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AN UPDATE ON THE BREEDING BIOLOGY AND BIOMETRY OF HAUXWELL'S THRUSH (*TURDUS HAUXWELLI*) FROM LOWLAND SOUTHWESTERN BRAZILIAN AMAZON

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Abstract · The Neotropical region is home to a large number of species of the genus *Turdus*. While the breeding biology of this genus is well known in general, data are scant for some Amazonian species, including Hauxwell's Thrush (*Turdus hauxwelli*). Here, we present new data on the breeding and biometry of *T. hauxwelli* based on field observations and captures in a fragment of terra firme forest in southwestern Amazonia, Brazil. We monitored six active nests between 2012 and 2014 and collected data on the incubation and nestling phases of five nests. The nests were built at a mean height of 1.9 m (range: 0.53–3.2 m) above the ground. We estimated incubation time as 13–14 days. We monitored the development of 11 nestlings in four nests. The mean weight of the newly-hatched nestlings was 6.56 g (range: 4.3–9.0 g [SD = 2.27]). The constant (K) of the growth rate in the nestlings was 0.43 (range: 0.31–0.51; SE = 0.03), with an asymptote of 51.1 g (range: 45.04–62.32; SE = 0.31). The daily survival rate of the nests during the incubation phase was 97% and the survival rate during the nestling phase was 90%. Mayfield's success was 70% during the incubation phase and 21% during the development of the nestlings, whereas apparent success was 75% in the incubation phase and 27% in the nestling phase. We banded and measured 64 adult individuals, 13 juveniles, and 4 nestlings in 2005 and between 2009 and 2017. Minimum longevity calculated from the recapture of banded individuals was 6 years, 3 months and 11 days (or 2298 days after banding). Our results indicate that *T. hauxwelli* has a breeding season restricted to a few months of the rainy season (November–March), which overlaps with molt.

Resumo · Novas informações sobre a nidificação e biometria do sabiá-bicolor (*Turdus hauxwelli*) nas terras baixas da Amazônia sul ocidental brasileira
A região Neotropical concentra uma grande diversidade de espécies do gênero *Turdus*. Apesar deste gênero ser um dos mais bem estudados do ponto de vista reprodutivo, para algumas espécies da Amazônia, como *Turdus hauxwelli*, estas informações são escassas. O objetivo aqui é apresentar novos dados sobre a reprodução e biometria de *T. hauxwelli*. No período de 2012 a 2014 encontramos seis ninhos ativos, dos quais cinco foram monitorados na fase de incubação e de ninhegos. Os ninhos foram construídos a uma altura média de 1,9 m (min–max: 0,53–3,2 m) acima do solo. Estimamos o tempo de incubação entre 13 e 14 dias. Acompanhamos o desenvolvimento de 11 ninhegos a partir de quatro ninhos. O peso médio dos filhotes no dia do nascimento foi de 6,56 g (min–max 4,3-9 [DP = 2,27]). A constante (K) da taxa de crescimento dos ninhegos foi de 0,43 (min–max = 0.31–0.51; EP = 0.03) com uma assíntota de 51,1 (min-max: 45.04–62.32; EP = 0.31). A taxa diária de sobrevivência dos ninhos durante a fase de incubação foi 97% e a taxa de sobrevivência diária na fase de ninhegos foi de 90%. O sucesso de Mayfield e o sucesso aparente foram respectivamente de 70 e 75% na fase de incubação e de 21 e 27% na fase de desenvolvimento dos ninhegos. No ano de 2005 e no período entre 2009 e 2017 anilhamos 64 indivíduos: 47 adultos, 13 jovens e quatro ninhegos. A longevidade mínima calculada a partir da recaptura de indivíduos anilhados foi de 6 anos 3 meses e 11 dias (ou 2298 dias após o anilhamento). Nossos resultados indicam que *T. hauxwelli* parece ter uma estação reprodutiva restrita a alguns meses do ano no período de maior pluviosidade na região, entre novembro e março, e que a muda de penas ocorre concomitante com o período de reprodução.

Key words: Longevity · Nest · Nestlings · Survival rate.

INTRODUCTION

Reproduction is a fundamental requisite for the existence of a species (Ridley 2004, Price 2008). Reproductive success guarantees a new generation and birds, like other animals, invest a great deal of effort in this life phase (Clutton-Brock 1988). During the reproductive period, the climate, choice of site, food supply, and the time dedicated to the process are all crucial to the survival of the young (Saether 1985, Poulin et al. 1992, Mezquida & Marone 2001, Tarroux & McNeil 2003). Given this, the study of reproduction in birds found in different geographic areas and distinct environmental conditions contribute to the understanding of population dynamics (James et al. 1992, Böhning-Gaese et al. 1993) and can provide important insights for the development of effective conservation measures for a species. Despite its importance, basic data on breeding patterns is scant for most Neotropical bird species and, in particular, in the Amazonia, which has a high bird diversity, but few detailed studies (del Hoyo et al. 2019).

