

BREEDING BIOLOGY OF AN ENDEMIC BORNEAN TURDID, THE FRUITHUNTER (*CHLAMYDOCHAERA JEFFERYI*), AND LIFE HISTORY COMPARISONS WITH *TURDUS* SPECIES OF THE WORLD

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ABSTRACT.—We present the first description of the breeding biology for the Fruithunter (*Chlamydochaera jefferyi*), a member of the cosmopolitan family Turdidae, and a montane endemic to the tropical Asian island of Borneo. We also compile breeding biology traits from the literature to make comparisons between the Fruithunter and the thrush genus *Turdus*. Our comparisons indicate that Fruithunters exhibit a slower life history strategy than both tropical and north temperate *Turdus*. We located and monitored 42 nests in 7 years in Kinabalu Park, Sabah, Malaysia. The mean clutch size was 1.89 ± 0.08 eggs, and the modal clutch size was 2 eggs. Mean fresh egg mass was 6.15 ± 0.13 g, representing 9.5% of adult female body mass. Average lengths of incubation and nestling periods were 14.56 ± 0.24 and 17.83 ± 0.31 days respectively. Only the female incubated and brooded the eggs and nestlings, but both the male and female fed nestlings. Female attentiveness during incubation was high throughout, reaching an asymptote around 85% with average on-bouts of 39.0 ± 2.5 mins. The daily nest survival probability was 0.951 ± 0.025 , and the daily predation rate was 0.045 ± 0.024 . Female feeding rate increased as brooding effort decreased, suggesting that female feeding rate may be constrained by the need to provide heat while nestlings are unable to thermoregulate. This contrasts with the feeding behavior of males, which showed much less of an increase across the nestling period. Furthermore, we describe a new vocalization which expands the vocal repertoire for Fruithunters, and we provide a brief audio clip and spectrogram. Received 22 February 2016. Accepted 26 May 2016.

Key words: avian life histories, bird nests, Fruithunter, Turdidae.

Descriptions of avian breeding biology traits have played a major role in the development and refinement of life history theory (Lack 1947, Skutch 1949, Cody 1966, Williams 1966, reviewed in Stearns 1976). Still, the breeding biology of many species is unknown, limiting our ability to fully recognize the global variation in life histories and understand the causal mechanisms that underlie this variation. In particular, studies from tropical regions are underrepresented despite the fact that the majority of avian diversity occurs near the equator (Sodhi et al. 2006, Jetz et al. 2012). Data are especially sparse for tropical Asian species (Sodhi et al. 2006), and this is particularly true for the thrushes (family Turdidae; Collar 2005). Additional breeding descriptions from this region and taxon will help overcome these deficiencies and advance our understanding of life history evolution.

Life history traits generally fall along a slow-fast gradient across latitudes (MacArthur and Wilson

1967; Pianka 1970, 1974). Tropical birds tend to be on the slow end of this gradient with smaller clutch sizes and slower growth and development trading off with higher adult survival and parental investment (Moreau and Moreau 1940, Skutch 1945, Ghalambor and Martin 2001, Jetz et al. 2008, Martin et al. 2015a). Interestingly, these patterns are not seen in all avian clades, for example, the thrush genus *Turdus* seems to be anomalous, showing relatively little life history variation between latitudes, at least in the new world (Snow and Snow 1963, Martin and Schwabl 2008). Because of the lack of life history data for tropical Asian thrushes, we have a poor understanding of the extent to which they differ from those in other tropical and north temperate regions.

The Fruithunter (*Chlamydochaera jefferyi*) is an elusive member of the thrush family (Turdidae), and a montane endemic to the tropical Asian island of Borneo. *Turdus* is the closest relative to *Chlamydochaera* with representatives in both north temperate and tropical latitudes (Voelker and Klicka 2008), and with available breeding data (Collar 2005). Thus, we present extensive breeding biology data for the Fruithunter, and in order to elucidate the range of life history variation between latitudes in Asian thrushes, we use literature data (Collar 2005) to make comparisons with members of north temperate and tropical

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Turdus. Furthermore, we describe a new vocalization that was recorded at a nest to expand the currently known vocal repertoire of this species. We provide an audio clip as well as a segment of the spectrogram to help future researchers cue into nesting habits.

METHODS

Study Site and Nest Monitoring.—We searched for nests in primary tropical rainforest ranging from 1350–1950 m asl in Kinabalu Park, Sabah, Malaysia (6° 05' N, 116° 33' E). Fieldwork was conducted from February to June, 2009–2015. Nests were located using a combination of behavioral observations and systematic search methods (see Martin and Geupel 1993). We typically monitored nests every 1–4 days, but up to two times per day during stage transitions (hatch and fledge) to improve the precision of our estimates of developmental periods. Nests were mostly in the canopy and were reached using ladders, climbing gear, and free-climbing techniques. We were not able to reach all nests for egg and nestling measurements, and so sample sizes are given for the subset of nests in which data could be collected. Nest heights are reported as visual estimations.

