



Contrasting latitudinal patterns of life-history divergence in two genera of new world thrushes (Turdinae)

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Several long-standing hypotheses have been proposed to explain latitudinal patterns of life-history strategies. Here, we test predictions of four such hypotheses (seasonality, food limitation, nest predation and adult survival probability) by examining life-history traits and age-specific mortality rates of several species of thrushes (Turdinae) based on field studies at temperate and tropical sites and data gathered from the literature. Thrushes in the genus *Catharus* showed the typical pattern of slower life-history strategies in the tropics while co-occurring *Turdus* thrushes differed much less across latitudes. Seasonality is a broadly accepted hypothesis for latitudinal patterns, but the lack of concordance in latitudinal patterns between co-existing genera that experience the same seasonal patterns suggests seasonality cannot fully explain latitudinal trait variation in thrushes. Nest-predation also could not explain patterns based on our field data and literature data for these two genera. Total feeding rates were similar, and per-nestling feeding rates were higher at tropical latitudes in both genera, suggesting food limitation does not explain trait differences in thrushes. Latitudinal patterns of life histories in these two genera were closely associated with adult survival probability. Thus, our data suggest that environmental influences on adult survival probability may play a particularly strong role in shaping latitudinal patterns of life-history traits.

Life history strategies vary broadly within and among taxa, but the reasons for this variation are poorly understood. Despite large variation in life-history traits, species largely fall along a 'slow-fast' gradient (MacArthur and Wilson 1967, Pianka 1970, Stearns 1976, Ghalambor and Martin 2001). Slow species are characterized by high adult survival, long developmental periods, low fecundity, and large offspring size, while fast species tend to show the opposite traits. A well-studied manifestation of this gradient is the life-history continuum observed across latitudes in Passerine birds, where species in the tropics tend to have slower life history strategies than their temperate counterparts (Lack 1947, Martin 1996, Ricklefs 1997, Martin et al. 2000a, 2015a, Jetz et al. 2008, Cox and Martin 2009). Several hypotheses, including food limitation (Lack 1947), seasonality (Ashmole 1963, Ricklefs 1980), nest predation (Skutch 1949, Robinson 1990, Martin 1995) and adult survival (Moreau 1944, Skutch 1949, Hussell 1972, Ghalambor and Martin 2001, Martin 2002, Martin et al. 2015a) have been proposed to explain this gradient in traits, but debate remains.

The latitudinal divergence in life-history traits between temperate and tropical relatives is often large (Martin and Schwabl 2008, Cox and Martin 2009, Gill and Haggerty 2012) and consistent across a broad range of sites and taxa (Ricklefs 1980, Skutch 1985, Jetz et al. 2008). Because of this obvious and apparently consistent geographic variation,

a broadly accepted hypothesis for latitudinal variation has focused on environmental drivers such as seasonality (Ashmole 1963, Ricklefs 1980, Skutch 1985, Jetz et al. 2008). In particular, high seasonality in temperate regions is argued to cause high mortality during lean periods, resulting in increased resource abundance per individual during the breeding season (Ashmole 1963, Ricklefs 1980, Martin 1996).

Food limitation has often been posited as the primary driver of clutch-size and life-history variation in birds (Lack 1947, 1954, Ricklefs 2010). Yet, subsequent work has suggested that food may influence life-histories within species, but is of minor importance for explaining differences in clutch size, developmental periods and feeding rates among conspecific populations (Ferretti et al. 2005), and among species and latitudes (Martin 1995, Martin et al. 2000a, Chalfoun and Martin 2007, Gill and Haggerty 2012).

High nest predation is thought to favor low nest visitation rate (Skutch 1949, 1985, Martin et al. 2000a, b, 2011), lower parental effort to conserve energy for future breeding attempts (Slagsvold 1982, 1984, Skutch 1985, Martin 1995, 2014, Martin et al. 2015a), and shorter developmental periods to reduce time-dependent mortality of nests (Lack 1968, Case 1978, Martin 1995, Martin et al. 2007, 2011, 2015a). However, nest predation rates are not consistently higher in the tropics (Snow and Snow 1963, Oniki 1979, Skutch

1985, Martin 1996, Martin et al. 2000a, 2006), calling into question the ability of nest predation rates to explain the smaller clutches and slower life-histories typically seen in tropical species.

Tropical birds often have higher adult survival probability than temperate relatives (Sandercock et al. 2000, Martin 2015, Martin et al. 2015a) which can favor a reduction in total energy expended in reproduction and parental care (Hirshfield and Tinkle 1975, Michod 1979, Roff 1993, Martin 2002, 2014, Martin et al. 2015a). Increased adult survival has been associated with smaller clutch sizes within and among latitudes (Bennett and Harvey 1988, Martin 1995, Ghalambor and Martin 2001), as well as reduced nest attentiveness that yields longer developmental periods (Martin 2002, Martin et al. 2015a). However, differences in adult survival probability across latitudes may not be as large and consistent as traditionally expected (Snow and Snow 1963, Karr et al. 1990, Blake and Loiselle 2008).

Examining latitudinal patterns of life-history variation in closely related species is a powerful tool to explore differing selection pressures across latitudes. Different strategies in closely related taxa are more likely to be the result of differing selection pressures than phylogenetic inertia (Cox and Martin 2009, Gill and Haggerty 2012, Llambias et al. 2015). Two genera of new world thrushes, *Turdus* and *Catharus*, constitute a particularly interesting suite of species for study because the magnitude of latitudinal divergence in life histories appears to differ between the two clades (Snow and Snow 1963, Johnston et al. 1997, Martin et al. 2000a, 2015a, Martin and Schwabl 2008). *Turdus* species have been the focus of several life-history studies (Snow and Snow 1963, Johnston et al. 1997, Ricklefs 1997) while *Catharus* has been largely overlooked despite being a closely related clade (Sibley and Monroe 1990, Voelker and Klicka 2008). Moreover, these two clades often coexist in the same habitat, thereby holding seasonality constant between clades. Thus, *Catharus* and *Turdus* provide an intriguing pair of clades to examine latitudinal patterns and possible causes of variation in life-history strategies.

