

Flexible breeding performance under unstable climatic conditions in a tropical passerine in Southwest China

DEAR EDITOR,

Parents may adjust their breeding time to optimize reproductive output and reduce reproductive costs associated with unpredictable climatic conditions, especially in the context of global warming. The breeding performance of tropical bird species in response to local climate change is relatively understudied compared with that of temperate bird species. Here, based on data from 361 white-rumped munia (*Lonchura striata*) nests, we determined that breeding season onset, which varied from 15 February to 22 June, was delayed by drought and high temperatures. Clutch size (4.52 ± 0.75) and daily survival rate but not egg mass (0.95 ± 0.10 g) were negatively affected by frequent rainfall. Daily nest survival during the rainy breeding season in 2018 (0.95 ± 0.04) was lower than that in 2017 (0.98 ± 0.01) and 2019 (0.97 ± 0.00). The overall nesting cycle was 40.37 ± 2.69 days, including an incubation period of 13.10 ± 1.18 days and nestling period of 23.22 ± 2.40 days. The nestling period in 2018 (25.11 ± 1.97 days) was longer than that in 2017 (22.90 ± 2.22 days) and 2019 (22.00 ± 2.48 days), possibly due to the cooler temperatures. Climate also affected the total number of successful fledglings, which was highest under moderate rainfall in 2017 (115 fledglings) and lowest during prolonged drought in 2019 (51 fledglings). Together, our results suggest that drought and frequent rainfall during the breeding season can decrease reproductive success. Thus, this study provides important insights into bird ecology and conservation in the context of global climate change.

Understanding breeding phenology is crucial for predicting how climate change may affect bird populations worldwide. Research on the breeding phenology of tropical birds, which live in relatively stable environments and generally display a long breeding season (Martin, 2004; Wiersma et al., 2007), remains limited compared to that on temperate species. Extreme events such as floods, droughts, and storms caused

by climate change are expected to occur more frequently (Beniston & Stephenson, 2004; Coumou & Rahmstorf, 2012). Furthermore, climate change has increased total annual precipitation in the mid- and high latitudes but has decreased precipitation in tropical and subtropical areas (Clark & Jäger, 1997). Thus, in a warming world, the flexibility of avian parents in response to unstable climatic conditions will influence reproductive success and population stability (Coumou & Rahmstorf, 2012; Gładalski et al., 2014).

Spring-time temperature and rainfall are thought to be the main climatic factors affecting the onset of breeding and reproductive performance in birds (Hidalgo Aranzamendi et al., 2019). Increasing atmospheric temperatures can alter resource availability peaks and breeding phenology of bird species in temperate regions (Both & Te Marvelde, 2007; Crick & Sparks, 1999; Stenseth et al., 2002). Bird species incapable of flexibility in response to climate change are likely to experience sharp declines in population size as atmospheric temperatures increase (Donnelly et al., 2015). For example, pied flycatcher (*Ficedula hypoleuca*) populations have declined by 90% over the past 20 years in areas where the timing of breeding has not coincided with resource peaks (Both et al., 2006). In contrast, the great reed warbler (*Acrocephalus arundinaceus*) has shown the ability to adapt to changes in climate by increasing its total breeding season, with expansions in both the earliest and median first egg-laying dates (Dyrce & Halupka, 2009). Drought can also affect avian community structure, population size, adult mortality, and reproductive success (Albright et al., 2010; Bourne et al., 2020b; Cruz-McDonnell & Wolf, 2016; Guindre-Parker & Rubenstein, 2020). In tropical areas with monsoon climates, most bird species breed seasonally, and reproductive performance often varies within and between breeding seasons (Delhey et al., 2010; Marques-Santos et al., 2015).

Received: 04 December 2020; Accepted: 23 February 2021; Online: 24 February 2021

Foundation items: The study was supported by the Lancang-Mekong Cooperation Special Fund (Biodiversity Monitoring and Network Construction along Lancang-Mekong River Basin project), Biodiversity Investigation, Observation, and Assessment Program (2019-2023) of the Ministry of Ecology and Environment of China, and CAS 135 (2017 XTBG-F03)

DOI: 10.24272/j.issn.2095-8137.2020.288

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Thus, extreme climatic events may pose greater challenges for tropical species, as populations in stable environments are often less able to adapt to sudden changes in conditions (Cavieres & Sabat, 2008).

