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BREEDING LIFE-HISTORY TRAITS OF THE PALE-BREASTED THRUSH (*TURDUS LEUCOMELAS*) IN SOUTHEASTERN BRAZIL

Paulo V. Davanço, Leonardo S. de Oliveira, Lívia M. S. Sousa, & Mercival R. Francisco

Universidade Federal de São Carlos, Campus de Sorocaba, Depto. de Ciências Ambientais,
Rod. João Leme dos Santos, Km 110, Bairro Itinga, CEP 18052-780, Sorocaba, SP, Brazil.
E-mail: mercival@ufscar.br

Resumo. – Parâmetros reprodutivos da história de vida do Sabiá-barranco (*Turdus leucomelas*) no sudeste do Brasil. – Apresentamos aqui informações sobre a biologia reprodutiva do Sabiá-barranco (*Turdus leucomelas*) no sudeste do Brasil, bem como comparações intra- e interespecíficas de parâmetros reprodutivos da história de vida. Testamos a premissa de que a fecundidade anual no Sabiá-barranco é menor do que no "Robin" norte americano (*T. migratorius*) e a premissa de que as ninhadas são maiores e as estações reprodutivas são menores em latitudes mais altas, comparando nossa população com populações do Sabiá-barranco de regiões equatoriais. Durante três estações reprodutivas analisamos 50 ninhos ativos do Sabiá-barranco. Os ninhos ativos se concentraram entre setembro e novembro. O tamanho das ninhadas foi de 2.52 ± 0.72 (média ± DP). Os períodos de incubação e permanência dos filhotes nos ninhos foram, respectivamente, 12.8 ± 0.81 e 15.5 ± 1.1 dias. O número de ninhadas mais freqüente foi dois. A taxa média de sucesso dos ninhos foi 57% e o número médio de filhotes que deixaram os ninhos com sucesso foi 2.46 ± 0.78. Embora as ninhadas do Sabiá-barranco tenham sido menores que do Robin norte-americano, o número de filhotes produzidos por ninho, o número de ninhadas por ano e as taxas de sobrevivência dos ninhos foram similares, indicando que o número de filhotes produzidos por estação seja similar. As estações reprodutivas do Sabiá-barranco foram maiores nas latitudes mais baixas, como encontrado em diversos passeriformes no hemisfério norte. Embora os tamanhos de ninhadas não tenham diferido significativamente, nós apresentamos evidências de que a fecundidade anual possa ser maior em baixas latitudes devido ao maior número de ninhadas por ano. Este estudo é um dos poucos que investigou uma série de parâmetros e rejeitou a premissa de maior fecundidade em um representante de ambientes temperados. Também sugerimos que possa haver variações na fecundidade anual dentro de espécies neotropicais devido a fatores que vão além do tamanho das ninhadas, revelando uma importante lacuna de conhecimento sobre a história de vida reprodutiva das aves.

Abstract. – Here we provide information on the reproductive biology of the Pale-breasted Thrush (*Turdus leucomelas*) from southeastern Brazil, and present inter- and intraspecific latitudinal comparisons of breeding life history traits. Specifically, we tested the prediction that annual fecundity in the Pale-breasted Thrush is lower than in the temperate American Robin (*T. migratorius*), and the prediction of larger clutch sizes and smaller breeding seasons at higher latitudes, by comparing our study population with equatorial populations of the Pale-breasted Thrush. During three breeding seasons we monitored 50 active nests of the Pale-breasted Thrush. Most active nests were observed from September to November. Clutch size was 2.52 ± 0.72 (mean ± SD). Incubation and nestling periods were respectively 12.8 ± 0.81, and 15.5 ± 1.1 days. The most frequent number of broods per season was two. Overall nesting success was 57%, and average number of fledglings per successful nests was 2.46 ± 0.78. Although clutch sizes of Pale-breasted Thrush were smaller, average number of fledglings per successful nests, number of clutches per season, and nest survival were similar to American Robin, resulting in similar annual offspring production. Pale-breasted Thrush breeding seasons were longer in lower latitudes, as reported for many passerines from the Northern Hemisphere, and this is the first study to demonstrate this tendency in Central/South America. Although clutch sizes did not differ, we provide evidence that annual fecundity in equatorial populations of the Pale-breasted Thrush is greater due to multiple broods. This study is one of a few that have investigated a suite of parameters and failed to support the prediction of greater annual fecundity in a temperate representative. We also suggest that variation in annual fecundity within Neotropical species due to parameters other than clutch size must be important and that there are gaps in our understanding of the breeding life history of birds. *Accepted 9 January 2014.*

Key words: Pale-breasted Thrush, *Turdus leucomelas*, American Robin, *Turdus migratorius*, annual fecundity, breeding behavior, latitudinal variation, South America, Turdidae.