Here, we test whether latitudinal divergence in life-histories in these two clades is explained by seasonality, food limitation or age-specific mortality (nest predation and/or adult survival probability). To accomplish this, we examine several measures of parental effort (nest-attentiveness, egg temperature, clutch size, total feeding rate), parental investment (relative egg mass, per-nestling feeding rate), developmental rates (incubation and nestling periods), and age-specific mortality probability (adult survival, nest predation) in coexisting species of *Turdus* and *Catharus* thrushes in temperate (Arizona, USA) and tropical (Lara, Venezuela) sites and across a broader suite of species from the literature.

Material and methods

Field data

We searched for nests at two mid-elevation sites, the Coconino National Forest, Arizona, USA (34°N latitude, 2250–2400 m), and Parque Nacional Yacambu, Lara, Venezuela (9°N latitude, 1350–2000 m). Fieldwork was conducted from

May–August (1993–2013) in Arizona and from February–June (2002–2008) in Venezuela. Habitat is characterized by deciduous snow-melt drainages and conifer-dominated ridges in Arizona and primary and secondary tropical cloud-forest in Venezuela (Martin et al. 2006).

Nests were found using parental behavior and systematic search techniques (Martin and Geupel 1993) and monitored following long-term protocols common to both field sites (Martin et al. 2007) to determine developmental periods and nest predation rates. Incubation period was measured in days, beginning at clutch completion and ending when the last egg hatched (Briskie and Sealy 1990). Nestling period was measured in days, beginning with the first egg hatching and ending the day the first nestling fledged. A subset of all nests was videotaped for 6–8 h starting within 30 min of dawn to determine nest-attentiveness and nestling feeding rates (Martin et al. 2000a, 2007, 2011, Martin 2002). A subset of these nests was videotaped more than once throughout the incubation stage to determine changes in nest attentiveness across the incubation stage. Nest attentiveness is defined here as the percentage of total observation time an adult spent on the nest during incubation. Video data were also analyzed to determine both total and per-nestling feeding rates. Feeding rates change over the nestling period (Gibb 1955, Hussell 1972), thus we measured feeding rates within 1 d of when nestling primary feathers first emerge from their sheaths to ensure that measurements were made at a standardized point of nestling development. We weighed eggs for each species during the first three days of incubation to control for the effect of water loss on mass over the course of incubation. Eggs were measured with Acculab (Elk Grove, IL, USA) portable balances with a precision of ± 0.001 g. Egg temperature was measured by inserting small thermistors into the center of eggs. These were then connected to HOBO Stowaway data-loggers (Onset Computer Corporation, Bourne, MA, USA) by threading the connecting cable through the nest (Martin et al. 2007). Thermistors were inserted during egg-laying or on the first day of incubation to capture the entirety of the incubation period. Data-loggers recorded internal egg temperature every 12 s, and were changed every 4–5 d. Introduction of thermistors to the egg arrested development of the embryos, thus, this procedure was only performed on a small subset of nests.

Adult survival was estimated by banding, resighting and recapturing birds at both Arizona and Venezuela field sites, again following long-term protocols common to both sites (Martin et al. 2015a). Birds were captured by passive mist-netting for 6 h each day starting at dawn. Twelve nets were deployed at each netting plot, which were distributed uniformly across the entire nest-searching area. Netting occurred at each subplot 3 times during each field-season, with three weeks in between sessions. Birds were marked with one alpha-numeric aluminum band, and three color-bands forming a unique combination. Birds were resighted daily by nest-searchers throughout each field season. Plot area and season length were consistent throughout the duration of study, so resighting effort was assumed to be constant. Resight and recapture data were combined to provide a robust estimate of average annual adult survival (see Statistical analyses). Estimates are based on 21 consecutive years of

banding and resighting at the Arizona site and 7 consecutive years in Venezuela.

Study species

Study species included 5 species of *Turdus*; American robin *T. migratorius*, yellow-legged thrush *T. flavipes*, black-hooded thrush *T. olivater*, glossy-black thrush *T. serranus* and pale-eyed thrush *T. leucops*, and 3 species of *Catharus*; hermit thrush *C. guttatus*, orange-billed nightingale-thrush *C. aurantirostris*, and slaty-backed nightingale-thrush *C. fuscater*. Clutch size, relative egg mass, and feeding rates are presented for all of the above species, however due to rarity of some taxa, data for other traits is limited to a subset of these species.

Literature data

We compiled data on clutch size, incubation and nestling periods, nest success and adult survival probability for *Turdus* and *Catharus* thrushes from reference volumes (del Hoyo et al. 2005) and from individual studies (Supplementary material Appendix 1). Our field data were not included in the literature dataset. Clutch size and developmental periods are frequently reported as a range of values in the literature. In such cases we used the midpoint value of the range of values given, excluding values indicated to be rare or non-typical. When multiple sources for a given species were available, we took the mean across sources. Most studies did not report nest predation rates, therefore we use nest success as our metric of nest predation rate due to its frequency of use. This may overestimate rates of nest predation. However, nest predation is the primary cause of nest failure (Nice 1957, Skutch 1985, Martin 1992), so nest success should be reasonably representative of nest predation rate. We assigned each species a designation of either 'tropical' or 'temperate'. Species were considered 'tropical' if the majority of their breeding range was between the Tropic of Cancer (23°26'N) and the Tropic of Capricorn (23°26'S). Field data were only included from sites that were within a species latitudinal designation. All others were considered 'temperate'.

