by one all terms not significant at the 0.01 level (0.05 divided by the number of predictor variables examined; the Bonferroni method, see Rice 1989).

Finally, I examined the relationship between a male’s feeding effort and its presumed and actual paternity for both DMs and DF-stepsons. Presumed paternity was indicated by the amount of time a male had spent within 2 m of the DF during her “fertile period,” while actual paternity (determined by DNA fingerprinting; see Rabenold et al. 1990) indicated, for a DM, whether he had sired all offspring or shared paternity with a DF-stepson, and for a DF-stepson, whether he had sired one or more offspring or no offspring.

LAPAROTOMIES

On 2, 4 and 13 May 1991, I used laparotomy (Piper and Wiley 1991) to measure the testes of four males in two wren groups whose genetic relationships were known but on which no behavioral observations were gathered. The laparotomized individuals flew strongly and behaved normally both upon release and 10 days after laparotomy.

RESULTS

DEPENDENCE OF BREEDING ON RAINFALL

The first heavy rainfalls of the wet season (which can occur anytime from March to June) were invariably followed by egg-laying in many wren groups. In 1991, for instance, the first pre-breeding rainfall of greater than 2 mm occurred on 5 April (21.0 mm of rain), was followed by four more days of heavy rain, and elicited egg-laying in 12 of 13 focal groups (a mean of 11.6 ± 4.4 SD days after the first day of rain; range 5–19 days).

The amount and timing of rainfall appeared also to affect the probability that a given social group would breed. For example, an isolated initial rainfall of 14.5 mm on 3 April 1990 followed by a period of 22 days without rain resulted in egg-laying in 6 of 24 focal groups, while an isolated initial rainfall of only 2.0 mm on 11–12 March 1991 followed by 24 days without rain elicited breeding attempts by only 1 of 13 groups.

TESTICULAR STATUS DURING THE BREEDING SEASON

Laparotomies suggested that all males, regardless of their capacity to breed, experienced enlargement of testes during the breeding season. All four subordinate males laparotomized in May of 1991 (29 days or more after the first major rainfall of the wet season) had testes that were substantially enlarged (7 mm or longer in anterior to posterior length) from the typical nonbreeding size in small passerines (1–2 mm). Three of these subordinates were DF-sons (and thus were unable to breed) in the HG group, and 1 was a DF-stepson in the FA group.

COURTSHIP: THE AGGRESSIVE CHASE

A conspicuous signal that Stripe-backed Wrens had begun breeding was the occurrence of the "aggressive chase," an apparent form of courtship directed by males in a group towards the dominant female. Aggressive chases were usually preceded by intent observation of the DF by a male that foraged intermittently or merely perched motionless. The aggressive chase itself consisted of several "runs" by a male at a flying DF. Each run by the male, in turn, consisted of two phases. In the first phase the male rapidly overtook and appeared to peck the DF in the cloacal area while a loud, staccato call (probably given by the pursuing male) was heard. In the

second phase of each run the male slowed down and allowed the female to fly a meter or so ahead of him as he prepared for the next run. The behavior of the dominant female did not seem to be affected by the male's behavior before, during or after aggressive chases; flights of DFs that elicited aggressive chases by males, appeared, from the DF's perspective, to be routine trips between foraging areas.

Although the vocalizations heard during aggressive chases were indistinguishable from those heard during chases of intruding birds (either wrens or heterospecifics), aggressive chases differed from chases during nest defense in two obvious ways. First, during nest defense the pursuer never made a series of runs at the bird it was chasing, but instead always flew directly towards the intruder and continued to pursue the intruder rapidly and without noticeably reducing speed until the intruder moved away from the nest. Second, the wren being pursued during an aggressive chase, unlike intruders pursued in nest defense, made no effort to evade its pursuer by flying more rapidly, swerving suddenly or darting towards cover. Never were aggressive chases that were actually seen by observers confused with nest defense, even when the bird being pursued was an intruding Stripe-backed Wren or a species of similar size (e.g., a Plain-fronted Thornbird).

PATTERNS IN THE OCCURRENCE OF AGGRESSIVE CHASES

The set of group members that took part in aggressive chases matched the set observed to be parents of offspring in wren groups (Rabenold et al. 1990). In 197 of the 201 cases wherein both birds involved in an aggressive chase were identified, the pursuer was a DM or a DF-stepson and the pursued bird the dominant female. DF-sons and subordinate females, the two nonreproductive classes of adults, did not participate in aggressive chases. The four aggressive chases that did not fit this general pattern were one aggressive chase of a subordinate female by a DM (her father), one aggressive chase of a DM by a DF, and two aggressive chases of a DF-son by his brother (another DF-son).

The seasonal timing of aggressive chases suggested a clear association with the onset of breeding. Aggressive chases did not occur in the dry season, peaked in frequency during a brief period early in the wet season when most wren groups were beginning to breed, and were clustered

