Jiang *et al. Avian Res (2017) 8:28*
DOI 10.1186/s40657-017-0086-1

Avian Research

RESEARCH Open Access

Nest-site selection and breeding ecology of Streaked Wren-Babbler (*Napothera brevicaudata*) in a tropical limestone forest of southern China

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Abstract

Background: The breeding information of most birds in Asian tropical areas, especially in limestone forests, is still poorly known. The Streaked Wren-Babbler (*Napothera brevicaudata*) is an uncommon tropical limestone bird with a small range. We studied its nest-site selection and breeding ecology, in order to understand the adaptations of birds to the conditions of tropical limestone forest in southern China.

Methods: We used methods of systematical searching and parent-following to locate the nests of the Streaked Wren-Babbler. We measured characteristics of nest sites and rock cavities. Data loggers and video cameras were used to monitor the breeding behavior.

Results: All the observed nests of the Streaked Wren-Babbler were placed in natural shallow cavities or deep holes in large boulders or limestone cliffs. The great majority (96.6%) of Streaked Wren-Babbler nests had three eggs with an average fresh weight of 3.46 ± 0.43 g ($n = 36$, range 2.52–4.20 g). Most (80.4%) females laid their first eggs between March and April ($n = 46$). The average incubation and nestling period of the Streaked Wren-Babbler was 10.2 ± 0.4 days ($n = 5$, range 10–11 days) and 10.5 ± 0.8 days ($n = 6$, range 9–11 days), respectively. Most (87.9%) nests had at least one nestling fledge between 2011 and 2013 ($n = 33$).

Conclusions: Our study suggests that several features of the breeding ecology of the Streaked Wren-Babbler, including building nests in rocky cavities, commencing breeding earlier than most species, and reducing foraging times during the incubation period, are well-adapted to the unique habitat of tropical limestone forest.

Keywords: Breeding season, Breeding strategy, Clutch size, Karst, Incubation rhythm, Nest predation, Nestling development, Parental care, Reproductive output

Background

Understanding why birds differ in their breeding strategies is a key question in the study of life history evolution. Tropical birds generally lay fewer eggs and suffer from higher nest predation pressure than temperate species (Stutchbury and Morton 2001; Brawn et al. 2011). Yet previous studies and evidence have often focused on birds in Neotropical (e.g. Wikelski et al. 2003; Styrsky et al. 2005) and Afrotropical forests (e.g. Du Plessis et al. 1995; Mkongewa et al. 2013). Basic natural history information about the breeding ecology of birds of Asian tropical areas is still very poorly known (Robson 2005).

Southeast Asia and southern China, which includes a limestone area of 800,000 km^2, and in which more than 90% of natural vegetation has been destroyed, is one of the most important karst regions in the world (Day and Urich 2000). Recently, these limestone areas have become a focus of research, due to their great endemic biodiversity and conservation value (Clements et al. 2006; Luo et al. 2016), as demonstrated by three newly discovered

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bird species in the last 10 years (Zhou and Jiang 2008; Woxvold et al. 2009; Alström et al. 2010). Unfortunately, basic information about the breeding ecology of birds in these limestone areas is poorly known (Jiang et al. 2014), although this situation has been improved in the last 5 years. New studies have suggested that birds inhabiting limestone forests adopt particular life history traits, such as preferring to nest in natural rocky holes, and suffering high nest predation (Jiang et al. 2013a, b, 2015). However, it is still necessary to conduct more research to explore the breeding ecology of birds, especially for species that are endemic to limestone areas.

