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FIRST RECORD OF COOPERATIVE BREEDING IN A *THRYOTHORUS* WREN

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ABSTRACT.—Although offspring delay dispersal past the age of independence in many *Thryothorus* species, cooperative breeding has not been recorded in this genus. Here, I present the first observation of cooperative breeding in a *Thryothorus* wren (Buff-breasted Wren, *T. leucotis*). Of 41 offspring that delayed dispersal past the age of independence, 4 individuals stayed on their natal territory until their parent's next breeding attempt, indicating a low potential for cooperative breeding. Of these four individuals, one male provisioned 11- to 15-day-old nestlings and one female approached her parents' nest but was repeatedly driven away from it by her father. The retained female was apparently tolerated when in the vicinity of fledglings, but feeding was never positively confirmed. *Received 10 May 2004, accepted 15 October 2004.*

In cooperatively breeding birds, more than two adults participate in a single breeding event, either by defending the nest, incubating eggs, or provisioning young (Brown 1987). This is the predominant social system in 18.5% of oscine passerine species with biparental care (383 of 2,067 species), and occurs occasionally in another 3.7% of oscines classified as pair breeders (Cockburn 2003). However, patterns of nestling care are unknown for most passerines (n = 2,385), particularly those in the Neotropics (Cockburn 2003); thus, cooperative breeding may occur in still other species. Intensive studies of populations of banded birds are needed to determine the extent of pair versus cooperative breeding in these species.

Cooperative breeding may arise in several different ways, including when (1) independent offspring remain on natal territories until their parents' next breeding period (Cockburn 1998), (2) individuals initially disperse and then preferentially immigrate into social groups composed of related individuals (Baglione et al. 2003), and (3) groups of unrelated individuals reproduce together (Davies 1992). In the first case, delayed dispersal by offspring is a necessary prerequisite for cooperation. However, in some species in which offspring remain on their natal territories for extended periods, helping never occurs (reviewed in Ekman et al. 2001). Delayed dispersal by offspring is often associated with high adult survival, low reproductive rates, and deferred maturation (Brown 1987), and may be a form of extended parental investment, in which parents permit or encourage offspring (via access to resources) to remain on natal territories (Ekman et al. 2001).

Wrens (Family Troglodytidae) have been among the most studied New World avian taxa in terms of cooperative breeding, with much of this research focusing on the genus *Campylorhynchus*, in which 9 of 13 species are known to breed cooperatively (e.g., Austad and Rabenold 1986, Rabenold 1990). Cooperative breeding occurs regularly in Black-capped Donacobius (*Donacobius atricapillus*) and has been reported in House Wrens (*Troglodytes aedon*; reviewed in Cockburn 2003). However, the breeding systems of most species in this family, especially those in tropical areas, have not been described and cooperative breeding may be more common than reported. For example, many species in other genera, in particular *Thyrothorus*, are often found in family groups (e.g., Skutch 1960, 2001; Slud 1964; Hilty and Brown 1986; Brewer 2001), suggesting that independent offspring may stay on natal territories for extended periods, potentially setting the stage for cooperative breeding. Here, I describe the first record of cooperative breeding in the genus *Thryothorus* made during a study of patterns of nestling provisioning in Buff-breasted Wrens (*T. leucotis*; SAG unpubl. data). Previous studies have reported that Buff-breasted Wrens are often found in groups of 3–4 individuals (Skutch 1968, Farabaugh 1983, Ahumada 2001), but none has recorded dis-

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persal delayed into the breeding season or cooperative breeding.

METHODS

Buff-breasted Wrens are small (16–23 g), monochromatic birds that inhabit secondary forest throughout their range from central Panama to northern South America (Ridgely and Tudor 1989). They maintain territories and partnerships throughout the year, and breed during the wet season (April to October; SAG unpubl. data); initiation of breeding is closely tied to the onset of rains (Ahumada 2001). Buff-breasted Wrens are socially and genetically monogamous: extra-pair young were detected in only 1 of 31 broods (Gill et al. 2005). Throughout the year, pairs produce antiphonal duets in which males and females give alternating sex-specific songs (Farabaugh 1983).

I studied a color-banded population of Buff-breasted Wrens in Gamboa, Republic of Panama (9° 7′ N, 79° 42′ W) during both dry and wet seasons (February–May 1997, February–July 1998, October 1998, February–June 1999). The study site was a 22-ha secondary forest bordered on three sides by Gamboa, the Rio Chagres, and the Panama Canal, and it was separated from the nearest forest by a 100-m grassy marsh. In 1997, both individuals in 15 of 18 pairs were banded, whereas in 1998 (n = 24) and 1999 (n = 19), both members of all pairs were banded. I banded a total of 65 adults, 17 adult philopatric offspring, 27 fledglings, and 13 nestlings. I sexed individuals based on body size (females are smaller than males; SAG unpubl. data), singing behavior (Farabaugh 1983), and egg laying and incubation (Gill 2003). When more than two adult birds resided on a given territory, I distinguished paired adult birds from their adult philopatric offspring by behavior, as paired individuals duetted more frequently, and spent more time in close association (<5 m apart) than with their offspring. I defined a philopatric offspring as one that remained on its natal territory for >3 months.