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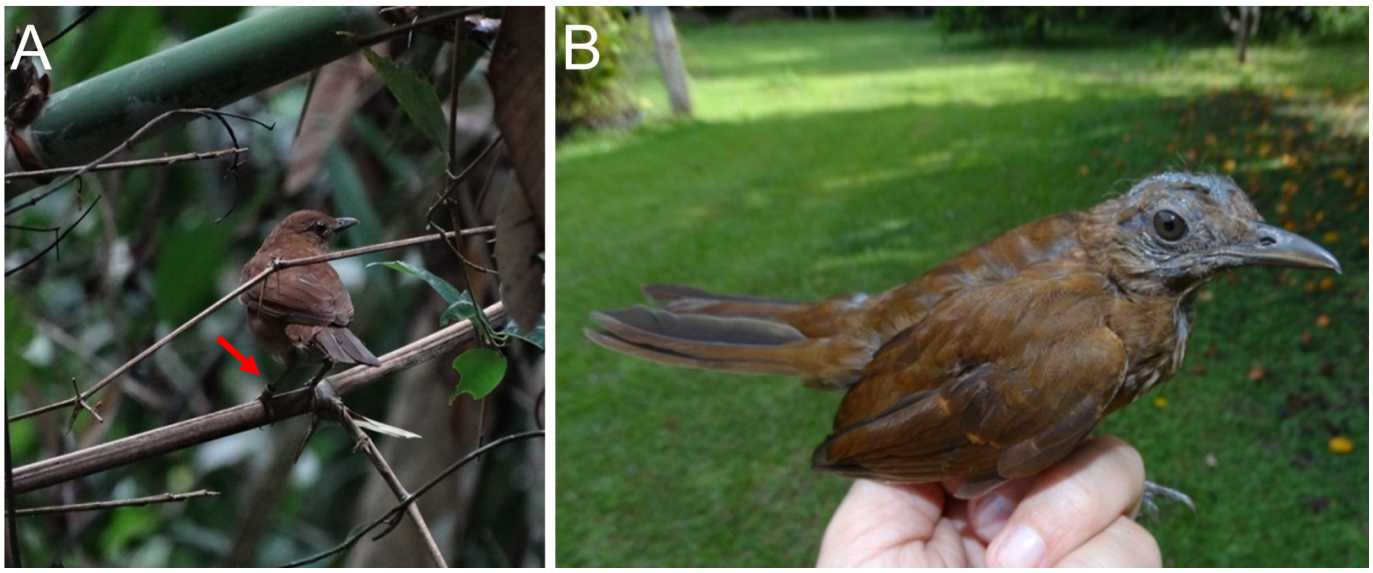

Figure 1. Hauxwell's Thrush (*Turdus hauxwelli*). A – Adult individual (the arrow indicates the band attached to the left leg; B – Individual with molting plumage. Photos: Edson Guilherme.

The family Turdidae is cosmopolitan and one of its most successful genus is *Turdus*, which has a worldwide distribution (Kentish et al. 1995, Collar 2005). There are 71 *Turdus* species, including the recently discovered Varzea Thrush (*Turdus sanchezorum*). Half of the species (36) are found in the Americas, mostly in the Neotropical region (del Hoyo et al. 2019), with at least 12 species found in the Amazon (Ridgely & Tudor 2009, O'Neill et al. 2011). One of these Amazonian species is Hauxwell's Thrush (*Turdus hauxwelli*). This monotypic species is found in southeastern Colombia, eastern Ecuador and Peru, and western Brazil, including parts of the states of Mato Grosso and Mato Grosso do Sul (Ridgely & Tudor 2009, Buainain et al. 2017). Despite this relatively broad geographic range, which includes parts of five different countries, the first data on the reproductive biology of the species was collected only very recently (Sandoval-H et al. 2018). Here, we aim to expand the information on the breeding biology and biometry of the Hauxwell's Thrush through the collection of data in a lowland *terra firme* forest in the southwestern Brazilian Amazonia.

METHODS

Study area. We conducted the study in the Zoobotanical Park (ZP) of the Federal University of Acre (UFAC) in Rio Branco, the capital of the Brazilian state of Acre. The ZP (9° 57'08.9" S, 67°52'22.5" W) is an urban forest fragment with a total area of a little over 100 ha. See Meneses-Filho et al. (1995) for a more detailed description of the vegetation in the study area, and Guilherme (2001) for details on the local bird fauna.

