

LETTER TO THE EDITOR

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# Breeding ecology of the Yellow-bellied Warbler (*Abroscopus superciliaris*)

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## Abstract

The life history of birds dictates their activities and is crucial to population success. However, the life history traits of only one-third of the world's bird species have been described; the rest are poorly understood. We studied the breeding ecology of the Yellow-bellied Warbler (*Abroscopus superciliaris*) and documented reproductive information throughout the egg and nestling periods. The data included natural nest sites, nest components, nest size, egg laying dates and time, egg morph, egg size, clutch size, egg incubation, nestling brooding and feeding, nestling morph and growth, and reproductive outcome. This study provided particular information of breeding ecology that has not been reported before in the Yellow-bellied Warbler.

**Keywords:** Behavioral patterns, Egg incubation, Life history, Nestling feeding, Reproductive success

## Correspondence

Avian reproduction has a series of complex behaviors, such as mate selection, nest site selection, egg laying, incubation, and nestling feeding (Zheng 2012). These behaviors are a sequence of adaptations formed through natural selection that are beneficial to individual and population survival (Saether and Bakke 2000). There are about 10,000 bird species (del Hoyo et al. 2013). The fundamental breeding information (nesting, incubation and nestling periods) of only about one-third of these species is known while the rest are poorly understood (Xiao et al. 2017). Passerines have the greatest number of species (6004) and inhabit all continents except Antarctica (Sibley et al. 1991; del Hoyo et al. 2013). Fewer than 7% of studies on passerines include breeding data (Pienaar et al. 2013). The tropics contain 73% of all bird species but breeding information have been well documented in only 20.2% of tropic bird species, compared to 57.9% of bird species in temperate areas (Kricher 2001; Levy 2008; Xiao et al. 2017). It is difficult to study the natural habitats and nests of birds in tropical forests because of the

hot and humid climate and dense vegetation (Xiao et al. 2017). Using artificial nest boxes facilitates studies of breeding biology of birds, especially for secondary cavity-nesting birds. Detailed information of avian reproduction can be obtained when birds accept and use nest boxes. Artificial nest boxes are convenient for breeding ecology studies but are also useful for other studies such as niche utilization (Ye et al. 2019).

We studied the Yellow-bellied Warbler (*Abroscopus superciliaris*) (Passeriformes, Cettiidae). There are three species in *Abroscopus*, including the Yellow-bellied Warbler, Rufous-faced Warbler (*A. albogularis*) and Black-faced Warbler (*A. schisticeps*). Knowledge of the breeding ecology of these three warblers is limited and little clutch size information has been reported (Xiao et al. 2017). We studied the breeding ecology of *A. superciliaris* and documented reproductive information throughout egg and nestling periods. Data collected included nest components, nest size, egg laying date and time, egg morph, egg size, clutch size, egg incubation, nestling brooding and feeding, nestling morph and growth, and reproductive outcome.

This study was performed in Nonggang village (23°39'N, 107°04'E), located in Guangxi Province of Southwest China, from April to July 2019. This location

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has a tropical monsoon climate with an average annual temperature ranging from 20.8–22.4 °C and an average annual rainfall ranging from 1150–1550 mm (Feng et al. 2019). *A. superciliaris* are resident birds mainly distributed in the eastern part of the Himalayas, Southern China and Southeast Asia. They are secondary cavity-nesters with similar morphology between males and females (del Hoyo et al. 2013).

We established 191 nest boxes to attract *A. superciliaris*. Nest boxes were made from pine wood and were 30 cm high  $\times$  15 cm long and wide, with a 6-cm diameter hole. They were attached to trees at a height of 3 m before the breeding season and inspected regularly for warbler activity. Nests in natural habitat were found by searching for holes in bamboo habitat. We recorded the nest materials, egg laying date, egg morph, clutch size, nestling morph, and measured the egg size, egg mass, nestling tarsus length, and nestling mass during nest inspection. Egg length, egg width, and nestling tarsus length were surveyed by a caliper. Egg mass and nestling mass were surveyed by an electric scale. For the calculation of egg size and mass, to avoid pseudo-replication, the average values from each nest represented one sample rather than using each egg as one sample. Two warbler nests in nest boxes were monitored 24 h continuously from egg laying to egg incubation and nestling feeding stages using a mini-camera (WJO3, Hisilicon, Shenzhen, P.R. China). A total of 77,760 min of video were recorded from nest T12 and J1. T12 included intact video data of both egg and nestling stages for analyses while for J1 only video data of nestling stage was included because the video data of egg stage was incomplete and excluded from analyses.

