Variation in maternal effects and embryonic development rates among passerine species

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Embryonic development rates are reflected by the length of incubation period in birds, and these vary substantially among species within and among geographical regions. The incubation periods are consistently shorter in North America (Arizona study site) than in tropical (Venezuela) and subtropical (Argentina) South America based on the study of 83 passerine species in 17 clades. Parents, mothers in particular, may influence incubation periods and resulting offspring quality through proximate pathways, while variation in maternal strategies among species can result from selection by adult and offspring mortality. Parents of long-lived species, as is common in the tropics and subtropics, may be under selection to minimize costs to themselves during incubation. Indeed, time spent incubating is often lower in the tropical and subtropical species than the related north temperate species, causing cooler average egg temperatures in the southern regions. Decreased egg temperatures result in longer incubation periods and reflect a cost imposed on offspring by parents because energy cost to the embryo and risk of offspring predation are both increased. Mothers may adjust egg size and constituents as a means to partially offset such costs. For example, reduced androgen concentrations in egg yolks may slow development rates, but may enhance offspring quality through physiological trade-offs that may be particularly beneficial in longer-lived species, as in the tropics and subtropics. We provide initial data to show that yolks of tropical birds contain substantially lower concentrations of growth-promoting androgens than north temperate relatives. Thus, maternal (and parental) effects on embryonic development rates may include contrasting and complementary proximate influences on offspring quality and deserve further field study among species.

Keywords: incubation period; physiological trade-offs; life history; nest attentiveness; nest predation; parental care

1. INTRODUCTION

The rate of embryonic development varies extensively among species (Rahn & Ar 1974; Arendt 1997; Martin 2002; Martin *et al.* 2007). Variation in the rate of embryonic development can influence offspring and adult phenotypes and create major fitness consequences (Arendt 1997; Gilbert 2001; West *et al.* 2003). For example, growth rates via cellular proliferation can trade off with intrinsic features (e.g. cellular repair mechanisms, locomotor performance, immune function, neural networks) that can enhance offspring quality and fitness of adults (Case 1978; Ricklefs 1993; Arendt 1997, 2003; Billerbeck *et al.* 2001; Brommer 2003; Shine & Olsson 2003). Yet, slower development (i.e. longer embryonic periods) increases the risk of time-dependent mortality caused by predation (Case 1978; Bosque & Bosque 1995; Martin 1995, 2002). As a result, any intrinsic benefits from slower development can be overshadowed by mortality if the predation risk of embryos is high. Resolution of such trade-offs may be achieved by differing proximate maternal strategies in response to selection imposed by offspring versus adult mortality (i.e. ultimate factors; Martin 2002, 2004).

Mothers can influence offspring quality and the rate of embryonic development through more than one proximate pathway. In particular, mothers (or both the parents when they share incubation) may influence embryonic development rates through incubation behaviour and resulting temperatures experienced by embryos (Boersma 1982; Martin 2002; Martin *et al.* 2007). Mothers may also influence development rates through embryo exposure to growth-promoting maternal steroids in the egg (Schwabl 1993, 1996; Gorman & Williams 2005; Groothuis *et al.* 2005; Groothuis & Schwabl 2008; Schwabl *et al.* 2007). Finally, mothers may affect offspring quality through egg size and quality (Styrsky *et al.* 1999; Martin *et al.* 2006; Whittingham *et al.* 2007; but see Krist *et al.* 2004). These proximate pathways may have contrasting or complementary influences on development rate and offspring quality, and such interactions need to be considered to understand interspecific variation in developmental strategies. Yet, the ultimate and proximate causes and consequences of differing developmental trajectories and the alternative maternal

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pathways for achieving them need exploration. Here, we consider these alternative proximate maternal pathways and discuss potential ultimate causes of differing strategies among species and the implications for offspring quality and development rates. We approach these issues based on examination and documentation of patterns from field studies of Passeriformes in three locations in the Americas, including north temperate (Arizona), tropical (Venezuela) and Southern Hemisphere subtropical (Argentina).

2. STUDY AREA AND METHODS

(a) *Study areas and bird species*
We studied 83 passerine species at three field sites in North and South America. Note that a recent analysis of relationships between incubation periods and nest predation and nest attentiveness (i.e. Martin *et al.* 2007) included 62 species from these three sites. Besides the new data for the additional 21 species included here, the previous analysis did not provide phylogenetic comparisons among the sites as is the focus here. Study sites were high-elevation (2300 m elevation) mixed forest in Arizona (34° N latitude), cloud or near-cloud tropical forest (1350–2000 m elevation) in the northern Andes of Venezuela (9° N) and Yungas subtropical dry forest (1000 m) in the northwestern Argentina (26° S; see Martin 1998, Martin *et al.* 2000, 2006 and Fierro-Calderón & Martin 2007 for further descriptions of these study sites).

(b) *Nest predation, incubation periods and parental care sampling*
Study sites were searched for nests during entire breeding seasons in 1988–2006 in Arizona, 1997–1999 in Argentina and 2002–2006 in Venezuela for all bird species encountered. Data were obtained on incubation period (78 spp.) or nest attentiveness (79 spp.) for 83 passerine species on these sites: 22 species in Arizona; 22 in Argentina; and 39 in Venezuela. For the species examined here, large numbers of nests were monitored for nest predation and duration of the incubation periods in Arizona (11 649 nests), Argentina (1716 nests) and Venezuela (2537 nests) following long-term protocols (Martin 1998, 2002; Martin *et al.* 2000). Embryonic (incubation) period was quantified as the difference in days between the last egg laid and the last egg hatched (Nice 1954; Briskie & Sealy 1990), but could not be determined at most nests due to predation or missing exact laying or hatching events. The nests were checked every 2–4 days to determine status and predation events, but were checked daily or twice daily near stage-changing events such as completion of laying, hatching and fledging. Nest predation was assumed when nest contents disappeared during incubation and was calculated as daily predation rate (Mayfield 1975; Hensler & Nichols 1981) during the incubation period.

