

2RRH: *Mitchell et al* – FRUITHUNTER BREEDING BIOLOGY

BREEDING BIOLOGY OF AN ENDEMIC BORNEAN TURDID: FRUITHUNTER
(*CHLAMYDOCHAERA JEFFERYI*)

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ABSTRACT.---We present the first description of the breeding biology of the endemic Bornean Fruithunter (*Chlamydochaera jefferyi*), a member of the pan-global family Turdidae. We located and monitored 32 nests in 4 years of field work and were able to observe the contents of 14. The mean clutch size was 1.86 ± 0.10 eggs. Mean fresh egg mass was 6.18 ± 0.22 g, representing 9.50 % of adult female body mass. Average lengths of incubation and nestling periods were 14.67 ± 0.33 days, and 18.42 ± 0.49 days respectively. Only the female incubated and brooded the clutch but the male fed the incubating female on the nest at a rate of $0.14 \pm .04$ trips/hr. Both parents fed the nestlings at an average rate of 2.71 trips/hr, and this rate steadily increased throughout the nestling period. Female attentiveness during incubation was 82.81 ± 1.60 % with average on-bouts of $42:03 \pm 1:55$ min. The daily nest survival probability was 0.96 ± 0.01 and the overall nest survival rate was 33.3%. 31% of the nests fledged young successfully and the daily predation rate was 0.03 ± 0.01 . Furthermore, we use literature to compare breeding biology traits of the Fruithunter to the sister clade *Turdus*.

Avian life histories are well studied in north temperate regions, but incomplete information regarding the much less-studied tropical species creates gaps in knowledge that need to be filled in order to improve our understanding of the range of differences between latitudes. Both early and modern ornithology has recognized that the breeding strategies of tropical birds commonly differ greatly from those of temperate birds (Moreau 1944, Lack 1947, Skutch 1949, Cody 1966, Macarthur 1972, Ricklefs 1980, Martin 2000). The mechanisms that underlie the causes of these differences are still poorly understood (Cox and Martin 2009, Martin 2014), in part due to a lack of available data for strong, among-species/region comparisons. Descriptions of life history traits for enigmatic species such as the Fruithunter are difficult to attain, and may permit the strong, among-species comparisons needed to further understand avian life history evolution (Martin 1996). Here, we present novel information on the breeding biology of the monotypic Fruithunter (*Chlamydochaera jefferyi*), a member of the Turdidae family in Malaysian Borneo, and compare its breeding biology with the cosmopolitan genus *Turdus*, a near-relative within Turdidae.

Turdus has a large latitudinal distribution and breeding information for the genus is relatively well described and widely available (Collar 2005). The fact that it is a sister group to the clade containing Fruithunter (Voelker and Klicka 2008: Fig. 3) makes *Turdus* suitable for the tropical-temperate comparisons offered here. Additionally, the Turdidae represent an interesting group for tropical-temperate comparisons because the genus *Turdus* sometimes shows relatively small life history differences between latitudes, whereas other turdid genera show larger differences, at least in the new world (e.g., Martin and Schwabl 2008). Because of the dearth of data on breeding biology of tropical

turdids in Asia, we have little sense of the extent to which turdid species there differ from those in the north temperate region. For example, it is unclear whether the Fruithunter exhibits slow life history strategies consistent with the tropical-temperate trend observed in most passerines, or shows low variability of traits across latitudes like the genus *Turdus*. Thus, the Fruithunter provides a unique opportunity to examine the breeding biology of a monotypic genera of tropical Asian Turdidae, and compare its life history traits using tropical-temperate life history theory.

The Fruithunter is a frugivorous passerine bird endemic to the mountains of North Borneo. It is found in primary and secondary forests at elevations ranging from 700-3200 meters (Myers 2009). The taxonomy of the Fruithunter has been heavily debated and was historically placed in Campephagidae (Sharpe 1887). It is presently accepted as a member of the pan-global family Turdidae, based on anatomy, DNA analysis, plumage, nidification, and behavior (Ames 1975, Clark Jr. 1981, Olson 1987, Ahlquist et al. 1984). The genus *Chlamydochaera* is monotypic, and sister to the subtropical/tropical genus *Cochoa* (Klicka et al. 2005). Very few life history traits are described for *Cochoa*, which makes the description of the breeding characteristics of the Fruithunter even more important, as it represents the majority of the available data for the clade. Our literature search yielded documentation of only one nest (Parr et al. 2002), with no description of the nest contents or developmental periods.

Finally, we present a digital recording and sonogram of a previously undescribed male vocalization which is likely the song. This was heard and recorded at and away from nest sites, typically in the presence of a female. This song expands the previously known range of vocalizations of this species.

