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Breeding biology of the Mountain Wren-Babbler (*Gypsophila crassus*)

Morgan C. Slevin,[1]* Enroe E. Bin Soudi,[2] and Thomas E. Martin[3]

ABSTRACT—Life history theory in ornithology has been mostly based on temperate birds in part because a relative paucity of biological data has been described for tropical species. Expanding our knowledge about life histories of tropical birds can help us to better understand global trends in life history strategies. To aid in this endeavor, we studied Mountain Wren-Babblers (*Gypsophila crassus*) breeding in Malaysian Borneo from 2009 to 2017. Relatively small (mean = 28.8 g), dark brown birds, they were cooperative breeders and foraged and cared for the nest in groups of typically 4 or 5 birds. We located 145 nests, which were globular and partially domed (91.8 mm mean opening height accounted for half of 180.7 mm total mean nest height), constructed from fern fronds on the outside and dead leaves on the inside, and most often placed on banks. Brooding attentiveness decreased with nestling age and was rare after day 7 once they began growing their primary feathers. Provisioning rate slightly increased with nestling age. Nestling growth rate constants were typical of many tropical birds, asymptoting a few days prior to fledging. Predation accounted for nearly all nest failures (87 of 88), with a daily nest predation rate for the total nesting period of 0.056 and nest success decreasing with elevation. Daily predation rate was highest during lay (0.117) and lowest during incubation (0.046). We compared these results with related species to identify potential explanations for the trends we described. The most notable result from these comparisons was that Mountain Wren-Babblers have a long incubation period (23.5 d) and adults only incubate for a small part of the day. This anomalous behavior emphasizes the importance of understanding the great variation in tropical life history strategies to ultimately improve life history theory. *Received 11 March 2019. Accepted 11 March 2020.*

Key words: Borneo, life history, nestling growth rate, nest survival, parental effort

Biología reproductiva de la ratina *Gypsophila crassus*

RESUMEN (Spanish)—La teoría de historias de vida en ornitología se basa principalmente en aves de la zona templada, en parte por la carencia de datos biológicos que se han descrito para especies tropicales. El incremento de nuestro conocimiento de historias de vida de aves tropicales puede ayudarnos a entender tendencias globales en dichas estrategias. Para contribuir en este propósito, estudiamos ratinas *Gypsophila crassus* que anidan en la parte malaya de Borneo de 2009 a 2017. Estas aves relativamente pequeñas (media = 28.8 g) de color café, anidan de manera cooperativa, forrajean y cuidan sus nidos en grupos típicamente de 4 o 5 individuos. Encontramos 145 nidos, que fueron globulares con domos parciales (la altura media de apertura de 91.8 mm es la mitad de la altura media del nido de 180.7 mm), construida de frondas de helechos en el exterior y hojas muertas en el interior, frecuentemente ubicados en laderas. La atención a la nidada declinó con la edad de los polluelos y fue rara después del día 7, una vez que comenzaron a emerger las plumas primarias. La tasa de aprovisionamiento se incremento ligeramente con la edad de los polluelos. La tasa de crecimiento tiene una constante típica de muchas aves tropicales que llega a una asíntota algunos días antes de la emancipación. La depredación fue responsable de casi todos los nidos fallidos (87 de 88), con una tasa diaria de depredación de nidos de 0.056 y el éxito del nido declina con la elevación. La tasa diaria de depredación fue más alta durante la puesta (0.117) y más baja durante la incubación (0.046). Comparamos esos resultados con aquellos de especies relacionadas para identificar potenciales explicaciones para las tendencias que describimos. El resultado más notable de estas comparaciones es que esta especie de ratina tiene un periodo de incubación alto (23.4 d) y los adultos solo incuban en una pequeña parte del día. Este comportamiento anómalo enfatiza la importancia de entender la gran variación de estrategias de historias de vida tropicales y finalmente mejorar la teoría la teoría de historias de vida.

Palabras clave: Borneo, esfuerzo parental, historias de vida, sobrevivencia de nidos tasa de crecimiento de los polluelos

Avian life history theory has been largely based on north-temperate birds (Martin 1996, 2004; Stutchbury and Morton 2008). However, most of the world's species of birds are found in tropical and south-temperate regions (Fisher 1960, Martin 2004, Stutchbury and Morton 2008). Furthermore, life history traits often strongly differ between north-temperate vs. tropical and south-temperate species (Lack 1948, Martin et al. 2000, 2011). Yet, reproductive biology of most tropical birds is still poorly described compared to north-temperate birds because of a paucity of tropical breeding biology studies, and because tropical birds can be secretive and difficult to monitor (Martin 1996, Jiang et al. 2017b, McCullough and Londoño 2017). Studying the life history of multiple species and in different regions of the world can help us understand geographic variation in life history (Martin 1996, Ricklefs and Wikelski 2002). Furthermore, life history theory in birds has often focused on clutch size and food limitation (Skutch 1985, Martin 2004). Many other life history traits, such as egg mass, developmental rate, parental

