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RESEARCH ARTICLE

Adaptive influence of extrinsic and intrinsic factors on variation of incubation periods among tropical and temperate passerines

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ABSTRACT

Understanding intrinsic (physiological) and extrinsic (e.g., temperature) causes of variation in embryonic development time (incubation period) is important because they can have different impacts on individual quality. Robert Ricklefs and colleagues have argued that longer incubation periods result primarily from intrinsic physiological programs that increase individual quality and adult survival. They claim that incubation periods are largely invariant and that extrinsic factors like temperature have little impact. We have argued that adult survival may be a cause rather than a consequence of much of the variation in embryonic development time. A reduction in extrinsic sources of annual adult mortality (e.g., migration, predation, nonbreeding-season mortality) favors reduced parental effort during incubation to minimize costs to future reproduction and survival. Reduced parental effort, in turn, manifests as cooler average egg temperatures that yield longer incubation periods. Ricklefs and colleagues mischaracterized our hypothesis and deconstructed their own incorrect version, while also making some incorrect statements. We show that reevaluation of previous evidence provided by this group actually supports a role of egg temperature for the variation in incubation periods. We also summarize other observational and experimental evidence that incubation periods are not invariant and that egg temperature has a strong causal influence on variation within and among species. In fact, egg temperature explains ∼60% of the difference in incubation periods among species. The remaining ∼40% reflects intrinsic physiological programs and other factors, potentially providing intrinsic benefits. Ultimately, annual adult mortality explains substantial variation in parental effort and egg temperature, and the latter strongly explains variation in incubation periods. Both intrinsic programs and extrinsic temperature effects need to be considered in attempts to understand incubation strategies.

Keywords: adult survival, egg temperature, parental effort, physiological trade-offs

Influencia adaptativa de factores extrínsecos e intrínsecos sobre la variación de los períodos de incubación en paseriformes de zonas tropicales y templadas

RESUMEN

Comprender las causas intrínsecas (fisiológicas) y extrínsecas (e.g., temperatura) por las que varían los tiempos de desarrollo embrionario (períodos de incubación) es importante porque éstas pueden tener diferentes impactos en la calidad de los individuos. Robert Ricklefs y sus colegas han argumentado que los períodos de incubación más largos se deben principalmente a programas fisiológicos intrínsecos que aumentan la calidad de los individuos y la supervivencia de los adultos. Ellos afirman que los períodos de incubación son en gran parte invariables y que los factores extrínsecos, como la temperatura, tienen poco impacto. Nosotros hemos argumentado que la supervivencia de adultos puede ser una causa en vez de una consecuencia de gran parte de la variación en el tiempo de desarrollo embrionario. Una reducción de las fuentes extrínsecas de mortalidad anual de los adultos (e.g., depredación, mortalidad durante la temporada no reproductiva, o por migración) favorece la reducción del esfuerzo parental durante la incubación, lo que minimiza los costos que afectan la futura reproducción y supervivencia. La reducción del esfuerzo parental, a su vez, se manifiesta en forma de temperaturas promedio de huevos más frías lo que produce periodos de incubación más largos. Ricklefs y sus colegas caracterizaron de manera errónea nuestra hipótesis y deconstruyeron su propia versión incorrecta, además de proporcionar algunos hechos incorrectos. Nosotros mostramos que una reevaluación de la evidencia presentada anteriormente por este grupo de hecho apoya el importante rol que juega la temperatura de los huevos en la variación de los períodos de incubación. También resumimos evidencia basada en observaciones y experimentos que muestra que los períodos de incubación no son invariables y que la temperatura de los huevos tiene una gran influencia causal en la variación inter- e intraespecífica. De hecho, la temperatura de los huevos explica aproximadamente el 60% de las diferencias en los períodos de incubación entre especies. El 40% restante refleja programas fisiológicos intrínsecos y otros factores, que potencialmente proporcionan beneficios intrínsecos. En definitiva, la mortalidad anual de adultos explica de manera sustancial la variación en el esfuerzo parental y la temperatura de los huevos, y esta última explica gran parte de la variación en los períodos de incubación. Tanto los programas intrínsecos como los efectos de la temperatura extrínseca deben ser considerados para comprender las estrategias de incubación.

Palabras clave: esfuerzo parental, supervivencia de los adultos, solución de compromiso fisiológico, temperatura de los huevos

INTRODUCTION

Understanding the relative roles of intrinsic (physiological) vs. extrinsic (e.g., temperature) causes of variation in embryonic development time is important because they yield different phenotypic consequences (Martin 2002, Martin et al. 2007, 2013). Slower embryonic development, resulting from physiological programs that reflect trade-offs favoring greater cellular differentiation over proliferation, can provide intrinsic benefits that enhance offspring quality and adult longevity (McCay 1933, Arendt 1997, Billerbeck et al. 2001, Metcalfe and Monaghan 2003, Martin et al. 2007, 2011, 2013). Robert Ricklefs and colleagues have championed the view that such intrinsic physiological programs are the primary determinant of incubation periods in birds and argued that extrinsic (e.g., temperature) effects are unimportant (Tieleman et al. 2004, Robinson et al. 2008, 2014, Ricklefs et al. 2017). Consequently, a correlation between incubation period and adult survival across species (e.g., Martin 2002, Martin et al. 2015a) is thought to reflect the influence of intrinsic physiological programs related to embryonic development rates (Ricklefs et al. 2017).