In this study, we analyzed the effects of rainfall and temperature on variation in breeding season onset, clutch size, egg mass, egg size, hatching span, nestling growth, nest cycle, and nest success of the white-rumped munia in Xishuangbanna, Yunnan, Southwest China. We predicted that: (1) parents would delay breeding season onset under decreasing dry season rainfall; (2) frequent rainfall during the nestling period would prolong its length; and (3) breeding success would decrease with increasing rainfall in the breeding season.

Our results showed that the onset of the breeding season varied greatly among years, i.e., 18 April, 15 February, 22 June, and 19 May for 2017, 2018, 2019, and 2020,

respectively. Mean laying date was 41.84 and 56.88 days later in 2019 than in 2017 and 2018, respectively ($t=3.80$, $P<0.001$ and $t=5.36$, $P<0.001$, respectively). Egg-laying within the breeding season also varied significantly by year ($F_{2,187}=14.50$, $P<0.001$), peaking in May and June in 2017 ($t=5.18$, $P<0.001$) but in July and August in 2019 ($t=2.94$, $P=0.004$), with relatively even distribution in 2018 ($t=0.80$, $P=0.42$) (Supplementary Figure S3). Increasing mean temperature in the 87 to 0 day window ($t=74.41$, $P<0.001$) and decreasing mean rainfall in the 134 to 104 day window ($t=-18.37$, $P<0.001$) before the first egg-laying date in each nest strongly delayed the onset of the breeding season (Figure 1A, C). Temperature and rainfall only showed a between-year effect on the onset of the breeding season ($P<0.001$ and $P=0.03$, respectively).

Eggs were laid on consecutive days ($n=292$ nests found in egg-laying period). Mean clutch size was 4.52 ± 0.75 (range:

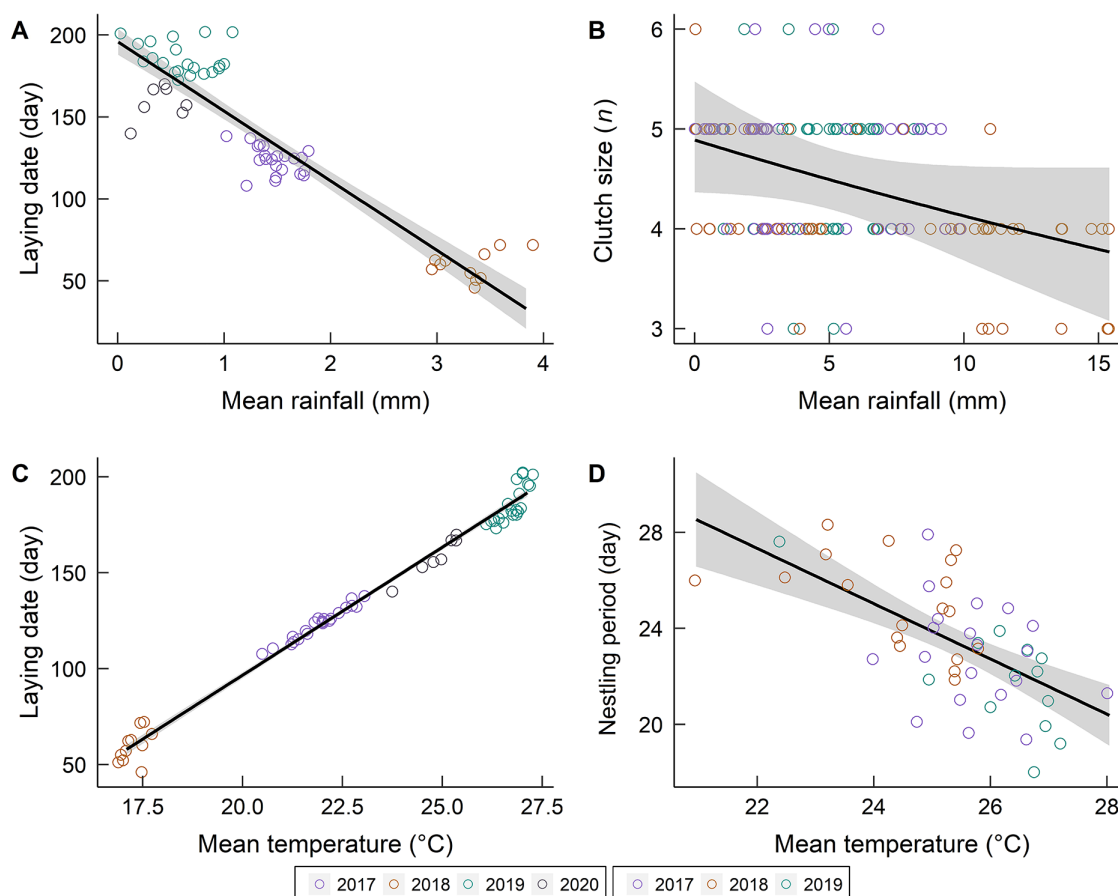


Figure 1 Laying date and breeding performance are affected by climatic variations

A: Increasing mean rainfall in climatic windows (134 to 104 days before egg-laying date) significantly advanced laying date (day 1=January 1) from 2017 to 2020. B: Clutch size decreased significantly with increasing mean rainfall in climatic windows (37 to 24 days before date of last egg laid in each nest) during 2017 and 2019. C, D: Increasing mean temperature in climatic windows (87 to 0 days before egg-laying, 14 and 11 days before fledging date) had a significant positive effect on laying date (C) and a negative effect on nestling period (D). Colored dots in (A) and (C) represent each laying day; in (B) represent clutch size of each nest; in (D) represent nestling period of each individual. Black lines and gray bands represent fitted lines of *lm*.

three to eight, $n=320$ nests), and was significantly smaller in 2018 (4.27 ± 0.63 , $n=104$ nests) than in 2017 (4.66 ± 0.67 , $n=86$ nests; $z=-4.27$, $P<0.001$) and 2019 (4.59 ± 0.70 , $n=56$ nests; $z=4.31$, $P<0.001$). Clutch size decreased as the breeding season progressed in 2018 (estimate $=-0.01$, $t=-6.12$, $P<0.001$), but showed no difference in 2017 (estimate $=-0.00$, $t=-1.08$, $P=0.28$) or 2019 (estimate $=0.01$, $t=1.62$, $P=0.11$). Average rainfall, which ranged from 37 to 24 days before the last egg-laying date in each nest, had a strong negative effect on clutch size (estimate $=-0.07$, $z=-6.25$, $P<0.001$, Figure 1B).

Mean egg mass was 0.95 ± 0.10 g ($n=904$ eggs), and mean egg size was $15.11 \text{ mm} \pm 0.87 \times 10.76 \text{ mm} \pm 0.58$ ($n=225$ eggs). Egg mass increased with the laying sequence ($\chi^2=58.76$, $P<0.001$), where later-laid eggs (eggs laid fourth to sixth) were heavier than early-laid ones (eggs laid first to third, Supplementary Table S2). We found no difference in egg mass with year ($F_{2,132}=0.26$, $P=0.77$), and no effect of proximate weather on variation in egg mass (temperature: $P=0.95$, rainfall: $P=0.93$).

Around 92% of broods hatched asynchronously ($n=180$). Hatching span varied from one to six days, and ~85% ($n=180$) of broods hatched within two or three days. Hatching span was positively related to clutch size but did not vary with egg-laying date or among years ($F_{2,132}=0.26$, $P=0.77$). However, the within-brood hatching span was longer later in the breeding season in 2019 ($F_{1,34}=16.45$, $P<0.001$). Proximate weather had no significant effect on variation in hatching span ($P=0.83$, $P=0.91$).

The mean nesting cycle was 40.37 ± 2.69 days ($n=51$), with a mean egg-laying period of 4.52 ± 0.75 days ($n=104$), mean incubation period of 13.10 ± 1.18 days ($n=122$), and mean nestling period of 23.22 ± 2.40 days ($n=67$). Incubation length showed no differences among years ($F_{2,95}=0.86$, $P=0.43$), but decreased with egg-laying date ($F_{1,95}=7.85$, $P=0.006$) and was negatively correlated with clutch size ($F_{1,95}=10.26$, $P=0.002$). Neither rain nor temperature in any climatic window had a significant effect on incubation length ($P=0.64$ and $P=0.95$ for rainfall and temperature, respectively). The nestling period was longer in 2018 (25.11 ± 1.97 , $n=18$) than in 2017 (22.90 ± 2.22 , $n=20$; $t=3.03$, $P=0.01$) and 2019 (22.00 ± 2.48 , $n=13$; $t=-3.87$, $P<0.01$). Number of hatchlings and egg-laying date did not affect nestling period length ($F_{1,46}=1.31$, $P=0.26$; $F_{1,46}=1.90$, $P=0.18$, respectively). Fledging occurred earlier when the temperatures from 14 to 11 days before the fledging date were higher ($t=-5.46$, $P<0.01$).