The Streaked Wren-Babbler (*Napothera brevicaudata*), including seven subspecies, is a medium-sized bird of the genus *Napothera*, which itself includes eight species mainly distributed in Southeast and South Asia (Gill and Donsker 2017). The Streaked Wren-Babbler has been traditionally considered to be an uncommon bird with a small range, mainly inhabiting broadleaf evergreen forest with rocky outcrops in southern China, northeastern India and Southeast Asia (Collar and Robson 2007). In China, there are two subspecies: *N. b. venningi* has been recorded in the far west of Yunnan Province, and *N. b. stevensi* is a resident in southern Guangxi and southeastern Yunnan Province (MacKinnon et al. 2000). In the limestone forests of southwestern Guangxi, the Streaked Wren-Babbler is a commonly observed bird (Jiang et al. 2014). It usually forages on insects from the surfaces of rocky outcrops in this area (Lu et al. 2013). The Streaked Wren-Babbler and the newly discovered and vulnerable Nonggang Babbler (*Stachyris nonggangensis*) share similar ecological niches in limestone forests of southern China (Zhou and Jiang 2008; Jiang et al. 2013a; Lu et al. 2015). Some information about the breeding season, nest and eggs of the Streaked Wren-Babbler has already been recorded in Southeast Asia, but the duration of incubation and the nestling period of the species are not well known (Collar and Robson 2007; Wells 2007). Although the Streaked Wren-Babbler is a common bird in some areas of China, almost nothing is known about its breeding ecology there (Zheng et al. 1987; Yang and Yang 2004). Interestingly, although both Streaked Wren-Babbler and Nonggang Babbler build their nests in rocky holes in similar positions, they have quite different nest predation rates, and different seasonal patterns (Jiang et al. 2013a). The Streaked Wren-Babbler has its peak of breeding in March rather than May, which is the peak of breeding for the Nonggang Babbler and most other species of the forest, and also lower nest predation rates, so we hypothesize that the Streaked Wren-Babbler avoids nest predation by breeding in a different season (Jiang et al. 2017). Moreover, due to the good heat preservation of these rocky holes, we also hypothesize that the Streaked Wren-Babbler has an incubation strategy of reducing the frequency of recess periods (times away from the nest) and prolonging the duration of such recesses, like Nonggang Babbler (Jiang et al. 2013a) and some pheasants (e.g. Jia et al. 2010).

In this paper, we present new data on the nest-site and breeding ecology of the Streaked Wren-Babbler in a typical tropical limestone forest, near the northeastern limit of its distribution. The main goal of this study was to report information about nest sites, breeding season, eggs, incubation rhythm, parental care, nestling development and breeding success of this species. We also assessed the importance of nest predation as an important factor of breeding failure in this area. Finally, we compared and discussed the breeding ecology of the Streaked Wren-Babbler in this limestone forest with that from other areas where it has been studied to better understand how the life history of birds has been shaped by this karst ecosystem.

Methods

Study site

This study was conducted in the limestone forest of the Nonggang Protected Section (22°28′N, 106°57′E; 5426 ha; altitudinal range from 150 to 650 m asl), the largest part of Nonggang National Nature Reserve, southwestern Guangxi Province, southern China. Nonggang has a tropical monsoon climate, with clear demarcation between the dry and wet season. Based on the data from Longzhou International Exchanging Meteorological Station (22°22.0′N, 106°45.0′E, 129 m asl, about 20 km from the study site) between 1980 and 2010, the annual rainfall was 1260.2 ± 246.2 mm, of which 73.3% was concentrated between May and September. The annual average temperature is 22.4 ± 0.5 °C. The great majority (96.6%) of Nonggang Protected Section is covered by tropical limestone hill seasonal rain forest. Although the altitude of Nonggang is low, the vegetation can be roughly divided into three ecological series, dominated by hygric, mesic, and xeric plants, respectively, based on the change of humidity and soil from the valley bottom to the peak elevations (Shu et al. 1988).

Nest searching and monitoring

Nest searching was conducted between January and July in the years of 2011–2015. The nests of the Streaked Wren-Babbler were located by following individual birds carrying nesting material or food to the nests and systematically searching the potential cavities of limestone around where we heard calls or songs. Potential habitat was searched with similar frequency each month. We noted the following characteristics of the cavity in which the nest was placed: nest height above ground,

width and height of cavity entrance, and depth of cavity. The active nests were checked every day to determine the time of egg laying, clutch size, start and duration of the incubation, and nestling period and fate of the nest. If the egg was not measured before it hatched, we estimated the fresh weight of eggs using the formula of Hoyt (1979): $W = K_w \cdot LB^2$, where W, L, and B are initial weight, maximum length and breadth of eggs, respectively; the species-specific constant K_w can be calculated from empirically measured data. We firstly calculated K_w using eggs that we measured before incubating, and then used this data to estimate the fresh weight of eggs that we measured after hatching. All data about nest and eggs are presented as mean ± SD.