Search for nests and biometry. We searched for Hauxwell's Thrush nests opportunistically in 2012–2014 and captured individuals of this species in 2005 and 2009–2017. We captured birds using mist-nets, 12 m long and 2.5 m high, with a 36-mm mesh and a capture effort of ca. 4.000 net/hours/year. Birds were banded using numbered metal rings (Figure 1A) supplied by CEMAVE (Brazilian National Center for Wild Bird Research and Conservation) within the scope of the project 1099, coordinated by EG (Senior Bird Bander, Registration Number: 324654). We weighed the birds and the nestlings using a Pesola® balance with 100 g capacity and 1-gram precision in 2005 and 2009–2014, and a digital scale (0.05 g precision) in 2015–2017. We collected standard morphometric data (wing chord length flattened, tarsus length, bill length, head-bill size, tail length and total length) following the protocol of Proctor & Lynch (1993). To measure wing, tail and total length we use a ruler with a millimeter scale and to measure other characters we used an analogical caliper (0.05 mm precision) in 2005 and 2009–2014, and a digital caliper (0.01 mm precision) in 2015–2017. We distinguished the juveniles and adults during banding, based on the presence of juvenile plumage, i.e. first-cycle juvenile and second-cycle basic plumage (see Sibley 2010, Johnson et al. 2011, Figure 1B). Each mist-netted bird was inspected to determine its molt status (body, wing and tail) (Sibley 2010; Figure 1B) and the presence of a well-defined brood patch (sensu Redfern 2010). We measured the cloacal temperature with a digital thermometer (measuring range of 32 °C to 42.9 °C and resolution of 0.1 °C) and calculated the minimum longevity based on the time between the day an individual was banded and its last recapture (Scholer et al. 2018).

Incubation and nestling development. We monitored active nests until either the last nestling fledged, or when no further reproductive activity was observed due to predation or the nest being abandoned. Nests found newly built or with eggs were monitored almost every day until the first laying or hatching. We weighed the eggs using a digital scale (0.05 g precision) and measured them with a digital caliper (0.01 mm precision). We calculated the incubation period (whenever possible) from the laying of the last egg to the hatching of the last chick. We weighed the nestlings every two days after hatching and individually marked the chicks, initially with a colored plastic ring, which was later replaced by a permanent metal ring. We calculated the nestling development period from the moment at which the first chick hatched, until the last chick left the nest. We determined the growth rate of the chicks using the logistic equation proposed by Ricklefs (1967): $W(t) = A / (1+e[-K(t-ti)])$, where W (t) = the mass of the chick at age t, A = the asymptote of the