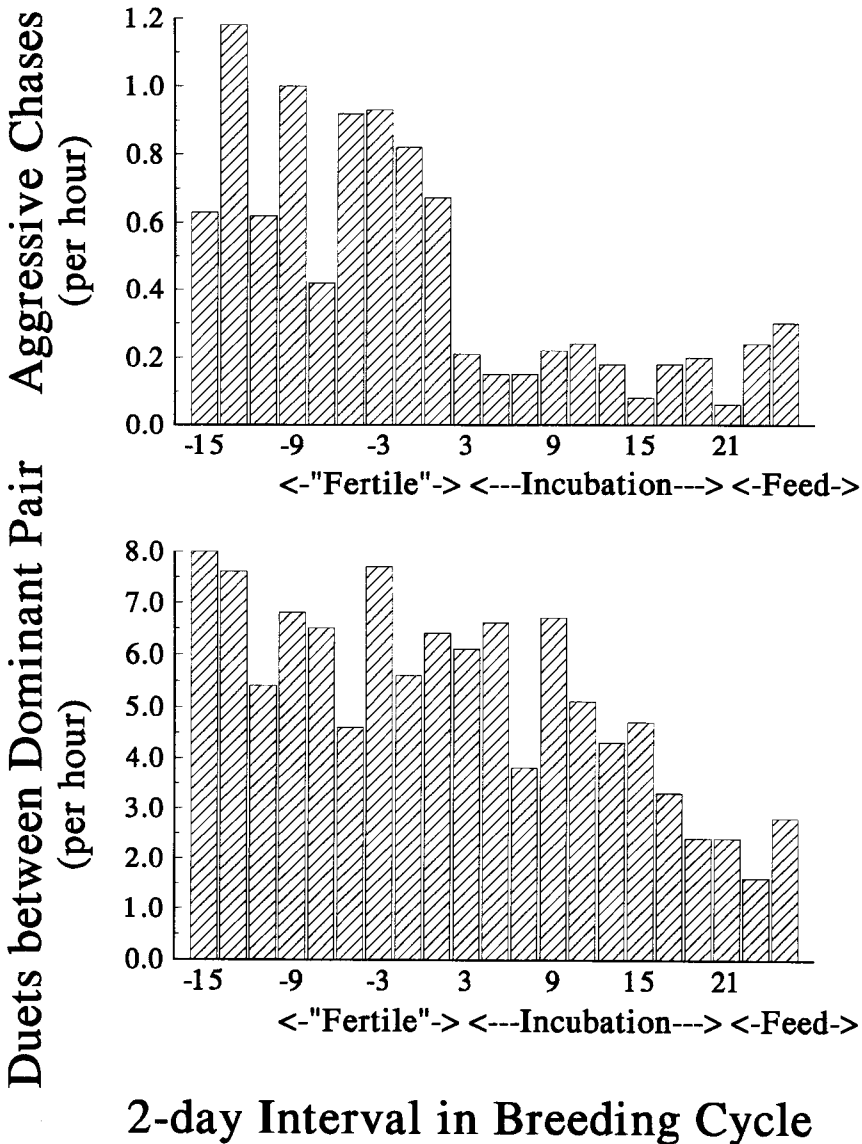


FIGURE 1. Occurrence of aggressive chases and duets during the breeding cycle. The figure shows that aggressive chases peaked sharply in frequency before and during the “fertile period” but that duets were common throughout the breeding cycle.

around the fertile periods of social groups (Fig. 1). The occurrence of aggressive chases contrasted with that of duets, which occurred throughout the year and showed no peak in frequency during the fertile period (Fig. 1).

Three unusual occurrences of aggressive chases in focal groups provide further evidence of the strong link between aggressive chases and the onset of breeding. First, aggressive chases oc-

curred at a rate of 7.7 per hr (in 0.65 hr) in the UV group in 1990 on a single day during the middle of the incubation of a first clutch, a point in the breeding cycle when this behavior is usually rare (see Fig. 1). I later discovered that this unusual occurrence of aggressive chases signified the beginning of a second fertile period for the DF, which was followed by the laying of a second clutch of eggs. Second, in the YO group in 1991,

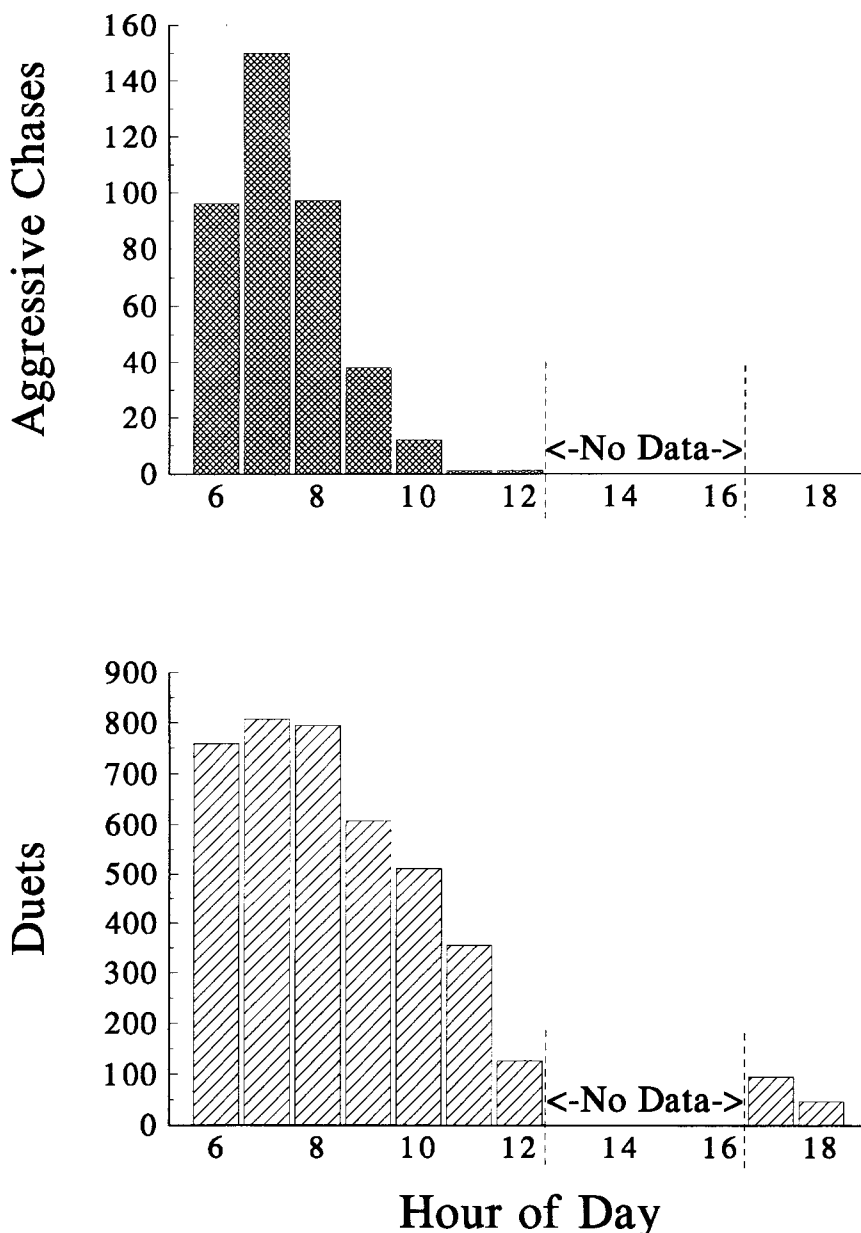


FIGURE 2. Hourly occurrence of aggressive chases and duets. "6" indicates the hour of 06:00–06:59 and so forth. (Data are not available for 13:00 through 16:59.) The figure shows that both aggressive chases and duets occurred most often in the early morning.

aggressive chases were observed at a rate of 2.9 per hr (in 2.4 hr) over three days just after a nest failure at which time the group was searching for a new nest. Finally, a prolonged period of frequent aggressive chases in the GL group in 1991 (2.1 per hr during 28 hr of observations over six

weeks), coincided with the failure of this group to initiate nesting during a period when all other focal groups laid eggs.

The hourly occurrence of aggressive chases within the day roughly paralleled the changes in foraging and social activity in the wrens (Fig. 2).

Aggressive chases began to occur in the first morning hour, from 06:00 to 06:59, peaked in frequency between 07:00 and 07:59, occurred with decreasing frequency as the morning progressed and were never observed after 13:00.

Although aggressive chases were often followed immediately by duets, there was no tendency for them to precede or follow any conspicuous breeding behavior such as copulation or construction of the brood chamber. In particular, the occurrence of aggressive chases and copulations seemed unrelated, since: (1) the two behaviors were never observed to occur within an hour of each other in a group, and (2) aggressive chases only occurred during the morning, while copulations occurred throughout the day.