Nest attentiveness was measured as the percentage of time birds were on the nest for the first 6–8 hours of the day. Nests were videotaped during incubation for the first 6–8 hours of the day, beginning within 0.5 h of sunrise from 1993 to 2006 in Arizona and in all study years in Argentina and Venezuela. This protocol standardized both time of day and sampling duration (Martin *et al.*

2000; Martin 2002). In addition, attentiveness was systematically sampled early (2–3 days after the last egg laid) and late (2–3 days prior to average hatching date) in the incubation period in all years in Venezuela and in the last 6 years in Arizona (Fierro-Calderón & Martin 2007; Martin *et al.* 2007). It was also opportunistically sampled in the middle to incorporate any stage changes in the overall estimates. In Argentina, and earlier years in Arizona, nest attentiveness was randomly sampled across the incubation period. Preliminary analyses indicate that nest attentiveness does not change over the incubation period in Arizona and Argentina, and so timing of sampling is not important. Attentiveness consistently increased across the incubation period among most species in Venezuela, but our systematic sampling there incorporated these effects.

(c) *Egg temperature measurements*
Egg temperatures were measured by inserting thermistors on the first or second day of incubation into the centre of the eggs through a small hole sealed with glue (Weathers & Sullivan 1989; Martin *et al.* 2007). The wire was threaded through the nest and connected to a HOBO Stowaway XTI datalogger that recorded temperatures every 12–24 s for 5–8 complete (i.e. 24 h) days per nest. We used data from days 2–6 to standardize sampling and minimize possible disturbance effects on the first day. We excluded nests where night-time temperatures systematically changed across days from failing batteries or poorly sealed holes; we used night-time temperature to identify any potential problems because it holds attentiveness constant, given that all birds incubated constantly at night. We sought to sample 6 nests per species, but the samples varied from 2 to 9, with an average of 4.8 nests per species over 37 species studied on these three sites. We include data through the 2007 field season, which include egg temperature data on nine new species not included in a recent analysis (i.e. Martin *et al.* 2007), and we provide phylogenetic comparisons here, which have not been presented previously.

(d) *Yolk androgen assays*
Yolk samples in Arizona and Venezuela were collected on the day an egg was laid and frozen until hormone analyses. Yolk concentrations of androstenedione (A_4), testosterone (T) and 5α-dihydrotestosterone (5α-DHT) of all species presented here were measured in Schwabl's laboratory using the same protocol and the same antibodies (Schwabl 1993). Briefly, steroids were extracted from the yolk homogenates with diethyl ether/petroleum ether, purified from lipids, separated by diatomaceous earth column chromatography and measured using radioimmunoassay. Antibodies used were as follows: T 3003 (Wien Laboratories, Inc.) for T and 5α-DHT and A 1707 (Wien Laboratories, Inc.) for A_4. ^{3}H-labelled steroids NET 553 (T), NET 544 (5α-DHT) and NET 469 (A_4) were obtained from PerkinElmer Life and Analytical Sciences. Previous analyses (i.e. Schwabl *et al.* 2007) indicated that A_4 was not associated with embryonic development rate and, consequently, we do not present these data here.
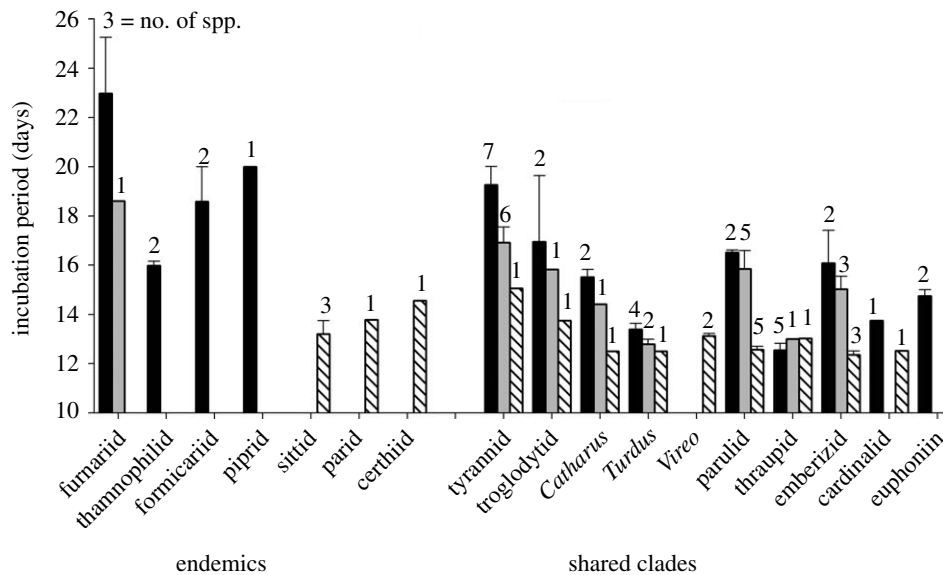
Figure 1. Average incubation periods of study species in endemic (i.e. not shared between North and South America) and clades (families or genera) of passerines that are shared between north temperate (Arizona, hatched bars), tropical (Venezuela, solid bars) and southern subtropical (Argentina, grey bars). Numbers above the bars reflect the numbers of species in the clade.

(e) *Analyses*

We used analysis of variance (ANOVA) with site and clade as fixed factors to examine geographical variation in the incubation periods, nest attentiveness, egg temperatures and egg androgens. We conducted analyses of raw data based only on clades shared between North and South America as a conservative approach to control for possible phylogenetic effects without complicated phylogenetic assumptions (Møller & Birkhead 1994). We also included any clades that are endemic to North or South America or unmatched between sites for broader comparisons. We analysed this broader set of all taxa with data using the BRUNCH option of program CAIC (Purvis & Rambaut 1995) to control for possible phylogenetic effects using independent contrasts (Felsenstein 1985) for binary comparisons. In these cases, independent contrasts were calculated at the nodes where two sites were represented in a clade (Purvis & Rambaut 1995). Clades and phylogenies were defined by standard phylogenies (Sibley & Ahlquist 1990) updated with the most recent information available for relevant taxa (e.g. Burns *et al.* 2002; Yuri & Mindell 2002; Klicka *et al.* 2005; Voelker *et al.* 2007; see other references in Martin *et al.* 2006).