Nestling mass exhibited a traditional S-shaped curve, which well fitted the logistic growth equation (Supplementary Figure S4). The growth rate constant (k) and asymptote (A) were 0.30 and 9.37 g in 2017, 0.27 and 8.83 g in 2018, and 0.29 and 9.73 g in 2019, respectively.

Overall nest success was 31.76% ($n=340$), while the mean hatching rate was 0.52 ($n=315$) and average fledging rate was 0.45 ($n=186$). The mean fledging number was 1.78 ($n=186$). The hatching rates were 0.54, 0.53, and 0.51 in 2017, 2018, and 2019 respectively, with no significant differences found among years ($F_{2,247}=0.10$, $P=0.91$). The fledging rates were

0.54, 0.40, and 0.40 for 2017, 2018, and 2019, respectively, which were not significantly different ($F_{2,150}=0.73$, $P=0.18$). Total number of fledglings was 115 in 2017 ($n=89$), 97 in 2018 ($n=118$), and 51 in 2019 ($n=56$). Compared to that found in 2017 and 2018, partial loss occurred significantly more frequently in 2019 ($z=2.47$, $P=0.04$ and $z=2.45$, $P=0.04$, respectively). Among nest failures, 63.19% were caused by predation (2017: 75%, 2018: 52.22%, 2019: 66.67%), 15.93% were caused by parasites (2017: 8.93%, 2018: 21%, 2019: 10.26%), and 14.84% were caused by nest desertion ($n=182$).

The daily survival rate (DSR) (0.97 ± 0.00) increased with nest age ($t=107.40$, $P<0.001$). The survival rate over the total nest cycle was 0.30, whereas the survival rates during the egg-laying, incubation, and nestling periods were 0.86, 0.64, and 0.52, respectively. Variation in DSR within each breeding season showed different patterns among the three sample years (Supplementary Figure S5).

Rainfall and temperature played an important role in breeding phenology and reproductive performance in the white-rumped munia. Drought and high temperature in the dry season significantly delayed the onset of breeding season. Frequent rainfall decreased the clutch size and prolonged the nestling period, suggesting that proximate rainfall could directly influence breeding performance. Total number of fledglings decreased sharply in 2019, which was mainly associated with the drought and shortened duration of the breeding season. Our results showed that rainfall, specifically drought, represents a major potential constraint on reproductive performance in white-rumped munia.

Selecting an optimal breeding period and season is critical for maximizing reproductive output (Sydeman et al., 1991). Certain species exhibit remarkable flexibility in their timing of breeding, allowing them to closely track changes in the climate (Lv et al., 2020; Senapathi et al., 2011). In our study, however, high temperatures and decreased rainfall in the dry season delayed the onset of the breeding season. Rain is known to affect resource abundance as well as seasonal breeding in tropical species (Hau et al., 2008; Hidalgo Aranzamendi et al., 2019). In the current study, early rainfall in the dry season advanced the onset of the breeding season in 2018, whereas drought delayed breeding by more than four months in 2019 (Supplementary Figures S1, S2). Drought can affect avian community structure, population size, adult mortality, and reproductive success (Albright et al., 2010; Cruz-McDonnell & Wolf, 2016; Saracco et al., 2018). Breeding season duration can affect the stability of populations (Tarwater & Arcese, 2018). Our study showed that white-rumped munia responded flexibly to climate variation, which should aid their ability to match the timing of their most resource-demanding activity (breeding) with the period when resources are most abundant; however, the length of the breeding season in 2019 was substantially shortened, which led to a sharp decline in the total number of fledglings. Thus, an increasing number of extreme climatic events caused by climate change, e.g., hot droughts (Bourne et al., 2020a, 2020b), may threaten the

stability of white-rumped munia populations.