COPULATIONS

Throughout the duration of the 15-year study of Stripe-backed Wren behavior, a total of nine solicitations of copulations by females (seven of which occurred during the present study in 1990 and 1991) have been observed in eight social groups. Thus, it is possible to describe the behavior in detail and begin to discern patterns in its occurrence.

Copulation in Stripe-backed Wrens was similar to that in many other passerines (Birkhead and Møller 1992). The dominant female flattened her body against a branch with her tail cocked upward and wings quivering and uttered a loud, distinctive vocalization similar to the querulous and provocative call often given by intruding females. A male (in all observed cases, the dominant male) then jumped on the female's back and remained there for about 2 sec, while fluttering his wings for balance.

Copulations occurred throughout the day and in a variety of locations. Females were observed to solicit copulations twice in early morning (07:05 and 08:50), a period characterized by high levels of social interaction and vocalization (Fig. 2). However, in six of the eight cases wherein the time of the event was recorded, solicitations occurred after 11:00 (11:33, 11:36, 12:37, 17:56, 18:07 and 18:40), when the wrens were, in general, less active (compare with Fig. 2). All solicitations and copulations occurred in plain view: three on the outside surface of the stick nest used for breeding, four in large trees and two in bushes.

The timing of solicitations and copulations relative to the breeding cycle indicated that not all

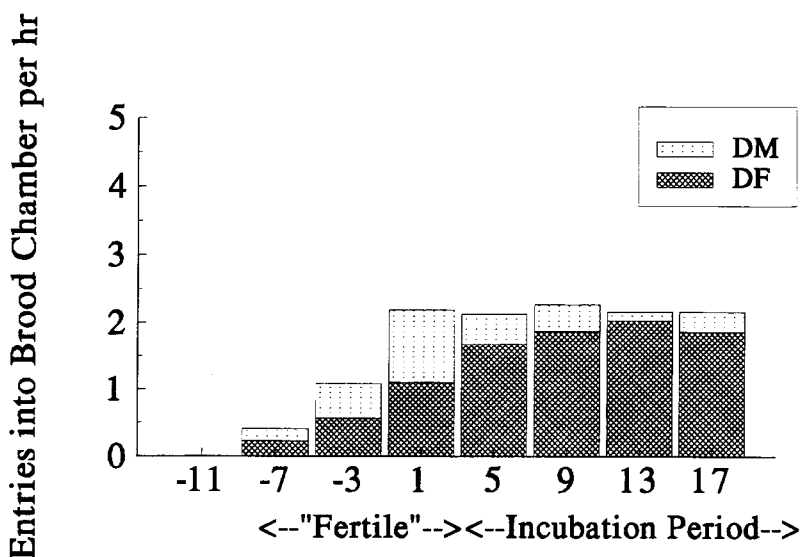
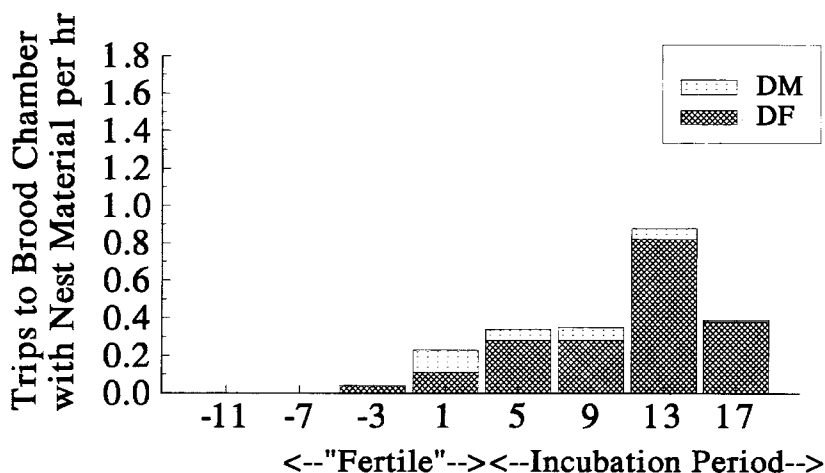
were capable of fertilizing eggs. Eight of the nine observed solicitations occurred in the wet season (15 April 1991, 5 May 1990, 6 May 1990, 9 May 1991, 13 May 1990, 15 May 1990, 24 May 1990 and 17 June 1986), while the other involved a newly-formed pair about to roost together for the first night late in the dry season (11 March 1989), 3 months before they attempted to reproduce. Of the six wet season copulations, one occurred on estimated day -1 of the 11-day fertile period, two occurred on day 0, one occurred on day 4 and the final two (both in the NC group in 1990) occurred on days 15 and 24, well after the end of the female's fertile period for the first clutch and more than two weeks before the beginning of the DF's fertile period for a second clutch.

The sample of solicitations for copulations was small, but there seemed to be no clear association between solicitations and other affiliative behaviors like duets or aggressive chases. The only feature consistent across all solicitations was the presence of a dominant male near the dominant female. Otherwise, females seemed to solicit copulations mechanically and without obvious stimulation.

I generated a crude estimate of the number of copulations per clutch in this population based on the number and timing of copulations observed and the amount of time spent observing dominant females during the fertile periods of focal groups. In computing the estimate, I assumed that copulations occurred with equal frequency throughout the day (as my data suggest). The estimate of the number of copulations occurring during a single fertile period for a single DF was thus:

$$(C_{\text{obs}})(T_{\text{fp}}/T_{\text{obs}}) = (3 \text{ copulations})(132\text{hr}/44.5 \text{ hr}) \\ = 9 \text{ copulations per clutch}$$

where C_{obs} was the number of copulations observed in all groups combined during the fertile period, T_{fp} was the total amount of daylight hours in a fertile period and T_{obs} was the total amount of time spent observing the DF during the fertile period for all groups combined. Although it is based on relatively few copulations, the estimate of copulations per clutch is robust to changes in the length of the fertile period because: (1) $T_{\text{fp}}/T_{\text{obs}}$ is relatively constant regardless of the duration of the fertile period and (2) all three copulations used in this estimate occurred in the last five days before incubation began.



4-day Interval in Reproductive Cycle

FIGURE 3. Entries into the brood chamber by dominant males and females with and without nesting material during different stages in the reproductive cycle (DF = dominant female; DM = dominant male). DFs and DMs differed in both the timing and numbers of visits made to the brood chamber and in the amount of nest material brought to the brood chamber.

NEST BUILDING AND NEST ATTENDANCE

Brood chambers, like chambers used for roosting, were built in stick or grass nests, but only the dominant pair participated in the preparation of the brood chamber. Entries into the brood chamber by the dominants began several days before the "fertile period" and continued to increase in frequency during the fertile period (Fig.

3). Once eggs were laid and incubation begun, the DF often carried additional soft material into the brood chamber when she returned from foraging to resume incubation. The DM visited the brood chamber infrequently during incubation (Fig. 3).