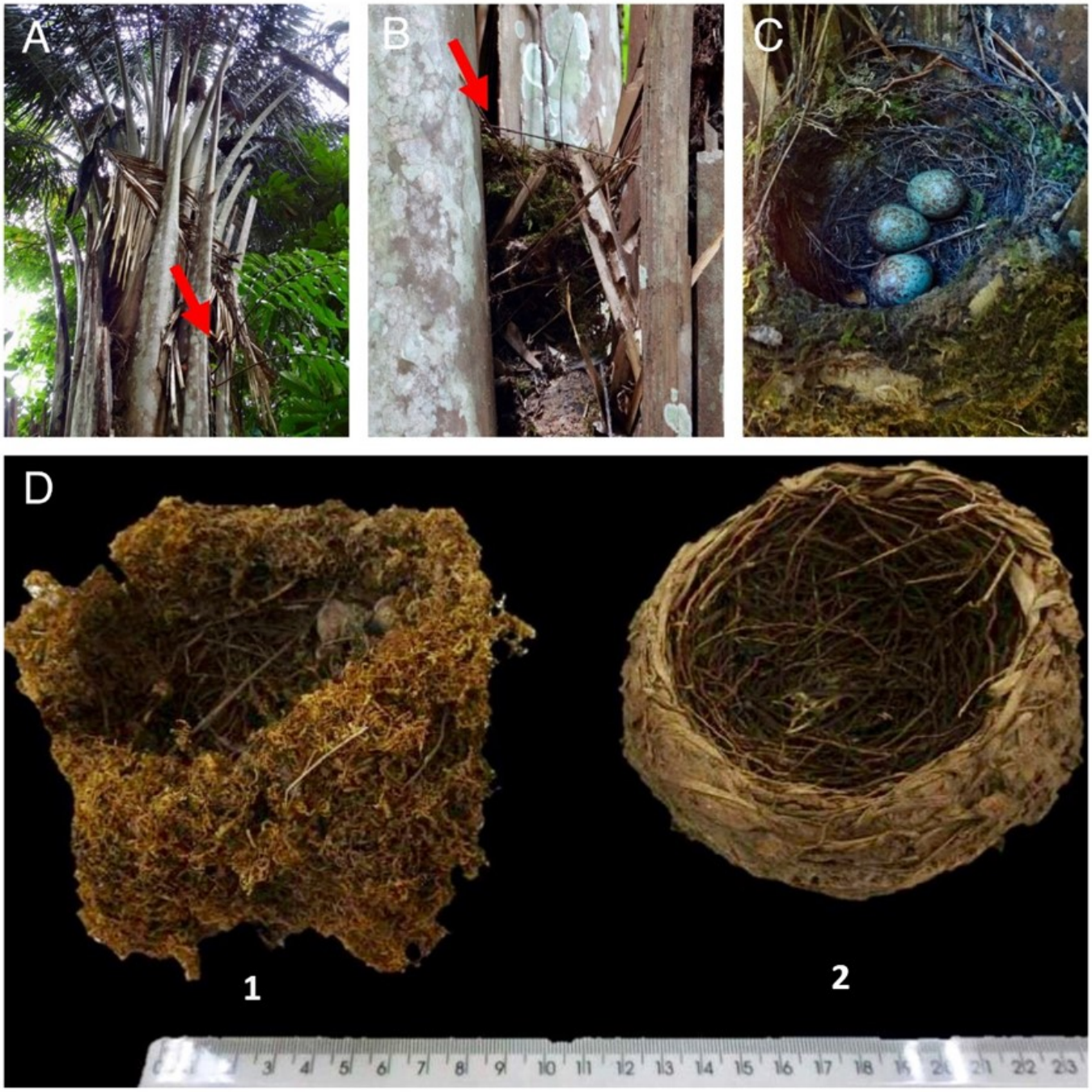

Figure 2. Nests of the Hauxwell's Thrush (*Turdus hauxwelli*). A – *Attalea tessmannii* palms, in which one of the Hauxwell's Thrush nests was built; B – Detail of the nest. In A and B, the arrows indicate the position of the nest; C – Nest with eggs seen from above; D – Comparison of a Hauxwell's Thrush nest (1) with that of the Black-billed Thrush (*Turdus ignobilis debilis*) (2). Photos: Edson Guilherme.

growth curve, K = the constant of the growth rate, and ti = the point of inflection of the time axis. We calculated reproductive success rates by Mayfield's method (Mayfield 1961) and determined the apparent success with the ratio of successful nests to the total number of nests identified (Jehle et al. 2004). During the monitoring of the nestlings we also observed opportunistically what type of food was being offered to the chicks by the adults.

RESULTS

We found six active Hauxwell's Thrush nests in the UFAC - ZP between 2012 and 2014 (Table 1). All the nests were built in plants located at the margin of the trails across the fragment, at a mean height of 1.9 m (range: 0.53–3.2 m) above the ground. Four nests had been built at the insertion of the leaves in the trunks of the palms *Attalea phalerata* (N = 3) and *Attalea tessmannii* (N = 1; Table1; Figure 2A, 2B). One nest was built just above the ground in a branch fork of the exotic shrub *Dracaena fragrans*, while the other nest was built on the trunk of an unidentified plant. Eggs were found in four of these nests (1, 2, 4 and 6; Table 1), while Nest 3 contained two recently-hatched chicks with an estimated age of three days (based on their weight). One (Nest 5) had been recently built, although the female did not lay a clutch (Table 1).

Nests. The nests were built primarily out of roots and moss (Figure 2D). The internal layer was made only of fine roots, while the external layer of the nest was cemented to the plant with a small amount of clay with live moss attached to it. This moss grows over the whole external portion of the

Figure 3. Development of the Hauxwell's Thrush (*Turdus hauxwelli*) nestlings. A – Recently-hatched chicks; B – Chicks at 5 days of life; C – Chick at 13 days of life (the arrow indicates the presence of ants of the genus *Dolichoderus* in the nest); D – Chick at 15 days of life; E – Chick at 17 days of life after leaving the nest, and moving on the adjacent branches (Photos: Edson Guilherme).

nest, including the edge of the chamber, or "cup", which confers a green hue to the whole structure (Figures 2C, 2D, 3A). The nests (collected after nestlings fledged or contents were depredated) weighed between 69.17 g and 201.36 g. Measurements of three nests revealed a mean internal diameter of 77.75 mm (SD = 1.3), a mean incubation chamber depth of 55.67 mm (SD = 8.14), a mean external width of 129.24 mm (SD = 10.88), a length of 140.42 mm (SD = 4.99), a mean external height of 101.33 mm (SD = 12.10), and a mean wall thickness of 26.61 mm (SD = 2.14).

Eggs and incubation. Mean egg mass was 3.7 g (range: 1–5 g) and the mean dimensions were 2.5 cm x 1.8 cm (range: 2.4–2.7 x 1.1–2.0). Clutches contained two (N = 1) or three (N = 3; Figure 2C) eggs. Eggs hatched in three of the four nests containing eggs, while in one case (Nest 2), the eggs suffered predation (Table 1). We estimated incubation time to be between 13 and 14 days.