METHODS

Our study site was Kinabalu National Park, Sabah, Malaysia, located in the northern part of the tropical island of Borneo ($6^{\circ} 05' N$, $116^{\circ} 33' E$). We searched for nests in primary and secondary tropical rainforest ranging from 1500 – 1900 m elevation. Our field work lasted from February to June, 2009 - 2012. Nests were located using a combination of behavioral observations and systematic search methods. Once nests were located they were monitored every 1 to 4 days, depending on the stage. Nests were monitored every day near laying, hatching, and fledging stages to increase precision of nest transition stages. Nests were reached using ladders, ascension gear, and free-climbing techniques. Eggs were weighed within 3 days of the start of incubation and again during the last 3 days of incubation to determine fresh egg mass and mass lost due to embryonic metabolism. When eggs were found without the exact incubation date known they were candled using a flashlight to estimate the embryo age and probable hatch date. Mass, tarsus, and wing chord measurements were taken on days 0, 1, and 2 of the nestling period, and repeated every other day until fledge. Additionally, the total length of the 8th primary feather (P8), the length of P8 broken out of the sheath, and tail were measured every other day once they started developing. We calculated growth rates, including *growth rate constant K*, following Remeš and Martin (2002).

Nests were filmed periodically across different stages for 4 to 7 hours per day starting within 30 minutes of sunrise in order to calculate parental attentiveness and nestling provisioning rates. Nest attentiveness was calculated as the amount of time the female was incubating eggs/brooding nestlings divided by the total time filmed for that

day. The incubation period was calculated as the number of days between when the last egg was laid and when the last egg hatched. The nestling period was the amount of time between when the first egg hatched and the date when the first nestling fledged from the nest. Daily survival rate and daily predation rate were calculated using the Mayfield method (Mayfield 1961, 1975, Hensler and Nichols 1981).

We compiled literature data using Handbook of the Birds of the World (Collar 2005) on clutch size, incubation periods, and nestling periods for all available *Turdus* species, sorted by latitude. The species were sorted into two categories, based on latitudinal distribution: temperate and tropical. Temperate species have breeding ranges primarily above 23° N, and below 23° S. The species breeding primarily between 23° north and south were treated as tropical. A few species were that were roughly distributed equally across temperate and tropical zones were omitted from analyses. Clutch size, incubation length, and nestling period were recorded by taking the midpoint of the reported range per species. Many traits were listed as a range of possible values, with a most common value also indicated. In this case, we used the most common value (i.e. 'clutch size 2-7, most commonly 3-4'—here, 3.5 was our midpoint value). These midpoints were averaged by latitude category in order to generate a table with the mean clutch size, length of incubation, and length of nestling periods.

Statistical Analyses.--IBM SPSS Version 22 (2013) was used for all statistical tests. All means are reported with ± 1 standard error. Analysis of variance (ANOVA) was used to test for changes in incubation attentiveness and mean on-bout length across the duration of the incubation period. Linear regressions were used to test for changes in

brooding effort and feeding rates across the nestling period. Independent-Samples *T* Tests were used to determine significance of life history trait variation within *Turdus*.

RESULTS

Nest description.--We found 32 Fruithunter nests, ranging from 1518 to 1879 m in elevation. The nests were open cups with fresh, green moss outside and dark brown rootlet fibers as lining (Photo 1). The vast majority (30 of 32 nests) were on live trees, one was on a vine, and one was built on a dead branch at the top of a snag. Nest height ranged from 3.2m to 19m, with a mean of $8.21 \pm 0.56\text{m}$ ($n=32$). Only one nest was measured for dimensions—the outside measured 14.5 cm and 11.5 cm in diameter and height, respectively. The inside of the cup measured 8.0 cm in diameter and 4.0 cm in height.

Timing of nesting.--Nest initiation (date first egg was laid) ranged from 20 February to 25 May with the median falling between the first and second week of April ($n=24$). The nesting season lasted for a minimum of 106 days, not including the highly variable nest-building stage. This is based on the duration between the earliest known initiation date and the latest known fledge/fail date. Aside from this project, a pair of adults was seen feeding a juvenile between 28 August and 6 September in W. Kalimantan (Prieme and Heegaard 1987).

Clutch and egg sizes.--The mean clutch size was 1.86 ± 0.10 eggs ($n=14$). The modal clutch size was 2, with 12 of 14 nests containing 2 eggs. The eggs were creamy

white with brown specks, sometimes concentrated around the blunt end of the egg. This gave the eggs an overall light-brownish appearance (Photo 2, 3).

The mean fresh egg mass was 6.18 ± 0.22 g (n=11), which represented 9.5% of the adult female body mass (65.06 ± 7.50 g, n=2). The eggs ranged from 5.09 to 7.10g and lost an average of 0.88 ± 0.09 g (n=5) between early and late incubation. This represents approximately 15.3% of the fresh egg mass (n=5).

Incubation period.--The mean incubation period was 14.67 ± 0.33 days (n=6) and the eggs were only incubated by the female. The eggs were incubated by the female 82.8 ± 1.6 % of the time (n=34 video records). Incubation attentiveness did not differ among early, middle, and late incubation periods (ANOVA, $F_{2,19} = 1.02$, $P = 0.38$). The average length of incubation on-bouts and off-bouts were $42:03 \pm 1:55$ and $8:13 \pm 0:40$ minutes respectively (n=34 video records), with no significant change across the incubation period (ANOVA for on-bouts-- $F_{2,18} = 1.86$, $P = 0.19$; ANOVA for off-bouts-- $F_{2,18} = 0.19$, $P = 0.83$). During incubation, the male visited the nest (near the nest for <60 seconds), guarded the nest (near the nest for >60 seconds), and fed the incubating female at an average rate of 0.12 ± 0.03 , 0.09 ± 0.03 , and 0.14 ± 0.04 trips/h, respectively (n=12 nests, from a total of 216.09 hours of incubation footage.)