We have advanced an alternative argument, that environmentally caused variation in adult survival (i.e. extrinsic sources of adult mortality such as migration, predation, and nonbreeding-season mortality) plays a strong, but not solitary, role in driving the evolution of physiological and life-history strategies that affect embryonic development. In particular, high annual adult survival resulting from relatively low environmentally caused mortality favors reduced parental effort during incubation that manifests in lower egg temperatures that cause longer developmental periods (Martin 2002, Martin et al. 2015a). This hypothesis is predicated on (1) the well-established fact that parental effort in incubation is energetically costly and can influence future reproduction and survival (Williams 1996, Bryan and Bryant 1999, Reid et al. 2000, Visser and Lessells 2001) and (2) the long-standing and broadly supported life-history prediction that long-lived species should expend less parental effort than shorter-lived species to reduce impacts on residual reproductive value (Williams 1966, Charnov and Schaffer 1973, Law 1979, Michod 1979, Barbraud and Weimerskirch 2001). Ultimately, long incubation periods caused by cool temperatures may benefit the parent over the offspring, emphasizing the importance of understanding the relative roles of temperature vs. intrinsic programs in the variation in incubation periods (Martin 2002, Martin et al. 2007, 2013, 2015a).

Ricklefs (1984) long ago disputed a similar egg-temperature hypothesis in seabirds (i.e. Wheelwright and Boersma 1979, Boersma 1982), reflecting a long-standing stance against a role of egg temperature in the incubation periods of birds. Ricklefs and colleagues produced a series of subsequent papers that continued this argument that egg temperature is not important for embryonic development time (Tieleman et al. 2004, Robinson et al. 2008, 2014, Ricklefs et al. 2017). Yet the role of egg temperature in driving extensive variation in the incubation periods and phenotypic quality of other taxa is widespread and unquestioned (e.g., Van Damme et al. 1992, Shine et al. 1997, Qualls and Andrews 1999, Matsuzawa et al. 2002, Hare et al. 2004). Similarly, later-life consequences of incubation temperatures in birds are well documented and demonstrate that intrinsic factors alone cannot explain phenotypic quality (e.g., Hepp et al. 2006, Nord and Nilsson 2011, Auer and Martin 2017). Moreover, we have provided extensive data showing a strong relationship between egg temperature and incubation periods across diverse songbird species (Martin et al. 2007, 2015a). We will show that the evidence and conclusions provided by Ricklefs and colleagues are flawed. Their description of our hypothesis was critically wrong, and they devoted much space to deconstructing this incorrect characterization, while making some incorrect statements. We will also show that reevaluation of evidence from their previous studies actually provides support for temperature effects on incubation periods in birds. We will summarize clear observational and experimental evidence that temperature causes substantial variation in incubation periods of birds. Finally, we will explain why extrinsic sources of adult mortality should play a stronger role than intrinsic programs in driving evolution of physiological and life-history strategies, but that intrinsic programs are also contributing and acting simultaneously.

Mischaracterization of the Argument

Ricklefs et al. (2017) mischaracterized our hypothesis as being based on predation risk to the incubating adult on the nest and spent much space in refuting this incorrect argument. In fact, the original argument, as stated in Martin (2002:309), was that "species with lower extrinsic rates of adult mortality should reduce their risk of added mortality from parental effort, assuming similar levels of juvenile mortality (Williams 1966; Ghalambor & Martin 2001)." Martin (2002:309) further stated:

> Incubation incurs energetic costs to parents that are as great as those when feeding nestlings (Williams 1996) and increased energy expenditure can increase mortality (Deerenberg et al. 1995; Bryant 1998 [*sic*; should be Bryant 1999]). Indeed, the energy costs of incubation have recently been shown to increase mortality (Visser and Lessells 2001); such energy costs are magnified because parents cannot forage when incubating and, in addition, incubating birds are further vulnerable to predation while sitting on the nest (Magrath 1988).

Similarly, Martin et al. (2007:2559) stated:

> Long-lived species should invest less effort in reproduction than shorter-lived species to reduce adult mortality risk, even at a cost to offspring (Williams 1966; Charnov and Schaffer 1973; Law 1979; Michod 1979; Barbraud and Weimerskirch 2001; Ghalambor and Martin 2001). Incubation is energetically expensive and can influence future reproduction and survival (Bryan and Bryant 1999; Reid et al. 2000; Visser and Lessells 2001).

The energetic cost of parental incubation effort was clearly the focus. Predation risk of incubating adults was only mentioned initially (Martin 2002) as a contributing, and not the main, cost of parental incubation effort and was not even mentioned in subsequent papers (i.e. Martin et al. 2007, 2013, 2015a).

Moreover, we argued that extrinsic adult mortality is largely the result of year-round environmental factors, rather than predation risk during incubation, and that year-round adult mortality drives parental effort. Indeed, Martin (2002:314) explicitly stated:

> Harsher lean (i.e. winter) seasons in northern compared with southern regions can yield greater extrinsic adult mortality either from direct winter effects or from migration that is favored by harsher winters (Rowley and Russell 1991; Martin 1996; Sandercock et al. 2000; Ghalambor and Martin 2001). These differences in extrinsic adult mortality should favor differences in reproductive effort among latitudes (Williams 1966; Charlesworth 1994).

Ultimately, our argument focused on the long-standing life-history prediction that species with lower adult mortality caused by the environment should reduce parental (incubation) effort to minimize energetic or predation costs to future reproduction and survival (Williams 1966, Charnov and Schaffer 1973, Law 1979, Michod 1979).

Our original argument (Martin 2002) acknowledged that mortality of incubating adults may form one component of mortality risk to parents. The idea of a predation cost of reproduction is not new (e.g., Magnhagen 1991), and despite the effort by Ricklefs et al. (2017) to refute this factor, we believe that it can play a role. A variety of studies have shown substantial predation of incubating adults. For example, predation on incubating females was the major influence on annual mortality in Mallards (*Anas platyrhynchos*; Arnold et al. 2012). Other studies have also found extensive predation of incubating females (15% to >20% of individuals; Reidy et al. 2009, Low et al. 2010), which can exceed adult predation during nestling or fledgling stages (Stoleson and Beissinger 2001). The importance of adult predation during incubation as an agent of selection is also reflected by evolved strategies. Evolution of nest-site choice was influenced by the effects of nest-site cover on predation risk of incubating adults (Amat and Masero 2004). Playback experiments to incubating females of a long-lived species demonstrated the greatest sensitivity to adult predation risk (Schneider and Griesser 2013). Incubating females may also be subject to increased predation risk during off-bouts because they must forage quickly in a limited amount of time, thereby favoring male-guarding (Fedy and Martin 2009). While predation of incubating adults may not always be high (Ricklefs et al. 2017), it is sufficiently common to influence the evolution of strategies. Nonetheless, this is only one component of adult mortality, and we have pointed out that adult mortality over the entire year should be the basis of selection on parental effort, with consequences for egg temperature and incubation periods.