A data logger (ZDR 21 automatic temperature recorder, made by Hangzhou Zeda Instruments Co., Ltd.) was placed in the nest after the first egg was laid to help analyze the timing of incubation. We also determined prey items brought to each nest by parents for nestlings with a Kodak Zx1 HD pocket video camera powered by a homemade battery in front of nest entrances from dawn until sundown. Prey items were only recorded to the order or family level because of the low light conditions close to the nests.

Breeding success

Hatching success was defined as the number of young in relation to the total number of eggs per nest. Fledging success was defined as the proportion of the hatchlings that successfully left the nest. Breeding success was defined as the number of fledglings in relation to the total number of eggs (Sanz et al. 2001). Nesting success was calculated as the observed numbers of successful nests (with at least one fledgling) in relation to the total number of nests (Ford 1999).

Results

Nests and nest sites

The nests of Streaked Wren-Babbler were built by both females and males (although the species is monomorphic, we saw two birds working together on multiple occasions). The typical nest is an open bowl (outer diameter: 13.5 ± 0.7 cm, inner diameter: 6.7 ± 0.3 cm, outer nest height: 9.1 ± 1.0 cm, bowl depth: 5.6 ± 0.3 cm, $n = 10$) with an obvious three-layered structure. The outmost layer was mainly constructed by dry twigs and leaves, the middle layer was built by crumpled leaves, and the inmost layer was composed of thin and soft plant fiber.

The nests of Streaked Wren-Babbler were placed in natural shallow cavities (Fig. 1a) or deep holes (Fig. 1b) in large boulders or limestone cliffs. Of 16 measured nest cavities, 56.3% were located in valley bottoms, where the nest was located in a rock boulder, and boulders tended to be fairly widely separated. The others selected the middle and upper parts of the limestone peaks. All the rocky holes used by the Streaked Wren-Babbler had a single entrance (long axis: 30.6 ± 22.1 cm; short axis: 20.4 ± 8.9 cm; distance above ground: 159.6 ± 79.4 cm, $n = 16$), with a mean depth of 33.2 ± 18.1 cm. All the nests were well protected from the rain and sunshine with at least 95% coverage by rock in an area of 100 cm × 100 cm above the nest.

Eggs

Female Streaked Wren-Babblers laid one white egg with tiny red brown spots each morning ($n = 12$ eggs in four nests monitored daily). We found a K_w of 0.4499, using 11 measured eggs to estimate 24 other ones. Fresh mass of eggs was 3.46 ± 0.43 g ($n = 36$, range 2.52–4.20 g), about 14.1% of the body mass (24.2 g) of the Streaked Wren-Babbler. Dimensions of 36 eggs from seven nests were 24.22 ± 1.32 mm (range 21.32–26.68 mm) in maximum length and 17.21 ± 0.74 mm (range 15.68–18.44 mm) in maximum breadth. Of all nests observed between 2009 and 2015, 96.6% (28 of 29) had a clutch size of 3 eggs. Only one nest was seen to have 4 eggs, in 2011.

Breeding season

Female Streaked Wren-Babblers laid their first eggs from February to June at Nonggang (Table 1). They showed a clear peak of breeding in March and April, when 80.4% (37 of 46) of nests received the first egg. Almost all (89.1%, $n = 46$) female Streaked Wren-Babblers laid their first eggs before May, when the rainy season usually arrives. The number of nests in each month had no significant relationship with rainfall ($t = 0.72$, $p = 0.49$) or mean temperature ($t = 0.50$, $p = 0.63$).

Incubation

The average incubation period of the Streaked Wren-Babbler was 10.2 ± 0.4 days ($n = 5$, range 10–11 days). From observations of 12 nests, it appears that the eggs of Streaked Wren-Babbler may only be incubated by one bird (probably the female, though potentially the male, since we could not differentiate the sexes in the field), because there was no evidence of switches, and recesses from the nest tended to be long. Incubating Streaked Wren-Babblers left the nest for foraging 4.3 ± 1.5 times per day (range 3–8, $n = 38$ days from six nests). Incubating birds spent 19.6 ± 4.3% (range 11.6–30.8%) of their whole day (dawn to sundown) away from the nest, probably foraging, with a total time ranging from 167 to 444 min. Generally, the first recess occurred from 6:19 a.m. to 7:30 a.m., and the incubating bird came back to the nest before 7:00 p.m. and then stayed on the nest during the night in 36 of 37 days.