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[1] Department of Biological Sciences, Florida Atlantic University, Davie, FL, USA

[2] Forever Sabah, Kota Kinabalu, Sabah, Malaysia

[3] U.S. Geological Survey, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT, USA

* Corresponding author: mslevin2018@fau.edu

care behavior, adult survival, and nesting phenology, also vary geographically among similar species and can provide important insight into causes of variation among species (Martin 2002, 2008; Martin et al. 2017b).

Here we describe a broad array of life history traits for the Mountain Wren-Babbler (*Gypsophila crassus*; Fig. 1A), including nest site construction, demographic parameters, phenology, and nest survival, as well as general information such as appearance and behavior that improve our understanding of the species. This species is a member of Pellorneidae, a large family of old world babblers (Cai et al. 2019). The Mountain Wren-Babbler is endemic to the Borneo mountains from 900 to 2,900 m above sea level (m.a.s.l.; Sheldon et al. 2001). This species' range is restricted to montane regions and its status is evaluated as Least Concern despite an unknown population estimate (BirdLife International 2016). A literature search revealed that detailed information on the breeding biology of the Mountain Wren-Babbler, as well as most birds in the Southeast Asian region, is still lacking. Thus, this paper aims to provide detailed information on the breeding biology of the Mountain Wren-Babbler, and compare this information with what is known for other species in the family Pellorneidae.

Methods

Study site

The study was conducted during 9 consecutive breeding seasons, from early February to early June in 2009–2017 near Kinabalu Park headquarters on Mount Kinabalu on the Malaysia part of the island of Borneo (6°5′N, 116°33′E). Annual rainfall at the park headquarters (1,560 m.a.s.l.) ranges from 1,800 to 3,300 mm (Kitayama and Aiba 2002). The study plots were located in rainforest from 1,450 to 1,950 m.a.s.l.

Figure 1. Mountain Wren-Babbler nests and eggs. (A) An adult Mountain Wren-Babbler (sex unknown) sitting on the rim of its nest built in a mossy bank in Kinabalu Park, Malaysia. (B) A Mountain Wren-Babbler nest in Kinabalu Park, Malaysia, built by the female, is a globular partial dome composed of fresh and dry fern fronds, dry leaves, moss, and dry plant fibers and then lined with dry leaf skeletons. The example shown here was placed in a mossy bank.

Field methods

We located Mountain Wren-Babbler nests by systematically searching preferred nesting substrates (moss-covered stone banks; see Results) or observing parental behavior (Martin and Geupel 1993), with equal search effort across elevation and study year. For each nest, we recorded elevation via GPS (Garmin, Olathe, Kansas, USA), the substrate on which the nest was built (e.g., bank, tree), substrate height, nest's height above ground, and nest opening orientation (nests are partially domed and globular with a small opening facing a horizontal direction; see Results). If nests were found before hatch, we measured the nest's inner diameter, inner height, outer diameter, outer height, and total height using a ruler with an accuracy of 0.1 cm. Nests were checked every other day, except during critical stages (such as hatch or fledge) when nests were checked once or twice a day.

Clutch size was measured only for nests found during building or egg-laying to ensure no partial egg-removal had occurred. Once eggs hatched, or upon finding a nest with nestlings, we used nontoxic permanent marker on the nestlings' legs to differentiate between nestlings on subsequent days for measurements. Nestlings were measured within 0.5 h of the same time each day. We measured nestlings every day for the first 3 d starting at hatch or, if found after hatch, the day the nest was found and then every second day until fledging. Egg and nestling mass were obtained using a portable electronic scale (ACCULAB, Elk Grove, Illinois, USA) with an accuracy of ±0.001 g. We measured nestling tarsus and wing chord with digital calipers (Mitutoyo, Kingsport, Tennessee, USA) with an accuracy of 0.01 mm.

We quantified parental nest attentiveness during incubation. Nests were not videotaped during incubation because this species only incubates for a short time late in the day (see Results). Estimates for incubation attentiveness were obtained by either inserting a thermistor into the center of an egg through a small opening in the shell and sealing it with glue (Weathers and Sullivan 1989, Martin et al. 2007) or by inserting a thermistor through the bottom of the nest just underneath the eggs. Fine wires were connected from the thermistor through the nest to a HOBO Stowaway XTI data logger (Onset, Bourne, Massachusetts, USA) that recorded temperature at 12 s intervals for as long as the nest remained active or until the eggs hatched. Sudden changes in temperature were recognized as the time parents arrived at or left the nest. Nest attentiveness was calculated as the percentage of time parents spent on the nest incubating during daytime from 0530 to 1900 h.