Statistical analyses

Field data

All means are reported with ± 1 standard error (SE). Sample sizes (n) represent number of nests for incubation period, nestling period and clutch size; number of eggs for relative egg mass; and number of videos for nest attentiveness. We used R for all statistical analyses (R Core Team).

To examine latitudinal variation within genera, we tested for differences in mean trait values across all species in a given genus using one-way ANOVA. We then conducted Tukey HSD post-hoc tests to determine whether pairwise differences existed between tropical and temperate species pairs. Each regional group of species is monophyletic and species-level phylogenetic relationships among tropical groups are not completely resolved (Voelker et al 2007, Hackett et al. 2008). Thus, we did not use phylogenetic analyses here and rely on within-genera comparisons to control for phylogenetic relatedness of species.

Nest attentiveness frequently increases throughout the incubation stage, so we controlled for stage day in our estimates of daily nest-attentiveness using the `lsmeans` package (Lenth 2014). We estimated the least-squares means of species-specific nest-attentiveness using a linear mixed model with species and log-transformed incubation day as fixed factors, nest-attentiveness as the response variable and nest as a random factor.

Relative egg mass was calculated as the studentized residual of a regression of log-transformed egg mass and log-transformed body mass (Martin 2008). We included data for 82 species of passerines present at our Arizona and Venezuela field sites in the regression to establish a general estimate of the relationship between egg mass and body mass. We examined latitudinal patterns within and between genera using a two-way ANOVA with genus and latitude as factors explaining variation in relative egg mass.

We used program RMARK (Laake 2013) to estimate both annual adult survival probability (Φ) and re-sighting probability (p) for each species (White and Burnham 1999, Burnham and Anderson 2002). We then built species-specific models with all possible combinations of (Φ) and (p) in which these parameters were assumed to be either constant, sex-specific, or a transient model based on the first year of capture versus all subsequent years. In Venezuela, where many species are not readily assigned to a sex, an additional 'unknown' category was included for ambiguous individuals. Final parameter estimates were estimated using model averaging across all iterations based on model weights (Burnham and Anderson 2002).

We estimated average 24-h egg temperature using a linear mixed model to account for repeated daily temperature measurements for a given nest, and for the asymptotic increase in nest-attentiveness as the incubation period progresses. We included nest identity and species as random factors and log-transformed stage day as a fixed factor to accomplish the above. Data are the same as those presented in Martin et al. (2015a).

Nest predation rates were estimated using the logistic exposure method (Shaffer 2004) in program R (R Core Team).

We tested for differences in latitudinal patterns between our field and literature datasets using a linear regression with genus, region (temperate or tropical) and dataset as fixed factors and mass as a covariate. We tested for correlations between life-history traits and adult survival probability using linear models with mass, genus and adult survival as fixed factors and a genus \times survival interaction. Mass was dropped from the final model when nonsignificant.

Literature data

We used linear regressions including log-transformed mass, genus, site, and a genus \times site interaction to determine how clutch size, incubation period, nestling period, nest success and adult survival probability varied within genera across latitudes and if latitudinal variation in traits differed between the two genera. We included mass as a fixed effect in all models given its known correlations with those traits (Sæther 1987, Speakman 2005). While it would be ideal for these analyses to be performed in a phylogenetic framework, the breadth and resolution of available genetic data are insufficient for

such analyses. Therefore, we cannot eliminate the possibility that differences within and across latitudes include an influence of phylogenetic relatedness.

Results

Clutch size

We determined clutch size in 1240 nests of eight species (Table 1A). Clutch sizes differed among *Turdus* species

(ANOVA, $F_{4, 298} = 148.2$; $p < 0.001$) and all four tropical *Turdus* had smaller clutches than temperate *T. migratorius* (Table 1A), with an average reduction of 39.3% in the tropical species. Clutches of *Catharus* also differed among species (ANOVA, $F_{2, 934} = 2741.7$, $p < 0.001$) with tropical species averaging 48.4% smaller clutches (Table 1A). Clutches were also smaller in the tropics in both genera based on literature data ($p < 0.01$, Fig. 1A) and the difference in clutch size between temperate and tropical species was similar for *Turdus* and *Catharus* ($p = 0.70$, Fig. 1A). Latitudinal differences

Table 1. Mean values, standard errors and sample sizes for A) clutch size, B) incubation period, C) nestling period, D) nest attentiveness, E) total feeding rate, and F) per-nestling feeding rate for temperate and tropical members *Turdus* and *Catharus* thrushes. Contrasts refer to the difference in trait values between each pairwise comparison of a tropical species and its temperate congener, positive contrast values indicate temperate values are greater. p-values are from Tukey HSD post-hoc tests. Sample sizes for all traits refer to numbers of nests.