Egg and Nestling Measurements and Nest Survival.—We weighed eggs within 3 days of the start of incubation and again within 3 days of hatching to determine fresh egg mass and mass lost because of embryonic metabolism. Mass loss was calculated only for eggs that were weighed both at the beginning and end of incubation. Mass, tarsus, and wing chord were measured on days 0 (hatch day), 1, and 2 of the nestling period, and repeated every other day until fledge. We fit exponential growth curves and calculated the growth rate constant K , following Remeš and Martin (2002). Nest predation was assumed if nests were found empty prior to 2 days before the mean nestling period length. This was verified by checking for visual signs of predation such as egg shell fragments, damaged nests, and/or absence of recently fledged juveniles in the vicinity. Predation is the primary cause of nest failure in songbirds (Ricklefs 1969, Martin 1992, Remeš et al. 2012), but all sources of mortality can be agents of selection on life history traits, and therefore we present general nest survival rate (1-mortality rate)

as well as predation rate to enhance the future utility of these data.

Parental Behavior and Developmental Periods.—We filmed nests for 4–8 hrs per day to calculate parental attentiveness and nestling provisioning rates. Nests were filmed opportunistically throughout the incubation and nestling stages with videos starting within 30 mins of sunrise to control for temporal changes in behavior. We used various models of Sony high-band Video8 (Hi-8; Sony Corp., Tokyo, Japan) handheld cameras mounted on tripods placed >5 m from the nests. Nest attentiveness was calculated as the amount of time the female spent incubating eggs or brooding nestlings divided by the total time filmed for that day. Nestling provisioning rates were calculated as the number of feeding trips per hour. We defined the incubation period as the number of days between the last egg laid and the last egg hatched (Martin et al. 2007), and the nestling period was the number of days between the last egg hatched and when the last nestling left the nest (Martin et al. 2011).

Literature Data.—We compiled literature data on clutch size, incubation periods, and nestling periods for north temperate and tropical *Turdus* species using Handbook of the Birds of the World (Collar 2005; see Appendix). All species were sorted into tropical or north temperate categories based on latitudinal distribution. North temperate species were defined as those with breeding ranges primarily above 23° N latitude. Species that breed primarily between 23° north and south were counted as tropical. Species breeding in the south temperate region (below 23° S) were excluded because south temperate species do not show latitudinal trends in life history traits to the same extent as north temperate species (Yom-Tov 1987; Martin 1996, 2004; Ricklefs and Wikelski 2002). Species with breeding ranges that heavily overlapped both tropical and north temperate latitudes were omitted to avoid bias because of the higher occurrence of published studies from north temperate regions. We calculated clutch size, incubation period, and nestling period of species from literature by taking the midpoint of the reported range for each species. We used the mode rather than midpoint when a modal value was reported, since it reflects higher confidence as the species average.



FIG. 1. Photograph of a Fruithunter's nest and eggs at 1695 m asl in Kinabalu National Park, Sabah, Malaysia. This nest was constructed in a 14 m tall tree and was ~7 m above the ground. Photograph by AEM, 2012.

Vocalization.—We recorded vocalizations using an Audio-Technica Cardioid Condenser Lavalier Microphone (model AT831C; Audio-Technica Corp., Tokyo, Japan) placed directly above the nest, 15 cm from the rim of the cup. The microphone was connected to a solid state recorder (Marantz model PMD 661; Marantz America LLC, Mahwah, NJ, USA) recording at a sampling rate of 48 kHz.

Statistical Analyses.—Parental behavior at the nest (attentiveness and nestling provisioning rates) was analyzed using repeated measures ANOVA (RM-ANOVA) to account for non-independence of data collected on multiple days from the same nest. We modeled clutch size, incubation period, and nestling period of literature data with latitude and mass as covariates in order to correct for any body mass effects for the mean values of these parameters. We also modeled nest survival following the logistic exposure method (Shaffer 2004), and included nest height as a fixed effect to detect changes in nest predation rates at different nest heights. All models were performed using Program R ver. 3.2.2 (R Core Team 2015) with packages lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2015), and lsmeans (Lenth 2016). For these analyses, the day of incubation and nestling periods were log-transformed. We used IBM SPSS (IBM Corp. 2013) for all other statistical analyses. All means are reported ± 1 standard error. SigmaPlot (Systat Software Inc. 2008) was used for graphical figures, except the

sound spectrogram segment, which was created using Raven Pro (Bioacoustics Research Program 2011).