Nestlings. We monitored the development of 11 nestlings in four nests (1, 3, 4, and 6; Figure 4). The nestlings are born naked, pinkish in color, with their eyes closed (Figure 3A). After five days, when the nestlings open their mouths to solicit food, their eyes are half open, and the first remiges' shafts begin to appear (Figure 3B). Three chicks hatched in three of the nests monitored from the incubation period onward (Nests 1, 4, and 6; Table 1). When hatching, the mean weight of the chicks was 6.56 g (range: 4.3–9.0 [SD = 2.27]). In all three cases (Nests 1, 4, and 6), only one nestling survived to reach a weight of over 30 g on days 11–15 (Figure 4). In Nest 1, two nestlings died on the 5th day. In Nest 4, one nestling died after the 8th day and, while the two others

Table 1. Characteristics of Hauxwell's Thrush's nests (*Turdus hauxwelli*) found in a fragment of *terra firme* forest in southwestern Amazonia between 2012 and 2014.

Nest	Date of finding	Plant support	Height from ground (m)	Clutch or Brood size	Date of laying	Incubation start	Date of hatch	Mortality (N)/ Cause	Fledging nestlings (N), date
1	16 Nov. 2012	*Attalea phalerata*	3.19	3 eggs	Nest found with eggs		23 Nov. 2012	2 nestlings/ possibly predated	1 – 09 Dec. 2012
2	31 Dec. 2012	Not ident.	0.53	2 eggs	Nest found with eggs			2 eggs/ predated	0
3	31 Dec. 2012	*Attalea phalerata*	2.4	2 nestlings				2 nestlings/jumped from the nest and were no longer seen	0
4	27 Nov. 2013	*Dracaena fragrans*	0.58	3 eggs	Nest found with eggs		07 Dec. 2013	2 nestlings/ inanition	1 – 22 Dec. 2013
5	05 Dec. 2013	*Attalea phalerata*	2.3	Empty					
6	11 Dec. 2014	*Attalea tessmannii*	2.59	3 eggs	19 Dec. 2014	24 Dec. 2014	02 Jan. 2015	2 nestlings/ inanition	1 – 6 Jan. 2015

survived until the 12th day, one began to lose weight from the 10th day onward, whereas the other nestling continued to gain weight (Figure 4). In Nest 3, in which two nestlings were found, both chicks reached a weight of over 40 g by the 11th day of life (Figure 4). On this day, after being weighed, both chicks were spooked, jumped from the nest, and were not seen again. In Nest 6 (Figure 3A-E), like Nest 1, two nestlings also died on the 5th day of life. The surviving nestling abandoned this nest when it weighed 32 g (Figures 3E and 4).

The growth rate constant (K) of the nestlings was 0.43 (range: 0.31–0.51; SE = 0.03), with an asymptote of 51.1 g (range: 45.04–62.32; SE = 0.31, Figure 5). The daily survival rate of the nests during the incubation phase was 97%, and during the nestling phase this rate was 90%. Mayfield's success was 70% in the incubation phase (assuming 14 days of incubation) and 21% in the nestling development phase (assuming it lasts 15 days). Apparent success was 75% in the incubation phase and 27% in the nestling phase.

Nestling feeding. During the first half of the nestling phase, the chicks were fed almost exclusively on animal protein (i.e., earthworms), while during the second half, the diet shifted to fruit, mainly açaí (*Euterpe* sp.). In Nest 6, as soon as the fruit diet was initiated (on the 7th day), ants of the genus *Dolichoderus* began to visit the nest (Figure 3C).

Breeding season. We captured adult Hauxwell's Thrushes during almost all months of the year (Figures 1A and 6), but we only captured juveniles between December and April (Figures 1B and 6). Active nests were found in November and December, although some remained active in January (Figure 6). However, we observed birds with brood patches only between January and March. We recorded molting adults between January and April (Figure 6).

Morphometrics. We banded 64 individuals, including 47 adults, 13 juveniles and 4 nestlings. The adults had a mean weight of 65.8 g (range: 55–79 g [SD = 5.9] N = 33). Mean wing length was 112.8 mm (range: 104–122 mm [SD = 3.9] N = 34), mean tarsal length was 27.1 mm (range: 22–33 mm [SD = 3.8] N =33), tail length was 89.85 mm (range: 76–95 [SD = 5.4] N = 34), total length was 228.8 mm (range: 205–256 mm [SD = 10.5] N = 28), bill length was 20.7 mm (range: 15–25 [SD = 2.2] N = 22), and head-bill size was 46.3 mm (range: 46–47 [SD = 0.6] (N = 3). Cloacal temperature was 42.8° C (N = 1).

Minimum longevity. Overall, we recaptured 12 of the 64 banded individuals. The greatest minimum longevity was recorded for individual H 41592, which was banded in 2005 as a juvenile, and recaptured in 2011 (6 years, 3 months, and 11 days later, or 2298 days after banding). Individual J 33048 was recaptured after 3 years, 10 months, and 2 days (1402 days after banding). Three individuals were recaptured 589, 431, and 384 days after the ringing, and the remaining seven were recaptured less than 20 days after the banding.