| A) | Genus | Species | Latitude | Clutch size | n | Contrast | p |
|-----------------|-------|-----------------------|-----------|--|-----|----------|--------|
| <i>Turdus</i> | | <i>migratorius</i> | Temperate | 3.30 ± 0.004 | 142 | | |
| | | <i>olivater</i> | Tropical | 1.95 ± 0.003 | 75 | 1.35 | <0.001 |
| | | <i>flavipes</i> | Tropical | 2.09 ± 0.01 | 65 | 1.21 | <0.001 |
| | | <i>serranus</i> | Tropical | 2.08 ± 0.02 | 12 | 1.41 | <0.001 |
| | | <i>leucops</i> | Tropical | 1.89 ± 0.04 | 9 | 1.22 | <0.001 |
| <i>Catharus</i> | | <i>guttatus</i> | Temperate | 3.81 ± 0.001 | 492 | | |
| | | <i>fuscater</i> | Tropical | 1.96 ± 0.001 | 372 | 1.86 | <0.001 |
| | | <i>aurantiiostris</i> | Tropical | 1.97 ± 0.003 | 73 | 1.85 | <0.001 |
| B) | Genus | Species | Latitude | Incubation period | n | Contrast | p |
| <i>Turdus</i> | | <i>migratorius</i> | Temperate | 12.76 ± 0.03 | 316 | | |
| | | <i>olivater</i> | Tropical | 13.27 ± 0.24 | 13 | -0.51 | 0.01 |
| | | <i>flavipes</i> | Tropical | 13.06 ± 0.21 | 9 | -0.3 | 0.5 |
| | | <i>serranus</i> | Tropical | 13.50 ± 0 | 2 | -0.74 | 0.32 |
| | | <i>leucops</i> | Tropical | 12.75 ± 0.25 | 2 | 0.01 | 1 |
| <i>Catharus</i> | | <i>guttatus</i> | Temperate | 12.56 ± 0.07 | 102 | | |
| | | <i>fuscater</i> | Tropical | 15.60 ± 0.09 | 95 | -3.04 | <0.001 |
| | | <i>aurantiiostris</i> | Tropical | 14.56 ± 0.20 | 16 | -2 | <0.001 |
| C) | Genus | Species | Latitude | Nestling period | n | Contrast | p |
| <i>Turdus</i> | | <i>migratorius</i> | Temperate | 14.79 ± 0.09 | 189 | | |
| | | <i>olivater</i> | Tropical | 14.86 ± 0.56 | 7 | -0.07 | 0.99 |
| | | <i>flavipes</i> | Tropical | 14.15 ± 0.49 | 10 | -0.71 | 0.24 |
| <i>Catharus</i> | | <i>guttatus</i> | Temperate | 12.38 ± 0.16 | 77 | | |
| | | <i>fuscater</i> | Tropical | 15.22 ± 0.16 | 23 | -2.83 | <0.001 |
| | | <i>aurantiiostris</i> | Tropical | 15.14 ± 0.39 | 7 | -2.76 | <0.001 |
| D) | Genus | Species | Latitude | Nest attentiveness (%) | n | Contrast | p |
| <i>Turdus</i> | | <i>migratorius</i> | Temperate | 80.41 ± 2.00 | 37 | | |
| | | <i>olivater</i> | Tropical | 72.53 ± 2.17 | 31 | 7.84 | 0.1 |
| | | <i>flavipes</i> | Tropical | 76.07 ± 2.15 | 31 | 4.25 | 0.77 |
| <i>Catharus</i> | | <i>guttatus</i> | Temperate | 78.96 ± 1.24 | 98 | | |
| | | <i>fuscater</i> | Tropical | 56.59 ± 0.87 | 195 | 22.31 | <0.001 |
| | | <i>aurantiiostris</i> | Tropical | 65.94 ± 1.83 | 44 | 12.96 | <0.001 |
| E) | Genus | Species | Latitude | Total feeding rate (trips h ⁻¹) | n | Contrast | p |
| <i>Turdus</i> | | <i>migratorius</i> | Temperate | 6.00 ± 0.36 | 38 | | |
| | | <i>olivater</i> | Tropical | 5.99 ± 0.79 | 11 | 0.61 | 0.83 |
| | | <i>flavipes</i> | Tropical | 5.06 ± 0.38 | 16 | 0.94 | 0.39 |
| <i>Catharus</i> | | <i>guttatus</i> | Temperate | 7.29 ± 0.32 | 64 | | |
| | | <i>fuscater</i> | Tropical | 5.67 ± 0.25 | 45 | 1.62 | <0.001 |
| | | <i>aurantiiostris</i> | Tropical | 8.65 ± 0.45 | 13 | -1.36 | 0.09 |
| F) | Genus | Species | Latitude | Nestling feeding rate (trips h ⁻¹) | n | Contrast | p |
| <i>Turdus</i> | | <i>migratorius</i> | Temperate | 1.97 ± 0.20 | 12 | | |
| | | <i>olivater</i> | Tropical | 3.33 ± 0.68 | 6 | -1.36 | 0.04 |
| | | <i>flavipes</i> | Tropical | 2.23 ± 0.17 | 8 | -0.25 | 0.98 |
| <i>Catharus</i> | | <i>guttatus</i> | Temperate | 2.05 ± 0.09 | 48 | | |
| | | <i>fuscater</i> | Tropical | 2.76 ± 0.19 | 19 | -0.71 | <0.001 |
| | | <i>aurantiiostris</i> | Tropical | 4.36 ± 0.30 | 9 | -2.31 | <0.001 |