We measured parental behaviors (brooding and provisioning) after hatching and opportunistically identified nest predators by videotaping nests during the nestling period for 6–8 h per day starting within 30 min of sunrise (Martin et al. 2015b). A subset of nests was videotaped every other day after hatch. Remaining nests were videotaped during the early nestling stage (2–3 d after hatch day), pin-break (the day when the eighth pin feather broke its sheath), and late stage (2–3 d before fledge day). We calculated brooding attentiveness per day as the percentage of time an adult spent on the nest. Provisioning rate was calculated per nestling age as number of visits to the nest with food divided by total time filmed.

To estimate sex ratio, morphometrically describe the adults, and identify individual effort during parental care, we captured Mountain Wren-Babblers with standard-effort netting throughout the study area and opportunistically by target-netting near nests (Martin et al. 2017b). For standard-effort netting, we opened nets at sunrise, closed them after 6 h, and sampled each location 3 times from February to June. We collected standard morphometrics of captured adults and determined sex, if possible, by presence of brood patch or cloacal protuberance. Sex was also confirmed after banding by observing nest building and incubation, which only females perform. We used a portable electronic scale (ACCULAB) with an accuracy of ±0.001 g for mass, digital calipers (Mitutoyo) with an accuracy of 0.01 mm for bill width, length of tarsus, tail, and exposed culmen, and wing rule accurate to 0.5 mm for wing chord.

Analyses

Incubation period was defined as the difference in days between the last egg laid (day 0) and the last egg hatched (Nice 1954, Briskie and Sealy 1990). Nestling period was defined as the period from the last egg hatched to the last young fledged (Martin et al. 2011). Hatching and fledging was synchronous, making determination of period lengths straightforward. Nests found in incubation and nestling stages were backdated based on known mean incubation and nestling period to estimate initiation date (Auer et al. 2007). Incubation and nestling periods were calculated only from nests in which the exact day the last egg was laid, exact day of hatch, and exact day of fledge were known. Mean egg mass was calculated only for eggs weighed from day 0 to day 2 of incubation (Martin et al. 2006). All means are presented ± one standard error (SE).

Measurements of nestling mass, tarsus length, and wing chord were used to calculate the growth rate of nestlings following Remeš and Martin

(2002) using the equation:

$$W(t) = \frac{A}{1 + e^{-k(t-t_i)}}$$

where $W(t)$ is body mass (or tarsus or wing chord length) at time t, A is the asymptotic body measurement (mass, tarsus, or wing chord), t_i is the inflection point on the time axis for the given body measurement, and k is the growth rate constant. We built various mixed effect models in Program R (R Core Team 2018) to determine the random effect structure with the best model fit following Sofaer et al. (2013). We removed all models that did not converge, that included any 2 random effects that were highly correlated ($r > 0.9$), or when the standard deviation of any random effect was (effectively) 0. After selecting the best model for body mass, tarsus length, and wing chord, respectively, we validated the model by examining the distribution of the residuals and comparing observed with predicted values.

Estimates of total nest survival and during egg-laying, incubation, and nestling periods were calculated by dividing nest failures by exposure days. For each nest stage, we also built logistic exposure models in Program R with nest site covariates potentially related to nest survival: nest initiation date, nest height above ground, substrate on which the nest was built, and elevation. We selected the best model by comparing AIC_c values and model weights and considered 2 models to be statistically equivalent in fit if $\Delta AIC_c < 2$. Finally, for all top models, we assessed the significance and directionality of the relationship between the nest covariate(s) and nest survival by inspecting the covariate effect's P-value and the sign of the covariate effect's slope (β), respectively. We considered the effect of a covariate to be significant if $P \leq 0.05$ and approaching significance if $0.05 < P \leq 0.10$.

Results

Nest sites and construction

We located 145 nests. Nests were found from 1,401 to 1,895 m.a.s.l. (mean = 1,655.34 ± 9.72 m.a.s.l.) with one outlier found at 2,702 m.a.s.l. Nest substrates included banks (nearly vertical walls covered in moss and ferns ranging from 0.5 to 15 m tall), against the base of large trees, rocks, snags, shrubs, stumps, and ground, with banks (39%) and the bases of trees (26%) being used most commonly. Nest height above the ground ranged from 0 to 5 m, with an average of 0.78 ± 0.07 m ($n = 134$). Each nest was partially domed and globular in shape and consisted of fresh and dry fern fronds, dry leaves, and fibers (Fig. 1B). Fresh fern fronds were used to construct the outer part while the inner part was composed of dried leaves and fibers. Occasionally, nests were found with only dry leaves and no fresh plant matter. The floor of the nest interior was lined with leaf skeletons. When building a nest, the breeding pair split off from the group to build, while the rest of the flock could usually be seen nearby making contact calls. Only the female built, occasionally traveling >100 m from the nest to collect material, but the male was almost always present and often seen mate-feeding. Other individuals in the cooperative group were occasionally seen picking up nest material, perhaps to help the female select appropriate material or to practice the behavior for future nesting attempts. However, these individuals did not contribute to actual building of the nest.