The egg laying date and time, egg incubation and nestling feeding behaviors were extracted by studying the monitoring videos. We summarized incubation rate and time per hour from 6:00 to 19:00 and daily incubation rate and time during egg incubation stage. During

the nestling stage, we summarized daily brooding (i.e. a behavior that keeps nestlings warm) frequency and time, feeding frequency per hour from 6:00 to 19:00, and daily feeding frequency. The evaluation of reproductive outcome included calculations of hatching rate, fledging rate, fledging success, and nesting success. Hatching rate was calculated by the proportion of hatching eggs from all eggs while fledging rate was calculated by the proportion of fledglings from all nestlings. Nesting success was defined as the percentage of nests that fledged at least one young and fledging success was calculated as the brood sizes at fledging (Yang et al. 2011). Figures were generated using SigmaPlot 14.0 for Windows (Systat Software Inc., USA). A Student's *t* test was used to compare the nest sizes in the nest boxes and natural nests. Spearman's rank correlation coefficient was used to test the correlation between incubation rate and time or egg turning frequency. Logistic regression was used to fit the growing curve of nestlings. Data were presented as mean  $\pm$  SD. Data analyses were performed using IBM SPSS 25.0 for Windows (IBM Inc., USA).

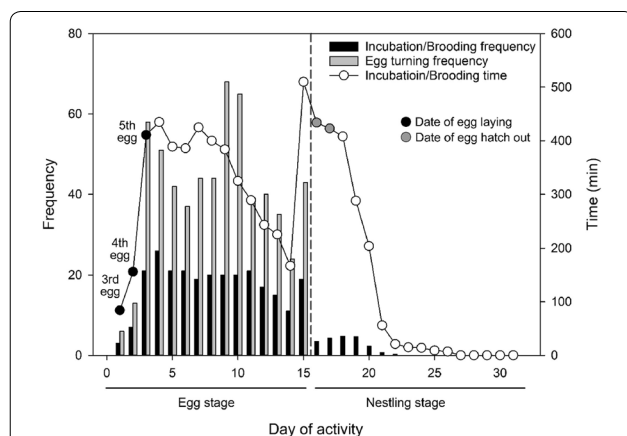
We found a total of 10 nests of *A. superciliaris* in nest boxes and 6 nests in natural habitats. Detailed information on breeding ecology was acquired from the nest boxes. We were unable to collect further information except for habitat, nest size, and nest fate because these nests were disturbed by local inhabitants. The nests of *A. superciliaris* in nest boxes were composed of an awn weaving nest cup surrounded by dry bamboo leaves. The nest cup included some feathers (Fig. 1a). In natural habitat *A. superciliaris* built nests in bamboo holes (hole diameter:  $2.5 \pm 0.2$  cm,  $n=6$ ) that were created by the White-browed Piculet (*Sasia ochracea*) (Fig. 1b). The holes were  $1.27 \pm 0.27$  m ( $n=6$ ) high. The nest materials were similar to those in the nest boxes but the nest shape differed (Fig. 1c). The nest cup diameter was similar between nest box and bamboo nests (nest



**Fig. 1** Nests and eggs of Yellow-bellied Warbler. **a** nest and eggs in nest box; **b** natural nest in bamboo hole; **c** interior of natural nest which was split after nestlings fledged

box:  $5.3 \pm 1.1$  cm,  $n=6$ , bamboo:  $5.1 \pm 1.5$  cm,  $n=6$ ;  $t=-0.359$ ,  $df=10$ ,  $P=0.727$ , Student's  $t$ -test), but the nest cup depth was different (nest box:  $4.2 \pm 0.3$  cm,  $n=6$ , bamboo:  $3.4 \pm 0.4$  cm,  $n=6$ ;  $t=-3.839$ ,  $df=10$ ,  $P=0.003$ , Student's  $t$ -test). Clutch size was  $4.3 \pm 1.2$  (range: 2–6,  $n=10$ ) and eggs were white in ground color but densely covered with brownish-red markings, which were mostly present on the blunt end (Fig. 1a). Egg size and mass were  $14.66 \pm 0.54$  mm  $\times$   $11.03 \pm 0.30$  mm and  $0.93 \pm 0.11$  g ( $n=7$ ), respectively.