Buff-breasted Wrens typically construct separate dormitory nests—in which they roost overnight—and breeding nests, although approximately 10% of dormitory nests are used for breeding (SAG unpubl. data). I located nests by searching areas from which pairs gave their first song of the morning (these are typically given when birds are close to their nests), during regular searches of territories, and by following individuals that were collecting or holding nesting materials. I did not mark nest locations, as they were easy to refind. Nests were checked every 2 days until clutch completion (modal clutch size = 3, range = 2–3, n = 42) and irregularly thereafter until the young fledged or the nest failed.

As part of a broader study examining male and female effort during nest construction and nestling provisioning, I made 1-hr observations of nestling provisioning every 2 days from the day after hatching (day 0) until the nestlings fledged (usually day 15). All observations were performed between 06:00 and 14:00 EST, from a position at least 5 m from nests, to avoid influencing the behavior of the parents as they returned to feed or brood (females only). During these observations, I quantified the number of visits per hour by male and female parents, as well as visits by the retained offspring. In addition, I noted the singing behavior of offspring, as well as aggressive interactions between them and their parents.

RESULTS

Of 57 offspring banded as nestlings, fledglings, or independent birds, 35 remained on their natal territories for >3 months after fledging. Another six unbanded individuals lived on territories with banded adults. I assumed that these unbanded individuals were the offspring of the banded adults because (1) their presence was consistent with the fledging of offspring in those territories in the previous breeding season; (2) 17 individuals, banded as adults and residing on territories with 2 other adult birds, were the genetic offspring of those adults (SAG unpubl. data); and (3) I have no evidence that groups formed other than by the retention of offspring. Thus, a total of 41 offspring (65.1% of offspring fledged) remained on their natal territories for >3 months. Prior to their parents' next breeding attempt, most philopatric offspring either dispersed to become territory holders in the study population (n = 13) or disappeared (n = 24). Only four individuals (9.8% of philopatric offspring) postponed dispersal for >1 year, staying on

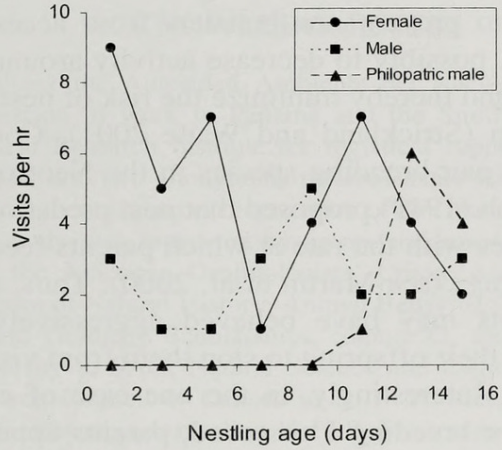

FIG. 1. Pattern of provisioning by a single pair of Buff-breasted Wrens and a philopatric, unbanded male when feeding three nestlings. Eggs hatched on day 0 and were observed every second day from days 1 to 15, at which time the young fledged. The philopatric male was not observed within 5 m of the nest area prior to day 11.

their natal territories through their parents' subsequent breeding season.

Between 6 and 10 June 1999, I observed helping at the nest by an unbanded male during the second breeding attempt of a banded pair that had been together for >2 years. This pair had fledged two males in the previous breeding season, one of which I captured and banded. Both male offspring were present on the territory at the start of my field season in February 1999, with the banded male dispersing to another territory before breeding commenced. The unbanded male was last observed on his natal territory on 30 June, a date that corresponded to the end of my field season.

Visitations by the parents and the unbanded male while provisioning a brood of three nestlings are summarized in Figure 1. Between days 1 and 9 after hatch, the unbanded male was not observed within 10 m of the nest, but often sang within the territory. On day 11 near the start of observations, the unbanded male entered the nest and stayed in it for approximately 10 sec. Shortly after the unbanded male left the nest there was a chase involving two unidentified wrens, and "aggressive" churring (such calls are heard only during aggressive encounters; SAG pers. obs.). Less than 30 sec later, a third unidentified wren approached this pair, and another chase ensued. The parental male did not visit the nest within 30 min of this interaction, while the female visited the nest four times within that period. Near the end of the 1-hr observation period, the unbanded male, with food in his bill, tried to approach the nest once more. The parental male was in the nest, exited it and then chased the unbanded male away from the nest. Soon after, the parental male and the unbanded male were observed foraging within 2 m of each other.