The nest attendance (visits to the outside of the nest without entry into the brood chamber) of various group members during the breeding

cycle appeared to be influenced by their sex and social status (Fig. 4 and Table 1). Dominant males had levels of nest attendance significantly higher than all other classes of group members (DF-sons, DF-stepsons, DF-daughters, and DF-stepdaughters), DF-sons and DF-stepsons did not differ from each other in nest attendance but had higher levels than DF-daughters and DF-stepdaughters, and DF-daughters had higher levels than DF-stepdaughters (Table 1). (Dominant females, which spent much of the time incubating eggs inside the nests, were excluded from statistical tests.)

Most entries into the brood chamber before incubation were by dominant females and males. For example, of 219 occasions (in 27 social groups) on which group members entered the brood chamber during the fertile period in 1990 and 1991, 152 (69%) were by the DF, 55 (25%) by the DM, 12 (5%) were by subordinate males, and never was a subordinate female observed to enter.

INCUBATION AND BROODING OF YOUNG

Diurnal incubation periods varied from less than 1 to 57 min in duration (mean = 8.7 ± 8.0 , $n = 168$ incubation periods in 10 groups). After periods of incubation, dominant females usually began to forage intensively. At night, DFs incubated the eggs, and the remaining group members roosted in a separate chamber in the same or a different nest. Frequent visits of 5 min or more to the brood chamber by DFs during the first 2–3 days after feeding began indicated that DFs brooded nestlings during this period.

FEEDING OF YOUNG

Analysis of feeding efforts by subordinates. The most striking pattern in the feeding behavior of subordinate Stripe-backed Wrens was the lack of strong association of feeding effort with age, sex or relatedness to dominant pair or offspring. There were weak and marginal simple correlations that indicated more feeding by males than females ($F_{1,78} = 7.1$, $P = 0.010$, $R^2 = 0.08$) and by older than younger birds ($F_{1,71} = 5.2$, $P = 0.026$, $R^2 = 0.06$; degrees of freedom differ from test of sex effect because of missing values), but neither was significant in the model that included both variables (age: $F_{1,70} = 0.9$, $P = 0.36$; sex: $F_{1,70} = 6.8$, $P = 0.011$), and together they explained only 15% of the total variance in the feeding effort of adult wrens. The only apparent pattern in feeding be-

havior was a weak but significant correlation between the feeding efforts of individuals in different breeding attempts in the same or consecutive seasons ($R^2 = 0.20$, $P = 0.006$, $n = 33$; see also Rabenold 1985).

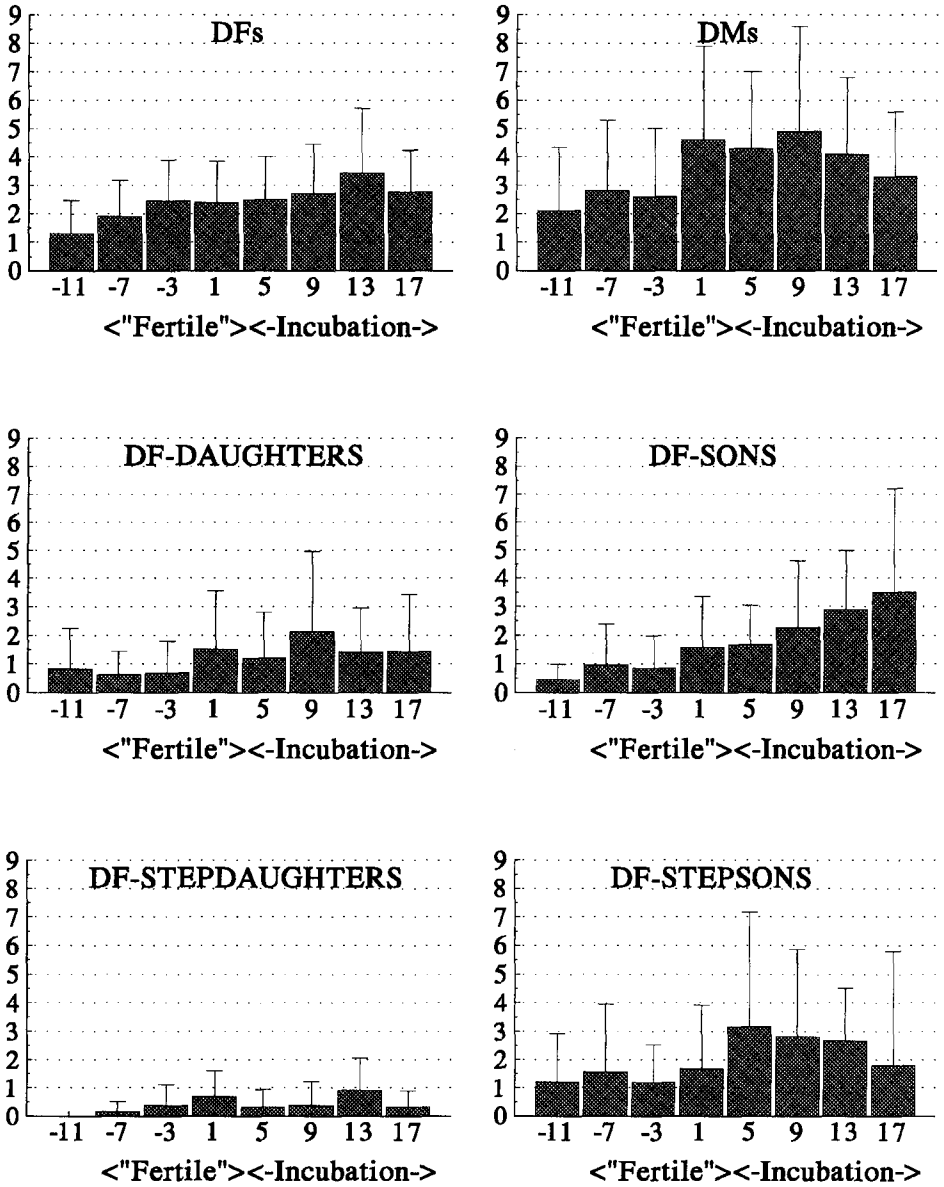
Relationship between feeding effort and paternity. In neither DMs nor DF-stepsons were feeding efforts proportional to their presumed likelihoods of having sired the young (the amount of time they had spent within 2 m of the dominant female), although for both DMs and DF-stepsons the correlation was positive ($r = 0.361$, $P > 0.2$, $n = 15$ for DMs; $r = 0.278$, $P > 0.2$, $n = 21$ for DF-stepsons; product-moment correlations).