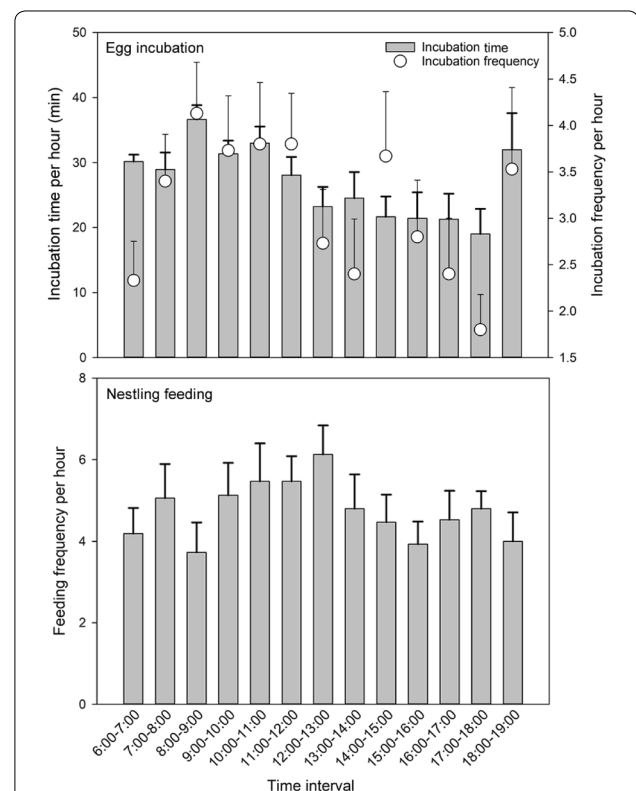
Nest box data showed that the earliest and latest laying dates of the 1st egg were 24 April and 31 May, respectively. *A. superciliosus* laid one egg each day during egg laying. The laying time of three eggs (3rd, 4th, and 5th egg) from nest T12 was recorded on 6:52, 6:18, and 6:54 in the morning. The egg incubation began after the last egg was laid. Before that, a short-time incubation was also found during the egg laying stage (Fig. 2). Although male and female warblers were sexually monomorphic, incubation appeared to be performed solely by the female. The incubation duration and absence intervals showed no signs of alternate incubation. The daily incubation rate was high and the duration was long initially but decreased during the latter part of the egg stage. On the day before the hatch of the first nestling, the incubation time increased to a peak (Fig. 2). Incubation rate was positively correlated with incubation time and egg turning frequency (frequency vs time:  $r=0.664$ ,  $P=0.007$ ; frequency vs turning:  $r=0.606$ ,  $P=0.017$ , Spearman's rank correlation coefficient). The incubation time per hour of a day from 6:00 to 19:00 was relatively longer in the morning compared to afternoon, but increased on the last