Nest orientation followed no discernible pattern. The internal dimensions of the nest averaged 69.9 ± 1.42 mm in diameter and 45.7 ± 1.39 mm in height (vertical distance between lowest point in cup to bottom lip of nest opening). Outer dimensions averaged 115.1 ± 2.99 mm in diameter and 88.9 ± 3.22 mm in height (bottom of nest mass to bottom lip of opening). Mean total height (bottom of nest mass to top of dome) was 180.7 ± 6.72 mm ($n = 38$).

Eggs and nest initiation

The Mountain Wren-Babbler nearly always laid a clutch of 2 ($n = 79$) cream-colored eggs with brown speckles that spanned the egg but were typically more concentrated around the thicker end of the egg. A 3-egg clutch was observed once. Although we only considered clutch size based on nests found during building or laying, no other nest found at later stages had more than 2 eggs or young. Eggs were laid early in the morning on consecutive days. The earliest nest initiation was 8 January (backwards-estimated) and the latest was 11 June, with the highest nesting activity in March and April (mean initiation date = 31 March ± 3.89 d; Fig. 2).

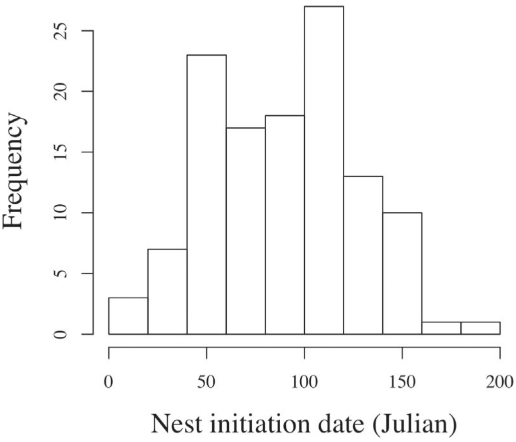

Figure 2. Timing of nest initiation from 2009 to 2017 for Mountain Wren-Babblers at Kinabalu Park, Malaysia. The earliest initiation was 8 January, the latest 11 June.

Fresh egg mass varied between 2.60 g and 4.76 g, with a mean of 3.91 ± 0.03 g (*n* = 138), which represented 14% of mean adult body mass (Table 1).

Incubation

Incubation started after the last egg was laid and only the female was observed incubating. The eggs hatched synchronously after 23–25 d of incubation, mean = 23.5 ± 0.4 d (*n* = 18 nests with precise incubation periods). The incubating female typically left the nest near dawn and was absent throughout the morning and into the afternoon, or about 8 h in the early incubation period, allowing eggs to cool to ambient temperatures of 16–18 °C for many hours (Fig. 3A). Females reduced the length of the off-bout in the late incubation period, but still remained off the nest for as much as 5.5 h in late incubation (Fig. 3B). The reduction in length of the off-bout reflected an increase in nest attentiveness as the embryos aged (Fig. 3C). Nest attentiveness during the daytime averaged 35.6 ± 0.57% over the entire incubation period, corrected for embryo age, and averaged less than 50% of the day during late incubation (Fig. 3C).

Table 1. Morphometrics of adult Mountain Wren-Babblers captured in Kinabalu Park, Malaysia, 2009–2017. Measurements presented are the mean ± standard error.

Measurement	Male	*n*	Female	*n*
Mass (g)	28.35 ± 0.24	39	29.29 ± 0.39	31
Tarsus length (mm)	28.86 ± 0.14	35	28.81 ± 0.21	26
Wing chord (mm)	68.86 ± 0.25	39	66.78 ± 0.39	30
Tail (mm)	49.36 ± 0.29	34	45.91 ± 0.44	23
Exposed culmen (mm)	14.26 ± 0.24	26	13.83 ± 0.31	19
Bill width (mm)	4.34 ± 0.06	26	4.46 ± 0.07	19