RESULTS

Nest Description.—We found 42 nests of Fruithunters, ranging from 1494–1904 m asl. The nests were open cups with fresh, green moss outside and dark brown rootlet fibers as lining (Fig. 1). Thirty-eight of 42 nests were on live trees, one was on a vine, and one was on a dead branch at the top of a snag. Two nests were on unrecorded substrates. Estimated nest height ranged from 1.5–15 m above ground, with a mean of 7.28 ± 0.42 m ($n = 42$). Mean nest measurements for two nests were 14.8 ± 1.2 and 12.2 ± 0.9 cm in outer diameter and outer height, respectively. The inside of the nest cups measured 8.8 ± 0.3 and 4.6 ± 0.8 cm in mean diameter and depth, respectively.

Timing of Nesting.—Estimated nest initiation (date the first egg was laid) ranged from 4 February to 25 May ($n = 32$). The nesting season lasted for a minimum of 111 days, not including the nest-building stage. This is based on the duration between the earliest known initiation date and the latest known fledge/fail date. These results are based on the duration of our field season, and Fruithunters may breed at other times of the year in other locations, depending on environmental conditions. For example, a pair of adults was seen feeding a juvenile between 28 August and 6 September in W. Kalimantan (Prieme and Heegaard 1988).

Clutch and Egg Sizes.—Eggs were creamy white with brown specks, sometimes concentrated around the blunt end of the egg, giving the eggs an overall tan appearance (Fig. 1). The modal clutch size was 2, with 16 of 18 nests containing 2 eggs. The mean clutch size was 1.89 ± 0.08 eggs ($n = 18$), which was smaller than both north temperate and tropical *Turdus* (4.33 ± 0.15 and 2.49 ± 0.12 respectively; Table 1). Indeed, tropical *Turdus* commonly lay 3 eggs (Collar 2005), whereas no Fruithunter nest was found with 3 eggs. Tropical *Turdus* laid fewer eggs per clutch than north temperate *Turdus* ($P < 0.001$), but clutch size was not affected by adult mass ($P = 0.38$).

Mean fresh egg mass was 6.15 ± 0.13 g ($n = 19$), which represented 9.5% of the adult female body mass (65.06 ± 7.50 g, $n = 2$). The eggs

TABLE 1 Comparisons of clutch size (\pm SE), incubation period (\pm SE), and nestling period (\pm SE) between Fruithunter, north temperate *Turdus* species, and tropical *Turdus* species. Values for Fruithunters are means of individual nests from our field study in Kinabalu National Park, Sabah, Malaysia, and values for north temperate and tropical *Turdus* are means of all species within each latitudinal group compiled from Handbook of the Birds of the World (Collar 2005). Literature means are corrected for mass (see Appendix). Sample size (n) = number of individual nests for Fruithunters, and numbers of species within *Turdus* for both north temperate and tropical latitudinal groups. 95% lower and upper bounds are the 95% confidence intervals of the means of all *Turdus* species taken from the literature for both north temperate and tropical breeding locations. Fruithunter is boldfaced to highlight the different type of data used for this group compared with the *Turdus* categories (see above).

Group	Clutch size \pm SE	n	95% lower	95% upper	Incubation period \pm SE	n	95% lower	95% upper	Nestling period \pm SE	n	95% lower	95% upper
Fruithunter	1.89 \pm 0.08	18			14.56 \pm 0.24	9			17.83 \pm 0.31	6		
N. Temperate <i>Turdus</i>	4.33 \pm 0.15	24	4.03	4.62	12.83 \pm 0.27	16	12.27	13.39	13.01 \pm 0.47	15	12.03	13.98
Tropical <i>Turdus</i>	2.49 \pm 0.12	30	2.24	2.73	13.60 \pm 0.36	8	12.86	14.35	15.32 \pm 0.57	9	14.13	16.51