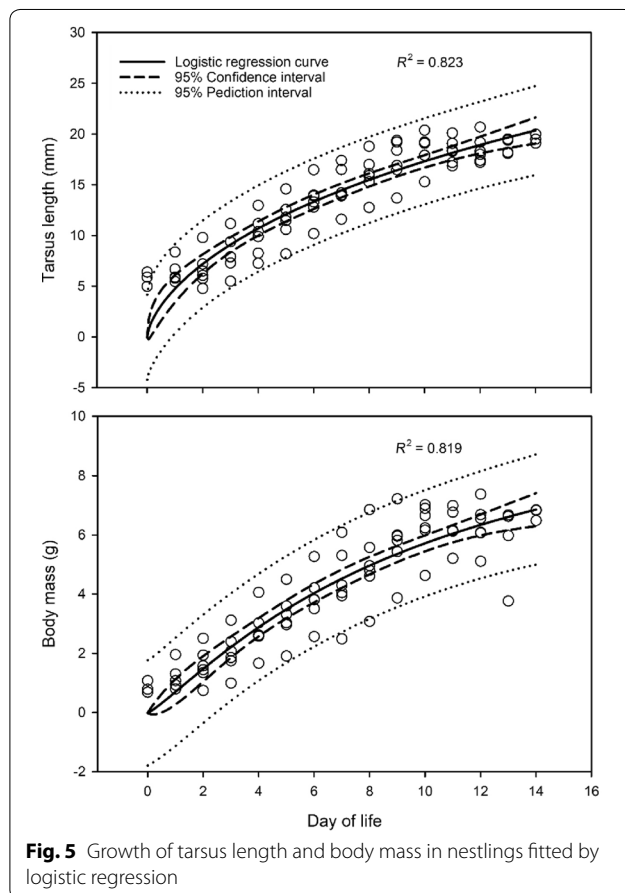
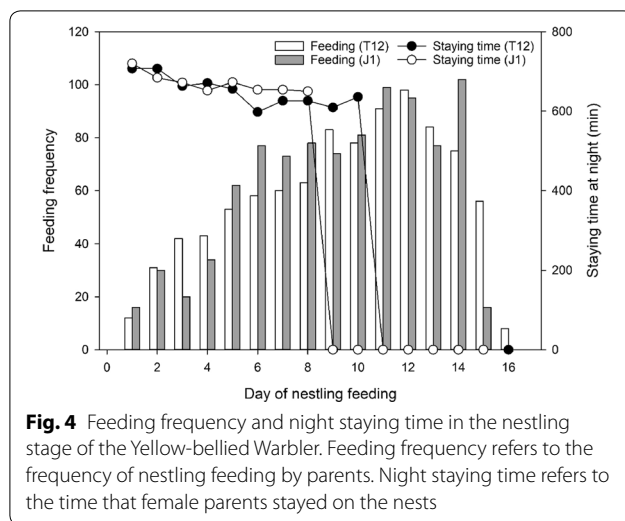
**Fig. 2** Breeding behaviors of Yellow-bellied Warbler (T12 nest) in egg and nestling stages. Incubation/brooding frequency refers to the frequency of egg incubation/nestling brooding (keeping eggs and nestlings warm) by the female parent; egg turning frequency refers to the frequency of turning eggs during incubation by female parent

hour (18:00–19:00) (Fig. 3). Compared with incubation time, incubation rate was more variable during the incubation period (Fig. 3). The egg incubation stage lasted  $13 \pm 1.7$  days (range: 12–15,  $n=3$ ), and females remained in the nest boxes at night during the entire incubation stage ( $701.5 \pm 26.3$  min/night,  $n=12$ ).

The hatching time of two nestlings in nest T12 was 6:55 and 6:26 on the mornings of two successive days. For nest J1, the hatching time of two nestlings was 11:35 and 12:55 on the same day. Eggshells were ejected by females after nestlings hatched. Females sat on the nest after nestlings hatched to keep the nestling warm (i.e., nestling brooding). The brooding time lasted 11 days, which accounted for 68.75% of nestling stage. It was high on the first 3 days, but decreased rapidly by the 6th day and was absent on the last 5 days (Fig. 2). The female parent remained in the nest box at night ( $649.9 \pm 37.8$  min/night,  $n=10$ ) until the end of nestling brooding (Fig. 4). Both males and females participated in nestling feeding. The feeding frequencies of T12 and J1 were similar. They increased gradually with nestling growth but decreased on the last 2 days



**Fig. 3** Incubation and feeding behaviors of Yellow-bellied Warbler on daytime (6:00–19:00). Data are presented as mean  $\pm$  SE. Incubation and feeding refer to the behaviors of egg incubation and nestling feeding by parents



(Fig. 4). The feeding frequency per hour of a day from 6:00 to 19:00 had minor fluctuations (Fig. 3).

The growth curves of tarsus length and body mass in nestlings were fitted by logistic regression (Fig. 5).