Similarly, feeding efforts of DMs and DF-stepsons were not related to their actual paternity. DMs that had sired all offspring in stepmother groups (mean feeding effort of 1.03 ± 0.32 SD, $n = 11$) fed no more (indeed, they fed less) than DMs that had shared paternity with DF-stepsons (1.24 ± 0.38 , $n = 6$); this result does not change when DMs from mother groups (who always sire all offspring) are combined with the DMs in stepmother groups who sired all offspring (combined mean = 1.11 ± 0.47 , $n = 21$). Moreover, DF-stepsons with paternity (0.86 ± 0.77 , $n = 6$) fed no more (actually less) than DF-stepsons without paternity (1.02 ± 0.55 , $n = 19$), whether or not DF-sons are added to the latter group (combined mean = 1.03 ± 0.47 , $n = 42$).

Changes in feeding rate during the nestling period. Both feeding rate and the size of food items brought to the nest varied during the nestling stage. Nestling Stripe-backed Wrens were fed an average of 10.1 times per hour during the first week of feeding ($n = 95$ hours in 28 groups), 15.6 times per hr during the second week ($n = 70$ hr in 25 groups) and 13.7 times per hr during the final 5–7 days before fledging ($n = 45$ hr in 22 groups). The sizes of food items increased gradually from 83% small and 17% large items ($n = 929$ items) during the first week of feeding to 49% small items ($n = 1,157$) during the second week to 32% small items ($n = 672$) during the third week. Food fed to young comprised mostly larval Lepidoptera, but included a wide range of other arthropods including spiders, moths, beetles, bugs, dragonflies and katydid.

Participation of juveniles in feeding of nestlings. Juveniles from broods fledged early in the wet season often fed later broods, and their contributions were sometimes substantial. For in-

Number of Arrivals to Nest per hr



4-day Interval in Reproductive Cycle

FIGURE 4. Nest attendance (arrivals to the nest; \pm SD) by group members during different stages in the reproductive cycle. (DFs = dominant females; DMs = dominant males; SFs = subordinate females; SMs = subordinate males). Patterns in nest visitation varied depending on sex and relatedness to dominant female.

TABLE 1. Results of Wilcoxon Signed Ranks Tests comparing nest attendance levels of dominant females (DFs), dominant males (DMs), sons of dominant females (DF-sons), stepsons of dominant females (DF-stepsons), daughters of dominant females (DF-daughters) and stepdaughters of dominant females (DF-stepdaughters). Dominant males had the highest level of nest attendance, followed by DF-sons and DF-stepsons, DF-daughters and DF-stepdaughters. All classes of group members differed significantly from all other classes except for DF-sons and DF-stepsons (see also Fig. 4).

Higher nest attendance	Lower nest attendance			
	DF-sons	DF-stepsons	DF-daughters	DF-step-daughters
DMs	$t_s = 1, P < 0.02$	$t_s = 0, P < 0.01$	$t_s = 0, P < 0.01$	$t_s = 0, P < 0.01$
DF-sons	X	$t_s = 10, P > 0.2$	$t_s = 1, P < 0.02$	$t_s = 0, P < 0.01$
DF-stepsons		X	$t_s = 0, P < 0.01$	$t_s = 0, P < 0.01$
DF-daughters			X	$t_s = 0, P < 0.01$

stance, three juveniles fledged on 16 or 17 May 1990 in the UV group had feeding efforts of 1.23, 0.58 and 0.14 in feeding nestlings from their group's third breeding attempt (4–8 August), which placed them within the range of values for adults (0.07 to 3.90). On the other hand, recently-fledged juveniles often seemed to cause confusion during the feeding of later broods because they pursued and begged for food from adults while the latter attempted to feed nestlings.

Idiosyncrasies in feeding behavior. There were several unusual patterns in feeding behavior recorded during the study. One of these, a behavior recorded in five of 33 groups, was premature feeding, in which an adult brought an item of food to the nest three or more days before the nestlings hatched but eventually swallowed it rather than attempting to enter the brood chamber. Secondly, some individuals had the peculiar trait of not being capable of transferring food to the dominant female or young on occasions when the DF was brooding the young. For example, the dominant male in the YO group was seen to enter the brood chamber four times while the DF was on the nest but exited each time with the food still in his bill. During the same period, the four subordinates in the YO group (a full brother and three offspring of the DM) dropped off 14 items of food while the DF was brooding the young. The DM in the NM group and a subordinate male in the C2 group did not even enter the nest when the DF was brooding the young. Instead, they arrived at the nest with food, gave the querulous 'where are you' call, waited for the DF to exit, and then fed the young. A third unusual occurrence was stealing of food from one group member by another, which happened on six occasions in four different groups. In each case, one bird brought food to within a meter of the brood chamber but a second bird dominant

to the first then took the food from the first and either fed it to the young or swallowed it.

NEST SANITATION

Like most passerines, Stripe-backed Wrens removed eggshells and fecal sacs from the brood chamber (Gill 1990). Eggshells were removed by dominant females soon after the nestlings hatched. Adult wrens seized and removed gelatinous fecal sacs after feeding nestlings as the latter turned completely around and excreted them in the direction of the adult as in other passerines (e.g., Sargent 1993). Both eggshells and fecal sacs were carried 10 m or more away from the nest and then dropped.

AGGRESSION DURING THE BREEDING SEASON

Intragroup aggression, which was relatively uncommon throughout the year in most wren groups, ranged from supplantations of one bird by another to protracted pursuits and pecking bouts directed by one wren towards a second accompanied by loud screaming from the victim. Aggression among males in polyandrous groups (usually attacks of dominant males on DF-stepsons) occurred frequently during the breeding season (Piper and Slater 1993). While less frequent than that between males, pecking and chasing also occurred between females in stable groups and nearly always involved DFs that were relatively new to a group and were unrelated to the subordinate females ("SFs") they attacked. Such attacks were recorded in five of eight focal groups where DFs had taken over within the last year and had not previously associated with SFs in the group (which were also unrelated to them). In contrast, DFs were never observed to attack SFs in groups where they had been the DF for more than a year (0 of 10 possible groups; $G =$

10.7, $P < 0.01$, G -test) and were familiar with all SFs (who were also their daughters in all cases).

PREDATION AND NEST DEFENSE

Species known to have attacked nests of Stripe-backed Wrens included Roadside Hawks (*Buteo magnirostris*), Yellow-headed Caracaras (*Milvago chimachima*), Crane Hawks (*Geranospiza caerulescens*) and Cebus Monkeys (*Cebus nigrivittatus*). A variety of arboreal snakes occurred on the ranch, and these were likely nest predators as well. When predators approached a nest containing eggs or nestlings, the wrens (especially those in large social groups) often mobbed them and emitted harsh rasping notes. On other occasions, both large and small groups only scolded intermittently or not at all when predators approached their nests.

In addition to the nest predators listed above, wrens encountered a wide variety of smaller birds ("nest intruders") near their nests. Almost invariably the wrens chased such intruders until they left the vicinity of their nests. Moreover, the close correlation between the mean levels of nest attendance for DMs, DF-sons, DF-stepsons, DF-daughters and DF-stepdaughters and the number of chases of nest intruders in which each sex/status class participated ($r = 0.995$, $P < 0.01$, $n = 5$) demonstrates that an adult's participation in nest defense depended solely on its presence near the nest and not on its sex and status within the group (i.e., DMs chased more intruders away from the nest simply because they were present at the nest more often; see Fig. 4). (DFs were excluded from this analysis because their nest attendance was usually related to incubation.)