Ricklefs et al. (2017) also make several arguments related to differences in nest attentiveness among species not explaining incubation periods to further their case that egg temperature is not important. However, they discount low attentiveness in early incubation, and cool temperatures in the early period are an important influence on variation in incubation periods (Kim and Monaghan 2006; see below). Moreover, while nest attentiveness varies extensively among species and represents an important component of parental effort during incubation, it is still a coarse indicator because it is not the sole determinant of effort and egg temperature (Martin et al. 2007, 2015a). Birds also invest considerable energy in regulation of blood flow to their brood patch to affect egg temperature (White and Kinney 1974, Webb 1987), and species differ in their brood-patch temperatures (Deeming 2008). Moreover, egg temperature is the real factor that we argue has an influence on incubation periods. Attentiveness explains 25–50% of the variation in egg temperature (Tieleman et al. 2004, Martin et al. 2007), leaving substantial residual variation that results from differential brood-patch blood regulation, clutch size, location of eggs in clutches, nest insulation, and other factors that influence egg temperature. In addition, some species have male-shared incubation, and males can differ in the temperature provided (Kleindorfer et al. 1995, Reid et al. 2002, Bartlett et al. 2005, Auer et al. 2007). Finally, species with larger clutch sizes rotate eggs to the edge of brood patches or stack eggs, with outer or bottom eggs experiencing cooler incubation while they are in those positions (Haftorn 1983).

In summary, we argue that environmental sources of mortality that determine annual adult survival should drive parental effort during incubation to determine egg temperature and influence incubation periods (Martin 2002, Martin et al. 2015a). Indeed, we have shown that variation in annual adult survival explains extensive variation in parental effort manifested as egg temperature (Martin et al. 2015a). Below, we will provide evidence of the importance of egg temperature for variation in incubation periods.

Sampling Methods and Measurement Error in Egg Temperature

A necessary first step is to understand the influence of sampling methods on egg temperature and how they can lead to measurement error. Egg-temperature estimates can vary depending on intervals of temperature measurement, temperature probe placement, and timing and duration of measurements; for example, 1 min sampling intervals yield cooler estimates during off-bouts than 3 min sampling intervals because of the relatively short nature of off-bouts in the temperate zone (Haftorn 1988). Shorter sampling intervals are better, and, given the advances in data loggers, reasonably short intervals are easy to accomplish. We sampled at 12 s intervals most commonly, and sometimes at 24 s intervals (Martin et al. 2007, 2015a).

The method used to probe and place eggs in the nest can have a strong influence on estimated egg temperatures. We placed temperature probes in the center of the egg (Martin et al. 2007, 2015a). This approach has the disadvantage that it may underestimate temperatures experienced by young embryos during the first few days of incubation when they float at the top of the egg, although it provides a consistent measure of temperature (e.g., Rahn et al. 1983). We put the probe in the center of the egg because we believe that it may more reliably measure natural variation in egg temperature over the incubation period. This approach allows parents to roll and move eggs, as they normally do, such that eggs can get positioned at the edge of the brood patch at times and experience cooler temperatures (Haftorn 1983). Indeed, we have observed such effects at night when birds are incubating full time; temperature cools for a period as parents shift themselves or their eggs in relation to their brood patches. This variation in egg temperature is a real component of average temperature and, therefore, should be included in measurements. By placing probes in the center of eggs and allowing eggs freedom to be moved, parents can roll and move eggs, allowing measurement of natural temperature variation.

A common alternative approach places the temperature probe inside the egg near the shell, and the egg is then fixed in the center of the nest with the probe at the top of the egg, ostensibly centering it on the brood patch. The advantage of this method is that it measures the temperature experienced by a young embryo that floats at the top of the egg when the egg and probe are placed in the correct position in relation to the brood patch. However, the embryo does not float at the top throughout incubation, and eggs are not always in the center of the nest such that this approach measures maximum temperatures experienced by embryos. More importantly, if the probe is rotated from top center or the fixed egg winds up in a position that is at the edge of the clutch and brood patch, then temperatures will be underestimated in relation to probes and eggs placed top and center (Haftorn 1983, Rahn et al. 1983) and thereby create spurious variation from measurement error. Of course, measurement error can occur in any study, but increased sample size is the best approach to reduce the magnitude of such effects. For example, the impact of small sample size on measurement error seems evident in measurements of egg temperature for 2 seedeater species (*Sporophila*) studied by Tieleman et al. (2004), who only sampled 1 nest for 2 days in each species. Tieleman et al. (2004) reported a large difference (1.4°C) in average egg temperature between these 2 congeners that they assumed had the same incubation period, which most likely reflects measurement error compounded by small sample size. The importance of measurement error is that it yields statistical noise that increases the chances of a type II error (i.e. concluding that a pattern does not exist when one does), and this problem is magnified by small sample size.