INTRODUCTION

A central element for understanding avian life histories is how breeding traits evolve to maximize fecundity at different latitudes (Martin 1995, Böhning-Gaese *et al.* 2000, Cooper *et al.* 2005). It has long been claimed that northern temperate birds have larger clutch sizes, fewer broods per year and shorter incubation and fledging periods than tropical and southern temperate species (Moreau 1944, Lack 1947, Skutch 1949, Lack & Moreau 1965, Ricklefs 1969; Martin 1996, 2002). Some of these trends also have been observed within Northern Hemisphere species, i.e. larger clutches and fewer broods per season at higher latitudes within their breeding ranges (Lack 1947, Young 1994, Baker 1995, Fargallo & Johnston 1997, Hendricks 1997, Dhondt *et al.* 2002, Cooper *et al.* 2005).

Food limitation and nest predation are usually integral parts of the hypotheses proposed to explain these patterns. For example, Lack (1947) suggested that females lay a number of eggs that maximizes the number of young they can rear successfully, and at higher latitudes the longer days would enable parents to gather more food per day, and to raise more young per clutch. Ashmole (1963) extended Lacks hypothesis suggesting that resources limit population size during the periods of scarcity (non-breeding season) and clutch size is related directly to resource availability in the breeding season and inversely to population density. If so, the greater seasonal resource fluctuation at higher latitudes would result in larger clutch sizes (Ricklefs 1980). Skutch (1949) proposed that nest predators use parental activities to find nests, and the greater nest predation rates in the tropics would favor smaller broods to reduce feeding trips and nest detection by diurnal and visually oriented predators (Skutch 1949, 1985; Martin *et al.* 2000). An alternative hypothesis is that greater nest predation rates and longer breeding seasons in the tropics may favor smaller clutch sizes to distribute the risks of nest predation over various broods. It is also predicted that longer breeding seasons permit more broods per year in lower latitudes (Cody 1966, Martin 1996, Robinson *et al.* 2000, Farnsworth & Simons 2001, Griebeler *et al.* 2010). In an attempt to explain why incubation and nestling periods are longer in the tropics, Martin (2002) proposed that the tropics has greater rates of nest predation and lower rates of adult mortality. In this scenario parents would gain more long-term fitness by reducing nest attentiveness to increase their own survival, resulting in longer breeding cycles.

However, many premises and assumptions related to these hypotheses, and their implications for annual reproductive output still deserves investigation because: 1) these patterns were based on extensive surveys of natural history from single-species (Moreau 1944, Lack 1947, Skutch 1949, Yom-Tov 1994, Geffen & Yom-Tov 2000), and, thus, comparative studies based on pairs of species (to control for phylogeny and ecology) are scarce (Martin *et al.* 2000, Ghalambor & Martin 2001, Freitas & Francisco 2012), 2) most comparisons of annual fecundity were based on clutch size alone (Yom-Tov 1994, Yom-Tov *et al.* 1994, Geffen & Yom-Tov 2000), while multi-broodedness (Martin 1995, Cooper *et al.* 2005, Griebeler *et al.* 2010) and numbers of fledglings per successful nests (Ricklefs 1969) should also be taken into account, and 3) interspecific comparisons could be confounded by intraspecific variations occurring within each hemisphere (for review, see Cooper *et al.* 2005). Intraspecific comparisons across the latitudinal range of Neotropical region, however, have received little attention (Yom-Tov 1994, Young 1994).

The thrush genus *Turdus* (Turdidae) is one of the most speciose and widespread passerine genera, with 65 species distributed throughout Eurasia, Africa, and Central, South, and North America (Collar 2005, Voelker *et al.* 2007). Molecular reconstruction indicates that the New World members of *Turdus* are monophyletic and originated from an African ancestor that colonized tropical Central America 5.7 million years ago, after which a large radiation took place into Central and South America (Voelker *et al.* 2009). Except for resident reproductive populations of the Clay-coloured Thrush (*T. grayi*) in southern Texas, radiation to temperate North America was limited to the American Robin (*T. migratorius*) (Collar 2005, Voelker *et al.* 2009). The monophyletic origin of the New World *Turdus* thrushes, followed by a radiation to different latitudes, indicates that they are appropriate for studying adaptations to tropical vs. temperate habitats, although detailed information about breeding is unavailable for many tropical species.