On average, chases of nest intruders occurred at a rate of about once per hour during the reproductive cycle (Fig. 5), and the list of 28 species chased in 1990 and 1991 fell into three general categories. One category comprised species that competed with the wrens for use of grass or stick nests. This group included Greater Kiskadee Flycatchers *Pitangus sulphuratus* (4.0% of all chases, $n = 450$ total chases), Troupials *Icterus icterus* (3.6%), Blue-gray Tanagers *Thraupis episcopus* (1.8%), intruding Stripe-backed Wrens from other groups (1.1%), and finally the Plain-fronted Thornbirds (26.4% of all chases) that built the stick nests used by many wren groups and often continued to roost in stick nests after wrens moved in. The second category comprised 23 species of small- to medium-sized birds that nei-

ther competed with nor parasitized the wrens but merely ventured close to wren nests (e.g., Saffron Finch *Sicalis flaveola*, 4.9% of all chases; Yellow-rumped Cacique *Cacicus cela*, 2.7%; Grayish Saltator *Saltator coerulescens*, 2.2%). The third category comprised only the Shiny Cowbird *Molothrus bonariensis*, a brood parasite and the species most often chased by wrens (33.6% of all chases, see below).

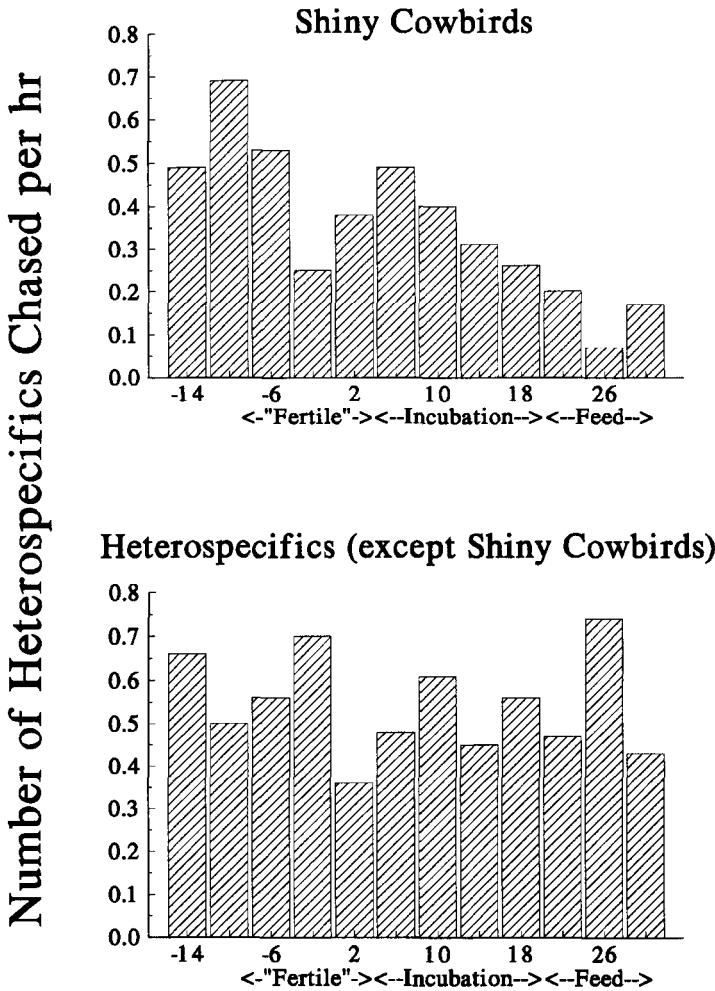
BROOD PARASITISM BY THE SHINY COWBIRD

The temporal pattern of nest defense against Shiny Cowbirds contrasted sharply with the pattern among other heterospecifics and indicated a clear tendency for cowbirds to approach wren nests during the incubation period, when parasitizing them was likely to result in the successful rearing of cowbird chicks (Fig. 5). It is important to note that, despite making frequent visits near wren nests, cowbirds only succeeded in entering brood chambers on 4 of 151 total visits (2.6%).

Anecdotal evidence suggested that cowbirds were capable of synchronizing their laying closely with that of the wrens. The nest of a pair of wrens without helpers that was checked on three consecutive days in 1991 contained two wren eggs on 20 April, three wren eggs on 21 April and four wren (two intact and two punctured) and three cowbird eggs on 22 April. Thus, three different female cowbirds laid eggs in the nest on a day that guaranteed the cowbird eggs hatching at least six days before the wren eggs.

Surveys of fledglings produced at wren nests showed that both large and small wren groups were important hosts for Shiny Cowbirds during 1990 and 1991. Of 43 groups observed within a week of fledging young in these years, five (11.6% of the total; three groups of four or more wrens and two pairs) fledged cowbirds only and two (4.7% of the total; both groups of four or more wrens) fledged both wrens and cowbirds. The overall estimate of the parasitism rate, 16.3%, is conservative since cowbirds appeared more successful in parasitizing pairs and trios (constituting 48% of all wren groups in 1991, $n = 56$), which were less often successful at producing fledglings than large groups and were not monitored as closely.

Male Shiny Cowbirds, as well as females, frequently ventured close to wren nests. Twenty-three percent of all cowbirds chased were males, and male cowbirds were pursued more frequently than any of the following more common birds:



4-day Interval in Reproductive Cycle

FIGURE 5. Number of heterospecifics chased away from active nests by wren groups during the reproductive cycle. Wrens chased more Shiny Cowbirds from their nests early in the reproductive cycle, but chases of other species did not depend on reproductive stage.

Greater Kiskadee Flycatcher, Troupial, Yellow-rumped Cacique, Grayish Saltator and Blue-gray Tanager. The high incidence of pursuits of male cowbirds by wrens did not appear to result from males simply following females to nests of potential hosts, for they rarely did so.

EFFECTS OF NEST CONSTRUCTION ON REPRODUCTIVE SUCCESS

During the course of the study, most wren groups bred in stick nests built by Plain-fronted Thorn-

birds, while a smaller number of groups bred in grass nests that they built themselves. Stick nests are sturdier than grass nests and thus would appear less likely to be lost to predators; moreover, they require lower maintenance (mean of 0.28 ± 0.33 SD trips to nest with nesting material per hr among 94 individuals for stick nests; 0.39 ± 0.40 SD among 67 wrens for grass; $P < 0.05$, two-tailed *t*-test). An apparent hazard to nesting in stick nests, however, was the danger of being trapped in them when they fell. In 1990 the dom-

inant female of the NM group was killed when the stick nest in which she was brooding nestlings fell during a storm.