The results of Tieleman et al. (2004) were used as a main source of evidence by Ricklefs et al. (2017) in arguing against egg-temperature effects, but the potential of type II error from small sample size was a serious problem. Indeed, in 7 (50%) of the 14 species studied by Tieleman et al. (2004), temperature was sampled at only 1 nest per species, and only for 1 day in 1 species, 2 days in 5 species, and 3 days in another species. The limited number of days sampled per nest increases chances of measurement error and creates biased sampling in relation to embryo age. Incubation effort and egg temperature commonly increase with embryo age in the tropics, especially in the first third to half of the incubation period (Skutch 1945, Ruggera and Martin 2010, Martin et al. 2015a). Yet species differ in the rate of the increase in egg temperature with embryo age (Figure 1). Most tropical species that we have studied show large changes in average 24 hr temperature during the early part of the incubation period, as exemplified by Mountain Leaf Warbler (*Phylloscopus trivirgatus*) in tropical Malaysia (Figure 1A). Some species show even larger changes, but other species show smaller changes (e.g., Figure 1B). These examples of temperature change with embryo age emphasize that 2 days of sampling, as was typical of Tieleman et al. (2004), cannot reliably measure average temperature over the incubation period. Ultimately, the pitfalls of probing methods, the potential for measurement error, and the consequences of small sample size are important to consider when assessing relationships with incubation periods.

Correlations of Egg Temperature and Incubation Periods

The title of Tieleman et al. (2004) declared that "Nest attentiveness and egg temperature do not explain the variation in incubation periods in tropical birds." They based this conclusion on not finding a significant correlation between egg temperatures in their 14 species in Panama and incubation periods obtained from the literature. However, the likelihood of a type II error was high because of small sample sizes that did not correct for embryo age. Indeed, we made 3 minor corrections to Tieleman et al.'s (2004) data and obtained a significant relationship. First, they set the incubation period for the 2 seedeater species as the same because that of one was unknown, even though temperature differed strongly given the small sample size (see above). In other words, they held incubation period constant while they allowed egg temperature to vary and tested whether the 2 traits covaried, which is an inappropriate test. We instead averaged the temperature measurements for the 2 seedeater species to compare with the single incubation estimate. Second, they did not have the incubation period for Ruddy Ground-Dove (*Columbina talpacoti*), so they used the incubation period (13 days) for Common Ground-Dove (*C. passerina*). Yet Cintra (1988) reported the incubation period for Ruddy Ground-Dove as averaging 12 days, based on the time between first egg laid and last egg hatched. Most of the incubation periods used in Tieleman et al.'s (2004) analysis were from Skutch (1954, 1960, 1969), who based his estimates on last egg laid to last egg hatched, as also argued by Briskie and Sealy (1990). Using this definition, the incubation estimate for the 2-egg clutch of Ruddy Ground-Dove based on Cintra (1988) is 11 days. Third, the incubation period (14.5 days) for White-lined Tanager (*Tachyphonus rufus*) used by Tieleman et al. (2004) was incorrect. Their estimate was taken from Geffen and Yom-Tov (2000), who used various sources, including field guides. We instead used the incubation period of 12.72 ± 0.222 days ($n = 9$) that we measured exactly for this species (i.e. we observed the day the last egg was laid and the day the last egg hatched; Martin et al. 2007, 2015a). With these 3 corrections, we obtained a marginally significant correlation ($r = -0.54$, $P = 0.055$; Figure 2) compared with Tieleman et al.'s (2004) original correlation ($r = -0.35$, $P = 0.22$).

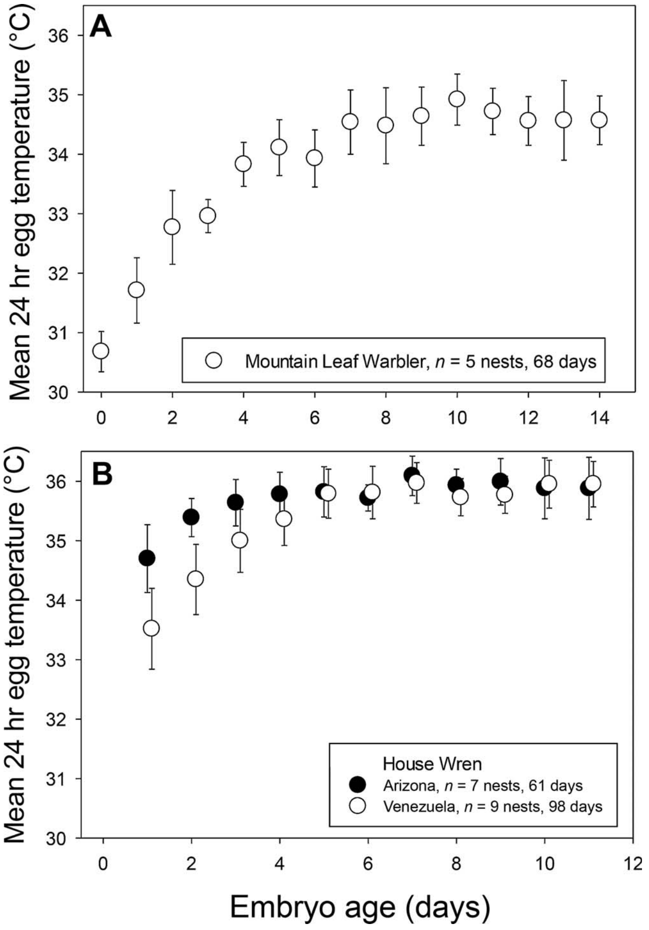

FIGURE 1. Mean (± SE) average egg temperatures among nests as a function of the age of embryos in (**A**) Mountain Leaf Warblers in Malaysia and (**B**) House Wrens in Arizona and Venezuela. Methods for egg-temperature measurement are described in Martin et al. (2007, 2015a).

The largest outlier was the only cavity-nesting species, House Wren (*Troglodytes aedon*), with the coldest estimated temperature (Figure 2). The temperature estimate for this species was again based on 1 nest for 2 days. If this outlier was removed, the significance of the inverse relationship was even stronger (i.e. $r = -0.62$, $P = 0.031$). The significant results from our minor corrections highlight the tenuous nature of any negative conclusions because of the high likelihood of type II error from measurement error associated with small sample sizes.