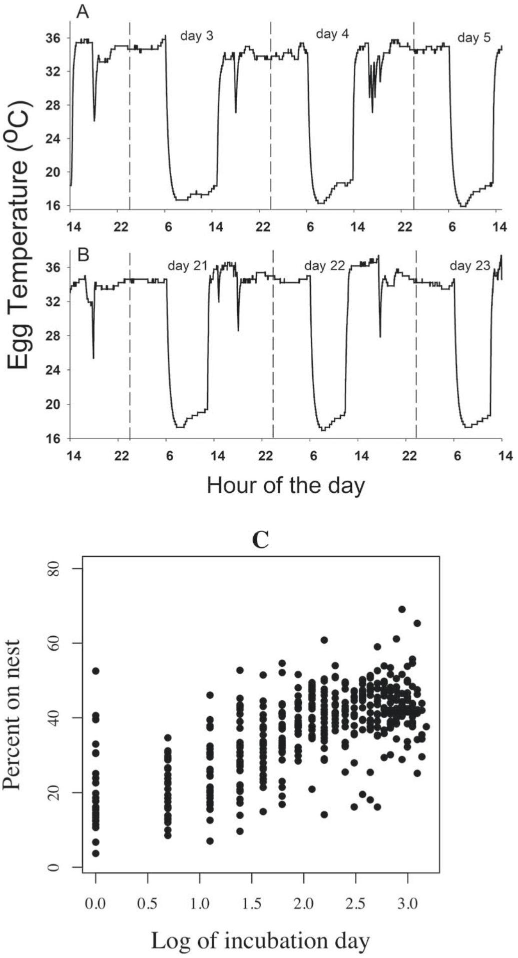

Figure 3. Incubation attentiveness and egg temperatures for Mountain Wren-Babblers nesting in Kinabalu Park, Malaysia. Egg probes show (A) that the female typically incubates overnight (temperature peaks) and is absent from the nest as much as 8 h during the day (temperature valleys) in the early portion of the incubation period. (B) Females reduced the length of the off-bout in the late incubation period, but still remained off the nest for as much as 5.5 h in late incubation. (C) Average daytime incubation attentiveness for Mountain Wren-Babbler females increased with age of the embryo, or incubation day ($\beta = 1.11 \pm 0.14$, $t_{87} = 7.89$, $P < 0.0001$, $r^2 = 0.41$).

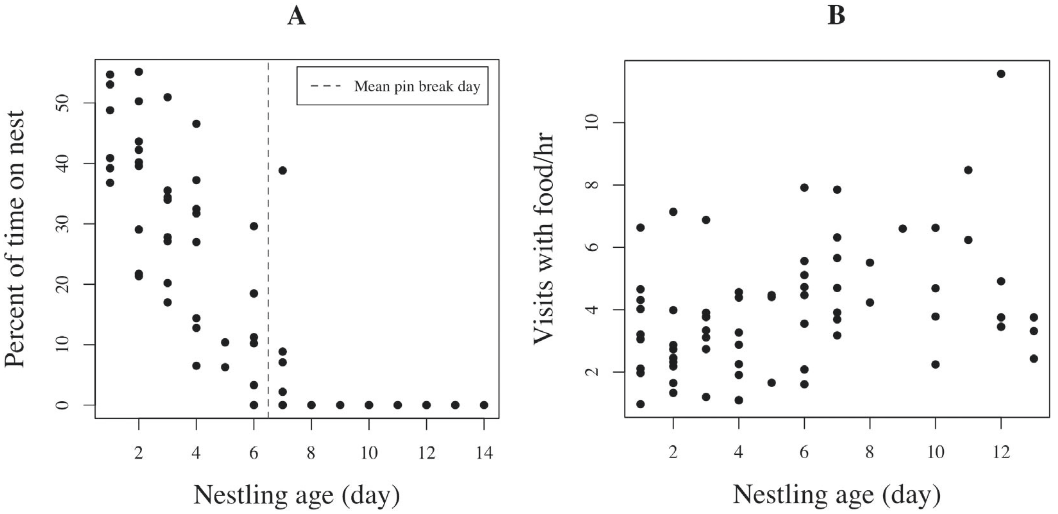

Figure 4. Adult behavior during the nestling period in Kinabalu Park, Malaysia. (A) Brooding attentiveness during the nestling period for Mountain Wren-Babblers decreased with nestling age ($\beta = -4.43 \pm 0.41$, $t_{69} = -10.9$, $P < 0.0001$, $r^2 = 0.637$). (B) Provisioning rates of adults increased with nestling age ($\beta = 0.19 \pm 0.06$, $z_{69} = 3.2$, $P = 0.002$, $r^2 = 0.129$).

Nestling period

Brooding and provisioning were provided cooperatively by the group with as many as 4 different individuals brooding based on observation of color-banded birds. All adults of the cooperative group were observed regularly feeding young with insects and larvae, and occasionally fruits and small lizards. Brooding attentiveness decreased with nestling age and was rare after day 7 (Fig. 4A). Provisioning rates by adults mildly increased with nestling age and averaged 3.9 ± 0.24 trips/h with food ($n = 70$ nests; 419.61 h of video recordings) across the nestling period (Fig. 4B).