Nestling period.--The nestlings remained in the nest after hatching for an average of 18.42 ± 0.49 days (n=6). Only the female brooded the nestlings, and to cater to increasing food demands of the nestlings, the percent of time the female spent on the nest decreased across the nestling period ($R^2 = 0.38$, $P < 0.001$; Fig. 2). Both parents fed the nestlings mostly fruits, with occasional insects and larva. A seed catchment trap below one nest collected very large numbers of two species of *Litsea* (Lauraceae), one *L.*

cylindrocarpa and the other unidentified. Both parents brought food to the nestlings and as expected, the feeding rate increased significantly as the nestlings aged ($R^2 = 0.31$, $P < 0.001$; Fig. 1). The male brought food 68.7 % of the time ($n = 952$ feeding trips over 360.65 h).

The mean nestling mass on the day of hatching (day 0) was 5.63 ± 0.71 g ($n=5$) and day 1 was 7.77 ± 0.55 g ($n=12$). Nestlings weighed an average of 34.90 ± 1.18 g ($n=10$) on pin break (the day the 8th primary feather broke from its sheath), which usually occurred on day 8. The growth rate constant K for mass was 0.37 ± 0.02 (fig 3). The growth rate constant K was 0.32 ± 0.01 (fig 4). Wing chord had a K value equal to 0.25 ± 0.01 (Fig. 5).

Nest survival.--10 of the 32 nests fledged young (31%) and 11 were depredated. The other 11 failed due to abandonment, weather, or unknown causes. The daily survival rate was 0.96 ± 0.01 ($n = 419.5$ exposure days, 32 nests), and the overall nest survival rate (likelihood of a nest fledging at least 1 young) was 33%, based on 34 days of combined incubation and nestling exposure.

None of the predation events were captured on film nor observed. Raptors, corvids, laughingthrushes, and treeshrews are the most common nest predators at the site and are likely to be responsible for the majority of the Fruithunter predations as well. Fruithunters can be aggressive towards potential nest predators and on one occasion a Bornean Green-magpie (*Cissa jefferyi*), a common nest predator, was successfully chased away from a nest by a female Fruithunter (A. Mitchell, pers. obs.). The overall daily predation rate was 0.03 ± 0.01 .

Vocalizations.--The male Fruithunter was seen and recorded singing a highly complex song on multiple occasions, usually at or near a nest site, and typically in the presence of a female (see attached sonogram and recording). Only single-noted calls have been described for this species thus far (Collar 2005, Myers 2009). We believe our recording to be the male song due to the locations and proximity to the nest and female while singing. The song, although clear and distinct when close, is remarkably quiet and may have been previously overlooked for this reason.

DISCUSSION

The slow-fast continuum is a central concept of life history theory and describes traits ranging from slow to fast, both within and among taxa (Wiersma et al. 2007, Hille and Copper 2014). This applies to most life history traits, including fecundity, length of development, adult survival, and parental investment in offspring. One of the most distinct trends of this gradient is observed across latitudes, with strategies shifting from faster to slower as latitudes decrease (Cody 1966, Wiersma et al. 2007, Robinson et al. 2010). To generalize, passerine bird communities with the slowest life histories live in tropical regions and the fastest in temperate regions. Interestingly, the thrush genus *Turdus*, a sister taxa of *Chlamydochaera*, exemplifies this trend with some life history traits, but shows less latitudinal variation with others (Martin and Schwabl 2008). For example, the mean clutch size of *Turdus* significantly declines from temperate regions (4.12 ± 0.17) to tropical regions (2.52 ± 0.10), $t(43) = 8.24$, $P < 0.001$; (Table 1), but the length of incubation and nestling periods do not—inc: $t(24) = 1.25$, $P = 0.22$; nstl: $t(24) =$

1.40, $P = 0.17$. Comparisons of life history traits between the Fruithunter and the near relative *Turdus* may help strengthen our understanding of these trends, especially within the family Turdidae.

Life history theory predicts the Fruithunter to have slower life history traits than temperate birds (Wiersma et al. 2007), and our data are consistent with this. Our data suggests that the Fruithunter are even slower than tropical-breeding *Turdus* on all parameters (Table 1). The mean clutch size of 1.86 ± 0.10 eggs/clutch is far less than the mean of temperate-breeding *Turdus*, and appx three-fourths of the mean of 2.48 eggs/clutch for tropical *Turdus*, which has the smallest mean clutch size between temperate and tropical *Turdus* (Table 1). The reduced clutch size may represent low annual fecundity, and may be driven by a reduction in parental investment per breeding attempt as a strategy to maintain a heightened adult body condition (Cody 1966), which may lead to higher adult survival (Martin 2002, Martin 2004). Due to the difficulty in catching large numbers of Fruithunters, survival estimates from mark-recapture techniques are not available from this study, but if they follow the same pattern as other large-bodied tropical passerines we would expect relatively high adult survival compared to temperate birds of equal size (McNamara et al. 2008). Furthermore, there are many potential advantages of laying small clutches in the presence of high nest predation including: reserving energy for subsequent broods, reducing the length of the vulnerable egg-laying period, and reducing the overall nestling feeding rate to minimize predator detection (Slagsvold 1982, Martin 1995). Reduction of clutch size due to high nest predation may be a viable hypothesis, as nest predation was the leading cause of nest

failure for the Fruithunter. With fewer than one out of three nests successfully fledging young, strong directional selection towards a smaller clutch size may result.