DISCUSSION

Hauxwell's Thrush appears on the first bird list of the UFAC - ZP as Cocoa Thrush (*Turdus fumigatus*; Guilherme 2001). The active nests found in the area, together with the recapture of banded individuals over the years, leave little doubt that the species is resident and locally common. Its more common and sympatric congener, the Black-billed Thrush (*Turdus ignobilis debilis*), inhabits open areas and urbanized habitats (Guilherme 2016), while Hauxwell's Thrush is found only in forests, although it may sometimes be encountered in clearings with tracts of açaí palms (*Euterpe* sp.). Hauxwell's Thrush is thus essentially a forest-dwelling species.

This thrush nests in plants located within and at the forest's edge; in the study area, it seemed to prefer the trunks of palms of the genus Attalea (Figure 2A, 2B). The nests were built at varying heights, which were consistent with the heights recorded by Sandoval-H et al. (2018) in Manu, Perú. Clutch size, egg weight, and incubation times were also similar to those recorded by Sandoval-H et al. (2018) and other species of the genus *Turdus* (Snow & Snow 1963).

The nest of the Hauxwell's Thrush is of the low cup/ base type (Simon & Pacheco 2005), which is typical for thrushes (Ruiz et al. 2017, Oliveira Jr. et al. 2014, Sainz-Borgo 2014), and the nest-building materials and the dimensions of the nest were similar to those recorded in Perú (Sandoval-H et al. 2018). This species, like the Spectacled Thrush (*Turdus nudigenis*, Sainz-Borgo 2014), does not typically use clay (or "mud") to line the exterior of the nest, and in the our study area, the nests were lined basically with mosses and roots, which makes the nests lighter and more irregular in shape than those of the Black-billed Thrush (Figure 2D).

The growth rates of the chicks based on their body mass and the asymptote of the growth curve were also consistent with the findings of Sandoval-H et al. (2018). The survival rate, on the other hand, was high in all three nests during the