Here we provide the first detailed description of the breeding life history traits of the Pale-breasted Thrush (*T. leucomelas leucomelas*) in tropical/subtropical South America, and we compare our data to literature information with the following specific objectives in mind: 1) to test the premise that annual fecundity is lower in the Pale-breasted Thrush than in the temperate American Robin when comparing clutch sizes, number of fledglings per nest, number of broods per season, and nest survival, 2) to test the premise that breeding season length and breeding cycle (incubation and nestling periods) are longer in the tropical species, and 3) to determine if clutch sizes and breeding season length vary between our tropical/subtropical study population and equatorial populations of Pale-breasted Thrushes.

METHODS

Study area. We studied the Pale-breasted Thrush on the campus of Faculdade de Engenharia de Sorocaba, in the city of Sorocaba, state of São Paulo, in southeastern Brazil (23°28'S, 47°25'W), and in an adjacent urban park. The 10 ha campus has extensive lawns, gardens and exotic trees (predominantly *Pinus* sp., *Eucalyptus* sp., *Mangifera* sp. and *Grevillea robusta*) mixed with native species typical of the original savanna-like formation (*cerrado*). Buildings and streets occupy about 30% of the area and an adjacent park (2 ha) is *cerrado.* Two streams cross the area and form a patch of partially open vegetation within an urban area. Climate is tropical, with a well-defined humid, hot season from October to March (average rainfall 919 mm, and mean daily temperatures varying from 15.7–32.4°C) and dry, cold season from April to September (average rainfall 294 mm, and mean daily temperatures varying from 11.4–30.6°C).

Study species. The Pale-breasted Thrush is widely distributed in South America, in semi open areas, such as forest borders, clearings, savannas, gallery forests, and a variety of anthropic settings, including orchards, agricultural fields, and urban areas (Ridgely & Tudor 1994, Sick 1997). Although fairly common, the breeding biology of Pale-breasted Thrushes is poorly documented and available information is limited to the subspecies *T. leucomelas albiventer*. The few studies include nest descriptions by Haverschmidt (1959), Oniki & Willis (1983), and Sick (1997). Incubation periods are reported for one nest observed in Surinam (5°N) and one nest from Belém, northern Brazil (1°S), and nestling periods for one nest from Suriname and three nests from Belém (Haverschmidt 1959, Oniki & Willis 1983).

We consider the comparisons between Pale-breasted Thrush and American Robin appropriate because they have close phylogenetic relationship (Voelker *et al.* 2007), use similar habitats, build similar nests, and have similar feeding habits. These similarities permit isolation of effects of latitude from those of phylogeny and ecology (Martin *et al.* 2000). Also, both of them have wide latitudinal distributions, ranging approx. from 10°N'–25°S, and 20–70°N, respectively (Collar 2005).

Field methods and statistical analyses. We conducted nest searches throughout the study area at least twice a week from August to May during three breeding seasons from late 2007 to early 2010. Breeding seasons overlap the change of years, and so, for example, the 2007 breeding season occurs in 2007 and early 2008. Hereafter, we will simply refer to the year in which the breeding season begins (hence, 2007, 2008 and 2009). Nests were located by following adult birds carrying nest materials or delivering food to the young. Nests were checked using a mirror every 13 days.

Clutch sizes were determined only from nests in which we could follow egg-laying from the first to the last egg, and we measured incubation period from the first day of incubation to the day before hatching. Because we performed daily 1-h observation sessions during the laying stage (06:00–09:00 h), we noted when females began incubation with respect to laying (Howell 1942, Rowe & Weatherhead 2009). We assume that laying order predicted hatching and fledging order. Laying dates were noted from nests found during construction or estimated by back-dating when hatching or fledging dates were known (using mean intervals). Nestlings were never touched to avoid stimulating early fledging (Skutch 1945). Repeated nesting was known for some pairs that were captured and individually color-banded during the non-breeding season.

We assumed nest predation when eggs or young nestlings disappeared (Pletschet & Kelly 1990). Nesting success (probability of survival) was estimated for the whole nesting cycle, and for incubation and nestling periods separately, using the Mayfield (1961) method, so that we could compare similar estimates from the literature for the American Robin. We estimated probability of success as the daily survival rate raised to the power of the length of the nesting cycle, and partial nest predations were not considered.

Information on clutch size, incubation and nestling periods, and breeding season length of American Robins was obtained from two studies (latitudes 42° and 43°N, respectively) comprising one from Ithaca, New York (Howell 1942) and the other from Madison, Wisconsin (Young 1955), and number of fledglings from Howell (1942) and Knupp *et al.* (1977) (northern Maine). We used similar methods as those used in the above mentioned studies to estimate reproductive parameters. Clutch sizes and breeding season length of equatorial populations of Pale-breasted Thrushes (*T. l. albiventer*) were obtained from Haverschmidt (1959) and Oniki & Willis (1983). Descriptive statistics are presented as mean ± SD (standard deviation). Large standard deviations in clutch size indicate non-normality and so we compared clutch sizes using Mann-Whitney *U*-test adjusted for large samples using *Z*-approximation (*ZU*). Incubation and nestling periods were compared using the parametric two-tailed t-test. All statistical analyses were performed using the software BioEstat 2.0 (Ayres *et al.* 2000).