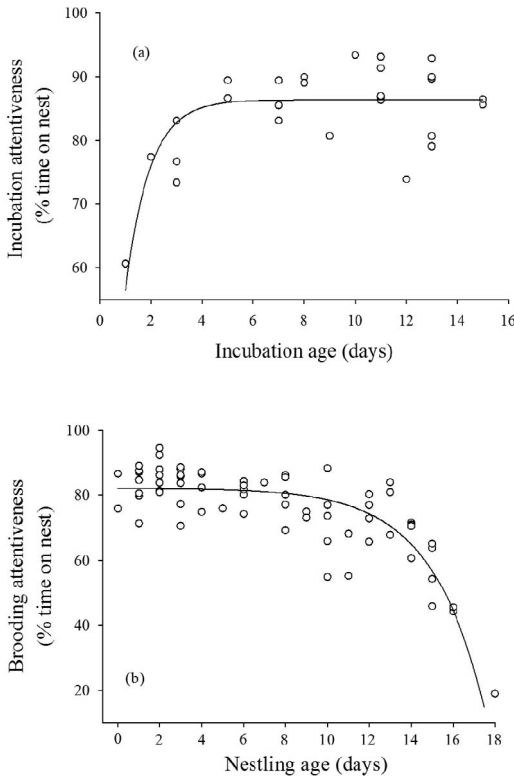


FIG. 2. Percentage of time adult Fruithunters in Kinabalu National Park spent (a) incubating eggs and (b) brooding nestlings (i.e., warming the young) across the duration of the incubation and nestling periods respectively. Parental effort changed significantly across the duration of both the incubation and nestling periods (RM-ANOVA, $P < 0.001$ for both). Each point represents the percent of time the female spent on the nest, for a given nest, from one 4–8-hr video record.

ranged from 5.09–7.10 g and lost an average of 0.88 ± 0.09 g across the duration of the incubation period ($n = 5$). This represented $\sim 14.8\%$ of the fresh egg mass.

Incubation Period.—Mean incubation period was 14.56 ± 0.24 days ($n = 9$; Table 1) and the eggs were incubated only by the female. Neither latitude ($P = 0.11$) nor adult body mass ($P = 0.28$) had an effect on incubation period within *Turdus* species. Results from our linear model accounting for mass indicate that the incubation period for Fruithunters was longer than both north temperate and tropical *Turdus* groups (12.83 ± 0.27 and 13.60 ± 0.36 days, respectively; Table 1).

Incubation effort changed significantly across the duration of the incubation period ($F_{1,18} = 19.55$, $P < 0.001$; Fig. 2a), and reached an asymptote at a fairly high level around 85% (Fig. 2a). The average lengths of incubation on-bouts and off-bouts were 39.0 ± 2.5 and 8.3 ± 0.8 mins, respectively. During incubation, the male visited the nest (near the nest for < 60 secs), guarded the nest (near the nest for > 60 secs), and fed the incubating female at an average rate of 0.12 ± 0.03 , 0.09 ± 0.03 , and 0.14 ± 0.04 trips/hr, respectively ($n = 12$ nests, 214.3 hrs of incubation video).

Nestling Period.—Fruithunter nestlings remained in the nest for an average of 17.83 ± 0.31 days after hatching ($n = 6$; Table 1), which was longer than both north temperate and tropical *Turdus* (Table 1). North temperate and tropical *Turdus* had mean nestling periods of 13.01 ± 0.47 and 15.32 ± 0.57 days, respectively (Table 1).

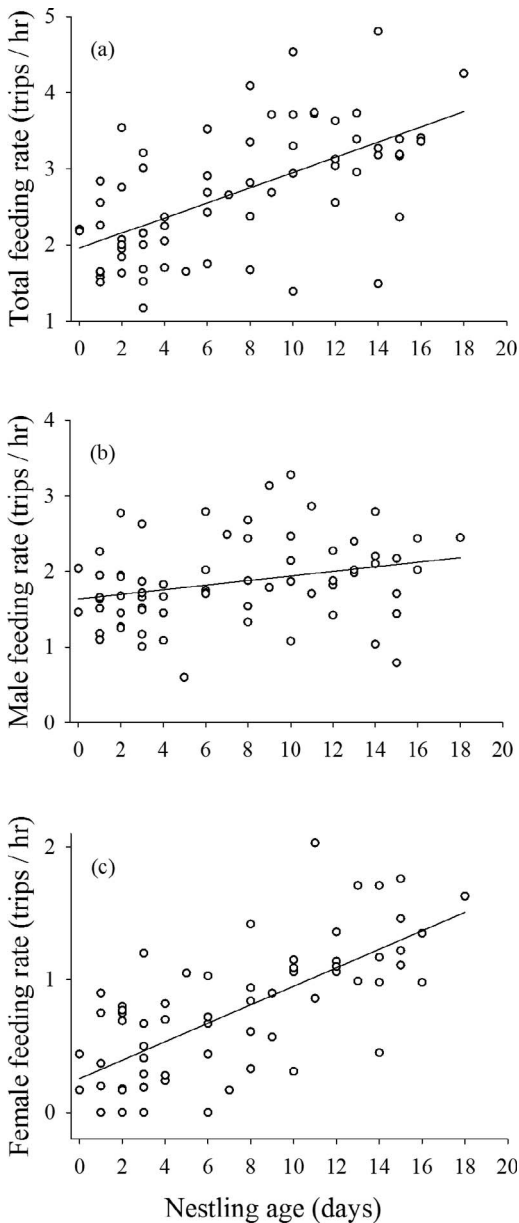


FIG. 3. Nestling provisioning rates of Fruithunters across the duration of the nestling period in Kinabalu National Park. Plots illustrate (a) total feeding rates, (b) male-only feeding rates, and (c) female-only feeding rates. Using RM-ANOVA, plots (a) and (c) increase significantly across the stage ($P < 0.001$), and plot (b) shows only a marginal increase ($P = 0.059$). Each point represents the number of times adults fed nestlings per hour, at a given nest, from one 4–8-hr video record.