3. RESULTS AND DISCUSSION

(a) *Patterns*

The incubation periods varied from 12 to 27 days across 78 passerine species in which the exact period lengths were measured in the north temperate (Arizona), tropical (Venezuela) and southern subtropical (Argentina) sites in the Americas. Body mass varied in comparable ranges among sites from 8 to 77 g in Arizona, 8 to 71 g in Venezuela and 6 to 61 g in Argentina. The incubation periods did not follow allometric expectations of being longer in the species with larger bodies or eggs (Rahn & Ar 1974; Case 1978; Arendt 1997) either within or among the sites for this set of species (T. E. Martin 2007, unpublished

data). Such results demonstrate that allometry is overridden by other factors in driving embryonic development rates in passerines.

Despite suggestions to the contrary (i.e. Geffen & Yom-Tov 2000), the tropical and Southern Hemisphere birds had longer incubation periods than the north temperate birds (figure 1) when comparing the relatives (site: $F_{2,37} = 9.4$, $p < 0.001$; clade: $F_{7,37} = 5.5$, $p < 0.001$; site $\times$ clade: $F_{13,37} = 1.3$, $p = 0.24$). The incubation periods in Venezuela were similar in length to those in Argentina (LSD, $p = 0.7$), but the incubation periods in both regions were longer than those in Arizona (LSD, $p < 0.001$). Differences were magnified when endemics and unmatched clades were included (figure 1). Independent contrasts for all taxa showed that incubation periods in Arizona were shorter than those in Venezuela ($F_{1,12} = 22.8$, $p < 0.001$) and Argentina ($F_{1,12} = 26.3$, $p < 0.001$), while those in Venezuela and Argentina did not differ ($F_{1,14} = 2.7$, $p = 0.12$).

These small (less than 100 g) bird species have a much narrower range of variation (figure 1) in the incubation periods in Arizona (12–15 days across species, also Martin 2002 for North American passerines in general) than that in Argentina (12.5–19 days across species) and especially in Venezuela (12–27 days across species). Such patterns raise the question of why incubation periods are seemingly constrained in north temperate passerines. More importantly, they emphasize that examinations of possible causes of variation in the incubation periods should be most fertile within the tropical and Southern Hemisphere regions owing to the greater variation there. Indeed, incubation periods vary from durations as short as some of the shortest north temperate species (e.g. 12 days in some tropical tanagers) to substantially longer periods (e.g. 27 days in *Premnoplex brunnescens*) among similarly sized and coexisting Venezuela passerines. Finally, the patterns also emphasize the value of comparisons among regions. The different ranges of variation may indicate that the relative importance of causal factors may differ among regions. Related species

with varying extents of differences in the incubation periods (figure 1, see below) can be compared between the regions to provide a powerful test of causal factors.

Not all clades showed large differences in the incubation periods among regions. For example, species of Thraupidae (tanagers) varied little among regions (figure 1). Also, within the family Turdidae (thrushes), species within the *Turdus* clade (which includes the genus *Platycichla*; Klicka *et al.* 2005, Voelker *et al.* 2007) show relatively small differences among regions, whereas species within *Catharus* show larger differences among regions (figure 1). Other clades show even larger differences among regions (figure 1). These sets of patterns are interesting because the variation among clades, where some clades (e.g. thraupids, *Turdus*) show little difference in the incubation periods between regions, while other clades (e.g. troglodytids, parulids) show large differences between regions (figure 1), provide a strong opportunity to examine possible causes of variation in the incubation periods. Possible proximate and ultimate causal factors (e.g. egg hormones, nest attentiveness, nest predation, adult mortality) should be more similar for related species between regions when the incubation periods are similar than those when they are different. Yet, such ultimate and proximate causes need investigation and some conceptual aspects will be considered in § 3*b,c* below.

(b) Ultimate determinants of variation in embryonic periods

Increased risk of time-dependent offspring mortality, such as predation risk, is expected to favour evolution of faster development and shorter periods of exposure to predators (Case 1978; Bosque & Bosque 1995; Martin 1995, 2002; Arendt 1997). Indeed, the length of incubation periods decreased with increased risk of nest predation within each site (Martin 2002; Martin *et al.* 2007), as predicted by theory. Thus, nest predation appears to be one evolutionary influence on interspecific variation in embryonic development rates and period lengths within regions, but not necessarily among latitudinal regions.

Nest predation rates are either similar or greater in the tropical and Southern Hemisphere locations compared with the north temperate locations (Skutch 1949; Maclean 1974; Robinson 1990; Major 1991; Martin *et al.* 2000, 2006), whereas incubation periods are longer in the southern locations (figure 1, also Martin 2002). As a result, nest predation does not explain much of the variation in the incubation periods among geographical regions (Martin 2002; Martin *et al.* 2007). Thus, the long incubation periods of many tropical and Southern Hemisphere species oppose expectations from nest predation risk (Martin 1996), and may reflect an interactive influence of adult mortality (Martin 2002, 2004).