RESULTS

During three breeding seasons (2007, 2008, 2009) we monitored 50 active nests of the Pale-breasted Thrush. The earliest clutch initiation was recorded on 30 August 2008, and the latest nesting activity (the last young observed in a nest) was recorded on 25 January 2009. Most active nests were observed from September to November (Fig. 1).

Clutch sizes, including three second broods of the same pairs, were 1 (n = 3), 2 (n = 14), 3 (n = 19) or 4 (n = 2) eggs, averaging 2.52 0.72 (n = 38 nests). Incubation periods were 12 (n = 7), 13 (n = 9), 14 (n = 1) or 15 days (n = 1) (12.8 ± 0.81; n = 18 eggs from nine nests), varying both within (but never more than one day) and between nests. Nestling stage lasted 13 to 18 days (15.5 ± 1.1, n = 34 young from 15 different nests), and fledging was always synchronous (n = 26 nests).

We observed six permanently resident color-banded pairs and all double-brooded successfully and a color-banded male triple-brooded successfully in two successive breeding seasons. Intervals between broods (fledging of the first nest to the next clutch initiation) averaged 21 ± 12 days (743, n = 10 observations from seven breeding pairs).

Of 39 clutches that were monitored for nest survival, 23 fledged young successfully (59%). Nest survival was 70% during incubation (seven lost to predation and three were abandoned in 364 nest days, n = 34 nests), and 82% during the nestling stage (five predation events in 384 nest days, n = 28 nests). Overall nesting success, from egg-laying to fledging, was 57% (748 nest days, n = 37 nests). The average number of fledglings per active nest was 1.6 ± 1.34 (n = 37). Considering only successful nests, this number was 2.46 ± 0.78 (n = 23).

In American Robins, clutch sizes averaged 3.4 ± 0.60 (range: 1–5, n = 273, Howell 1942, Young 1955), incubation period was 12.8 ± 0.73 days (range: 12–14, n = 17 eggs, Howell 1942), and nestling stage was 13.9 ± 1.05 (range: 11–17, n = 67 young, Howell 1942, Young 1955). The clutch size of the Pale-breasted Thrush was smaller than that of the American Robin ($U = 1986$, $ZU = 6.16$, $P < 0.001$) but the nestling period was longer (t = 7.20, $P < 0.001$). Incubation period was of similar length (t = 0.17, $P = 0.43$). The breeding season length (earliest egg laying to latest fledging) of the American Robin (middle April to middle August) was at least one month shorter than that of the Pale-breasted Thrush (late August to late January). Clutch sizes of birds in our study area did not differ from equatorial populations of the Pale-breasted Thrush (2.4 ± 0.5, n = 16, t = 0.88, $P = 0.38$), but breeding season in Paramaribo, Suriname (5°N), lasted from November to June (n = 9 nests) (Haverschmidt 1959), and in Pará, Brazilian Amazon (1°S), from July to February (n = 32) (Carvalho 1957, Oniki & Willis 1983), being at least three months longer than in our study site.

DISCUSSION

Pale-breasted Thrush vs. American Robin. Our comparison between the Pale-breasted Thrush and the American Robin is consistent with the idea that clutch sizes of Southern Hemisphere passerines are smaller than temperate species (Moreau 1944, Skutch 1949, Geffen & Yom-Tov 2000) and agrees with Martin *et al.* (2000) who compared, among other species, a population of the American