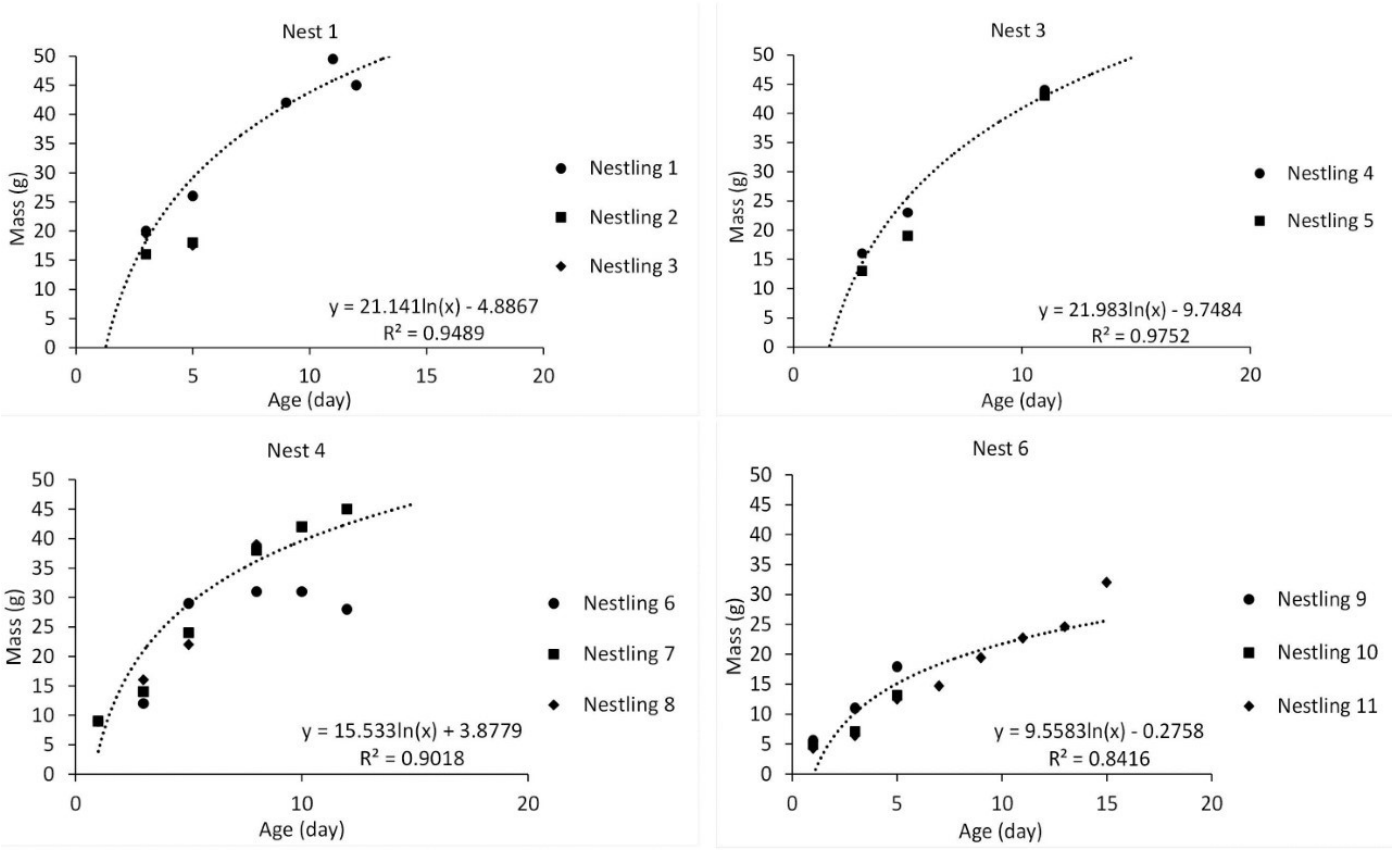

Figure 4. Weight gain and development of nestlings from four active Hauxwell's Thrush (*Turdus hauxwelli*) nests monitored in a fragment of *terra firme* forest in southwestern Amazonia between 2012 and 2014. The nestling numbers were assigned according to the order in which the nests were encountered. The line of the logarithmic equation was calculated only for the best developed nestling in each nest. Nests 2 and 5 are not shown here because they have not reached the nestling phase.

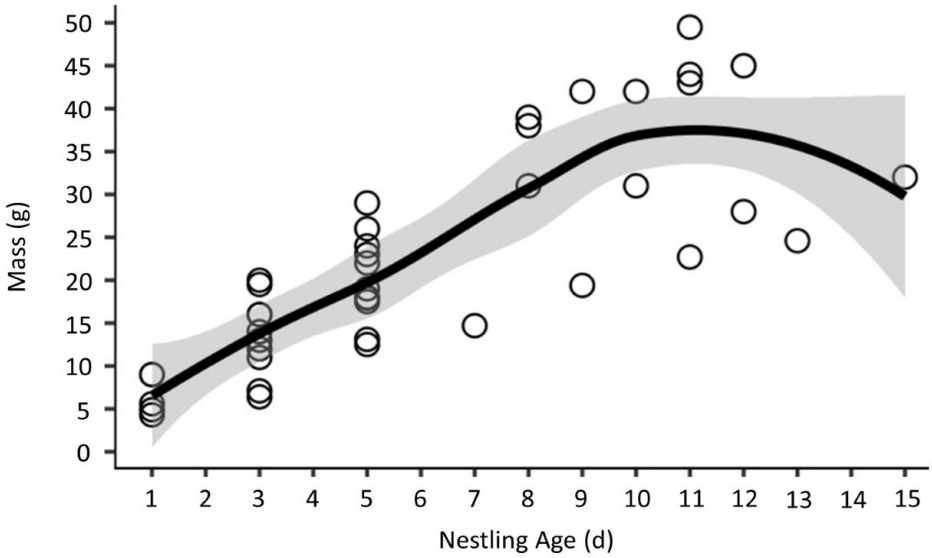

Figure 5. Logistic growth curve for Hauxwell's Thrush (*Turdus hauxwelli*) based on the development of the 11 nestlings monitored in the present study. Each circle represents a different nestling.

incubation phase, and similar to that recorded for the Pale-eyed Thrush (*Turdus leucops*) in Ecuador (Halupka & Greeney 2009). Apparent success during the nestling development phase was relatively low due to the high mortality rate. As a small number of nests was monitored in different breeding seasons, it is not possible to confirm conclusively that this is typical of an entire breeding season in this species. Sandoval-H et al. (2018) also reported a low success rate for Hauxwell's Thrush nests in Perú, mainly because of the nestlings' mortality caused by predation. In the present study, the nestlings of at least two of the five nests monitored appeared to have died from inanition (Table 1). The fact that some chicks started losing weight a few days after hatching (Figure 4) indicates that they had, for some reason, stopped feeding. It was not possible to determine whether the nestling stopped feeding on the initiative of the parents or due to