Increased longevity may be more important than increased risk of offspring mortality in species with low extrinsic adult mortality that depend on iteroparity across years to enhance fitness (Williams 1966; Law 1979; Barbraud & Weimerskirch 2001; Martin 2002, 2004). The tropical and Southern Hemisphere species often experience lower adult mortality than

the north temperate species (Sandercock *et al.* 2000; Ghalambor & Martin 2001). The species with low adult mortality may develop slower even at the risk of prolonged exposure to predators owing to physiological trade-offs. Slower embryonic development may allow increased investment in differentiation of specialized cells (e.g. neural systems, immune function) to enhance offspring quality and adult longevity (Ricklefs 1993; Arendt 1997, 2003; Arendt *et al.* 2001; Billerbeck *et al.* 2001; Brommer 2003; Shine & Olsson 2003), and be favoured in species with low adult mortality risk. The positive correlation observed between the length of the incubation period and adult survival probability (Ricklefs 1993; Martin 2002), thus, may reflect enhanced internal mechanisms for survival afforded by slower development, although direct tests of such functional relationships are lacking. Nonetheless, adult mortality may serve as an ultimate factor favouring intrinsic developmental programmes that yield slower embryo development.

Adult mortality may alternatively proximately influence the length of embryonic development through selection as an ultimate factor on maternal (or parental) effects rather than direct selection on developmental programmes. Adults of long-lived species compared with shorter-lived species should invest less effort in reproduction and reduce exposure to predators to reduce mortality risk to themselves, even at a cost to their offspring (Williams 1966; Charnov & Schaffer 1973; Law 1979; Michod 1979; Barbraud & Weimerskirch 2001; Ghalambor & Martin 2001). Incubation is energetically expensive and can influence future reproduction and adult mortality (Bryan & Bryant 1999; Reid *et al.* 2000; Visser & Lessells 2001). Longer-lived species, as commonly seen in the tropics and Southern Hemisphere (see above), therefore should invest less time and effort in incubation, which may be expressed as lower nest attentiveness (i.e. percentage of time spent on the nest incubating; Martin 2002). Nest attentiveness was indeed generally lower for the tropical and Southern Hemisphere birds than for the north temperate species (figure 2, also see Martin 2002 and Chalfoun & Martin 2007) when comparing the relatives (ANOVA; site: $F_{2,40} = 18.2$, $p < 0.001$; clade: $F_{7,40} = 2.6$, $p = 0.028$; site×clade: $F_{13,40} = 1.1$, $p = 0.4$); nest attentiveness was greater in the north temperate site than in the tropical or southern subtropical sites (LSD, $p < 0.001$ in both cases), but the latter two did not differ from each other (LSD, $p = 0.30$). Some clades (e.g. *Turdus*, thraupids) showed smaller differences in nest attentiveness between the northern and southern locations as also reflected in their incubation periods (figure 1), but most clades showed the geographical pattern. Independent contrasts confirmed the broader pattern for all taxa; nest attentiveness was greater in Arizona than in Venezuela ($F_{1,11} = 11.9$, $p < 0.001$) or Argentina ($F_{1,13} = 80.4$, $p < 0.001$), while Venezuela and Argentina did not differ ($F_{1,15} = 0.3$, $p = 0.6$).

Both sexes share incubation in some tropical groups (Furnariidae, Thamnophilidae, Formicariidae), as well as a few temperate species (e.g. *Vireo*, *Pheucticus*). Combined nest attentiveness can be high in many of
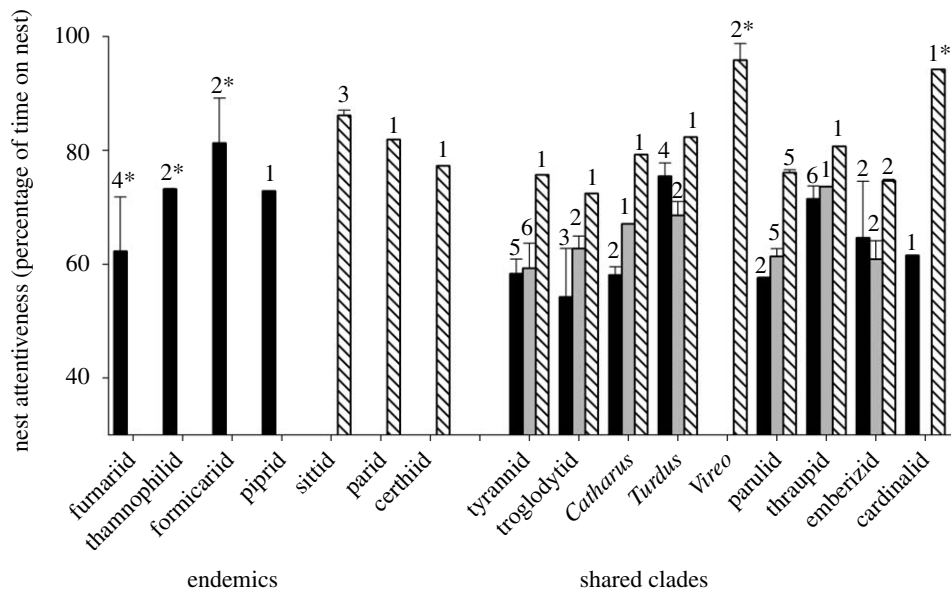
Figure 2. Average nest attentiveness for study species in endemic (i.e. not shared between North and South America) and clades (families or genera) of passerines that are shared between north temperate (Arizona, hatched bars), tropical (Venezuela, filled bars) and southern subtropical (Argentina, grey bars). Both sexes share incubation in a few groups or species, and the remaining study species have female-only incubation. Numbers above the bars reflect the numbers of species in the clade, and an asterisk reflects clades/species with biparental incubation.

these species (figure 2), while time spent by each individual is relatively low. However, not all of the tropical species with biparental incubation showed high combined nest attentiveness. For example, *P. brunnescens* is a furnariid with shared incubation and the longest incubation period (27 days) which we measured. Yet, both parents remained off the nest for extended bouts of 3–5 hours each day (figure 3). As a result, nest attentiveness is relatively low for this and other furnariid species which we studied as typical of most tropical species (figure 2), despite sharing duties between both sexes. In the end, adult mortality may serve as an ultimate factor influencing maternal (or parental) investment in incubation behaviour. This effect is important to consider because attentiveness can proximately affect incubation period (see below) with consequences for offspring quality that oppose those arising from direct selection of adult mortality on intrinsic developmental programmes.