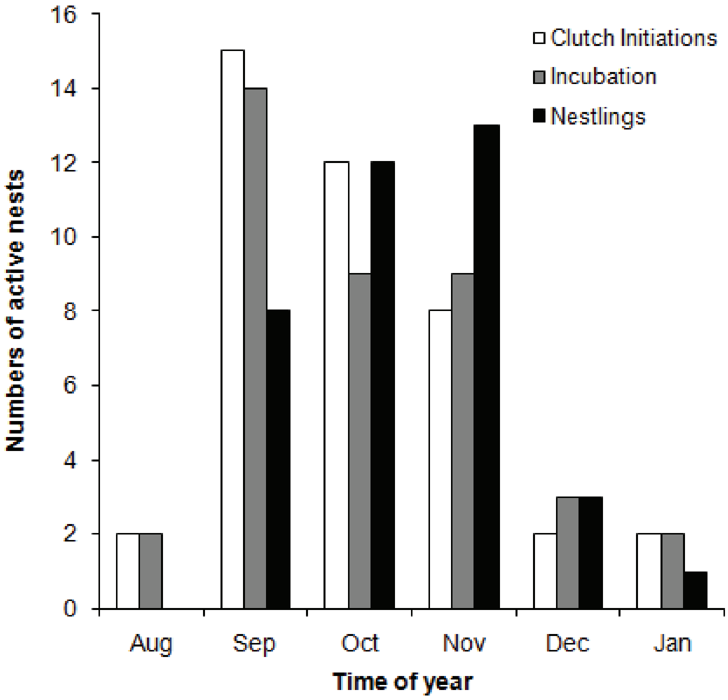

FIG. 1. Numbers of clutch initiations and numbers of active nests (incubation and nestling stages) of the Pale-breasted Thrush (*Turdus leucomelas*) averaged throughout three breeding seasons (2007–2009).

Robin from Arizona (34°N) with a subtropical population of the Rufous-bellied Thrush (*T. rufiventris*) from Argentina (26°S). However, our data fail to support the predictions of many life-history hypotheses that annual offspring production differs between Northern and Southern Hemispheres (Lack 1947, Skutch 1949, Ashmole 1963; Ricklefs 1980, 2000), because 1) the average number of fledglings per successful nests of the Pale-breasted Thrush (2.5) is similar to that found for American Robin populations, i.e., 2.4 in Ithaca, New York (Howell 1942), and 2.5 in northern Maine (Knupp *et al.* 1977), 2) the assumption that Southern Hemisphere species lay more clutches per season is not supported (Lack & Moreau 1965, Ricklefs 1969, Martin 1996), since both American Robin and Pale-breasted Thrush are typically double-brooded, with occasional records of triple-brooded pairs (Brackbill 1952), and 3) overall nesting success in our studied Pale-breasted Thrush population (60%) is higher than in most populations of the American Robin (Knupp *et al.* 1977).

The number of fledglings is an important fecundity parameter that was shown to affect thrush reproductive output in model based-analyses (Powell *et al.* 1999). The similar average number of fledglings per successful nest, despite clutch size differences, may have resulted from a higher frequency of partial brood loss in the populations of the American Robin (Ricklefs 1969), which we observed only once in Pale-breasted Thrushes, indicating that this feature should be considered in latitudinal life-history comparisons.

Our data agree with the idea of longer breeding seasons and nesting cycles in tropical species, but disagree with the idea that the extended breeding season results in more broods per year (but see discussion below about multiple broods in equatorial populations of the Pale-breasted Thrush). The number of broods seems to be balanced by shorter breeding cycles in American Robins (due to the shorter nestling stage). Intraspecific comparisons of another temperate thrush, the Eastern Bluebird (*Sialia sialis*), found a positive correlation between breeding season duration and nesting cycle length (compressed incubation period and re-nesting interval in northern populations) (Cooper *et al.* 2005). Although insufficient information exists on re-nesting intervals of American Robins to evaluate its importance, it could be another important parameter leading to similar numbers of broods per season, since the intervals of the Pale-breasted Thrushes seem to be long (averaging 21 days) when compared, for instance, to the northern temperate Wood Thrush (*Hylocichla mustelina*, 13.4 days) (Friesen *et al.* 2000).

Overall nesting success in our studied Pale-breasted Thrush population (60%) is higher than in most populations of American Robins (for a review, see Knupp *et al.* 1977), which might be due to the moderate urbanization in our study site (see also Morneau *et al.* 1995). Thrushes are tolerant of people, and nests are sometimes built in man-made structures. Such proximity to humans is probably beneficial and likely results in reduced predation (see Møller 2010). Despite this particularity of our study area, nest survival in other tropical thrushes has often been similar or greater than in the American Robin (Snow & Snow 1963, Knupp *et al.* 1977, Ferreti *et al.* 2005). For instance, nest survival of the Rufous-bellied Thrush in an undisturbed subtropical forested savanna from Buenos Aires Province was 61% (Ferreti *et al.* 2005). Also, similar or lower nest predation rates in subtropical Argentina than in Arizona (species paired by phylogeny and ecology) do not support one of the most important assumptions of the Skutch hypothesis (Martin *et al.* 2000). Analyzing the effects of nest survival in annual offspring output is complex because it is highly variable among thrush populations within a species in both hemispheres, but in general, fledgling production is not lower in tropical thrushes due to increased nest predation rates. Annual reproductive output could be affected ultimately by post-fledging survival. Although we have no data to test this hypothesis, it is suggested to be higher in the tropics. Russell (2000) found that post-fledging survival averaged 27.6% for 22 northern temperate passerines, and 37.4% for 34 Southern Hemisphere species. If this pattern is applicable here, it would support our results that annual offspring production is not greater in temperate latitudes.