The Fruithunter has a longer mean incubation period (14.67 ± 0.33 days) than both temperate and tropical *Turdus*. As it has strictly a tropical range, this is consistent with current theory (Wiersma et al. 2007). The mean nestling period of 18.42 ± 0.49 days is also far longer than all other latitude categories. The longer developmental periods may be a result of lower mean incubation temperatures due to longer off-bouts, and reduced brooding/feeding rates after hatching (Martin et al 2013). Along with a reduced clutch size, the longer developmental periods may represent a strategy of reduced parental investment while trading off with higher adult survival (Martin 2002). This could allow for more lifetime breeding attempts and therefore increased lifetime fecundity.

Our results suggest that the tropical-breeding Fruithunter exhibits life history strategies that are slower than temperate relatives. This is consistent with tropical-temperate life history theory (Wiersma et al. 2007), despite the fact that the sister clade *Turdus* shows less variation across latitudes (Martin and Schwabl 2008; Table 1). Understanding the evolutionary mechanisms that cause these trait shifts along with why some taxonomic groups show larger shifts than others will require further studies.

ACKNOWLEDGEMENTS

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FIGURE LEGENDS

FIG. 1. Scatter plot of adult provisioning rate (trips/hr) per nestling age.

FIG. 2. Scatter plot of adult brooding effort (as percent of time on nest brooding nestlings) per nestling age.

FIG. 3. Fruithunter growth rate (mass) per day of nestling age. Estimated asymptote A is shown with a dotted line.

FIG. 4. Fruithunter growth rate (tarsus) per day of nestling age. Estimated asymptote A is shown with a dotted line.

FIG. 5. Fruithunter growth rate (wing chord) per day of nestling age. Estimated asymptote A is shown with a dotted line.

PHOTO 1. Fruithunter nest structure from 1684 m elevation.

PHOTO 2. Fruithunter eggs.

PHOTO 3. Fruithunter nest and eggs.

Table 1

Latitude	cs	cs_SE	CS_n	inc	inc_SE	inc_n	nstl	nstl_SE	nstl_n
Temperate	4.12	0.165	26	13.03	0.225	17	13.78	0.387	16
Tropical	2.52	0.102	31	13.56	0.395	9	14.85	0.746	10
Fruithunter	1.86	0.1	14	14.67	0.33	6	18.42	0.49	6