(c) Possible proximate mechanisms: maternal effects

(i) Parental effort and egg temperatures

Passerine embryos are effectively ectothermic and subject to temperature fluctuations from the presence or absence of incubating parents (White & Kinney 1974). As a result, the variation in nest attentiveness among species (figure 2) can influence the average temperature experienced by embryos. Evidence from a large diversity of species across avian orders suggests that optimum development occurs in a temperature zone of 35.5–38.5°C for all species, although the exact temperature may differ among species within this zone (see review in Webb 1987). By contrast, evidence from chicken and quail has been used to suggest that 25–26°C is a general benchmark level where little development occurs in birds (White & Kinney 1974;
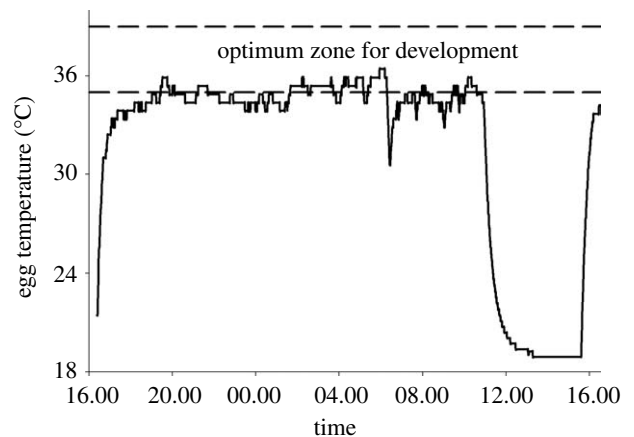

Figure 3. Representative example of daily egg temperature fluctuations in *P. brunnescens* in Venezuela. The two dashed lines at the top represent the optimum temperature zone for development for all bird species that have been examined (White & Kinney 1974; Webb 1987). The drop in temperature reflects off-bouts of parents. In this species, both parents incubate, but both are off the nest for a long period (3–5 hours) each day, reflected by the large drop in temperature to ambient.

Miller & Wilson 1975; Webb 1987; Haftorn 1988). Yet, apparently only the average temperature needs to be reduced because temperatures maintained at a constant level and not allowed to drop to cold levels still showed slower development with cooler average temperatures (e.g. Strausberger 1998; Hepp *et al.* 2006). Nonetheless, lower daytime attentiveness of southern species reflects long off-bouts that cause egg temperatures to regularly fall to low levels that reduce average temperatures (Martin *et al.* 2007). For example, the long off-bouts by both sexes of *P. brunnescens* caused egg temperatures to drop to ambient temperatures that are substantially below
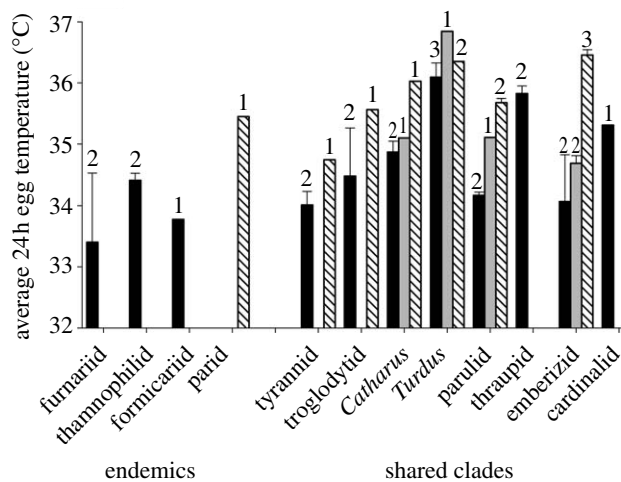
Figure 4. Average egg temperatures over 24 h periods for study species in endemic (i.e. not shared between North and South America) and related clades (families or genera) of passerines in north temperate (Arizona, hatched bars), tropical (Venezuela, filled bars), and southern subtropical (Argentina, grey bars). Numbers above the bars reflect the numbers of species in the clade.

optimum levels and remain there for a long period (figure 3). As a result, both minimum and average egg temperatures were lower in the southern compared with the north temperate regions (figure 4) for related species (ANOVA; sites: $F_{2,13}=9.1$, $p=0.003$; clade: $F_{7,13}=4.5$, $p=0.010$; site×clade: $F_{8,13}=2.1$, $p=0.11$). When all taxa were examined through independent contrasts, egg temperatures were warmer in Arizona than Venezuela ($F_{1,9}=10.1$, $p=0.011$) and only marginally warmer ($F_{1,4}=5.7$, $p=0.075$) than those in Argentina due to low power from the small sample size. Argentina and Venezuela did not differ ($F_{1,4}=3.7$, $p=0.12$). Nonetheless, embryos experience substantial temperature variation within and among regions.

The cooler egg temperatures (figure 4) resulting from lower parental effort (decreased nest attentiveness; figure 2) of many tropical and Southern Hemisphere bird species are strongly correlated (Martin 2002; Martin et al. 2007) with their longer incubation periods (figure 1). Indeed, the causal influence of temperature from parental effort in explaining variation in the incubation periods was verified through an egg swap experiment (Martin et al. 2007). Eggs were swapped between species of similar egg mass but that differed in egg temperatures and associated incubation periods. Incubation periods were shortened when the eggs of species with cool egg temperatures were placed in the nests of species with warm incubation temperatures in South Africa (Martin et al. 2007). Many previous studies found longer incubation periods when nest attentiveness and egg temperatures were reduced (White & Kinney 1974; Boersma & Wheelwright 1979; Lyon & Montgomerie 1985; Lifjeld et al. 1987; Reid et al. 2002; Martin et al. 2007). However, shortening of incubation periods below normal period lengths measured in the field caused by warmer temperatures is relatively untested with the exception of one anecdotal test; *Menura superba* in tropical Australia has 7 hour off-bouts (Lill 1979) and a single egg placed

under a constant incubating chicken reduced the incubation period from 50 to 28 days (Ward 1940). The off-bout is unusually long, but is reminiscent of *Premnoplex* in Venezuela (figure 3) and is a magnified version of the commonly lower nest attentiveness (figure 2) and cooler egg temperatures (figure 4) of many tropical and Southern Hemisphere species. Thus, variation in maternal effects (or parental effects in species with shared incubation) through egg temperatures potentially explain substantial amounts of variation in rates of embryonic development within and among geographical regions (Martin 2002; Martin et al. 2007).