Fig. 1 Nests, eggs and nestlings of the Streaked Wren-Babbler. **a** Nest and eggs in shallow cavity; **b** nest in deep hole; dprc: nestlings on hatching day; **d** nestlings on 5th day; **e** nestlings on 8th day; **f** nestlings on 11th day; **g** nestling preyed by mountain crab; **h** nestling we hypothesize was killed by a large invertebrate

Table 1 Breeding season of the Streaked Wren-Babbler at Nonggang limestone forest between 2011 and 2015

Month	Number of nests in which the first egg was laid	Rainfall (mm)	Mean temperature (°C)
Jan	0	34.6	14.2
Feb	4	32.6	15.9
Mar	23	55.2	19
Apr	14	84.6	23.5
May	4	166.2	26.6
Jun	1	217.1	28.1
Jul	0	220.2	28.3
Aug	0	205.7	28
Sep	0	115	26.7
Oct	0	66.9	23.7
Nov	0	43.6	19.5
Dec	0	18.5	15.5

Parental care

The nestlings of Streaked Wren-Babbler were fed by both females and males, as demonstrated by observations of both adult birds feeding nestlings at the same time. Parents fed their nestlings 8.2 ± 2.5 times per hour, as measured by the monitoring video recordings on two nests, totaling 16 h of observations. Every feeding visit lasted for 18.7 ± 17.2 s with an interval between visits of 6.85 ± 6.76 min. Removal of fecal sacs of nestlings was also practiced by the parents. Parents removed the fecal sac 38 times, 32 of which were directly swallowed.

We recorded 135 feeding visits to two broods of Streaked Wren-Babblers. Of these, 54.1% of 135 food items could not be identified due to poor light and the small size of the prey. Of the food items that were identified, 91.9% of 62 items were insects, including adult Lepidoptera (18), Lepidoptera larvae (13), walking sticks (2) and unidentified insects (24). The other five identified food items were eggs of spiders.

Nestling development

The nestling period of Streaked Wren-Babbler is 10.5 ± 0.8 days (range 9–11 days, $n = 6$). At hatching the nestlings had closed eyes, but were already covered by gray downy feathers on their heads, backs and legs (Fig. 1c). The primary, secondary and tail feathers had broken through the skin by the fourth day after hatching, and the eyes also began to open on that day. By the fifth day after hatching, the egg tooth and yellow yolk sac had disappeared (Fig. 1d). By the eighth day, they had begun to stand and extend their necks to beg for food (Fig. 1e). By the eleventh day, the feathers of the nestlings were similar in their position to that of the adults except forehead and wing tip (Fig. 1f). After the young left the nest, the parents continued to feed them for about 1 week nearby the nest.

Breeding success and nest predator

Among 33 nests of Streaked Wren-Babbler that had a known fate between 2011 and 2013, 87.9% (29 of 33) of the nests had at least one nestling fledge. Nest success did not differ by year ($\chi^2 = 0.10$; $p = 0.95$). Although the birds which laid the first egg after April 1 had lower nest success (66.7%, 8 of 12 nests) than those that laid earlier, this difference was not significant. Among 63 eggs of Streaked Wren-Babbler that were monitored during the whole incubation and nestling period, 92.1% of 63 eggs hatched and 84.5% of 58 nestlings fledged successfully.

Nest predation was the most important factor that led to breeding failure. Of the four nest failures, one nest was destroyed by a mountain crab (Fig. 1g). One nestling of another nest was found dead under the nest, meanwhile, the other two nestlings disappeared. We believe that this nest was attacked by a large invertebrate because the corpse was broken but not consumed (Fig. 1h). In two nests, all the nestlings (three in each nest) disappeared in 1 day, although the nest was intact, and we believe they were preyed on by a snake. All the nest predation events occurred in the nestling period.