A poorly tested hypothesis proposes that higher adult survival in Southern Hemisphere birds would favor reduced annual reproductive effort, and that investments in reproduction would be distributed along their extended life time (Skutch 1985, Martin *et al.* 2000). Although smaller clutch sizes in the Pale-breasted Thrush than in the American Robin corroborate this hypothesis, the similar annual reproductive output suggests that life-time offspring production are different between these species, being higher in the tropical representative.

Tropical/subtropical vs. equatorial Pale-breasted Thrushes. Our study area in southeast Brazil is at least 22° latitude (ca. 2440 km) away from the previously studied equatorial populations of the Pale-breasted Thrush. Although such a distance is comparable to studies conducted in the Northern Hemisphere, in which significant clinal variations in clutch size have been found (Bell 1996, Dhondt *et al.* 2002, Cooper *et al.* 2005), our comparison is not consistent with the pattern of larger clutch sizes at higher latitudes. Assuming that the Ashmole hypothesis is applicable to the Southern Hemisphere, resource seasonality and adult mortality in the non-breeding season must be moderate and may not influence Pale-breasted Thrush clutch size within the latitudinal range we examined. Data on intraspecific latitudinal clutch size variation in the Neotropics is limited to the widely distributed House Wren (*Troglodytes aedon*), for which a significant clinal increase in clutch size with latitude was observed in both South (18.553°S) and North America (Young 1994). Differently from House Wrens, the Pale-breasted Thrush is distributed throughout equatorial, tropical, and subtropical South America, not including the regions of harsh winters that may have influenced variation among House Wren populations (Young 1994). Even in North America, where climate is more extreme, clutch size changes in the Eastern Bluebird begin to occur north of latitude 30°N (Dhondt *et al.* 2002), which is at least 10° farther from the equator than our study range.

On the other hand, our comparison is the first in Central or South America to support the idea that the breeding season is extended in lower latitudes, as reported for many passerines in the Northern Hemisphere (Johnston 1954, Hemborg *et al.* 2001, Cooper *et al.* 2005, Renner & McCaffery 2006). Some evidences suggest that longer breeding seasons in these populations may result in a greater number of broods. While color-banded individuals in our study population often raised two clutches per season, two pairs observed by Haverschmidt (1959) reared four consecutive broods. This pattern is also supported by interspecific comparisons of Neotropical thrushes. For example, breeding seasons of the usually single-brooded Rufous-bellied Thrush and Creamy-bellied Thrush (*T. amaurochalinus*) from Argentina were two months shorter (OctoberJanuary, 26°S, Di Giácomo 2005, Ferreti *et al.* 2005) than that found in our study population. On the other hand, in Trinidad (10°N), active nests of the Cocoa Thrush (*T. fumigatus*) and White-necked Thrush (*T. albicollis*) were found throughout the year, except in September/October, and three pairs of Cocoa Thrush reared four successful clutches in one season (Snow & Snow 1963). Because local effects do not appear to influence general climatic conditions, we suggest breeding season length is likely influenced by latitude. Thus, although clutch size of the Neotropical Pale-breasted Thrush varies little over our latitudinal scale, annual fecundity can be greater in lower latitudes due to multiple broods as a consequence of extended breeding seasons.

Life-history hypotheses were proposed more than 50 years ago (Moreau 1944, Lack 1947, Skutch 1949), but differences in annual fecundity between hemispheres are still poorly understood because the number of broods and number of fledglings per nest rarely have been evaluated, especially in the Southern Hemisphere. Our study is one of few that analyze a suite of parameters involved in annual fecundity. In conclusion, we found similar number of broods per season and similar nest survival, whereas the clutch size differences are balanced by the numbers of fledglings per nest. These results reject the premise of greater annual offspring production in the temperate American Robin when compared to Pale-breasted Thrushes from a tropical/subtropical latitude. The broader application of this conclusion should be investigated by addressing other groups of species paired by phylogeny and ecology. Our comparisons also show for the first time that breeding life-history traits can vary within a Neotropical species due to variables other than clutch size (i.e., multiple broods), which may result in annual fecundity variation. Our study clearly indicates that there is still much information relevant to bird breeding life histories yet to be discovered in this vast region.

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REFERENCES

Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103: 458–473.