Embryonic temperature variation is characteristic of many true ectotherms owing to variation in their incubation environments. A critical consequence of such variation is that eggs placed in cooler incubation environments among conspecific true ectotherms yielded slower development and lower quality hatchlings (Webb & Cooper-Preston 1989; Shine et al. 1997; Qualls & Andrews 1999; Shine & Olsson 2003; Hare et al. 2004). Cooler embryonic temperatures (figure 4), caused by low nest attentiveness (figure 2), may similarly compromise hatchling quality in birds (figure 5a) because greater energy may be needed by embryos to develop at suboptimal temperatures (Booth 1987). Indeed, even subtle cooling of embryos caused slower development and produced smaller hatchlings (Olson et al. 2006; Hepp et al. 2006; Hammond et al. 2007). Also, one measure of immune function was reduced among passerine species with longer incubation periods in Arizona (Palacios & Martin 2006). Thus, the longer incubation periods of many tropical and Southern Hemisphere species (figure 1) may result in large part from reduced parental effort and resulting cool egg temperatures (figures 2 and 4) to allow long-lived parents to reduce costs to themselves (Martin 2002), but imposing a cost on offspring quality (figure 5a). As a result, proximate maternal effects that cause slower development through greater parental neglect may compromise quality of offspring. Note that this effect is opposite to that expected when slow development results from physiological trade-offs (figure 5a).

The above effects highlight potential contrasting ways that adult mortality can act as an ultimate factor to influence offspring quality and development rate based on alternative proximate pathways (figure 5a). Under the parental effort hypothesis, adult mortality can favour reduced effort that yields cool egg temperatures and proximately slows embryonic development (i.e. longer incubation periods) and compromise offspring quality. By contrast, under the physiological trade-off hypothesis, adult mortality may act on developmental programmes of embryos to favour increased resources for cell differentiation that proximately slows growth rate to enhance offspring quality (Ricklefs 1993; Arendt 1997, 2000, 2003; Arendt et al. 2001). Indeed, growth rate of post-natal offspring have been found to trade off with the development of the immune system (e.g. Brommer 2003; Soler et al. 2003). Thus, these two pathways may have contrasting effects on offspring quality (figure 5a).
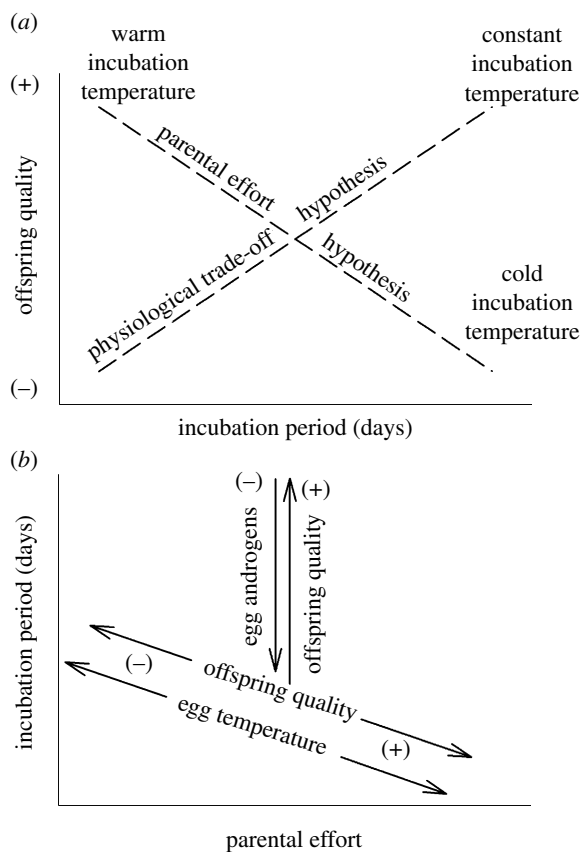
(a)

(b)

Figure 5. Conceptual model for the possible interacting roles of embryonic temperature versus physiological trade-offs on offspring quality. Note that these reflect effects of temperature and physiological trade-offs within species that might differ among species. (a) Longer incubation periods (slower embryonic development) can produce higher quality offspring under the physiological trade-off hypothesis, where embryonic temperature is held constant and slower development reflects physiological trade-offs to enhance offspring quality. Longer incubation periods can have the opposite result and yield lower quality offspring under the parental effort hypothesis where decreased parental effort during incubation causes reduced incubation temperature that causes longer incubation periods. (b) Embryonic temperatures and physiological trade-offs can interact to influence offspring quality. Increasing parental effort (often this is a maternal effect, but in species that share incubation, it is a parental effect) can yield increasing egg temperature that leads to shorter incubation periods, shown by the arrows associated with 'egg temperature'. Changes in incubation period related to egg temperature may yield correlated changes in offspring quality, as shown by the arrow with 'offspring quality' adjacent to egg temperature. For a constant parental effort (and egg temperature), increases in incubation period can reflect physiological trade-offs that enhance offspring quality (the up arrow), and may offset detrimental temperature effects. Maternal effects, through increased or decreased egg androgen concentrations, may provide one key proximate mechanism whereby mothers can shorten or lengthen incubation period and affect physiological trade-offs that determine offspring quality for a given parental effort (down arrow).