Hatchlings on 0 d were naked with some fluffy down on the head. Their skin was a reddish color on 0 d but was yellowish from 1 d forward (Fig. 6). Feather buds appeared on the forelegs and the center of the back at 4 d and began to grow within capsules. From 13 d the wing feathers had emerged from the capsules and at the time of fledging the nestling was similar in color to that of adult bird with a white brow and yellow belly (Fig. 6). The nestling stage lasted  $13.7 \pm 1.5$  days and ranged from 12 to 15 days ( $n=3$ ).

In the 10 nest box nests, the hatching and fledging rates of *A. superciliaris* were 25.58% (11 out of 43) and 54.55% (6 out of 11), respectively. Occupation by White-rumped Shama (*Kittacincla malabarica*), predation, and desertion led to nest failure. The nesting success was 40%, with an average fledging success of 1.1 fledglings per nest. All nests from bamboo holes successfully fledged, with a nesting success of 100%, but other information including eggs and nestlings were not studied.

The incubation time of *A. superciliaris* gradually decreased during the latter part of the egg stage, but significantly increased on the day before the first nestling hatched (Fig. 2). Female parents spent much more time in the nest immediately before the egg hatch. The parent could perceive that the eggs were near hatch. Egg embryos are sensitive to ambient temperature but tolerance to temperature can vary during different development stages (Webb 1987). The parent may modify its incubating behavior according to the development of the egg embryo. Several studies have documented parent-embryo communication in birds (Colombelli-Négrel et al. 2012; Mariette and Buhanan 2016; Katsis et al. 2018; Mariette et al. 2018). It is possible that *A. superciliaris* parents can either perceive the progress of embryo development or communicate with the embryo to achieve synchronism. Further studies are needed to test these hypotheses.

According to the allocation of incubation time per hour during the day, females invested more time in the morning than in the afternoon (Fig. 3). This suggests that parental foraging time mainly occurred in the afternoon. Birds balance their own survival and reproduction during breeding season (Dammhahn et al. 2018); therefore, such pattern of time allocation may be the result of trade-off between parent survival and embryo development. Allocating more time for foraging in the afternoon is reasonable because the temperature may be warmer for egg embryos than in the morning. Although the incubation time was similar between some time intervals, the incubation rate was not necessarily consistent. For example, the incubation time between 6:00–7:00 and 18:00–19:00 was similar, but the incubation rate of the former was lower than the latter (Fig. 3). This suggests that the parent





**Fig. 6** Nestlings during growth and adult Yellow-bellied Warblers

can maintain the incubation time by modifying the incubation rate. The parent may allocate more time per incubation during 6:00–7:00 than during 18:00–19:00, but maintain a similar total incubation time. This is

reasonable because during the last hour before nightfall, parents may come out more frequently to search for food.

This study provides information on the breeding ecology of *A. superciliosus*. The breeding ecology of the other two species in *Abroscopus* is poorly known. According

to the phylogeny of old-world warblers, the most closely related warbler clades are *Cettia*, *Tesia*, and *Urosphena* (Alström et al. 2011; Jetz et al. 2012). However, the breeding ecology of only two *Cettia* warblers (*C. diphone* and *C. cetti*) is known (Xiao et al. 2017). Unlike *A. supercilialis*, these warblers generally built nests in shrubby vegetation rather than in cavities (del Hoyo et al. 2013). For *Cettia* warblers, egg incubation and nestling feeding are solely performed by females (Kenzo and Takeshi 1970; Bibby 1982; Tasinazzo 1993; del Hoyo et al. 2013). In *A. supercilialis* males did not incubate eggs but they did participate in nestling feeding. Further studies on the breeding ecology of the other two *Abroscopus* species might help us to understand their evolution in relation to *A. supercilialis*.

#### Acknowledgements

We thank anonymous reviewers for their helpful comments on an earlier version of this manuscript. We thank Accdon for linguistic assistance during manuscript preparation.

#### Authors' contributions

CY conceived and designed the study. JB and YJ conducted the experiments in the field. JB and CY performed the data analyses and wrote the manuscript. All authors read and approved the final manuscript.

#### Funding

This work was supported by the National Natural Science Foundation of China (Nos. 31672303 to CY).

#### Ethics approval and consent to participate

This article does not contain any studies with human participants performed by any of the authors. The experiments comply with the current laws of China.