Figure 1

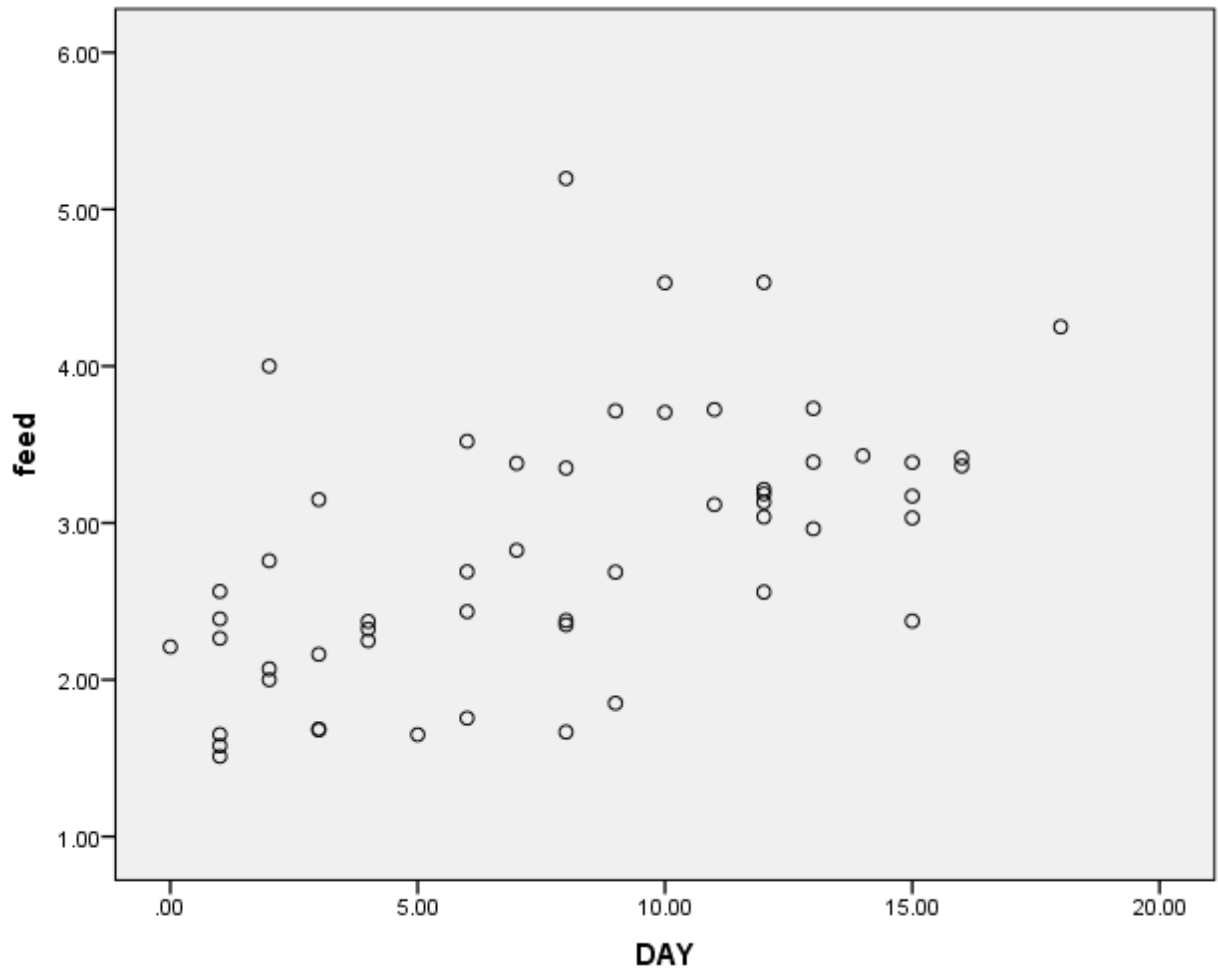


Figure 2

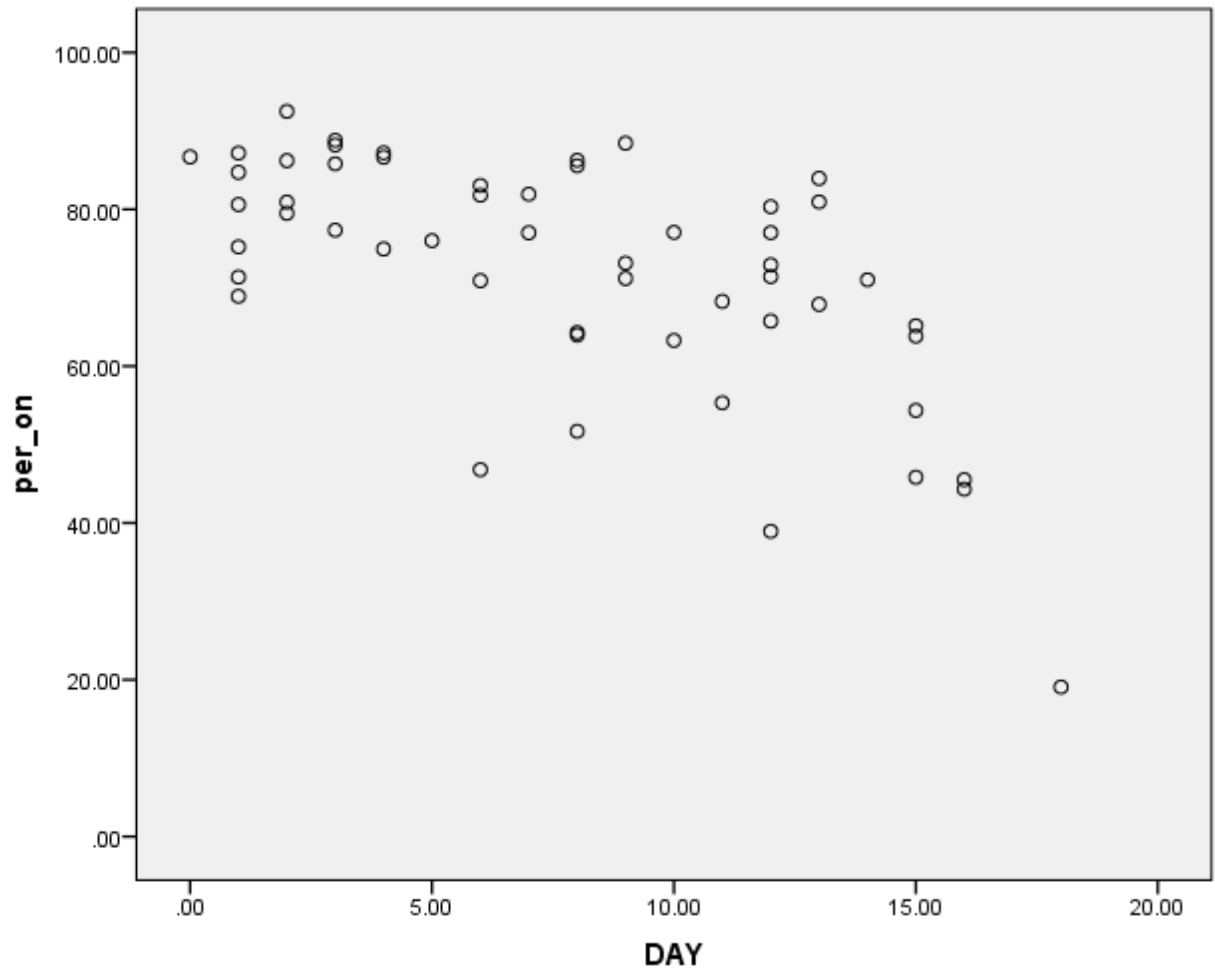