Discussion

Nest sites

Streaked Wren-Babblers only build nests in rocky cavities or holes, ignoring other potential suitable places in the study area. Collar and Robson (2007) noted that Streaked Wren-Babblers often place their nests on the ground or in the banks of roads or trails. Wells (2007), working in the Thai-Malay Peninsula, found that Streaked Wren-Babblers there occasionally bred in crevices of dead trees. Although these habitats were also common in limestone forest in Nonggang, Streaked Wren-Babblers did not use them. Interestingly, there are also some other species that are reported to elsewhere build nests in holes or the ground, but prefer rock cavities in limestone areas (Jiang et al. 2013b, 2014). For example, the Oriental Pied Hornbills (*Anthracoceros albirostris*) mainly build nests in rocky holes in limestone forests in Nonggang, but prefer tree holes in non-limestone forests (Chen et al. 2007).

One possible hypothesis to explain this strong attachment to rocky cavities is that such cavities provide both heat insulation and escape from rain (Jiang et al. 2013a). Generally, both boulders and limestone cliffs overhang the nest entrance, making them well protected from rain and direct sunshine. In our study, all the holes or cavities used by Streaked Wren-Babblers had only one entrance, making the nest drier and warmer than if it had two or more entrances, which would increase exposure to

rain and wind. Although these rocky holes help to supply a comfortable (warm/dry) nest for birds, they may be accessible for some predators, such as small mammals, snakes that use the ground, and large invertebrates. Indeed, the nest predation of some babblers breeding in rocky holes was very high in this limestone area, e.g. 75% nests of the Nonggang Babbler were destroyed by nest predators (Jiang et al. 2013a); note that the Nonggang Babbler also nests in a later season, after April, and this may be a large factor in its high predation rate, as argued by Jiang et al. (2017). We believe the comfortable nest environment and potential high nest predation risk after April in this area are two key factors influencing the life history strategy of Streaked Wren-Babblers.

Breeding season

Most Streaked Wren-Babblers laid their first eggs before April in Nonggang limestone forest. This is unusual for birds in Nonggang: most species breed after April (Jiang et al. 2013a, b, 2015). It is also unusual for babblers, as most babbler species' breeding behavior is associated with an increasing day length and temperature in the northern hemisphere (Collar and Robson 2007).

Despite relatively constant temperatures, tropical birds are known to show strong seasonality of breeding, influenced by different kinds of environmental factors, especially rainfall (Stutchbury and Morton 2001). Some of this seasonality may be related to food availability (Lack 1954). As yet, however, there has been no experimental study conducted to determine the effects of food-supply on forest bird ecology in Southeast Asia forests (Sodhi 2002). As for the case of the Streaked Wren-Babbler, it would seem that food availability would be higher when they complete their breeding process. Both parents and nestlings of the Streaked Wren-Babbler forage on invertebrates (Collar and Robson 2007; Lu et al. 2013). In our research, adult Lepidoptera were the most common insects that appeared in the diet of Streaked Wren-Babbler nestlings. Generally, the population and abundance of adult Lepidoptera has a strong positive correlation with daily temperature and monthly rainfall in tropical forests of Southeast Asia (Intachat et al. 2001), and the weather of Nonggang becomes warmer after April with more rainfall starting from May. All this suggests that the key factor controlling this species' breeding is not food availability, but more likely potential nest predation after April in this area (Jiang et al. 2017), as has been also suggested for other tropical birds, e.g. the Clay-Colored Robin (*Turdus grayi*) (Morton 1971).

Nest predation

High nest predation is an important life history trait of tropical birds (Stutchbury and Morton 2001). Some birds breeding in limestone areas have been reported to suffer a higher nest predation pressure compared to temperate areas (Jiang et al. 2013a, b, 2015). Streaked Wren-Babbler appears to be an exception, however, as it showed a very low nest predation rate in our research (12% of 33 nests).

Nest predation has been shown to be affected by several different factors, such as nest sites, breeding season, and checking frequency of the researchers (Morton 1971; Ibáñez-Álamo et al. 2012; Vetter et al. 2013). Regarding the last factor, in a previous study (Jiang et al. 2017) we found that checking the nest once a day (predation in 37% of 59 artificial nests), or checking once every 3 days (31% of 49 nests), was associated with lower predation rates than checking just once in a 12-day period (57% of 74 nests). However, this effect was not as large as seasonal differences (predation in 17% of 83 artificial nests in March, vs. 66% of 99 nests in May). Hence, we believe that this study's once-a-day checking may be one factor that contributed to the low predation rate, but that natural rates of predation are likely to be low, at least before April.