Tropical *Turdus* had a longer mean nestling period than north temperate *Turdus* species ($P = 0.008$), but nestling period was not influenced by adult mass ($P = 0.095$). Only the female Fruithunter brooded the nestlings, and the percent of time the female spent on the nest decreased across the nestling period ($F_{1,64} = 37.23$, $P < 0.001$), although brooding remained relatively elevated through fledging (Fig. 2b). Both parents fed the nestlings, and the adults fed primarily fruits, which were regurgitated for the nestlings. Adults also occasionally fed insects and insect larva. A seed catchment trap below one nest collected large numbers of seeds from two species of *Litsea* (Lauraceae). One species was identified as *L. cylindrocarpa* and the other was unidentified. The rate that both parents brought food to the nestlings increased with nestling age ($F_{1,60} = 41.89$, $P < 0.001$; Fig. 3a). When divided by sex, the increase in female feeding rate over time was highly significant ($F_{1,59} = 95.18$, $P < 0.001$; Fig. 3c), whereas the increase in male feeding rate across the stage was only marginal ($F_{1,58} = 3.72$, $P = 0.059$; Fig. 3b). The proportion of total feeding trips made by males decreased across the nestling period ($F_{1,57} = 55.26$, $P < 0.001$; Fig. 4a), reflecting an increase in female feeding rate as brooding time was reduced (Fig. 4b).

The mean nestling mass on the day of hatching (day 0) was 4.78 ± 0.24 g ($n = 7$; Fig. 5a). Nestlings weighed an average of 35.80 ± 0.79 g ($n = 18$) on pin break (the day the 8th primary feather broke from its sheath), which most commonly occurred on day 8. The growth rate constant K for mass was 0.399 ± 0.017 (Fig. 5a). The growth rate constants K for tarsus and wing chord were 0.325 ± 0.011 (Fig. 5b) and 0.247 ± 0.007 (Fig. 5c), respectively.

Nest Survival.—Twelve of the 42 nests fledged young and 17 were depredated, 9 of the remaining nests failed because of abandonment, weather, or other unknown causes, and 4 nests were in progress during the end of our study and therefore no final fate was obtained. Total daily survival rate was 0.951 ± 0.025 and the daily predation rate was 0.045 ± 0.024 . Nest height did not affect daily predation rate ($P = 0.56$), and was dropped from the model.

Vocalization.—Male Fruithunters were observed making a previously undescribed vocalization on several occasions, mostly at or near a nest site, and

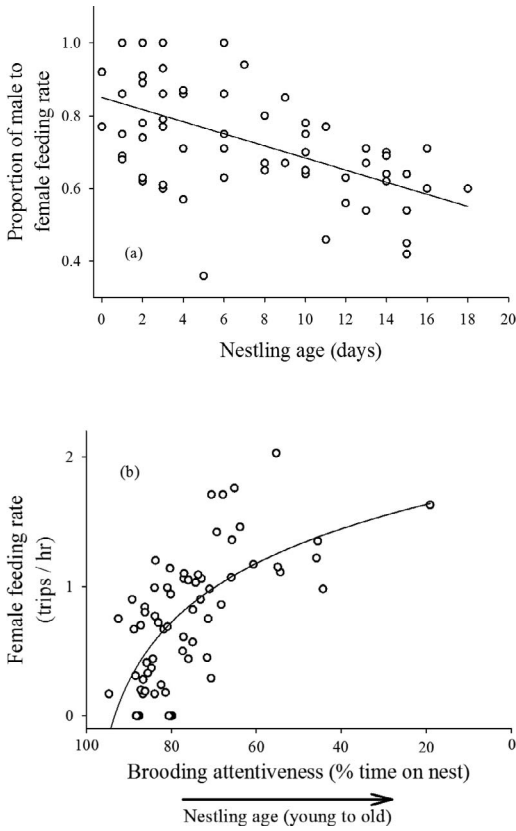


FIG. 4. Nestling provisioning rates of Fruithunters in Kinabalu National Park showing (a) proportion of total feeding trips made by the male and (b) female feeding rate as a function of female brooding attentiveness. Each point represents one nest video recorded for 4–8 hrs on a given day. Some nests were filmed multiple times and have multiple video records across the stage.

in the presence of a female. We recorded this complex vocalization on one occasion as the male perched near the nest during a nest-guarding event. Examination of the spectrogram shows clear examples of polyphonic sounds at different frequencies (see Fig. 6: 7.4 secs). The primary notes were generally in the range of 1–7 kHz, and many had multiple harmonics as high as 20 kHz (Fig. 6). Our recording of the vocalization lasted 28 secs (see supplemental recording). Previously documented vocalizations for Fruithunters are limited to a single-noted, high-pitched call (Collar 2005, Myers 2009), which we also observed as the most common vocalization at our field site.