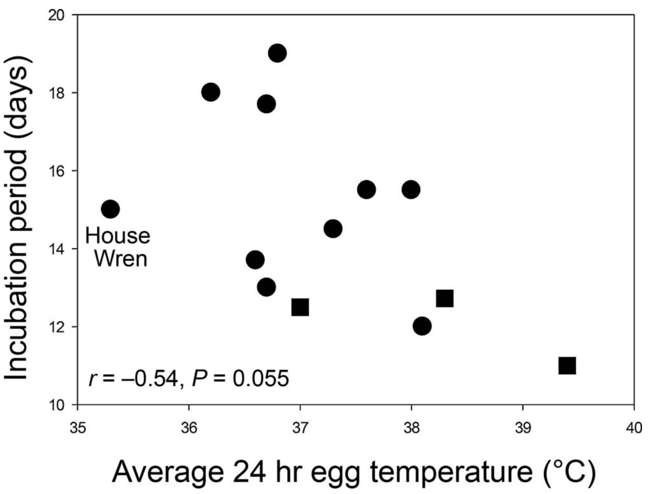

FIGURE 2. Relationship between incubation period and average egg temperature based on data from Tieleman et al. (2004), with 3 minor corrections (see text) represented by squares.

Indeed, the results actually support a role of egg temperature.

A negative relationship between incubation period and egg temperature was quite strong when based on extensive sample sizes and correction for embryo age (2,424 days of measurements across 63 species; Martin et al. 2015a). Similarly, incubation periods decreased with increasing brood patch temperature among 76 species (Deeming 2008). Other studies also have measured changes in incubation periods with changes in incubation attentiveness and egg temperature within various individual species (Haftorn 1983, Lyon and Montgomerie 1985, Lifjeld and Slagsvold 1986, Nilsson and Smith 1988, Reid et al. 2002, Eiby and Booth 2008). Thus, a variety of studies have demonstrated clear correlative effects of nest attentiveness and egg temperature on variation in incubation periods within and among species.

Manipulations of Egg Temperature

The most definitive evidence comes from direct manipulations of egg temperature, ideally performed in nature. Robinson et al. (2014) manipulated egg temperature using an incubator, and the conclusion declared in that article's title—"Incubation temperature does not explain variation in the embryo development periods in a sample of Neotropical passerine birds"—was based on the fact that incubation periods were either longer than (5 species) or similar to (3 species) those in natural nests, despite the elimination of cooling off-bouts. One problem with their conclusion is the inability of incubators to simulate incubation in the wild (Klimstra et al. 2009). Indeed, only 64% of Robinson et al.'s (2014) eggs hatched, which is much lower than natural hatching rates of ~90% (Briskie and Mackintosh 2004). These developmental problems are common for wild eggs in incubators (Klimstra et al. 2009) and may compromise incubation-period estimates. More importantly, Robinson et al.'s (2014) results appear to support temperature effects. They set the incubator at 36.5°C, whereas the average egg temperature across 14 species at the same site was 37.2 ± 0.28°C (Tieleman et al. 2004). The cooler incubator temperature predicts similar or slightly longer incubation periods compared to those in nature, exactly as Robinson et al. (2014) found; thus, their data actually support a role of egg temperature, contrary to their title.

Robinson et al. (2008) similarly incubated eggs of temperate and tropical House Wrens in an incubator. These 2 subspecies showed a difference of 1.2 days in incubation period in nature, and this difference remained when temperature was controlled in incubators. They concluded that "parental attendance patterns do not account for latitudinal differences in incubation periods" and that intrinsic physiological programs were paramount. However, some issues were not considered. First, as pointed out above, incubators create developmental abnormalities. They found that both subspecies took longer to hatch in the incubator than in nature, suggesting developmental problems and raising questions about the reliability of incubation-period estimates from incubators, although they did not report the number of eggs that did not hatch. Second, we found significant differences in egg temperatures of tropical and temperate House Wrens during the early part of incubation (Figure 1B), which may contribute to some of the difference in incubation periods. Llambías et al. (2015) found nearly identical regional differences in incubation attentiveness between northern and southern House Wrens (Llambías et al. 2015: 72% vs. 60%; Martin et al. 2015a: 72.4% vs. 60.6%; northern vs. southern subspecies, respectively). Temperature differences during early incubation are an important part of the variation in incubation periods (also see Kim and Monaghan 2006). Third, we have repeatedly acknowledged that intrinsic physiological programs explain part of the variation in incubation periods among species (see below). We differ in that the evidence is clear that egg temperature explains an even larger part of the variation in incubation periods among species.

The causal influence of temperature on incubation period was verified by experiments we conducted on 3 continents. First, we swapped freshly laid eggs of species that maintain cooler incubation temperatures into the nest of other species with a similar egg size but warmer incubation temperatures in South Africa and shortened incubation periods by 1–3 days (Martin et al. 2007, 2015a). Ricklefs et al. (2017:546) incorrectly stated that "the shifts were considerably smaller than the difference between natural incubation periods of the donor and foster species." The natural incubation periods at this South African site exhibited limited variation near the shorter end of incubation periods, and the shifts actually represented an average of 60.4% of the difference between species (Martin et al. 2015a:340). Thus, Ricklefs et al. (2017) incorrectly represented the extent of shifts, and egg temperature actually explained the majority of the difference between species.