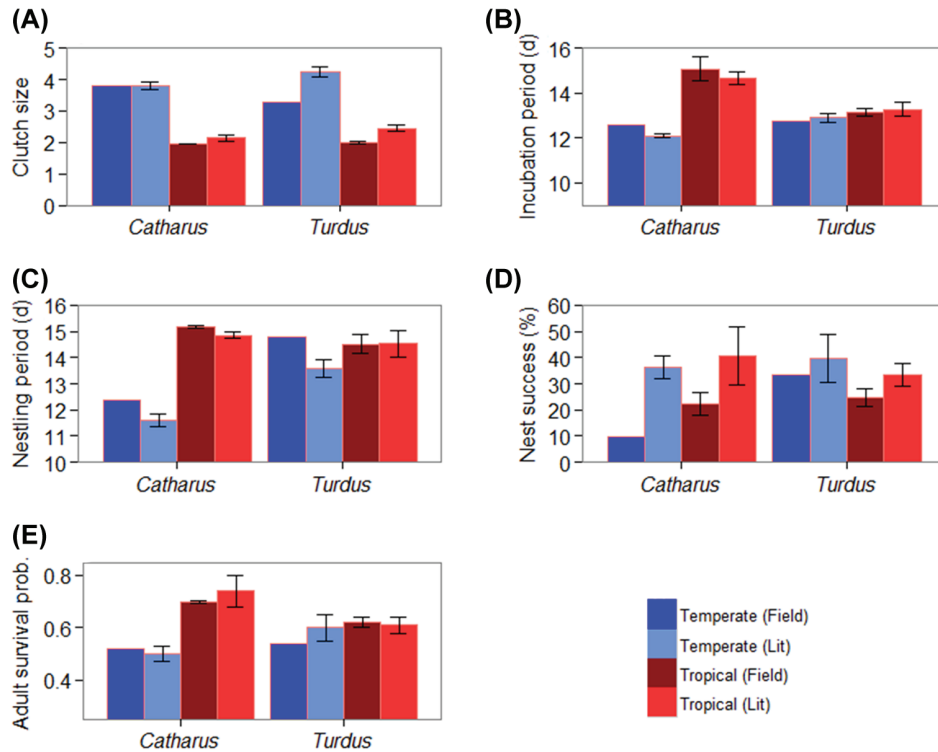


Figure 1. Life-history traits for temperate and tropical representatives of *Turdus* and *Catharus* thrushes based on field and literature data. Values for each trait are means \pm SE for each genus in that region. Tropical species are red, and temperate species are blue.

were similar between field and literature datasets ($p = 0.74$; Fig 1A).

Relative egg mass

Tropical species had larger eggs relative to adult body mass than their temperate congeners in both genera (Fig. 2A, ANOVA, $F_{1,3} = 27.3$; $p = 0.01$). Eggs of *Catharus* showed the largest difference in relative size across latitudes, while eggs of *Turdus* species were only slightly larger in the tropics (Fig. 2A), however this difference was not statistically significant (ANOVA, $F_{1,3} = 0.9$; $p = 0.41$) based on our limited sample of species. Within species variation is relatively small compared with among species variation for both egg mass (ANOVA, $F_{7,1026} = 1324.4$; $p < 0.001$) and body mass (ANOVA, $F_{7,2267} = 8268.6$; $p < 0.001$) in our dataset. Egg mass data were not available in the literature.

Incubation period

We obtained accurate incubation periods for 555 nests of 8 species. Incubation periods differed among species in *Catharus* (ANOVA, $F_{2,210} = 357.7$; $p < 0.001$) and were two to three days longer in the tropics (Table 1B). A difference was less obvious within *Turdus* however. Despite differences in incubation period among species (ANOVA, $F_{4,337} = 4.1$; $p < 0.01$), only one tropical species, *T. olivater*, had a longer incubation period compared to the temperate *T. migratorius* (Table 1B). This difference was small however, averaging only 4.0% longer. Literature data demonstrated a similar pattern in that incubation periods were longer in the tropics across both genera ($p < 0.01$, Fig. 1B), but the

average difference in *Catharus* (2.6 d) was much larger than in *Turdus* (0.4 d) ($p < 0.01$, Fig. 1B). Latitudinal variation in incubation periods were the same for field and literature data ($p = 0.83$; Fig. 1B).

Nest attentiveness

Nest-attentiveness in *Turdus* did not change over the course of the incubation period (*T. migratorius*; $p = 0.61$, *T. flavipes*; $p = 0.69$, *T. olivater*; $p = 0.11$), and did not differ between temperate versus tropical species (Table 1D). Nest-attentiveness did not change over the incubation period in temperate *C. guttatus* ($p = 0.64$). However, nest attentiveness increased over time in both tropical species (*C. fuscater*; $p < 0.001$, *C. aurantirostris*; $p = 0.03$). Temperate *C. guttatus* had higher mean attentiveness controlled for embryonic age than tropical *C. fuscater* and *C. aurantirostris* (Table 1D). Data on nest attentiveness was not available in the literature. Patterns in average 24 h egg temperature mirrored nest attentiveness as expected. Egg temperature was lower in tropical species in both *Turdus* and *Catharus*. However, the difference in *Catharus* was larger (1.2–1.3°C) than in *Turdus* (0.2–0.6°C, Fig. 2).

Nestling period

We observed nestling periods for 313 nests of 6 species. Within *Turdus*, nestling periods were similar among all tropical and temperate species (ANOVA, $F_{2,203} = 1.33$, $p = 0.27$, Table 1C). Contrastingly, nestling periods differed among species in *Catharus* (ANOVA, $F_{2,104} = 53.41$, $p < 0.001$) and both species of tropical *Catharus* had significantly