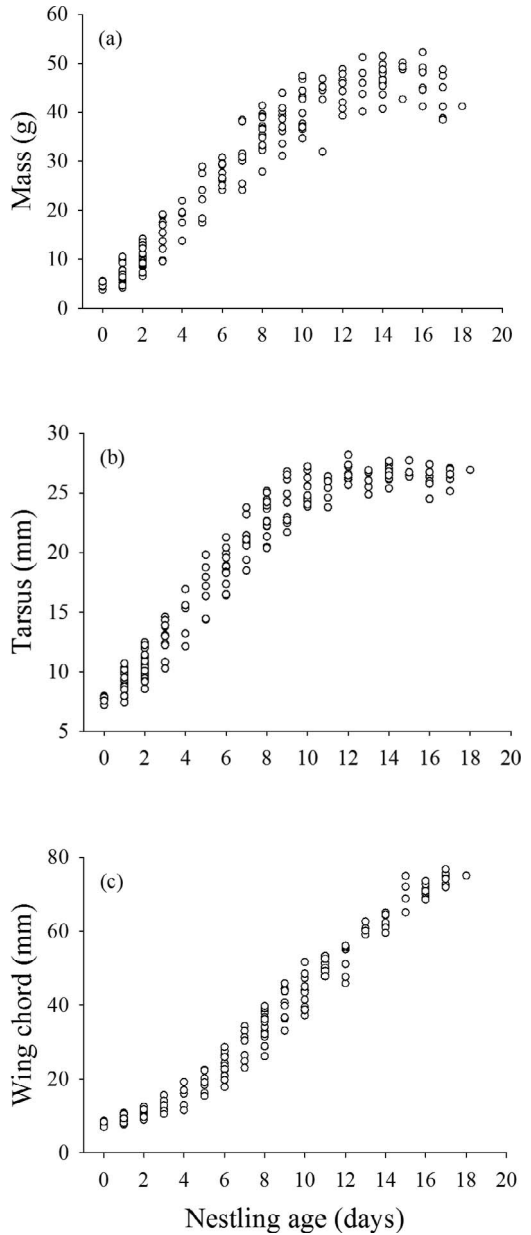


FIG. 5. Growth curves of nestling Fruithunters in Kinabalu National Park. Nestling growth parameters (a) nestling mass, (b) nestling tarsus, and (c) nestling wing chord are plotted against nestling age (days). Wing chord (c) never reaches an asymptote, indicating that the young fledge with less developed wings. Growth rate constants K for mass, tarsus, and wing chord were 0.399, 0.325, and 0.247 respectively. Each point represents a measurement from an individual nestling on a given day.

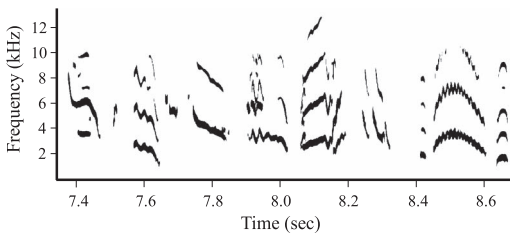


FIG. 6. Spectrograph showing frequency of newly identified calls of Fruithunters in Kinabalu National Park. At time 7.4 secs, the polyphony consists of two different notes being sung at the same time. The total song lasted ~28 secs.

DISCUSSION

Fruithunters have slower life histories than north temperate relatives, at least for the traits examined here (Table 1). Interestingly, Fruithunters also appear to have slower life histories than tropical-breeding relatives in the genus *Turdus* (Table 1).

Fruithunters have a smaller mean clutch size than temperate-breeding *Turdus*, and still ~25% less than the mean for tropical *Turdus* (Table 1). Small, tropical clutches have been attributed to high nest predation rates (Skutch 1949, Slagsvold 1982), yet nest predation is not always high in the tropics and cannot easily explain smaller clutch sizes throughout the tropics and subtropics (Martin 1996, Martin et al. 2000, Remeš et al. 2012). Indeed, nest predation also is unlikely to explain the small clutch sizes of Fruithunters, since the overall daily nest predation rate of 0.045 ± 0.024 is not especially high for tropical, non-cavity nesting birds (see Martin et al. 2015a: table 1). Instead, the reduced clutch size may reflect trade-offs resulting from low mortality rates of adults as well as offspring after leaving the nest (Williams 1966; Sæther 1988; Martin 1995, 2015; Ghalambor and Martin 2001), although we lack data to test this hypothesis.