On day 13, the unbanded male visited the nest six times within an hour, equaling the contribution of the parents combined. His first visit was apparently undetected by the parents as they were not in the immediate nest area at the time. While approaching the nest for his second visit, the unbanded male was supplanted by the male parent, who gave an aggressive churr, but the unbanded male was not chased out of the area. Rather, he continued to move around the nest, with the male parent following 1–2 m behind. The unbanded male then entered the nest and fed the young. On the next four visits, the unbanded male was followed several times by the male parent, but no aggression was exhibited. On the day of fledgling (day 15), the unbanded male made four visits to the nest, more than the individual effort of either parent (Fig. 1). No aggression between the unbanded male and the parental male was observed at this time, and no aggression between the unbanded male and the female was ever recorded. Three young fledged from the nest on 10 June. I made three additional untimed observations of this pair after the young fledged, during which the unbanded male perched within 2 m of the fledglings and their parents, and once fed the fledglings.

During observations at a second nest in June 1999, I witnessed aggressive encounters between a banded female offspring (hatch year 1998) and her banded father around the breeding nest, but never observed the female enter the nest to feed the young. On day 5, the philopatric female approached within 5 m of the nest and was chased by the male 3–4 times. She moved to 2 m from the nest and was chased again by the male parent, who gave several aggressive churrs. When the nestlings were 13 days old, the philopatric female perched 4–5 m from the nest and was immediately chased by the male, who uttered

aggressive churrs (the philopatric female did not approach the nest during observations made before day 5, between days 7 and 11, or on day 15). Two nestlings fledged on 6 June, and I observed the philopatric female within 3 m of them on the day of fledging as well as during observations 2 weeks later. At both times, the family was in thick vegetation and I made few definitive observations of feeding by any adult. No aggression was noted between the male and the philopatric female after the young fledged, nor was aggression observed at any time between the parental and philopatric females.

Two other banded offspring were observed on their natal territories during subsequent breeding attempts of their banded parents, but helping was not observed. I observed a banded, second-year female offspring on her natal territory 1 day before her parents began constructing their second breeding nest, but did not see her during 4 hr of observation of nestling provisioning. However, this female apparently stayed on her natal territory while her parents bred, as she was observed with them in the post-breeding season. Finally, a banded male was observed repeatedly foraging and singing with his banded parents over the course of their four breeding attempts. The philopatric male built a dormitory nest with his father (while the female incubated eggs), but did not participate in the construction of two breeding nests during timed observations. Although I did not observe this pair during nestling provisioning, the male offspring was still present on the territory at that time.

DISCUSSION

The potential for observing cooperative breeding in Buff-breasted Wrens was low, as only 4 of 41 independent offspring postponed dispersal for >1 year. All four offspring that delayed dispersal may have participated in territorial defense by singing on their own or with their parents. One male helped by feeding young, and one female appeared to try to provision nestlings and may have successfully fed fledglings. The latter cases were marked by aggression by male, but not female, parents toward their adult offspring during the nestling period. Similar aggressive interactions between parents and non-breeders occur in some small-bodied corvids during nestling care to prevent non-breeders from accessing nests, possibly to decrease activity around the nest and thereby minimize the risk of nest predation (Strickland and Waite 2001). Considering pair-breeding species in the Neotropics, Skutch (1949) proposed that nest predation increases with the rate at which parents feed the nestlings (see Martin et al. 2000). Thus, male parents may have behaved aggressively toward their offspring to stop them from visiting nests. Interestingly, in the one case of cooperative breeding I observed, parents appeared to visit their nest less once their male offspring started to provision the young (Fig. 1). Alternatively, parental aggression toward philopatric offspring may occur when resources become depleted and competition for the remaining resources intensifies (Strickland and Waite 2001). This hypothesis seems unlikely to apply to Buff-breasted Wrens, as breeding occurs during the wet season, when arthropod prey are abundant (e.g., Wolda 1996). Prey depletion seems more likely to occur during the dry season, yet I witnessed little or no parental aggression toward philopatric offspring at that time.

Most offspring that delayed dispersal did not stay on their natal territories long enough to help with reproductive activities of their parents. On average, offspring dispersed just prior to the onset of their parents' reproductive period (SAG unpubl. data). Prior to dispersing, however, some offspring participated in the construction of dormitory nests, and most sang either as part of territory defense or to advertise themselves to potential mates. Further studies are needed to determine the role of offspring in these activities, as well as the benefits and costs of philopatry for both parents and their offspring. The phenomenon of delayed dispersal in the absence of cooperative breeding is underappreciated, yet its study is a logical step toward understanding the evolution of cooperation (Brown 1987). The monophyletic wren family (Barker 2004) offers an exceptional opportunity to study the evolution of delayed dispersal and cooperative breeding due to the diversity of breeding and dispersal patterns, ranging from pair breeders with early dispersal by juveniles, to those with delayed juvenile dispersal without cooperation, to truly cooperative breeders.

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