In 1990 and 1991, a greater proportion of groups than average (22 of 47 observed groups, 47%) bred in grass nests, and it was possible to compare the reproductive success of grass- and stick-nesting groups. Groups in stick nests tended to fledge more young per adult than groups in grass nests (0.53 ± 0.44 SD, $n = 25$ for stick nests, versus 0.31 ± 0.33 , $n = 21$ for grass nests), although the difference was not significant ($t = 1.67$, $0.05 < P < 0.1$, two-tailed Mann-Whitney U test).

DISCUSSION

THE ONSET OF BREEDING

Two patterns emerged from the data on the timing of breeding relative to the occurrence of rain. First, rainfall, or some other cue resulting directly from it such as plant growth or insect emergence, triggered the onset of breeding in Stripe-backed Wrens. Second, breeding by the wren population was not "all or none"; instead the amount of rain required to elicit breeding behavior varied among wren groups. The importance of rain in eliciting breeding is well-documented in birds, especially in desert species (Immelmann 1972).

The fact that the first rainfall of a wet season preceded courtship and nest building by only a day or two in some groups suggests that wrens might have been prepared for breeding before the rains actually occurred. Perhaps testis growth in Stripe-backed Wrens is partially under endogenous control as in other tropical passerines (e.g., Miller 1962, Gwinner and Dittami 1990). Endogenous control of testicular growth might help explain the observation that all male wrens, even sons of the dominant female that could not breed because of the strict incest avoidance in this species, possessed enlarged testes during the breeding season. Selander (1964) found enlarged testes in all males in groups of a cooperatively-breeding congener (*C. griseus*), an indication that testicular growth in the breeding season regardless of breeding status might be widespread.

COURTSHIP: THE AGGRESSIVE CHASE

Courtship is defined generally as behavior that facilitates pairing and/or copulation between males and females (e.g., Beer 1972). Although it is not possible to ascertain precisely the rela-

tionship between the occurrence of aggressive chases and initiation of breeding, the occurrence of most aggressive chases during the early part of the fertile period suggests that they might have been an indication of sexual readiness on the part of males.

It is possible that aggressive chases by male Stripe-backed Wrens served to stimulate reproductive behavior in females just as male territorial song apparently does in other songbirds (Hinde and Steel 1976). Territorial song cannot be a reliable stimulus for reproduction in Stripe-backed Wrens because it takes the form of duets, which are carried out by both sexes (including DF-sons and subordinate females, which do not breed) and in many contexts throughout the year (see Fig. 1).

Insofar as male Stripe-backed Wrens pecked repeatedly at the cloacal area of a reproductive female, the aggressive chase superficially resembled the distinctive pre-copulatory cloaca-pecking by male Dunnocks (*Prunella modularis*; Davies 1983) and other passerines (e.g., the House Sparrow *Passer domesticus*, Summers-Smith 1954; Blue Tit *Parus caeruleus*, Boyle 1951). However, the cloaca-pecking of Stripe-backed Wrens occurred in flight, was not seen to elicit sperm ejection (as in the polyandrous Dunnock) and was not a prelude to copulation. It seems, therefore, that cloaca-pecking by male wrens was not a means of dislodging sperm of competing males from the female's cloaca.

The similarity between the aggressive chases of dominant females that serve as courtship and simple chases of heterospecifics away from wren nests is remarkable and seems unlikely to have resulted by chance. Both aggressive chases and nest defense involve chases by a wren of another bird accompanied by a distinctive staccato vocalization. It is reasonable to presume that the aggressive chase represents a ritualized form of nest defense that now functions as a breeding signal. Perhaps it should not be surprising that, in a species for which nest defense is so frequent and conspicuous, we should see a slightly-altered form of this behavior take on a completely different function.

COPULATION

Copulations in the Stripe-backed Wren occur at a frequency during the fertile period that places them well within the published range for passerines (see Birkhead et al. 1987, Birkhead and

Møller 1992). By virtue of its infrequent copulation and conspicuous mate-guarding (see Piper and Slater 1993), the Stripe-backed Wren falls into the category of birds that use mate-guarding (in this case, against other males within the group) as the primary means of paternity assurance (see Møller and Birkhead 1991). The wrens are typical of this category because the fertile period appears to be relatively short and because the occurrence of rainfall just before the fertile period permits males to predict when guarding should occur.

The hourly pattern of copulations lends further insight into the issues of fertilization and sperm competition. Since copulations immediately following the laying of an egg stand the greatest chance of fertilizing the following day's egg, copulations might be expected to occur soon after egg-laying (Birkhead and Møller 1992). Although this pattern holds in many birds (Møller 1987), it appears not to hold for Stripe-backed Wrens, which probably lay eggs in the morning (the common pattern in small passerines; Skutch 1952) but copulate throughout the day.

The tendency of copulations to occur at times other than those that maximized their likelihood of fertilizing eggs might be explained quite simply: female wrens, not males, might use solicitations to influence the paternity of offspring (Birkhead and Møller 1993). By soliciting copulations from certain males at times when they are unlikely to fertilize eggs (e.g., well after laying an egg), females might be able to minimize the chances of those males siring offspring; conversely, females might maximize the likelihood of paternity by favored males if copulations are solicited from them just after laying has occurred. Since I cannot be certain that forced copulations do not occur in Stripe-backed Wrens, statements regarding female control of paternity must remain tentative. In any event, the genetic consequences of such a phenomenon would not be so great in Stripe-backed Wrens as in many monogamous passerines, because most potential sires of offspring in the wrens are first-order relatives (fathers and sons or full brothers).

AGGRESSION DURING THE BREEDING CYCLE

Dominant females appeared to use aggression as a means of reinforcing their dominance over subordinates and avoiding being "deposed." Dominant females were occasionally deposed by unrelated females (six cases in 363 group-years of

observation since 1985) that joined their groups. Two of five subordinate females attacked by DFs in 1990 and 1991 had themselves been DFs in the group previously. In the remaining three cases, however, the subordinate female was the daughter of the DM and therefore unable to breed (see Rabenold 1990). Apparently a female that has just become the DF shows aggression towards all unfamiliar females in her group because she is unable to distinguish possible breeders from those unable to breed (daughters of the DM).

The tendency for DFs to behave aggressively towards SFs in their groups without regard for the likelihood that the SFs might depose them is reminiscent of a pattern in mate-guarding by dominant males. Mate-guarding increases as the number of DF-sons in groups increases (Piper and Slater 1993), even though DF-sons are no threat to the DM's paternity (Rabenold et al. 1990).