Small clutch sizes are commonly associated with lower adult mortality and longer lives (Martin 1995, Ghalambor and Martin 2001). If Fruithunters are long-lived as suggested by their tropical distribution and small clutch sizes, their increased longevity might be facilitated by slower growth and development (McCay 1933, Arendt 1997, Metcalfe and Monaghan 2003; but see Martin et al. 2015b). Indeed, eggs of Fruithunters take longer to develop than those of north

temperate and tropical *Turdus* (Table 1). Long incubation periods in some tropical species reflect relatively cool egg temperatures from low incubation attentiveness and effort (Boersma 1982; Martin 2002; Hepp et al. 2006; Martin et al. 2007, 2013, 2015a), which is associated with higher adult survival (Martin et al. 2015a: fig. 2a). Yet, Fruithunters exhibited high incubation attentiveness (~85%) compared with other tropical, and even north temperate species (Martin et al. 2015a). This may be facilitated by their relatively large size, as larger species can have higher attentiveness (Martin et al. 2007). Thus, their slow embryonic development seems to reflect intrinsic processes.

Fruithunters have a longer nestling period than both north temperate and tropical *Turdus* even after taking into account body size (Table 1). This may reflect a development rate-longevity trade-off (McCay 1933, Arendt 1997, Metcalfe and Monaghan 2003) or a nutrient-deficient diet (Morton 1973, Ricklefs et al. 1998). Furthermore, this additional time in the nest may allow the nestlings to be more developed upon fledging, increasing their juvenile survival probability (Martin 2014, 2015). Comparative studies of fledgling survival rates and juvenile development times can test this hypothesis, although these data are currently lacking.

Feeding rates across the nestling period differed between sexes (Figs. 3b, c), because brooding duties (i.e., keeping nestlings warm) constrained female feeding rate at younger nestling ages. Nestlings require less warmth from their brooding mothers as they develop endothermy (Visser 1998), and this extra time may be used to increase nestling provisioning rates (Figs. 3c, 4b). This contrasts with male feeding behavior, which hardly differs across the nestling period (Fig. 3b). Indeed, the proportional increase in female to male feeding rates indicates the heightened role in female provisioning over the course of the stage (Fig. 4a). It should be noted, however, that males still provide more than half of the food, on average, even as nestlings are ready to fledge (Fig. 4a).

Our vocalization recording expands the previously-known vocal repertoire for Fruithunters (Collar 2005, Myers 2009). The complex polyphonic notes are typical of thrushes (Turdidae), but are not previously described for Fruithunters, or their nearest relatives, *Cochoa* spp. (Collar 2005).

We speculate that the faintness of the vocalization has prevented previous detection and/or identification of this unique call. Furthermore, the description of this vocalization may help researchers identify breeding behavior and locate nests of Fruithunters in future studies.

In conclusion, Fruithunters exhibit traits that are suggestive of a slower life history strategy than temperate or tropical relatives in the genus *Turdus*. These slower traits, namely reduced clutch size and slower development, may be associated with higher adult survival, making the Fruithunter a long-lived tropical thrush. Annual adult survival estimates are not currently available for Fruithunters, and would be a great advancement towards elucidating the complete life history strategy of this species, and this unique clade of Turdidae.

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APPENDIX. Compiled literature data of life history traits: clutch size (number of eggs), length of incubation period (days), length of nestling period (days), and adult body mass (g) for all north temperate and tropical *Turdus* (see Methods for excluded species) with data published in Handbook of the Birds of the World, Volume 10 (Collar 2005).

Species	Clutch size	Incubation period	Nestling period	Adult mass
North temperate				
Mistle Thrush (<i>Turdus viscivorus</i>)	4.0	13.5	15.0	130.0
Song Thrush (<i>T. philomelos</i>)	4.0	13.5 ^b	13.0 ^b	78.5
Chinese Thrush (<i>T. mupinensis</i>)	5.0			63.0 ^a
Redwing (<i>T. iliacus</i>)	5.0	12.5 ^b	13.5	63.0

APPENDIX. Continued.