What about Streaked Wren-Babbler's nesting biology might explain their low nest predation rate? Some nests are located in inaccessible places, such as high on a vertical cliff or on the roof of big cave; such locations would make predation from common predators, such as raptors and big or medium carnivores, difficult. Even if predators arrive at the hole, the small and deep entrance may block predator access. Some of the larger invertebrates and snakes are the main threats for the eggs and nestlings of Nonggang Babbler, which builds nests at sites similar to those selected by Streaked Wren-Babblers (Jiang et al. 2013a). These animals also appear to be the main nest predators for other babblers in southwestern China (Fu et al. 2017). These ectotherms become more active with increased temperature (Cox et al. 2013). We suggest that Streaked Wren-Babbler finishes the breeding process before April to avoid the attacks from these ectothermal animals, and thus escapes nest predation.

Clutch size

The Streaked Wren-Babbler mainly laid three eggs in our study area, similar to birds in India and Myanmar (Collar and Robson 2007). However, this is different from birds in Peninsular Malaysia, where two eggs are usually laid (Wells 2007). Nonggang has the similar latitude with India and Myanmar, but is substantially further north than Peninsular Malaysia. Generally, clutch sizes of birds increase with an increasing latitude (Lack 1947), similar to the pattern shown here. However, the clutch size of Streaked Wren-Babbler is less than most birds breeding in the Nonggang area, which mostly laid more than three eggs (Jiang et al. 2013a, b, 2014, 2015). Small clutch sizes

may be explained by high nest predation or limited food supply for nestlings (Styrsky et al. 2005). In our research, the Streaked Wren-Babbler has low nest predation but breeds in early spring, suggesting that limited food for nestlings may drive the relatively small clutch sizes (relative to other species) of the Streaked Wren-Babbler in Nonggang limestone forest.

Incubation

The incubation rhythm of the Streaked Wren-Babbler is similar to that of the Nonggang Babbler in having only a few relatively long recess periods (Jiang et al. 2013a). Indeed, adults were away from the nest about 20% time of whole day. The incubation rhythm of birds is affected by environmental factors of the nests and the body size of the incubator (Afton 1980), and the incubation strategy of birds is a trade-off between keeping adequate egg temperature and foraging (Jia et al. 2010). Generally, small-sized birds leave nests to search for food more frequently than bigger or medium sized birds (Afton 1980). Perhaps rocky holes regulate heat well and thus allow incubating birds to forage more. However, to confirm this hypothesis it is necessary to do more observations with individually identified birds.

Conclusions

Our study suggests that several characteristics of the Streaked Wren-Babbler's breeding biology are specially adapted to the unique conditions of tropical limestone forest. They prefer to build nests in rocky cavities, which make their nests warm and dry, but vulnerable. Streaked Wren-Babblers use several strategies, such as breeding earlier in the year than other species, and reducing movements back and forth to the nest in the incubation period, to escape nest predation. Possibly as a consequence of their early nesting season, and consequent low food availability, Streaked Wren-Babblers have a lower clutch size than most birds in the Nonggang area.

Authors' contributions

AJ, DJ and FZ conceived and designed the project. AJ and DJ performed the project. AJ, EB, DJ and FZ analyzed the data and drafted the manuscript. All authors read and approved the final manuscript.

Acknowledgements

This study was supported by the National Natural Science Foundation of China (30970381, 31460567) and Guangxi (2010GXNSFB013044), and a postdoctoral start-up project of Guangxi University (Y336002006, B41049). We thank Guangxi Forestry Department and Nonggang National Nature Reserve for granting the research permits. We are very grateful to Rong Lu and Weihong Nong for their assistance in field work and logistics. We would like to give special thanks to China Meteorological Data Service Center for sharing their data.

Competing interests

The authors declare that they have no competing interests.

Received: 12 August 2017 Accepted: 16 October 2017
Published online: 20 October 2017

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