FEEDING EFFORT BY SUBORDINATES

While in other cooperative breeders provisioning of nestlings by subordinates is related to age (Purple Gallinules *Porphyryla martinica*: Hunter 1987; Galapagos Mockingbirds *Nesomimus parvulus*: Curry 1988) and sex (Curry 1988) of the adults and relatedness to offspring (Pied Kingfisher *Ceryle rudis*: Reyer 1984), the amount of food provided by subordinate Stripe-backed Wrens showed no strong pattern of this kind. It is possible that the weak tendency of older wrens to provision more than young wrens (also reported by Rabenold 1984) reflected the tendency for wrens to improve their provisioning efficiency over time by learning (see Lawton and Guindon 1981).

FEEDING EFFORT AND PATERNITY

If DMs and DF-stepsons competed with such intensity for access to DFs during the "fertile period," why did they later provision nestlings without regard to their success at gaining this access? There are probably two answers: (1) both DMs and DF-stepsons were related to the young sired by the other by $r = 0.22$ (coefficient of relatedness) on average, because of the fact that most DF-stepsons were first-order relatives (sons or full brothers) of the DM, and (2) most juveniles raised by a group remained with the group and increased the likelihood that the group reproduced successfully in future years, which benefited both DMs and DF-stepsons. Thus, it is

not surprising that male wrens differed from males in the polyandrous Dunnock (Davies et al. 1992) and Pied Kingfisher (Reyer 1984), which fine tune their feeding efforts according to their relatedness to the nestlings they feed. In the Dunnock, males are related to young they help raise by either $r = 0.5$ or 0 , so a male mistakenly feeding young not his own gains nothing in terms of fitness. Furthermore, a male Dunnock cannot increase his future productive success by raising more young, since young Dunnocks do not help their parents reproduce in subsequent years but instead disperse immediately to breed on their own. A similar disparity exists in the relatedness between helpers and nestlings in the Pied Kingfisher, wherein primary helpers show substantial feeding effort in raising full or half-siblings, while secondary helpers provide relatively little food to nestlings unrelated to them in order to associate with the female breeder with which they often mate in a future year.

GROUP FEEDING RATES OVER THE BREEDING CYCLE

The observed rise and fall in the feeding rate during the nestling phase is typical of passerines that fledge volant young (Nice 1943, Bussmann 1953). It seems likely that the maximal rate of food delivery during the middle of the nestling phase corresponds to the period of maximal absolute growth of nestlings (Ricklefs 1968). Since prey size increased steadily during the nestling phase, however, the actual mass of food brought to nestlings probably levelled off rather than decreasing during the last week of feeding.

PREMATURE FEEDING TRIPS AND FOOD-STEALING

The common tendency of wrens to bring food to the brood chamber before the eggs hatched suggests that Stripe-backed Wrens did not begin feeding as a simple response to the stimulus of begging nestlings but instead were primed for feeding by some other, perhaps physiological, means.

Food stealing between group members such as I observed in Stripe-backed Wrens occurs widely in cooperative breeders. Ligon and Stacey (1989) interpret similar food-stealing by Arabian Babblers and Green Woodhoopoes that is followed by feeding of young by the thief as an attempt on the thief's part to cement personal bonds between itself and nestling. If Stripe-backed Wrens

had stolen food from others in order to increase their feedings of nestlings and thus form strong relationships with them, dominant individuals could have waited at the nest and intercepted all incoming food brought by subordinates. I regard food-stealing by Stripe-backed Wrens, which always involved one adult stealing from a second wren subordinate to it, as simply an assertion of dominance, possibly as a means of strengthening the dominance relationship.

NEST ATTENDANCE BY DOMINANTS AND SUBORDINATES

Nest attendance by an individual appeared to be an indication both of its tendency to defend the group nest and its likelihood of producing offspring. Dominant females, for example, simply arrived many times in the course of building the brood chamber and incubating the eggs. Dominant males showed even greater nest attendance than DFs and guarded the nest frequently during incubation. For their part, DF-stepsons showed the expected high rate of nest attendance before and during the fertile period (like DMs), which declined as incubation progressed. DF-sons, which did not attempt to reproduce, visited the nest infrequently during courtship and the fertile period and became frequent visitors during incubation. DF-daughters had a pattern of nest attendance similar to that of DF-sons, but they visited less frequently overall. Finally, DF-stepdaughters, which were often attacked by DFs, showed very low nest attendance throughout the nesting period. The low rate of visitation by subordinate females generally probably reflected the tendency of females to leave the group territory often while scouting for breeding vacancies in other groups.

BROOD PARASITISM

Based on data gathered between 1978 and 1985, Rabenold (1990) estimated that fewer than 10% of all wren nests were parasitized by Shiny Cowbirds, while I observed cowbird fledglings at over 16% of all nests with fledglings in 1990 and 1991 and regard 30% as a good estimate of the actual rate of parasitism in these years. Deforestation and conversion of most of the land surrounding Hato Masaguaral to farming and ranching has probably increased the density of Shiny Cowbirds in the study area (see Post et al. 1990) and thus the incidence of cowbird parasitism. The increase in brood parasitism might, at least in

part, explain the 71% drop in the original study population between 1978 and 1991.

A number of factors appear to render the wrens vulnerable to brood parasitism by the cowbird. These factors include the conspicuousness of the bulky stick and grass nests used by wrens, the loudness of the wrens themselves generally and of their nest defense in particular (which aids cowbirds in finding nests; Wiley 1988) and the willingness of the wrens to accept cowbird eggs (no rejection of a cowbird egg has ever been recorded).

An additional factor that probably made the wrens especially appealing hosts for cowbirds was the seven-day difference between the incubation periods of the two species. Indeed, this difference might have provided cowbirds with substantial room for error in their laying dates in wren nests and thus might have compensated for the apparent difficulty that cowbirds experienced in viewing the wren eggs so that they could use them as a cue in synchronizing their laying date with their hosts' (see Wiley 1988).

A curious finding of this study was that male Shiny Cowbirds visited wren nests frequently on their own. Although Wiley (1988) observed male Shiny Cowbirds in the company of females when the latter searched for host nests, he reported no tendency for male cowbirds to visit nests alone. Two possible explanations for male visitation of wren nests are: (1) male cowbirds attempt to find females by visiting nests of potential hosts, or (2) like females, male cowbirds monitor the progress of hosts' nests, perhaps as a means of maintaining breeding synchrony with their mates.

ACKNOWLEDGMENTS

Gary Slater helped gather much of the data described herein during both 1990 and 1991, and Joseph Haydock recorded the first observation of copulation in this species (on 17 June 1986). Kerry Rabenold, Patricia Parker, Steven Zack, Joseph Haydock, Haven Wiley and numerous field assistants contributed countless hours of field work to earlier aspects of the 14-year study from which the present research developed. Walt Koenig, Peter Stacey, Haven Wiley, Patricia Parker, Joseph Haydock and Kerry Rabenold made useful suggestions that improved the manuscript. Carlos Ruiz-Miranda translated the abstract. Finally, I thank Tomás Blohm, owner of Hato Masaguaral, for allowing me to conduct my research there. This work was funded by NSF grants BNS-9100841 and BSR-8818038.

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