Ayres, M., M. Ayres Jr., D. L. Ayres, & A. S. Santos. 2000. BioEstat 2.0: aplicações estatísticas nas áreas das ciências biológicas e médicas. Sociedade Civil Mamirauá/MCT-CNPq, Brazil.

Baker, M. 1995. Environmental component of latitudinal clutch-size variation in House Sparrows (*Passer domesticus*). Auk 112: 249–252.

Bell, C. P. 1996. The relationship between geographic variation in clutch size and migration pattern in the Yellow Wagtail. Bird Study 43: 333–341.

Böhning-Gaese, K., B. Halbe, N. Lemoine, & R. Oberrath. 2000. Factors influencing the clutch size, number of broods and annual fecundity of North American and European land birds. Evol. Ecol. Res. 2: 823–839.

Brackbill, H. 1952. Three-brooded American Robins. J. Field Ornithol. 23: 29.

Carvalho, C. T. 1957. A nidificação de *Turdus l. albiventer* Spix (Passeres: Turdidae). Bol. Mus. Paraense Emílio Goeldi 4: 1–13.

Cody, M. L. 1966. A general theory of clutch size. Evolution 20: 174–184.

Collar, N. 2005. Family Turdidae (Thrushes). Pp. 514–807 *in* del Hoyo, J., A. Elliott, & D. A. Christie (eds). Handbook of the birds of the world. Volume 10: Cuckoo-shrikes to thrushes. Lynx Edicions, Barcelona, Spain.

Cooper, C. B., W. M. Hochachka, & A. A. Dhondt. 2005. Latitudinal trends in within-year reoccupation of nest boxes and their implications. J. Avian Biol. 36: 31–39.

Dhondt, A. A., T. L. Kast, & P. E. Allen. 2002. Geographical differences in seasonal clutch size variation in multi-brooded bird species. Ibis 144: 646–651.

Di Giácomo, A. 2005. Aves de la Reserva El Bagual. Pp. 201–465 *in* Di Giácomo, A., & S. F. Krapovickas (eds). Historia natural y paisaje de la Reserva El Bagual, provincia de Formosa, Argentina. Inventario de fauna de vertebrados y de la flora vascular de un área protegida del Chaco Húmedo. Asociación Ornitológica del Plata, Buenos Aires, Argentina.

Fargallo, J. A., & R. D. Johnston. 1997. Breeding biology of the Blue Tit *Parus caeruleus* in a montane Mediterranean deciduous forest: the interaction of latitude and altitude. J. Ornithol. 138: 83–92.

Farnsworth, G. L., & T. R. Simons. 2001. How many baskets? Clutch sizes that maximize annual fecundity of multiple-brooded birds. Auk 118: 973–982.

Ferretti, V., P. E. Llambías, & T. E. Martin. 2005. Life-history variation of a Neotropical thrush challenges food limitation theory. Proc. R. Soc. Lond. B. 272: 769–773.

Freitas, M. S., & M. R. Francisco. 2012. Reproductive life history traits of the Yellowish Pipit (*Anthus lutescens*). Wilson J. Ornithol. 124: 119–126.

Friesen, L. E., V. E. Wyatt, M. D. Cadman, R. J. Mackay, E. D. Cheskey, M. L. Allen, & D. Ramsay. 2000. Extent of double-brooding and seasonal movement of nesting females in a northern population of wood thrushes. Wilson Bull. 112: 505–509.

Ghalambor, C. K., & T. E. Martin. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. Science 292: 494–497.

Geffen, E., & Y. Yom-Tov. 2000. Are incubation and fledging periods longer in the tropics? J. Anim. Ecol. 69: 59–73.

Griebeler, E. M., J. Caprano, & K. Bohning-Gaese. 2010. Evolution of avian clutch size along latitudinal gradients: do seasonality, nest predation or breeding season length matter? J. Evol. Biol. 23: 888–901.

Haverschmidt, F. 1959. Notes on the nesting of *Turdus leucomelas* in Surinam. Wilson Bull. 71: 175–177.

Hemborg, C., J. J. Sanz, & A. Lundberg. 2001. Effects of latitude on the trade-off between reproduction and moult: a long-term study with Pied Flycatcher. Oecologia 129: 206–212.

Hendricks, P. 1997. Geographical trends in clutch size: a range-wide relationship with laying date in American Pipits. Auk 114: 773–778.

Howell, J. C. 1942. Notes on the nesting habits of the American Robin (*Turdus migratorius* L.). The Am. Midl. Nat. 28: 529–603.

Johnston, R. F. 1954. Variation in breeding season and clutch size in Song Sparrows of the Pacific Coast. Condor 56: 268–273.