The eighth primary feather of the nestling broke its sheath on day 6 ($n = 15$), 7 ($n = 10$), or 8 ($n = 4$). Nestlings fledged 13–14 d after hatching ($n = 15$). Growth rate constants (k) for mass (Fig. 5A), tarsus (Fig. 5B), and wing chord (Fig. 5C) were typical of many tropical birds (Martin et al. 2015a, 2015b). Mean nestling mass at fledging (day 13 and 14) was 19.8 ± 0.59 g ($n = 13$), which was 69% of mean adult mass (Table 1). Mean nestling tarsus length on day 13 and 14 was 27.9 ± 0.37 mm ($n = 13$), which was 96% of mean adult tarsus length (Table 1). Wing chord length averaged 47.8 ± 0.82 mm ($n = 13$) at fledging, which was 70% of mean adult size (Table 1).

Nest success and predation

Cause of one nest failure was unknown, but all remaining failures could be attributed to predation (87 of 88 nest failures); predators included tree shrews (e.g., Kinabalu shrew [*Crocidura baluensis*]) and birds (e.g., Bornean Green-Magpie [*Cissa jefferyi*], Bornean Whistling Thrush [*Myophonus borneensis*]) based on videos of depredated nests. The daily predation rate for the total nesting period (lay, incubation, and nestling) was 0.056 ± 0.0058 ($n = 123$ nests, 1,554 exposure days). Daily nest success decreased with increasing elevation within our study range of 1,450–1,950 m.a.s.l. ($\beta = -0.003 \pm 0.001$, $z_{102} = -2.43$, $P = 0.015$).

Broken down into the 3 stages of the nest cycle, daily nest predation rate during the egg-laying period was 0.117 ± 0.036 ($n = 77$ exposure days), 0.046 ± 0.006 during incubation ($n = 1{,}126$ nest days), and 0.074 ± 0.014 during the nestling period ($n = 351$ nest days). Nest survival increased with nest height during incubation ($\beta = 0.52 \pm 0.26$, $z_{79} = 1.99$, $P = 0.047$), but decreased with greater nest height during the nestling period ($\beta = -1.04 \pm 0.38$, $z_{42} = -2.74$, $P = 0.006$).

Appearance and behavior

The adult Mountain Wren-Babbler is a stout, sexually monomorphic songbird with a dark brown back and head with lighter brown streaks,