Figure 3

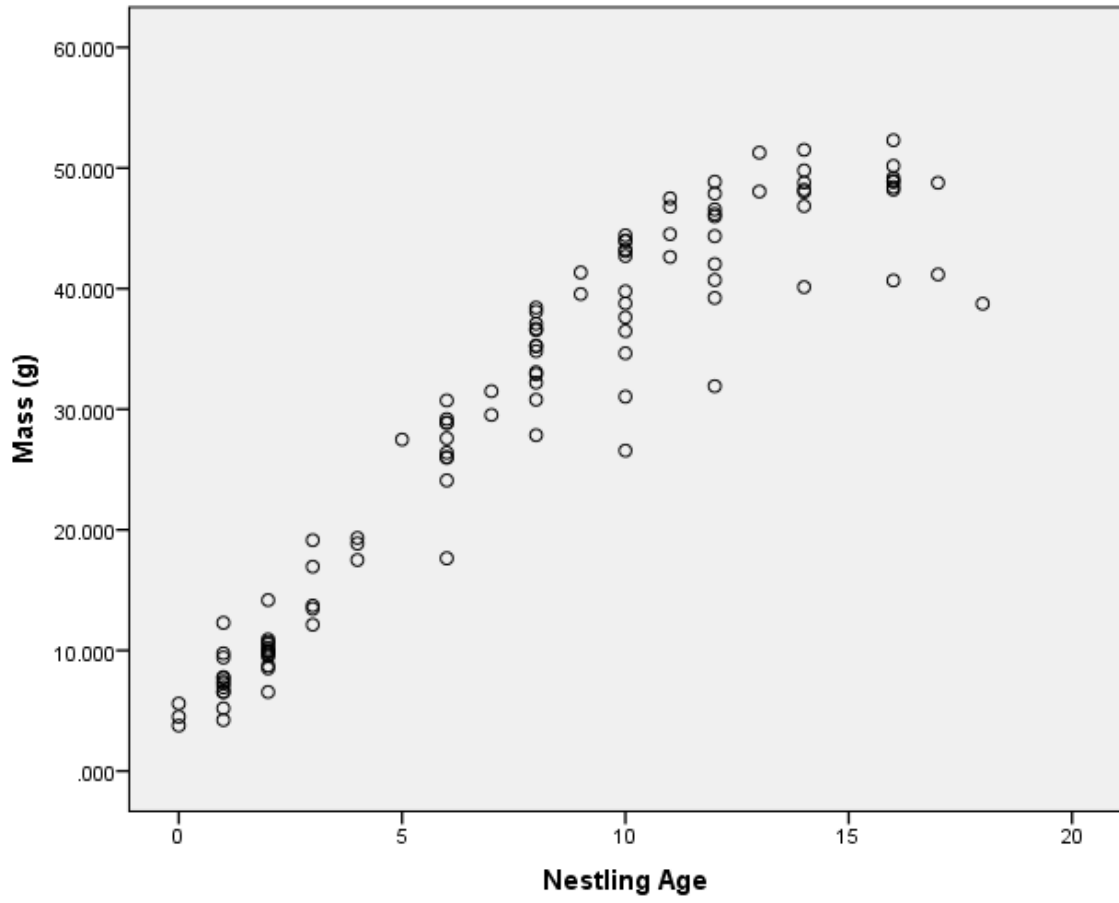


Figure 4