The breeding performance of white-rumped munia varied significantly among years. The average clutch size was larger in 2017 when rainfall and temperature were moderate. In normal years, higher rainfall could increase female body condition because of higher food availability, which could, in turn, increase clutch size and fecundity (Boulton et al., 2011; Hidalgo Aranzamendi et al., 2019; Oppel et al., 2013). However, we found that clutch sizes in 2019 under drought conditions were even larger than those in 2018 with earlier and more frequent rainfall (Supplementary Figure S1), which may be a compensatory mechanism in response to the shorter breeding season (Bourne et al., 2020a). Clutch size decreased with rainfall in 2018, which may be associated with higher predation pressure under wetter conditions. In environments with high predation risk, small clutch size could lower feeding visits as well as the exposure of nests to predators (Ghalambor et al., 2013). The main predators at our study site were snakes, which generally show increased activity with rain events (Li et al., 2019). Clutch size decreased as the season progressed in 2018, as reported in most temperate species and some tropical species (Delhey et al., 2010; Both et al., 2006; Shave et al., 2019). The seasonal decline in clutch size may be related to a scarcity of resources in the late breeding season or declining female quality (Christians et al., 2001).

Egg mass of later-laid eggs was significantly greater than that of early-laid eggs. In addition, asynchronous hatching was the main hatching pattern observed in this study. Parents may invest more energy in eggs laid later to improve their growth and competitive ability after hatching in asynchronously hatching species (Jeon, 2008; Muriel et al., 2019). Hatching asynchrony is a strategy for coping with unpredictable resources, and hatching span often increases in years with poor conditions and low resource abundances (Barrientos et al., 2016). In our study, however, hatching span did not vary among the three sample years.

The growth rate of the white-rumped munia nestlings was significantly lower in 2018 than in 2017 and 2019, which may be associated with the wetter and colder conditions observed in 2018 (Supplementary Figures S1, S2) (de Zwaan et al., 2019). Increasing rainfall during the nestling period is related to declines in nestling body mass (Cox et al., 2019). Furthermore, cold weather increases the energy costs of thermoregulation for nestlings and can constrain their growth (Abdullahi, 1990). Indeed, nestlings in experimentally heated nests grow faster than nestlings in control nests (Dawson et al., 2005). We also found that low temperatures prolonged the nestling period, which may be caused by slower nestling growth under cooler conditions.

The DSR of the white-rumped munia varied significantly with nest age and laying date (Supplementary Figure S5). Rainfall generally has a negative effect on nest survival (Boulton et al., 2011; Mwangi et al., 2018). Here, parasites caused ~21% of nest failures in 2018, significantly higher than the parasite infestation rates in 2017 and 2019. High parasite infestations may be related to the high humidity caused by

frequent rainfall (Cantarero et al., 2013; Heeb et al., 2000).

Our results highlight the potential effects of proximate rainfall and temperature on the timing of breeding and reproductive performance in a tropical bird species. This highly plastic reproductive performance contributed to the ability of white-rumped munia to persist in the face of climate variability. Furthermore, we also found that drought, which is predicted to increase in severity and frequency as climate change advances (Dai, 2011; Trenberth et al., 2003, 2014), was associated with a shorter breeding season and the production of fewer surviving offspring. These findings are similar to recent reports on arid-zone birds (Bourne et al., 2020a; Iknayan & Beissinger, 2018; Sharpe et al., 2019; van de Ven et al., 2020). Our findings suggest that increasing drought events under future climate change will have serious implications for population replacement and persistence in tropical birds.

SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

Permission for field surveys in Xishuangbanna Tropical Botanical Garden was provided by the Administrative Panel on the Ethics of Animal Experiments of Xishuangbanna Tropical Botanical Garden (2016-003).

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

R.C.Q. conceived and designed the study and experiments, and substantially edited the paper; C.Y.L. collected data and wrote the paper; U.G. conceived the study and developed the methods; R.C.H. analyzed the data; H.L. collected the data and edited the paper. All authors read and approved the final version of the manuscript.

ACKNOWLEDGMENTS

We thank our field assistant Meng Li for help searching for nests during the breeding seasons over the past nine years. We thank Lei Lv for providing useful comments on this study. We also thank the National Field Scientific Observation and Research Station of Forest Ecosystem, Xishuangbanna, for sharing climate data.

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