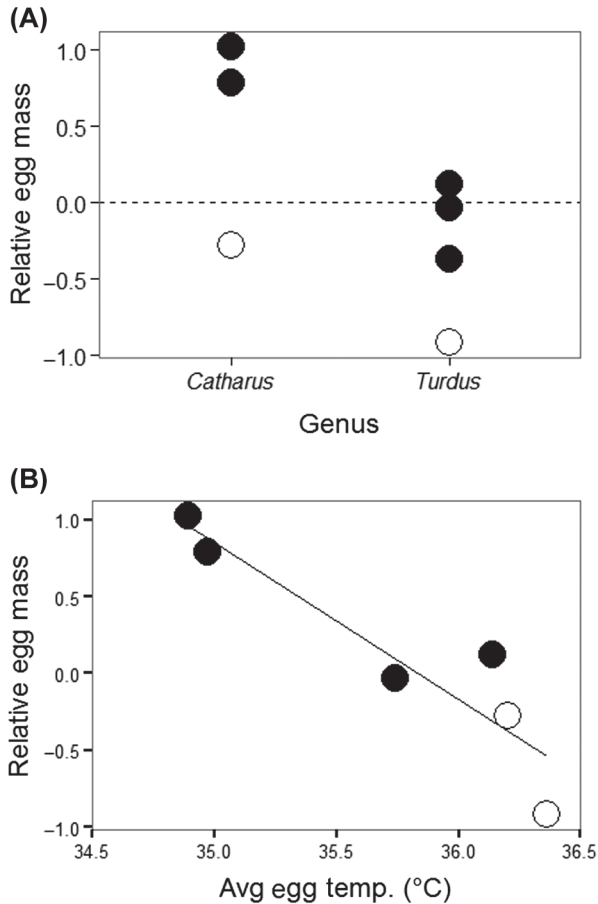


Figure 2. (A) Variation in relative egg mass in tropical and temperate members of *Turdus* and *Catharus* thrushes. Tropical species are closed circles, temperate species are open circles. A relative egg mass value of zero would indicate an egg of average size based on egg and body mass values of 82 Passerine species sampled at the Arizona and Venezuela field sites. Tropical species lay larger eggs than their temperate congeners across both genera. However, the difference in relative egg mass between tropical and temperate species is larger in *Catharus* than in *Turdus*, where all species have either average, or relatively small eggs given their body mass. (B) Larger eggs are associated with lower average egg temperatures during incubation ($p < 0.01$, $R^2 = 0.85$).

longer nestling periods compared with their temperate congener (Table 1C). Nestling periods were longer in the tropics across both genera in the literature ($p < 0.01$, Fig. 1C), but the elongation of nestling periods in the tropics was much greater in *Catharus* (3.6 d) than in *Turdus* (1.0 d, $p = 0.04$, Fig. 1C). There was no difference in latitudinal variation in nestling periods between our field and literature datasets ($p = 0.37$; Fig. 1C).

Feeding rate

Total feeding rates did not differ among tropical and temperate species of *Turdus* (ANOVA, $F_{3,64} = 0.98$, $p = 0.40$). Total feeding rates differed among species of *Catharus* (ANOVA, $F_{2,119} = 12.69$, $p < 0.001$), but with no consistent pattern across latitudes (Table 1E). Temperate *C. guttatus* had a higher feeding rate than tropical *C. fusca*, but a similar rate to tropical *C. aurantirostris* (Table 4). Per-nestling

feeding rates were not different among species for *Turdus* (ANOVA, $F_{3,24} = 2.90$, $p = 0.06$) and latitudinal differences were not consistent (Table 1F), while among *Catharus*, per-nestling feeding rates were consistently higher in tropical species (Table 1F). Feeding rate data were not available in the literature.

Nest predation

Daily nest predation rates were lower in temperate *Turdus* than in tropical species (Fig. 1D). However, the opposite was true for *Catharus*, where nest predation rates were higher in the temperate species than in either tropical species (Fig. 1D). Nest success did not differ across latitudes ($p = 0.71$, Fig. 1D) or between the two genera ($p = 0.76$, Fig. 1D) based on estimates from the literature. Our field estimates for nest success were lower than those in the literature ($p = 0.03$).

Adult survival

Estimated annual adult survival probability was higher in the tropics across both genera (Fig. 1E). However, the magnitude of difference between tropical and temperate species was greater in *Catharus* ($p = 0.04$, Fig. 1E). Annual survival probability of tropical *Catharus* averaged 34.9% higher than their temperate congener, while tropical *Turdus* were only 15.5% higher than their temperate counterpart. Adult survival probability was higher in the tropics across both genera in the literature ($p < 0.01$) but the difference across latitudes was larger in *Catharus* ($p < 0.01$) which concurs with our field data. Adult survival estimates were similar between field and literature datasets ($p = 0.66$; Fig. 1E).

Adult survival probability explained latitudinal variation in a variety of life-history traits (Fig. 3). High survival, typical of tropical species was correlated with small clutches ($p < 0.01$), and long incubation ($p < 0.01$) and nestling ($p < 0.01$) periods across genera when field and literature datasets were combined. High adult survival probability was also correlated with decreased nest attentiveness ($p = 0.02$), lower egg temperature ($p = 0.03$), higher per-nestling feeding rate ($p = 0.07$) and large relative egg mass ($p = 0.01$) based on field data alone (Fig. 3).

Discussion

Overall, the relatively small or nonexistent difference in many life-history traits in *Turdus* thrushes is an exception to the typical latitudinal differences commonly described among relatives (Martin et al. 2000a, Martin 2002, Martin and Schwabl 2008, Cox and Martin 2009, Gill and Haggerty 2012). *Catharus* thrushes sampled at the same sites (Table 1, Fig. 3) and more broadly in the literature (Fig. 1) exhibit typical differences between latitudes. The divergent latitudinal patterns in these two genera are particularly interesting given their close phylogenetic relatedness. The differences in latitudinal divergence between genera, as well as the interspecific differences within latitudes suggest that environmental factors may be more important than phylogenetic relatedness in explaining variation in their life-history strategies.