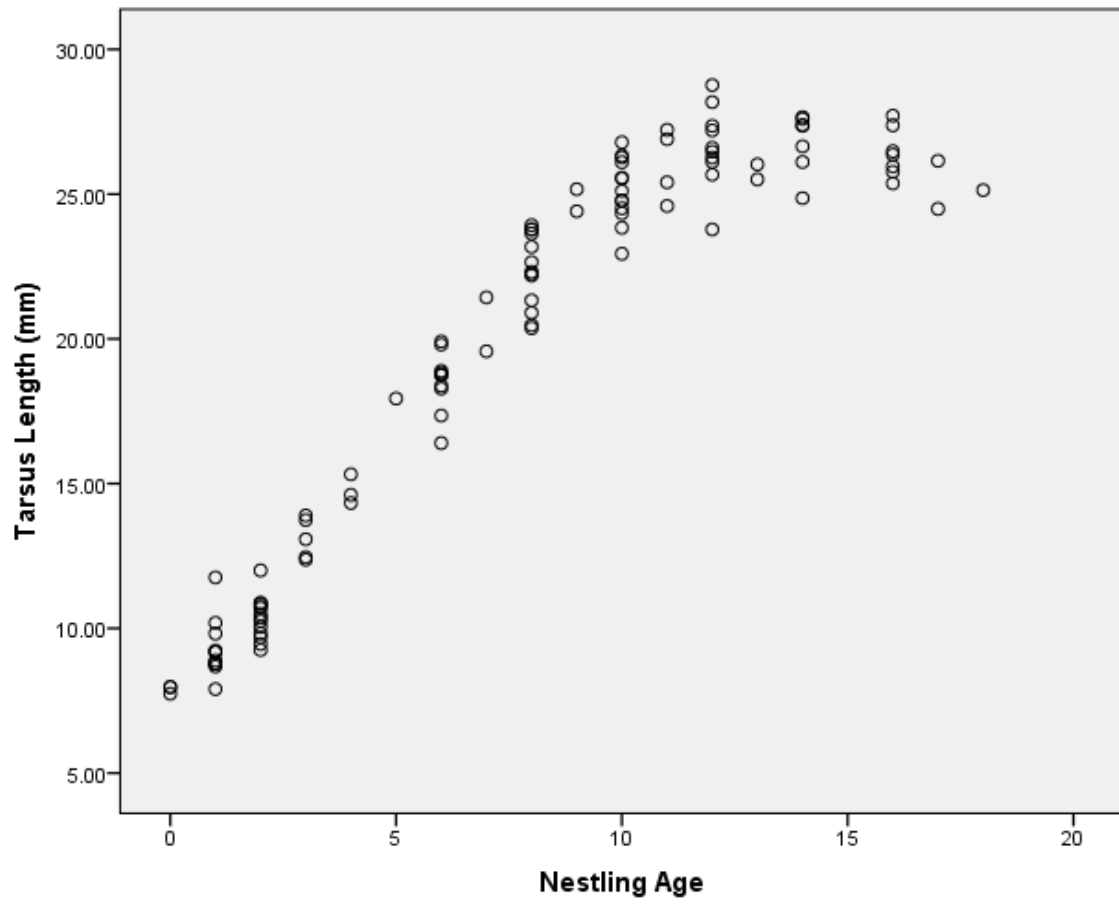
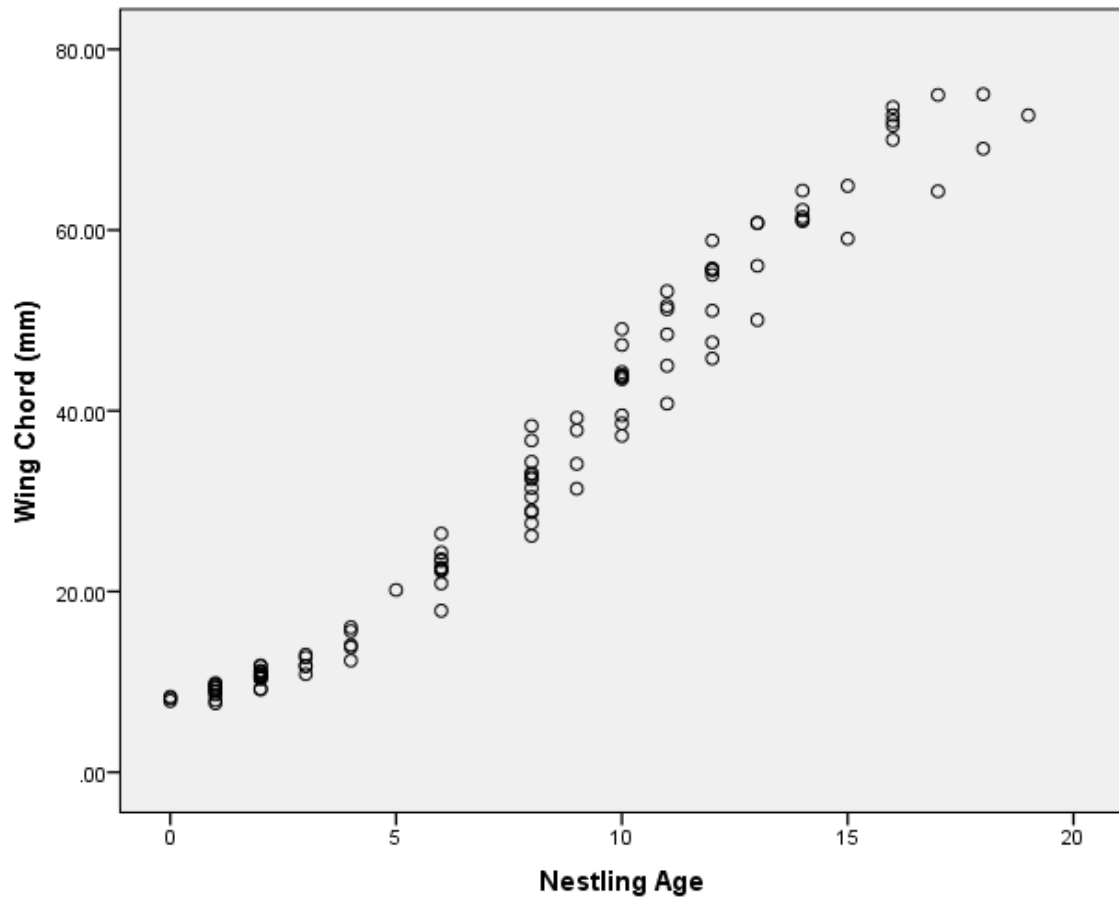