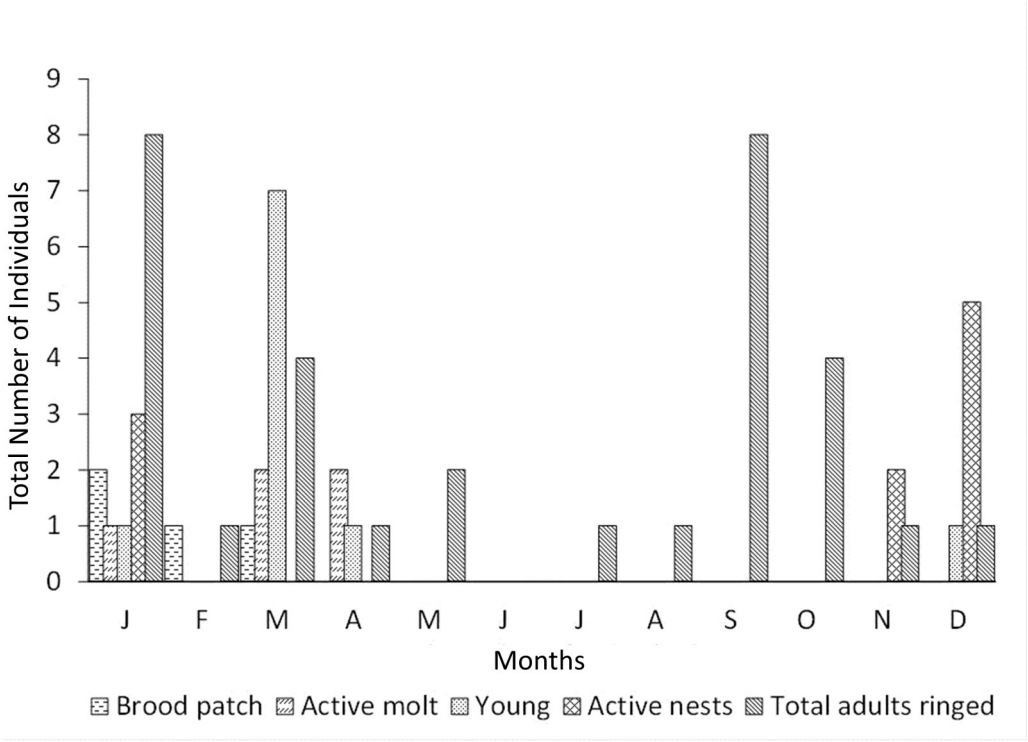

Figure 6. Hauxwell's thrushes (*Turdus hauxwelli*) captured during the study period in a fragment of *terra firme* forest in southwestern Amazonia in 2005 and between 2009 and 2017, showing the numbers of banded adults and juveniles, molting, the presence of vascularized brood patches and active nests. Recaptures are not shown.

competition from the older siblings, as observed in some birds (Mock & Parker 1997). We believe that the most likely factor was feeding constraint (Slagsvold & Wiebe 2007); in this case, when the chicks hatch asynchronously, the parents may begin to prioritize the older nestlings over the younger ones and provide them with larger and more succulent prey or fruit, causing the youngest to starve (Slagsvold & Wiebe 2007). Low nestling survival rates have been recorded not only in other *Turdus* species (Halupka & Greeney 2009, Ruiz et al. 2017), but also in many other passerine species (Mezquida & Marone 2001).

The nestlings are initially fed on animal protein and, subsequently, with fruit. The presence of *Dolichoderus* ants inside one of the nests (Figure 3C) may reflect a commensalistic relationship since the ants remained in the nest until the young bird departed, but did not interfere with its development. These ants appeared when the diet of the nestling shifted to fruit (mainly açaí). One occasion, we observed the nestling regurgitating seeds in the nest, after which the ants foraged for the organic residue still attached to the seeds.

The measurements of the Hauxwell's Thrushes in the ZP are consistent with those registered for this species in other areas of the geographic distribution of the species (O'Neill et al. 2011, Buainain et al. 2017, Sandoval-H et al. 2018). The cloacal temperature was recorded in Hauxwell's Thrush here for the first time, and it is similar to that recorded for the Pale-breasted Thrush (*Turdus leucomelas*) in the Brazilian state of Mato Grosso by Oniki & Willis (1999). In contrast to other *Turdus* species (i.e., *T. leucomelas*), which reproduce throughout the year (for a review, see Ruiz et al. 2017), Hauxwell's Thrush appears to have a breeding season restricted to a few months of the rainy season in the Rio Branco's region (Duarte 2007), between November and March, which matches the period of greatest abundance of feeding resources in the equatorial region (Poulin et al. 1992). For Hauxwell's Thrush, the molt also appears to coincide with the breeding season, as observed in the Pale-breasted Thrush (Ruiz et al. 2017). This differs from the White-throated Thrush (*Turdus albicollis*) in Central Amazonia, where Johnson et al. (2011) recorded no overlap between molt and breeding season.

The minimum longevity of Hauxwell's Thrush presented here is also the first published estimate for this species. In a brief literature search, we encountered longevity data for five Neotropical *Turdus* species (Snow & Lill 1974, Lopes et al. 1980, Lentino et al. 2003, Scholer et al. 2018). The longest-lived was the White-throated Thrush, at 14 years and 10 months (see Scholer et al. 2018 - mistyped as *Turdis albicollis*), followed by the Cocoa Thrush, which survived for 10.5 years after banding (Snow & Lill 1974). This suggests that the individual banded as a juvenile in the present study, recaptured more than six years later, is likely to survive for a number of years based on the lifespans recorded for other species of this genus.

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