#### Consent for publication

Not applicable.

#### Competing interests

The authors declare that they have no competing interests.

Received: 1 July 2020 Accepted: 20 October 2020

Published online: 25 October 2020

#### References

Alström P, Höhna S, Gelang M, Ericson PGP, Olsson U. Non-monophyly and intricate morphological evolution within the avian family Cettiidae

- revealed by multilocus analysis of a taxonomically densely sampled dataset. *BMC Evol Biol*. 2011;11:352.
- Bibby CJ. Polygyny and breeding ecology of the Cetti's warbler *Cettia Cetti*. *Ibis*. 1982;124:288–301.
- Colombelli-Négrel D, Hauber ME, Robertson J, Sulloway FJ, Hoi H, Griggio M, et al. Embryonic learning of vocal passwords in superb fairy-wrens reveals intruder cuckoo nestlings. *Curr Biol*. 2012;22:2155–60.
- Dammhahn M, Dingemanse NJ, Niemelä PT, Réale D. Pace-of-life syndromes: a framework for the adaptive integration of behaviour, physiology and life history. *Behav Ecol Sociobiol*. 2018;72:62.
- del Hoyo J, Elliott A, Sargatal J. *Handbook of the birds of the world*, Vol 1–17. Spain: Lynx Edicions; 2013.
- Feng CZ, Yang CC, Liang W. Nest sanitation facilitates egg recognition in the common tailorbird, a plaintive cuckoo host. *Zool Res*. 2019;40:466–70.
- Jetz W, Thomas GH, Joy JB, Hartmann K, Moores AO. The global diversity of birds in space and time. *Nature*. 2012;491:444–8.
- Katsis AC, Davies MH, Buchanan KL, Kleindorfer S, Hauber ME, Mariette MM. Prenatal exposure to incubation calls affects song learning in the zebra finch. *Sci Rep*. 2018;8:15232.
- Kenzo H, Takeshi O. The life history of *Cettia diphone*: 1. Breeding ecology. *J Yamashina Inst Ornithol*. 1970;6:131–40.
- Kricher J. Behavioral ecology of tropical birds. *Wilson Bull*. 2001;113:357–8.
- Levy C. History of ornithology in the Caribbean. *Ornitol Neotrop*. 2008;19:415–26.
- Mariette MM, Buchanan KL. Prenatal acoustic communication programs offspring for high posthatching temperatures in a songbird. *Science*. 2016;353:812–4.
- Mariette MM, Pessato A, Buttemer WA, McKechnie AE, Udino E, Collins RN, et al. Parent-embryo acoustic communication: a specialised heat vocalisation allowing embryonic eavesdropping. *Sci Rep*. 2018;8:17721.
- Pienaar J, Ilany A, Geffen E, Yom-Tov Y. Macroevolution of life-history traits in passerine birds: adaptation and phylogenetic inertia. *Ecol Lett*. 2013;16:571–6.
- Saether B-E, Bakke Ø. Avian life history variation and contribution of demographic traits to the population growth rate. *Evolution*. 2000;54:642–53.
- Sibley CG, Ahlquist JE, Houde P. Phylogeny and classification of birds: a study in molecular evolution. *Q Rev Biol*. 1991;252:1003–5.
- Tasinazzo S. Breeding ecology of Cetti's warbler (*Cettia cetti*, Aves) in northeastern Italy. *Boll Zool*. 1993;60:185–92.
- Webb DR. Thermal tolerance of avian embryos: a review. *Condor*. 1987;89:847–98.
- Xiao H, Hu Y, Lang Z, Fang B, Guo W, Zhang Q, et al. How much do we know about the breeding biology of bird species in the world? *J Avian Biol*. 2017;48:513–8.
- Yang C, Cai Y, Liang W, Antonov A. Breeding biology of the golden parrotbill (*Paradoxornis verreauxi*) (Aves: Timaliidae) in southwestern China. *J Nat Hist*. 2011;45:1817–22.
- Ye P, Yang C, Liang W. Nest site availability and niche differentiation between two cavity-nesting birds in time and space. *Ecol Evol*. 2019;9:11904–10.
- Zheng GM. *Ornithology*. Beijing: Beijing Normal University Press; 2012.

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