Figure 5



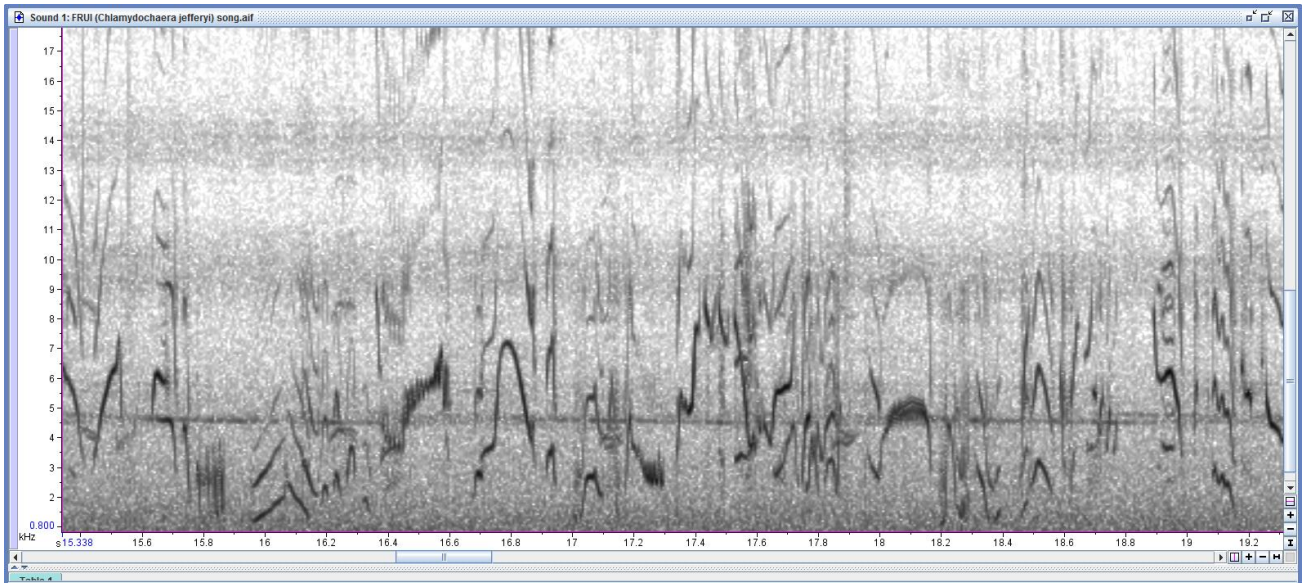
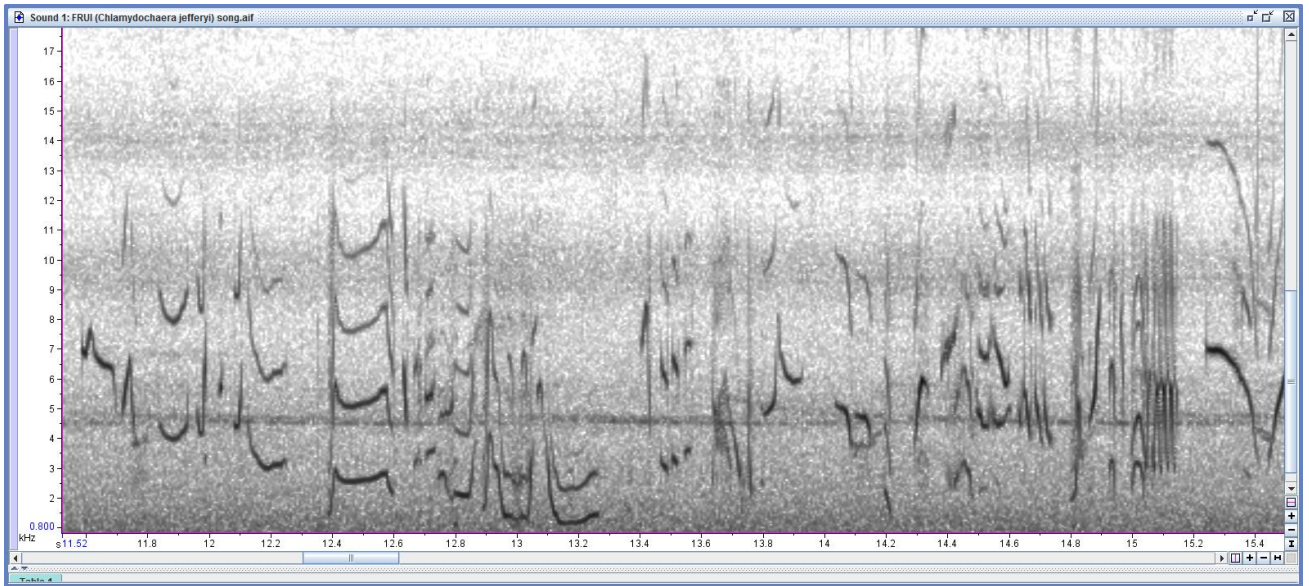


Photo 1



Photo 2



Photo 3