(ii) *Egg androgens*

Of course, physiological trade-offs may simultaneously exist and interact with parental effort and egg temperature effects (figure 5). Indeed, the incubation periods still vary substantially among species with

similar egg temperatures (Martin *et al.* 2007). Moreover, in the egg transfer experiment in South Africa, transferred eggs developed at a different rate than host eggs and in a direction that suggested evolved intrinsic differences (Martin *et al.* 2007). Thus, the results of the transfer experiment clearly demonstrated both maternal egg temperature effects and intrinsic influences on development rates.

Ultimate factors may exert selection on the evolution of intrinsic differences in development (see above), but achieved through selection on maternal effects that act internally. For example, nest predation may favour evolution of faster development (Case 1978; Bosque & Bosque 1995; Martin 1995, 2002; Arendt 1997) that is achieved through internal hormonal mechanisms. In particular, mothers may be able to adaptively modify development and differentiation by supplementing the embryo with growth-promoting steroid hormones in their eggs (Schwabl 1993, 1996, 1997; Groothuis *et al.* 2005; Groothuis & Schwabl 2008). Concentrations of the androgens 5α-DHT and its precursor, testosterone (T), in passerine eggs were positively associated with nest predation rates across north temperate species (Schwabl *et al.* 2007). 5α-DHT is the most potent androgen and endpoint in the androgen synthesis chain, and can only act via the androgen receptor pathway. Indeed, it was the most strongly correlated yolk androgen with the length of the incubation period (Schwabl *et al.* 2007), although yolk T concentrations were also negatively correlated with incubation periods (also see Gorman & Williams 2005). Moreover, these androgens were more strongly correlated with duration of the embryonic (incubation) than nestling period, suggesting that maternal hormones in the egg most strongly influenced embryonic rather than post-natal development rate (Schwabl *et al.* 2007).

These correlations suggest a causal relationship between yolk androgens and development rate (Schwabl *et al.* 2007), but the mechanisms by which these yolk androgens speed up development remain unclear (Groothuis & Schwabl 2008). They probably involve the androgen receptor pathway because development rate was most strongly correlated with 5α-DHT that, in contrast to T, can only act via the androgen receptor (Groothuis & Schwabl 2008; Schwabl *et al.* 2007). Tests for a causal relationship between androgens and development rate require carefully controlled, manipulative comparative experiments, although some experiments have already shown that yolk androgens influence embryonic development (e.g. Sockman & Schwabl 2000; Von Engelhardt *et al.* 2006) and nestling growth within species (e.g. Schwabl 1996; Eising *et al.* 2001; Pilz *et al.* 2004; Tschirren *et al.* 2005). Moreover, the biosynthesis pathway for these two androgens may easily respond to selection: T is synthesized from A_4 and 5α-DHT from T (Johnson 2000; Payne & Hales 2004). Both conversions are single-step enzymatic reactions that probably reflect single gene control and, therefore, may respond easily to natural selection on embryo development rate. Thus, maternally produced androgens in eggs may provide a key maternal effect on developmental programmes that can easily respond to selection.

Variation in development rates caused by such internal mechanisms might trade off with offspring quality for a constant temperature (figure 5b), as predicted by the physiological trade-off hypothesis demonstrated in other taxa (Arendt 1997, 2003; Arendt *et al.* 2001; Billerbeck *et al.* 2001; Brommer 2003; Shine & Olsson 2003). In other words, some of the variation in embryonic period might be caused by the rate of cell growth and proliferation, cell differentiation, organo- and morphogenesis and ontogeny of regulatory systems (e.g. thermoregulation, nervous and sensory systems, neuroendocrine systems). Experimental approaches, e.g. manipulation of embryo exposure to hormones by injections of androgens or anti-androgens, could help to test the trade-off hypothesis.

Incubation effort and maternal hormones probably differ radically in how they affect these processes. Incubation effort influences embryo temperature; therefore, we expect increased effort and temperature to enhance all of these processes and all cells via the general effect of temperature on chemical reactions and metabolism (Q_{10}). Yolk androgens, in contrast, can only affect those cells and tissues that are hormone sensitive—have developed functional response pathways (e.g. receptors) for the hormone signal. Thus, the two maternal effect mediators, egg temperature and yolk steroids, probably represent different pathways with different physiological trade-offs (figure 5).

Assuming that fast development reflects increased cell metabolism, production of reactive oxygen species (ROS) is also potentially increased and represents a physiological cost in the form of oxidative damage. In general, the ROS trade-off theory holds that high performance of mitochondria in young animals is bought at the expense of unavoidable ROS-related damage accumulation that manifests itself later in life (Partridge & Gems 2002). Thus, yolk androgens may increase metabolic rate (e.g. Buchanan *et al.* 2001, but see Wikelski *et al.* 1999 and Buttemer & Astheimer 2000) and cause a physiological trade-off between development rate and damage from the production of ROS as by-products of high metabolism (Hofhaus *et al.* 2003). Here, it is of interest that androgen receptors have been identified in mitochondria of hatchlings (Godsave *et al.* 2002). However, it is presently unknown if and how yolk androgens affect embryo metabolic rate and results for nestling metabolic rate are conflicting (Eising *et al.* 2003; Tobler *et al.* 2007).