We also tested this issue in tropical species with larger differences in incubation periods. We swapped freshly laid eggs of Bornean Stubtail (*Urosphena whiteheadi*) into nests of Chestnut-crested Yuhina (*Yuhina everetti*) at a tropical site in Malaysia (Ton and Martin 2017). Bornean Stubtails take long (6–8 hr) off-bouts each day, declining to around 4–5 hr late in incubation, similar to Spotted Barbtails (*Premnoplex brunnescens*) in Venezuela (Martin and Schwabl 2008, Muñoz and Martin 2014). This behavior caused cool average incubation temperatures associated with long (24-day) incubation periods for Bornean Stubtails (Martin et al. 2013). By contrast, Chestnut-crested Yuhinas take short off-bouts and produce much warmer average egg temperatures and shorter (14-day) incubation periods, whereas egg mass does not differ between the 2 species (Martin et al. 2013, 2015a). This swap caused a mean 6-day decrease in the incubation period of Bornean Stubtails that accounted for 60% of the difference in incubation periods of the paired nests of these 2 species (Figure 3; Ton and Martin 2017), nearly identical to the South African results (see above). Also, as previously pointed out (i.e. Martin et al. 2007), Ward (1940) conducted a similar experiment in Superb Lyrebird (*Menura superba*). This species has an unusually long incubation period associated with extended off-bouts during incubation (Lill 1979). Ward (1940) transferred a newly laid egg of the Lyrebird to a domestic hen that was bred for constant incubation attentiveness, with the result that the normal 50-day incubation period was reduced by 22 days. Thus, these egg-swap experiments clearly demonstrate that long incubation periods of tropical and Southern Hemisphere species can be dramatically shortened through warmer temperatures from greater incubation effort.

Finally, we conducted a nest-warming experiment across 6 temperate and 3 tropical species. We used heating strips around the outside of nests to increase average egg temperature by about 1.3 ± 0.13°C for these 9 species (Ton and Martin 2017). We found that species differed in their responses, but all species showed decreases in incubation periods with warming. The tropical species showed the greatest decreases (up to 7 days) in response to heating associated with their naturally colder incubation temperatures (Ton and Martin 2017). Species with warm egg temperatures and short incubation periods showed the smallest change in incubation period, potentially because they are near the physiological maximum possible for embryos (Ton and Martin 2017). Unlike incubators, swapping and warming experiments yielded hatching success of 92% (Ton and Martin 2017), typical of wild birds (Briskie and Mackintosh 2004). Other studies have also documented changes in incubation periods with manipulated temperatures (e.g., Hepp et al. 2006, Nord and Nilsson 2011, Auer and Martin 2017, Zhao et al. 2017). All of these experiments produced significant changes in incubation periods and clearly verified temperature as a major driver of incubation-period duration.

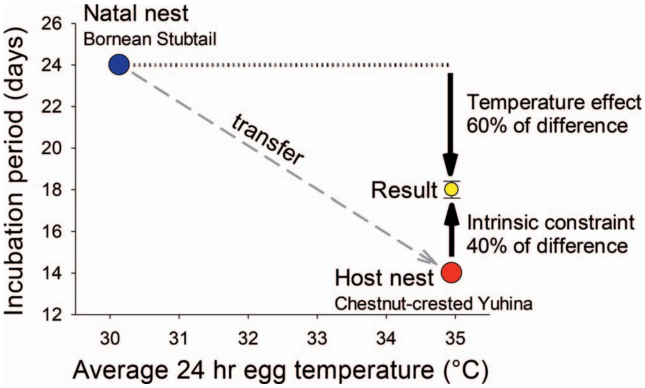

FIGURE 3. Results of a transfer experiment in which a freshly laid egg of a Bornean Stubtail was transferred to the nest of a Chestnut-crested Yuhina during egg laying ($n = 4$; data from Ton and Martin 2017). The 10-day difference in incubation period between the 2 species was reduced by 6 days as a result of temperature effects (60% of the difference), leaving a 4-day difference (40%) due to intrinsic and other constraints.

Extrinsic Temperature vs. Intrinsic Physiological Programs

Ricklefs et al. (2017) argued that intrinsic growth programs are the primary determinant of incubation periods and that egg temperature is of minor importance. However, our swapping and warming experiments demonstrated that egg temperature explained a majority (i.e. 60%; Figure 3) of the difference in incubation periods between species. At the same time, we have pointed out that physiological programs explain part of the variation (Martin et al. 2007, 2011, 2013, 2015a, Ton and Martin 2017). Indeed, we noted from our swap experiment that ∼40% of the variation in incubation periods among species could be attributed to intrinsic or other factors (Figure 3; also see Martin et al. 2015a, Ton and Martin 2017).

Ricklefs et al. (2017) suggested that incubation periods are largely invariant within species and that this was evidence for robust intrinsic growth programs that minimize temperature effects. Arguing for invariant incubation periods is equivalent to arguing that avian embryonic development has little plasticity or, in other words, no environmental effects on embryonic development time. Ricklefs et al. (2017:544) also stated: “The rate