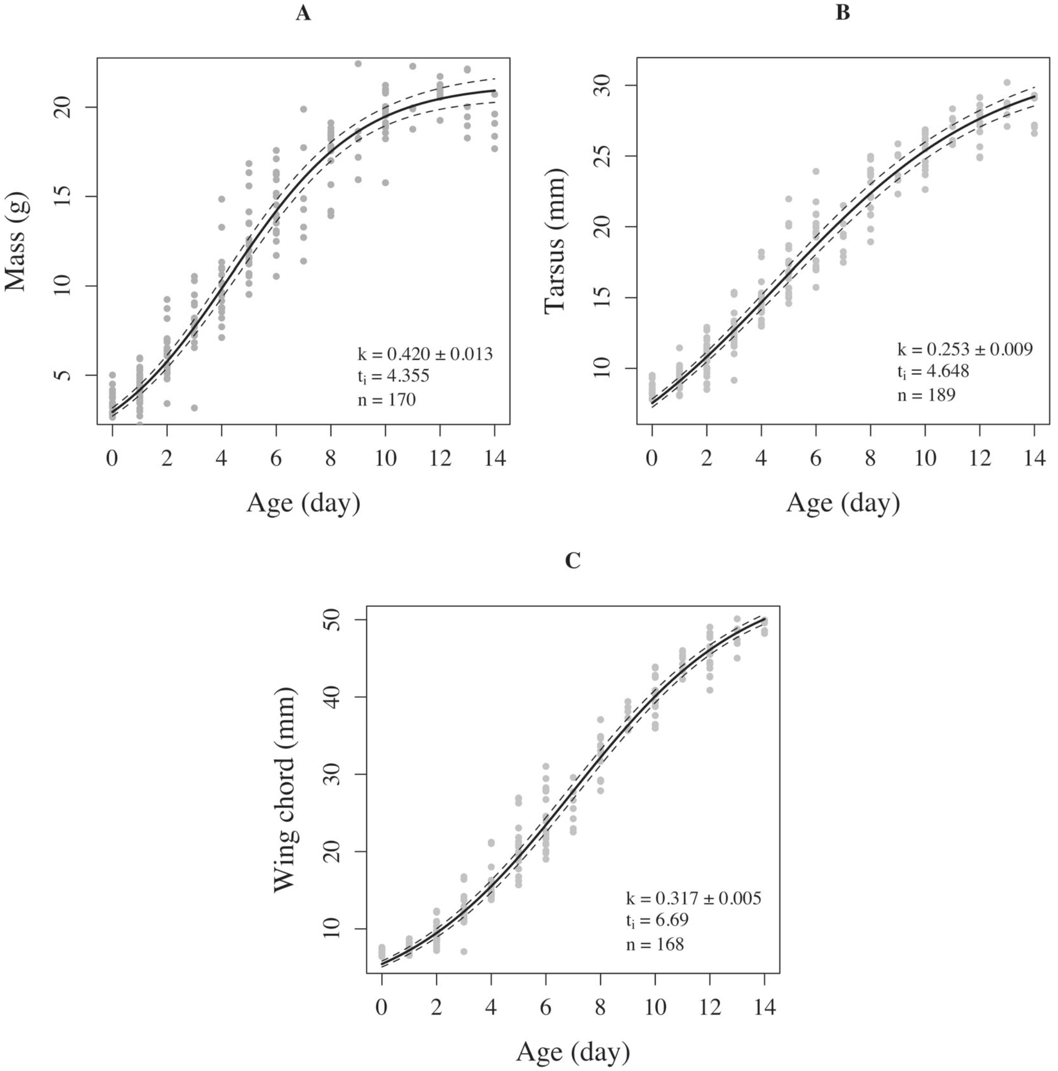

Figure 5. Fitted curve describing growth rate for mass (A), tarsus (B), and wing chord (C) for Mountain Wren-Babbler nestlings measured February–June, 2009–2016, in Kinabalu Park, Malaysia.

an incomplete eye ring with rusty iris, a gray supercilium, bill, throat, and legs, a light brown breast with streaked flanks, short brown wings, and a tail with darker brown coverts (Fig. 1A). Juveniles, when seen following adults post-fledging, had similar plumage to adults but with shorter tails. This is a cooperatively breeding species that always foraged as a group consisting of 3–7 individuals (typical group size = 4 or 5). Based on video data, the majority of the breeding effort (from nest construction through fledge) was accomplished by the main breeding pair, with females alone incubating, but the group also provisioned nestlings. Based on resighting adult color bands, territories were estimated to be very large, often comprising 50–150 ha.

Discussion

The aim of this research was to add to the understanding of avian life history theory by studying a poorly described species in a non-temperate region. Below, we discuss our findings for the Mountain Wren-Babbler and, when applicable, compare them with those from a detailed breeding account of the Streaked Wren-Babbler (*Gypsophila brevicaudata*) breeding in limestone forests of southern China (Jiang et al. 2017b) and with published data for Temminck's Babbler (*Trichastoma pyrrogenys*) from our study site (Martin et al. 2015a, 2015b), both of which are in the same Pellorneidae family as the Mountain Wren-Babbler.

Perhaps the most unusual trait of Mountain Wren-Babblers compared with other passerines of similar size and ecology is that they took 8 h off-bouts that allowed eggs to cool to quite cold temperatures for many hours of each day (Fig. 3A). Even in the late incubation stage, parents took 5–6 h off-bouts that allowed embryos to cool to 16 °C (Fig. 3B), which is well below the optimal incubation temperatures for most birds (≥35 °C; Webb 1987). Older embryos are often thought to be more sensitive to cooling that can lead to mortality (Webb 1987), yet our data show that old embryos experience very cold temperatures for extended periods. This suggests that at least some species can evolve cold tolerance in old embryos. At the same time, given the importance of egg temperature to embryonic development rates (Martin et al. 2007, 2015a; Ton and Martin 2017), these cold temperatures coincided with a relatively long incubation period of 23–25 d. This is more than twice the length of the incubation period of the Streaked Wren-Babbler (10.2 ± 0.4 d), which averaged 80% incubation attentiveness from dawn to sundown (Jiang et al. 2017b). In contrast, Mountain Wren-Babblers never exceeded an average of 50% attentiveness even at the peak of their effort (Fig. 3C). Interestingly, their strategy of unusually long off-bouts was observed in another species nesting in Kinabalu Park that also has long incubation periods, the Bornean Stubtail (*Urosphena whiteheadi*; 23.00 ± 0.58 d; Martin et al. 2013), as well as in Spotted Barbtails (*Premnoplex brunnescens*) in Venezuela with even longer incubation periods (27.2 ± 0.16 d, $n = 16$; Muñoz and Martin 2014). Egg-warming and egg-swapping experiments verified that the long incubation periods of the Mountain Wren-Babbler, as well as the Bornean Stubtail, were largely caused by the cold incubation temperatures from long off-bouts (Ton and Martin 2017). The long off-bouts potentially reflect a life history tradeoff in favor of adult survival vs. nest survival (Martin 2002, Martin et al. 2015a). Apparent annual adult survival for Mountain Wren-Babblers is quite high for a small passerine, averaging 89% (Martin et al. 2017b). High adult survival, which underlies greater longevity, can favor risk-averse behavior through low parental effort (Ghalambor and Martin 2001, Martin et al. 2015a). Nonetheless, the off-bouts are unusually long even for long-lived songbirds. Despite this apparent tradeoff, long off-bouts may also have evolved to reduce nest and adult depredation by reducing the number of parental nest visits, thus reducing the chance a predator can use this behavioral cue to locate the nest (i.e., Skutch 1949). Indeed, nest predation rates were much lower during the incubation period when parents visited the nest much less often than during the very active nestling phase.