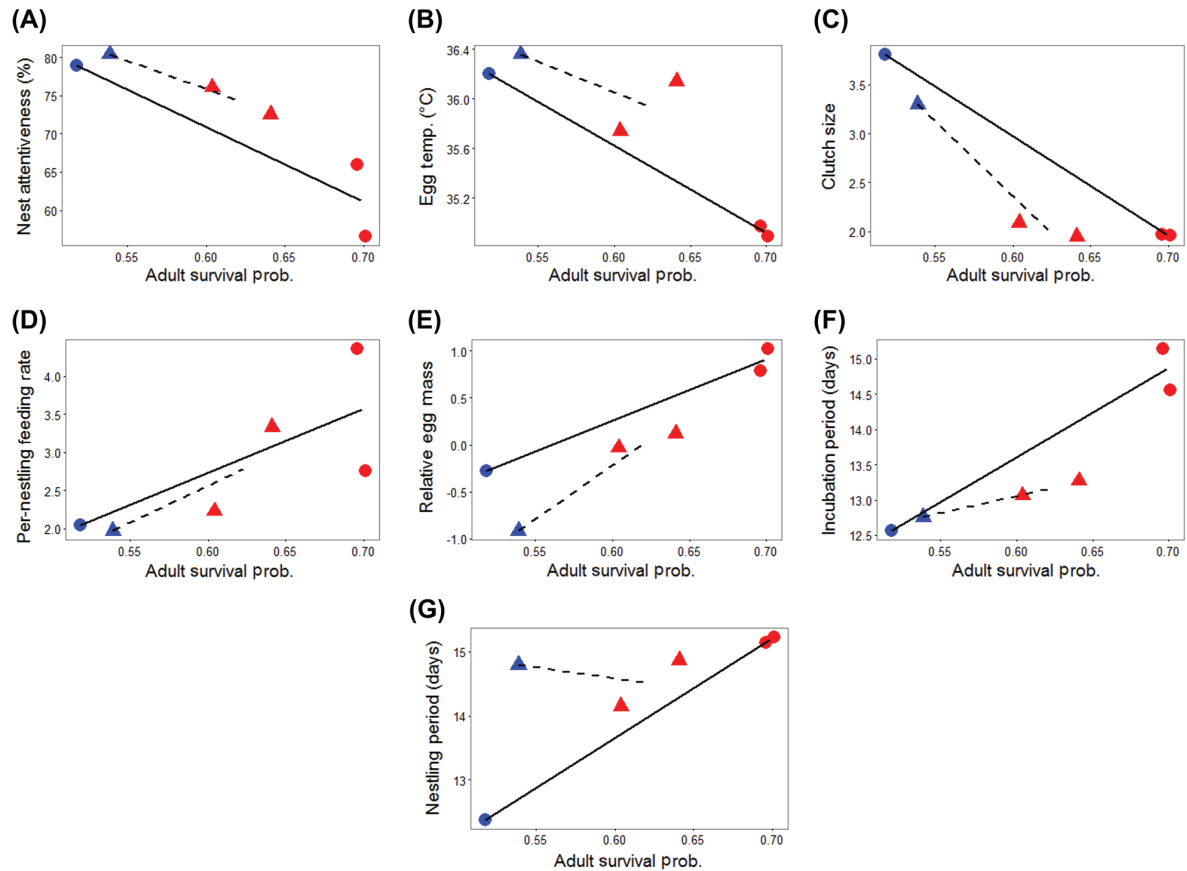


Figure 3. Changes in life-history traits describing variation in parental effort (A–C), parental investment (D, E) and developmental periods (F, G) versus adult survival probability across latitudes in *Turdus* and *Catharus* thrushes. *Turdus* species are represented by triangles and *Catharus* species by circles. Temperate species are in blue and tropical species are in red. Lines represent the magnitude of change in traits and adult survival probability between the temperate species and the mean trait values for tropical species. Dashed lines correspond to *Turdus*, solid lines to *Catharus*. Both genera show reduced parental effort and increased parental investment in tropical species, but the magnitude of these differences is dramatically reduced or insignificant in *Turdus* in association with a reduced difference in adult survival probability across latitudes. *Catharus* thrushes also show lengthened developmental periods in the tropics, where *Turdus* are either relatively invariant (incubation) or the same (nestling) across latitude.

Seasonality is arguably the most broadly accepted explanation for latitudinal variation in life histories (Ricklefs 1980, Jetz et al. 2008, McNamara et al. 2008). Yet, our results raise critical questions about the seasonality hypothesis. Comparisons of coexisting *Turdus* and *Catharus* in the same temperate and tropical sites should yield similar latitudinal differences in life-histories given that seasonality differences are the same for all study species. Clutch size shows reasonably similar latitudinal differences in the two genera, and this trait is where the bulk of latitudinal life history studies have focused. Yet, consideration of the broader life history paints a very different picture. Our field data show a general lack of latitudinal variation in a large number of traits in *Turdus* in contrast to strong variation in co-occurring *Catharus*. Additionally, the generally similar total feeding rates across latitudes and genera (Table 1E) suggest that per-individual resources are not lower in the tropics as predicted by the seasonality hypothesis (Ashmole 1963, Ricklefs 1980, Martin 1996, Martin et al. 2000a, 2011). Furthermore, when coexisting communities of species are compared across latitudes yielding identical variation in seasonality, closely-related species can show large, small, or no latitudinal differences

in life-histories (Snow and Snow 1963, Martin and Schwabl 2008). The difference in latitudinal patterns of life-histories despite identical variation in seasonality suggests that seasonality may not be able to adequately explain latitudinal patterns of life histories.

Food limitation also does not appear to be a valid explanation for latitudinal trait variation in thrushes. Clutches are universally smaller in tropical thrushes and nestling periods are generally longer (Table 1A, C, Fig. 1), as expected if food is limited in the tropics (Martin 1996, Martin et al. 2000a, Chalfoun and Martin 2007, Ricklefs 2010, Gill and Haggerty 2012). However total feeding rates were similar for both genera across latitudes (Table 1E), suggesting that tropical species are not struggling to find food more than temperate relatives. Total provisioning rates were also similar across latitudes in two genera of wrens (Troglodytidae) with typically divergent life-history syndromes (Gill and Haggerty 2012, Llambias et al. 2015) and did not explain latitudinal differences in clutch size across a broad array of passerine clades (Martin et al. 2000a), suggesting that this pattern may be general beyond thrushes.