Given the possible negative influences on offspring quality and adult longevity from faster development rate caused by internal embryo mechanisms, we might expect mothers of longer-lived tropical and Southern Hemisphere species to reduce such costs through lower concentrations of androgens in eggs. Moreover, the possible negative consequence for offspring quality from lower egg temperatures of the tropical and subtropical species (figure 4) might also favour reduced androgen concentrations to offset the costs of cool temperatures to embryos. In this regard, the Arizona–Venezuela comparison is instructive because nest predation rates are similar between the two sites (Martin *et al.* 2006, 2007) to control for possible offspring mortality selection on comparisons. Initial data show substantially lower
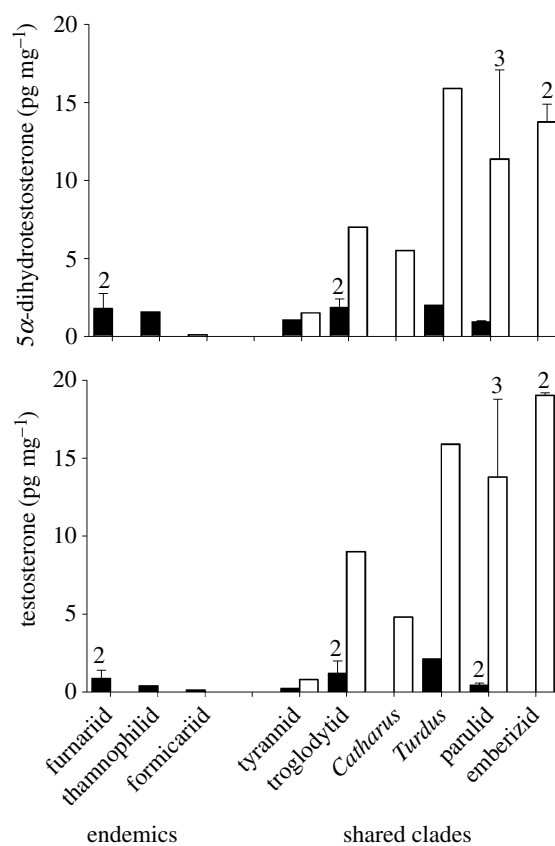

Figure 6. Average yolk concentrations for the androgens (*a*) testosterone (T) and (*b*) 5α-dihydrotestosterone (5α-DHT for study species in endemic (i.e. not shared between North and South America) and clades (families or genera) of passerines that are shared between north temperate (Arizona, open bars) and tropical (Venezuela, filled bars) sites. Numbers above the bars reflect the numbers of species in the clade; the absence of a number indicates a sample of one species.

concentrations of T and 5α-DHT in the eggs of tropical birds in Venezuela compared with north temperate birds in Arizona (figure 6). Thus, for a constant temperature, longer-lived species might reduce costs on offspring quality from physiological trade-offs and offset costs from cooler egg temperatures by reducing androgen concentrations (i.e. the vertical arrow in figure 5b).

As an alternative, however, plasma androgen concentrations of adult tropical species tend to be very low (e.g. Wikelski *et al.* 2003; Goymann *et al.* 2004; Gill *et al.* 2007) compared with temperate zone species (Ketterson *et al.* 2005). While information on plasma androgens of female tropical species is still scarce, this might indicate that the evolutionary pathway for varying yolk or plasma androgens involves a common mechanism that couples plasma and yolk androgens and might prevent their independent regulation (for an in-depth discussion of the relationship of yolk and plasma androgens and its consequences for the evolution of adaptive maternal hormonal effects, see Groothuis & Schwabl 2008). Thus, the low androgen concentrations in the eggs of tropical birds may simply reflect selection on adult plasma levels rather than on development rates *per se*. This possibility could be tested by examining whether incubation periods of tropical birds are correlated with

androgen levels across species, and by experimental manipulation of androgen concentrations to examine effects on developmental rates within species.

Of course, physiological trade-offs interact with egg temperature costs (figure 5b). In particular, parental effort may influence egg temperature to affect incubation period and offspring quality at one level, while maternal effects through differential yolk androgen concentrations in eggs may allow physiological trade-offs for a given level of parental effort (figure 5b). In fact, reduced androgen concentrations and slower development from physiological trade-offs may offset costs to offspring quality from cooler egg temperatures. In the end, the interplay of incubation temperature, maternal hormones, egg quality and ROS damage reflect proximate physiological mechanisms mediating evolved developmental strategies along a slow/fast gradient. In other words, fast species exert high parental effort that costs parents but provides optimum temperature for embryos for fast development. By contrast, fast development resulting from increased androgen concentrations benefits embryos by lowering nest predation risk but balanced by possible longevity costs from ROS damage or other intrinsic trade-offs. Slow-paced species may reduce parental costs by lower parental effort that imposes costs on young through cooler incubation temperatures, but offset these costs through reduced yolk hormone levels that reduce physiological trade-off costs, and pay for it by risking higher offspring predation.

(iii) Egg quality

Egg androgens represent one axis of variation in eggs that mothers can manipulate to influence embryonic development rates and offspring quality, but mothers can also modify other aspects of egg quality. For example, egg mass is substantially greater in Venezuela and Argentina than in Arizona for the same body mass (Martin *et al.* 2006). The proportion of this mass increase devoted to yolk versus albumin is unknown, but if we assume that yolk increases allometrically with egg mass as found in temperate birds (Carey *et al.* 1980), then tropical birds are provisioning their young with more yolk resources than north temperate species. Given that reduced egg temperatures cause greater use of resources that produce smaller hatchlings (Hepp *et al.* 2006; Olson *et al.* 2006; Hammond *et al.* 2007), another way that birds could offset such costs is to advance provision their young with additional resources. Indeed, the eggs of tropical Venezuela and subtropical Argentina were larger than those of related species in Arizona and were larger in species with lower adult mortality (Martin *et al.* 2006). Thus, production of larger eggs may be a relatively cheap way for long-lived birds to enhance offspring and partially offset the costs of cooler incubation, while minimizing costs to themselves. Yet, such possibilities await critical tests.

Clearly, mothers (and fathers), in response to ultimate selection pressures, can evolve a number of alternative strategies that exert strong influences on embryonic development rates and resulting offspring quality. The physiological trade-off hypothesis has dominated thinking, but the roles of parental effort, embryonic temperature, egg androgens and egg quality can all play critical interacting roles that may be currently underestimated in understanding interspecific and geographical variation in embryonic development rates and offspring quality.

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