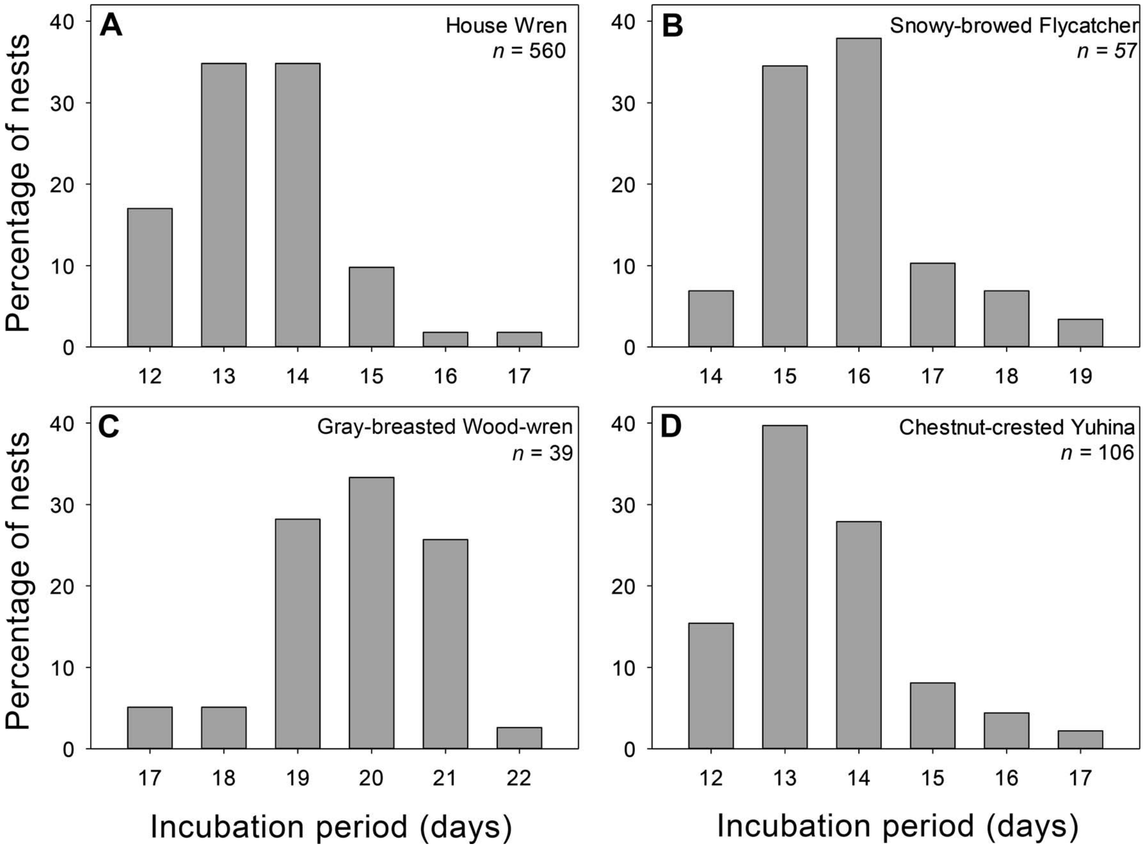

FIGURE 4. Variation in the incubation periods of 1 temperate species (House Wren), a relative in tropical Venezuela (Gray-breasted Woodwren), and 2 species from tropical Malaysia (Snowy-browed Flycatcher [*Ficedula hyperythra*] and Chestnut-crested Yuhina). Incubation periods are from nests for which the laying date of the last egg and its date of hatching were observed by checking near the beginning and end of the field day (Martin et al. 2007, 2015a).

of embryo growth and developmental periods varies little within a species; eggs incubated at the same temperature normally hatch within a few hours (e.g., Ricklefs and Smeraski 1983)." Yet the issue is not minimal variation "at the same temperature" but, rather, whether variation in temperature explains variation in incubation periods. Moreover, it is simply not true that incubation periods vary little within species in nature. Incubation periods of House Wrens varied from 12 to 17 days at our Arizona site (Figure 4), as did those of Western Bluebirds (*Sialia mexicana*) at the same site. Similarly, incubation periods of Tree Swallows (*Tachycineta bicolor*) varied from 13 to 18 days (Ardia et al. 2006). Such variation is common among temperate species but is not restricted to the temperate zone. A tropical wren, the Gray-breasted Wood-Wren (*Henicorhina leucophrys*), shows similar variation, as do tropical species from Malaysian Borneo (Figure 4). Incubation periods of White-browed Scrubwrens (*Sericornis frontalis*) varied from 17 to 22 days in southern Australia (Magrath et al. 2000). In each case, temperature was invoked as partly causing the variation. Haftorn (1983) reported a 5-day range of incubation periods in Great Tits (*Parus major*) that was strongly correlated with egg temperatures. Of course, the majority of nests are represented by a 3-day range of incubation periods (Figure 4), but this is not surprising because species have evolved incubation effort and brood patches that regulate egg temperature. Yet behavior and egg temperatures can vary among individuals to some extent as a result of environmental conditions (temperature, precipitation, food) and yield variation in incubation periods (Haftorn 1983, Bryan and Bryant 1999, Ardia et al. 2006, Kim and Monaghan 2006, Nord et al. 2010). Ultimately, variation in incubation periods is pervasive within species and variation in temperature seems to play a critical role.

Incubation periods of passerines <100 g in body mass vary extensively across species but do not vary with body mass (Martin 2002, Martin et al. 2007). For example, among 15–16 g species at our Venezuela site, Spotted Barbtail has an average incubation period of 27 days (Muñoz and Martin 2014), whereas Rusty-breasted Antpitta (*Grallaricula ferrugineipectus*) averages 17 days (Niklison et al. 2008) and Blue-necked Tanager (*Tangara cyanicollis*) averages 13 days (T. E. Martin et al. personal observation). Such extensive variation independent of mass is opposite of expectations based on physiological allometry considerations (i.e. Rahn and Ar 1974), raising serious questions about an overriding importance of physiological programs.

Similarly, metabolism is expected to be a major determinant of development rate, but mass-specific metabolic rates of embryos were not correlated with length of incubation periods across 49 passerine species (Martin et al. 2013). Yet, once egg temperature was taken into account, metabolic rates explained a significant portion of the residual variation in incubation periods (Martin et al. 2013). As in our swap experiments, egg temperature explained more of the variation in incubation periods than intrinsic metabolism (Martin et al. 2013). Also, longer incubation periods caused by intrinsic programs are thought to increase offspring quality, but we found that nestling immune responses were not correlated with incubation periods across 34 species of passerines (Martin et al. 2011). Again, once the influence of egg temperature on incubation periods was taken into account, the residual variation in incubation periods explained immune responses (Martin et al. 2011). These studies emphasize the importance of egg temperature to variation in incubation periods but also demonstrate that once the large effects of egg temperature are taken into account, physiological programs are revealed as also playing a role. These studies demonstrate that both temperature and physiological programs are acting on variation in incubation periods of birds, and the results are highly coincident with the results of the swap experiments (Figure 3; Martin et al. 2015a, Ton and Martin 2017).