Mountain Wren-Babblers and Temminck's Babblers both build partially domed nests. In contrast, Streaked Wren-Babblers built open cup nests, and placed nests in shallow or deep rock crevices (Jiang et al. 2017b). The Streaked Wren-Babbler was studied in the northern subtropics (22°N; Jiang et al. 2017b) and this nest structure difference fits with the broader pattern of domed nests being more common in the tropics than in northern latitudes (Martin et al. 2017a). Mean clutch size of Mountain Wren-Babblers was equal to that of Temminck's Babblers at the same site (Martin et al. 2015a) but smaller than that of Streaked Wren-Babblers (3 eggs, $n = 28$; Jiang et al. 2017b). Again, this clutch size difference fits with classic latitudinal patterns. The larger clutch size of Streaked Wren-Babblers may also reflect greater nest survival than Mountain Wren-Babblers. Streaked Wren-Babbler nest survival was quite high at 88%, perhaps due to their strategy of nesting relatively earlier in the year (Jiang et al. 2017a) and in protected natural crevices in limestone boulders (Jiang et al. 2017b), whereas it was only 11% for the Mountain Wren-Babbler.

The Mountain Wren-Babbler's nestling period was 13.7 d, which was 3 d longer than the Streaked Wren-Babbler (10.5 ± 0.8 d, $n = 6$; Jiang et al. 2017) despite the higher rates of nest predation for Mountain Wren-Babblers. Although higher nest predation rates can favor faster nestling development, this pattern fits with the fact that tropical species often show slower growth than northern relatives despite higher predation risk (Martin et al. 2011, 2015b). Nonetheless, this difference in nestling periods (33% longer than Streaked Wren-Babbler) was much smaller than the difference in incubation periods. The reasons why incubation periods show greater latitudinal differences than nestling periods remain to be uncovered.

The strong inverse relationship between Mountain Wren-Babbler nest survival and nest height during the nestling period may explain why nest height averaged only 0.78 m. Based on our video evidence, the 3 predators recorded depredating nests (tree shrews and 2 bird species) may forage at multiple forest strata, but typically do so at least a few meters above the ground (MCS, 2017, pers. observ.). Therefore, Mountain Wren-Babbler nests built closer to the forest floor may escape the attention of predators that forage higher. Other studies support this, showing that ground-nesting forest birds generally have higher nest survival rates than above-ground nesting birds (Martin 1993, Pierce et al. 2019). It may also be that predators are denser higher above the ground. Finally, the increased strength of our observed effect during the nestling period may indicate that predators cue on nestling sounds or smell, or increased parental visit rates (Skutch 1949). Much like birdsong, which has greater transmission properties when emitted from higher above ground (Hebets and Papaj 2005), perhaps nestling begging calls from nests that are lower to the ground degrade faster and travel less far, reducing the chance of discovery by a predator. Overall, because the nest height–survival relationship can differ between bird species depending on which predator guild is responsible for nest predation, nest depredation data specific to the nesting species are necessary to truly understand selection pressures on nest site preferences.

Future steps to advance our understanding of Mountain Wren-Babbler life history, and tropical species in general, include the continued collection of basic biological data such as those reported here. Detailed breeding data on more tropical species would make large-scale life history comparisons possible (e.g., Londoño et al. 2014, Martin et al. 2015a, 2015b) and will improve future comparisons among related species and their life history strategies. Such data are currently rare for babblers in family Pellorneidae. On the global scale, expanding the range of traits studied when comparing life histories across regions and latitudes, and studying species that exhibit an extreme end of the life history spectrum (e.g., very long or short incubation length, large or small parental behavior investment, very large or small clutch size), should contribute to improving our understanding of life history variation.

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Ethics statement

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