Higher per-nestling feeding rates in tropical species may indicate a lack of food limitation in the tropics (Martin 1996, Martin et al. 2011, Gill and Haggerty 2012, Llambias et al. 2015) and our results concur (Table 1F). However, higher parental investment per nestling may simply reflect increased investment to produce high-quality young achieved through reduced clutch size rather than an increase in food availability in tropical regions (Martin 2015). Because development of physiological components such as immune function appear to tradeoff with offspring growth (Korfel et al. 2015), higher per-nestling feeding rates could facilitate increased offspring quality, reducing juvenile and adult mortality, without sacrificing growth. It is important to note that nest predation can influence feeding rates (Skutch 1949, Martin et al. 2000a, b, 2011). Consequently, variation in feeding rates may not be solely driven by food availability, which limits our ability to assess the validity of the food limitation hypothesis using feeding rates alone. However, as nest predation rates do not differ consistently across latitudes (Martin 1996, Martin et al. 2006), the potentially confounding effect of nest predation on feeding rates should be minimal.

Nest predation rates do not explain the differential patterns of latitudinal trait variation in the two clades based on either field or literature data. Contrary evidence is provided, most clearly by *Catharus*. Tropical *Catharus* had reduced nest predation rates compared to their temperate congener (Fig. 1D), which violates the assumption of higher nest predation in the tropics. Moreover, lower nest predation in the tropics occurred in concert with a large reduction in clutch size in our field data (Table 1). These results suggest that nest predation does not drive latitudinal variation in these traits in our *Catharus* species. Nest predation was higher in tropical *Turdus* than in our temperate species (Fig. 1D), but was associated with a relatively small reduction in clutch size, no change in nestling period, and similar total feeding rates (Table 1), all contradicting predictions of this hypothesis. Furthermore, nest predation rates did not differ between temperate and tropical regions for either clade of thrushes based on literature data (Fig. 1D), nor do they vary consistently across latitudes for passerine birds on a global scale (Remeš et al. 2012, Martin et al. 2015a). Overall, nest predation alone is unable to explain latitudinal patterns of life-history trait variation in thrushes (Martin et al. 2000a).

The adult survival hypothesis appears to be supported by the data presented here. Similar adult survival probability across latitudes in *Turdus* is associated with similar levels of parental effort and investment and similar developmental periods in temperate and tropical species. In contrast, a large increase in adult survival probability in tropical *Catharus* is associated with a reduction in parental effort, an increase in parental investment and longer developmental periods (Fig. 3). The generality of this result is unclear however. Two studies of latitudinal variation in life-histories and survival probability in wrens yielded supporting evidence in one study and unclear results in the other. Both studies found 'slower' reproductive strategies in the southern species (Gill and Haggerty 2012, Llambias et al. 2015), and one shows increased adult survival probability in the southern population (Gill and Haggerty 2012), as we found here. However, the other study found similar adult survival across latitudes, but methodological issues may have caused an overestimate

of adult survival probability at the northern site (Llambias et al. 2015), which leaves open the possibility of correlated survival differences.

Patterns of relative egg mass were also consistent with the adult survival hypothesis. Longer-lived tropical species typically lay larger eggs, potentially to compensate for lower nest-attentiveness and associated lower egg-temperatures (Martin 2008, Martin et al. 2015b). Alternatively, larger eggs may facilitate the production of higher quality offspring which should be favored in an environmentally stable, highly competitive, tropical environment (MacArthur and Wilson 1967, Pianka 1970, Martin 1996). In thrushes, we found that relative egg-mass was associated with low egg temperatures (Fig. 2B) and was larger in tropical species (Fig. 2A), with a more dramatic difference in *Catharus* thrushes, mirroring the pattern in adult survival (Fig. 3). Thus, we find support for the both the adult survival and advanced provisioning hypotheses (Martin 2008), the latter of which has gained other support (Heming and Marini 2015, LaManna and Martin 2016). It is important to note that these two hypotheses are not mutually exclusive and that large tropical eggs may be a product of selection for both reduced parental effort during incubation and high quality offspring (Martin 2008).

Together, our results suggest that traits typically associated with tropical species are not correlated with seasonality, food limitation or nest predation but with high adult survival. Thus, our results are consistent with the hypothesis that variation in adult survival probability is an important driver of broad patterns of latitudinal trait variation in birds. The small sample size of species in our field studies limit the inference we can make about latitudinal patterns based on those data alone, especially since comparisons across latitudes rely on data from only one temperate species in each genus. However, broader data from the literature show similar patterns of latitudinal divergence in traits both within and across genera. Thus, the literature data further support our conclusions and minimize the possibility of spurious results based on field data alone. Beyond thrushes, more data combining age-specific mortality rates and broad suites of life-history traits are required to determine the generality of this relationship. Future studies examining ecological correlates of divergent latitudinal patterns in life history strategies within clades may provide great insight into the evolutionary drivers of life history variation. Additionally, the fact that clades differ in the extent of latitudinal difference in life-history traits provides an axis of variation that deserves further exploration. Given the correlated importance of adult survival, a remaining question is: what causes variation in adult survival across species? This is a large and complex question, with possible explanations involving metabolic rate (Wiersma et al. 2007, Williams et al. 2010, Londoño et al. 2015), migratory strategy (Sillert and Holmes 2002) and a wide variety of sources of extrinsic mortality. Solving this question will necessitate large scale studies of the aforementioned factors, in conjunction with estimates of adult survival probability.

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Supplementary material (Appendix JAV-01113 at <www.avianbiology.org/appendix/jav-01113>). Appendix 1.