Knupp, D. M., R. B. Owen Jr., & J. B. Dimond. 1977. Reproductive biology of American Robins in northern Maine. Auk 94: 80–85.

Lack, D. 1947. The significance of clutch size. Ibis 89: 302–352.

Lack, D., & R. E. Moreau. 1965. Clutch size in tropical passerine birds of forest and savanna. Oiseau Rev. Fr. Ornithol. 35: 76–89.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecol. Monogr. 65: 101–127.

Martin, T. E. 1996. Life history evolution in tropical and south temperate birds: what do we really know? J. Avian Biol. 27: 263–271.

Martin, T. E. 2002. A new view of avian life-history evolution tested on an incubation paradox. Proc. R. Soc. Lond. B. 269: 309–316.

Martin, T. E., P. R. Martin, C. R. Olson, B. J. Heidinger, & J. J. Fontana. 2000. Parental care and clutch sizes in North and South American birds. Science 287: 1482–1485.

Mayfield, H. 1961. Nesting success calculated from exposure. Wilson Bull. 73: 255–261.

Møller, A. P. 2010. The fitness benefit of association with humans: elevated success of birds breeding indoors. Behav. Ecol. 21: 913–918.

Moreau, R. E. 1944. Clutch size: a comparative study, with reference to African birds. Ibis 86: 286–347.

Morneau, F., C. Lépine, R. Décaric, M. A. Villard, & J. L. DesGranges. 1995. Reproduction of American Robin (*Turdus migratorius*) in a suburban environment. Landsc. Urban Plann. 32: 55–62.

Oniki, Y., & E. O. Willis. 1983. Breeding records of birds from Manaus, Brazil: V. Icteridae to Fringillidae. Rev. Bras. Biol. 43: 55–64.

Pletschet, S. M., & J. F. Kelly. 1990. Breeding biology and nest success of Palila. Condor 92: 1012–1021.

Powell, L. A., M. J. Conroy, D. G. Krementz, & J. D. Lang. 1999. A model to predict breeding-season productivity for multibrooded songbirds. Auk 116: 1001–1008.

Renner, H. M., & B. J. McCaffery. 2006. Nesting biology of Eastern Yellow Wagtails at Cape Romanzof, Alaska. J. Field Ornithol. 77: 250–258.

Ridgely, R. S., & G. Tudor. 1994. The birds of South America. Volume 2. Univ. of Texas Press, Austin, Texas, USA.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smith. Contr. Zool. 9: 1–48.

Ricklefs, R. E. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. Auk 97: 38–49.

Ricklefs, R. E. 2000. Lack, Skutch and Moreau: the early development of life-history thinking. Condor 102: 3–8.

Robinson, W. D., T. R. Robinson, S. K. Robinson, & J. D. Brawn. 2000. Nesting success of understory forest birds in Central Panama. J. Avian Biol. 31: 151–164.

Rowe, M. C., & P. J. Weatherhead. 2009. A third incubation tactic: delayed incubation by American Robins (*Turdus migratorius*). Auk 126: 141–146.

Russell, E. M. 2000. Avian life histories: Is extended parental care the southern secret? Emu 100: 377–399.

Sick, H. 1997. Ornitologia brasileira. Editora Nova Fronteira, Rio de Janeiro, Brasil.

Snow, D. W., & B. K. Snow. 1963. Breeding and the annual cycle in three Trinidad thrushes. Wilson Bull. 75: 27–41.

Skutch, A. F. 1945. Incubation and nestling periods of Central American birds. Auk 62: 8–37.

Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91: 430–455.

Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. Ornithol. Monogr. 36: 575–594.

Voelker, G., S. Rohwer, R.C.K. Bowie, & D. C. Outlaw. 2007. Molecular systematic of a speciose, cosmopolitan songbird genus: defining the limits of, and the relationships among the *Turdus* thrushes. Mol. Phylogenet. Evol. 42: 422–434.

Voelker, G., S. Rohwer, D. C. Outlaw, & R. C. K Bowie. 2009. Repeated trans-Atlantic dispersal catalyzed a global songbird radiation. Global Ecol. Biogeogr. 18: 41–49.

Yom-Tov, Y. 1994. Clutch size of passerines at mid-latitudes: the possible effect of competition with migrants. Ibis 136: 161–165.

Yom-Tov, Y., M. I. Christie, & G. J. Iglesias. 1994. Clutch size in passerines of southern South America. Condor 96: 170–177.

Young, H. 1955. Breeding behavior and nesting of the eastern Robin. Am. Midl. Nat. 53: 329–352.

Young, B. E. 1994. Geographic and seasonal patterns of clutch size variation in House Wrens. Auk 111: 545–555.