Species	Clutch size	Incubation period	Nestling period	Adult mass
Fieldfare (<i>T. pilaris</i>)	5.5	13.0 ^b	13.5	110.5
Naumann's Thrush (<i>T. naumanni</i>)	5.0			72.0
Dusky Thrush (<i>T. eunomus</i>)	5.0			80.5
Rufous-throated Thrush (<i>T. ruficollis</i>)	4.5	11.0	12.0	83.0
Black-throated Thrush (<i>T. atrogularis</i>)	5.5	11.5	12.0	82.0
Japanese Thrush (<i>T. cardis</i>)	4.0 ^b	12.5	14.0	59.0 ^a
Common Blackbird (<i>T. merula</i>)	3.5 ^b	13.0 ^b	13.5	95.0
Tibetan Blackbird (<i>T. maximus</i>)	3.5	12.5	17.0	
Ring Ouzel (<i>T. torquatus</i>)	4.5 ^b	13.5	15.0	114.0
White-backed Thrush (<i>T. kessleri</i>)	3.5			92.5
Chestnut Thrush (<i>T. rubrocanus</i>)	3.0			100.5
White-collared Thrush (<i>T. albocinctus</i>)	3.5			77.0
Brown-headed Thrush (<i>T. chrysolaus</i>)	3.5 ^b	13.5	13.0	85.0 ^a
Izu Thrush (<i>T. celaenops</i>)	3.5 ^b			77.0
Pale Thrush (<i>T. pallidus</i>)	5.0	13.5	14.0	89.0
Eyebrowed Thrush (<i>T. obscurus</i>)	5.0			71.0 ^a
Grey-sided Thrush (<i>T. feae</i>)	4.5	14.0	13.0	66.5
Tickell's Thrush (<i>T. unicolor</i>)	4.0	13.5		65.0
Grey-backed Thrush (<i>T. hortulorum</i>)	4.0	12.5	12.0	76.5
American Robin (<i>T. migratorius</i>)	3.0	13.0	13.0 ^b	
Tropical				
Indian Blackbird (<i>T. simillimus</i>)	4.0			77.0
Island Thrush (<i>T. poliocephalus</i>)	2.0	14.0 ^c	16.5 ^c	63.0
African Thrush (<i>T. pelios</i>)	2.5 ^b			62.0
Taita Thrush (<i>T. helleri</i>)	2.0	14.5		71.0
Somali Thrush (<i>T. ludoviciae</i>)	2.0			62.0
Bare-eyed Thrush (<i>T. tephronotus</i>)	2.5			50.0
Kurrichane Thrush (<i>T. libonyanus</i>)	3.0 ^b	13.0	14.5	64.0
Yemen Thrush (<i>T. menachensis</i>)	2.0 ^b			75.5
Comoro Thrush (<i>T. bewsheri</i>)	2.0			62.5
Gulf of Guinea Thrush (<i>T. olivaceofuscus</i>)	2.0			84.5
White-throated Thrush (<i>T. albicollis</i>)	2.5	12.5	14.0	58.5
Rufous-backed Thrush (<i>T. rufopalliatus</i>)	3.0			78.5
Black-billed Thrush (<i>T. ignobilis</i>)	2.0		15.0	55.0
Pale-breasted Thrush (<i>T. leucomelas</i>)	3.0 ^b	12.5	16.5	62.5
White-eyed Thrush (<i>T. jamaicensis</i>)	2.5			59.0
Pale-vented Thrush (<i>T. obsoletus</i>)	2.5			71.5
Cocoa Thrush (<i>T. fumigatus</i>)	3.0	13.0	14.0	69.0
Clay-colored Thrush (<i>T. grayi</i>)	3.0	12.5	13.0	75.5
Spectacled Thrush (<i>T. nudigenis</i>)	3.5			62.5
Ecuadorian Thrush (<i>T. maculirostris</i>)	3.0			69.0
American Mountain Thrush (<i>T. plebejus</i>)	2.5		20.0	86.0
Sooty Thrush (<i>T. nigrescens</i>)	2.0			96.0
Yellow-legged Thrush (<i>T. flavipes</i>)	2.0			63.5
Glossy-black-Thrush (<i>T. serranus</i>)	2.0			80.0
Black Thrush (<i>T. infuscatus</i>)	1.5			76.0
Great Thrush (<i>T. fusculator</i>)	2.0			151.5
La Selle Thrush (<i>T. swalesi</i>)	2.5			99.0
Red-legged Thrush (<i>T. plumbeus</i>)	3.5		11.5	66.0
White-chinned Thrush (<i>T. aurantius</i>)	2.5	16.0		82.0
Black-hooded Thrush (<i>T. olivater</i>)	2.5			77.5

^a Adult masses from Dunning (2007).^b Life history traits using modal values rather than midpoints of the range.^c Means from field site on Mt. Kinabalu, Sabah, Malaysia (TEM, unpubl. data).