Direction of Causality

The direction of causality is a critical contrast in arguments about the correlation between incubation period and adult survival. Ricklefs et al. (2017) argued that longer incubation periods cause higher adult survival due to physiological benefits of slower development. By contrast, we proposed that extrinsic sources of annual adult mortality create selection on parental effort (manifested as egg temperature) to influence incubation periods (Figure 5), which was supported by a strong negative relationship between adult mortality and egg temperature (Martin 2002, Martin et al. 2015a). Ricklefs et al. (2017:545) suggested that our perspective disregarded the cost of low egg temperature to embryos and stated that the “assumption that embryo fitness is unaffected by lower adult attendance—and, thus, by lower incubation temperatures—is questionable, at least in species in which selection has not favored egg neglect.” We have explicitly hypothesized that selection has indeed favored greater egg neglect and lower effort at warming eggs in species with greater annual adult survival, thereby benefiting parents despite potential costs to embryos (Martin 2002, Martin et al. 2007, 2015a). We have noted that lower temperatures can impose costs on embryos (Martin et al. 2007, 2011, 2015a). However, incubation is energetically expensive and can also impose costs on future reproduction and survival in parents (Williams 1996, Bryan and Bryant 1999, Reid et al. 2000, Visser and Lessells 2001). Species with lower adult mortality should minimize such costs of reproduction, even at a cost to offspring, to enhance residual reproductive value (Law 1979, Michod 1979, Barbraud and Weimerskirch 2001, Ghalambor and Martin 2001). At the same time, costs to offspring are not manifested as embryo mortality, given that species with long (5–8 hr) off-bouts that experience cold egg temperatures show normal

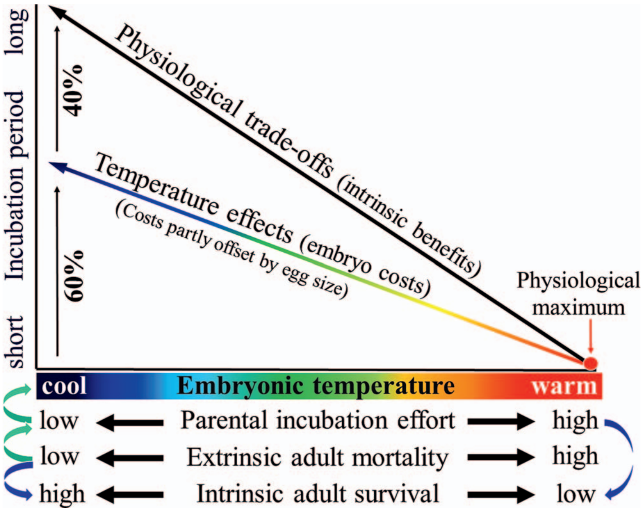

FIGURE 5. Summary of potential extrinsic and intrinsic mechanisms influencing incubation periods across species. High adult mortality from extrinsic environmental sources favors high parental incubation effort and warmer embryonic temperature. Greater parental effort can also lower intrinsic adult survival (through oxidative stress, DNA damage, etc.). Starting at the warmest temperatures and highest extrinsic adult mortality, embryos are at a physiological maximum. As extrinsic mortality declines, selection favors lower parental effort, causing longer incubation periods from cooler temperatures and explaining ~60% of the variation among species. However, cooler temperatures can create energy costs to embryos that may be partly offset by evolution of larger egg size (Martin 2008) or other physiological mechanisms. Parents with low extrinsic mortality and long life should accept costs to offspring over intrinsic survival costs to themselves. At the same time, lower extrinsic mortality should also favor physiological trade-offs that provide intrinsic benefits to phenotypic quality and adult survival, creating constraints on development time that account for ~40% of the variation among species. Physiological trade-offs during development that provide intrinsic benefits that promote longevity should be favored only if extrinsic mortality is low and thereby allow the opportunity to reap survival benefits. Ultimately, incubation periods increase in duration from both temperature effects and physiological trade-offs, causing them to covary with each other and with adult survival.

hatching success of 91.5–93.5%. Moreover, selection may favor evolution of strategies to mitigate physiological costs to embryos of cooler temperatures (Zhao et al. 2017). For example, parents of species with lower adult mortality and greater neglect may advance-provision embryos with more resources (larger egg size) to help offset costs of cooler temperatures (Martin 2008). This hypothesis has received other support (e.g., Martin 2008, Heming and Marini 2015, LaManna and Martin 2016). These patterns suggest that selection from annual adult mortality can influence interacting life-history traits (i.e. parental effort, egg size, development time) in the evolution of incubation strategies (Figure 5).

Annual adult mortality is strongly influenced by extrinsic environmental factors such as predation, migration, or nonbreeding-season mortality risks (e.g., Rowley and Russell 1991, Sillett and Holmes 2002, Evans et al. 2006, Turbill et al. 2011, Paxton et al. 2017). Lower extrinsic adult mortality can favor intrinsic mechanisms to further enhance longevity and survival; these mechanisms can include reduced reproductive (i.e. incubation) effort to minimize the costs of reproduction, as well as intrinsic programs (e.g., physiological trade-offs) that delay the onset of senescence and enhance adult survival (Law 1979, Michod 1979, Charlesworth 1994, Metcalfe and Monaghan 2003). However, costly physiological programs that require longer incubation periods to enhance longevity should not evolve if high extrinsic mortality inhibits any opportunity to benefit from such mechanisms. As a result, extrinsic mortality should act as the primary directional source of selection, rather than physiology driving mortality (Figure 5; Martin 2002; also see Martin et al. 2015b).

Ultimately, both juvenile and adult mortality should exert selection on life history and incubation strategies and should do so via both mechanistic pathways: intrinsic programs and parental effort (Figure 5; Martin 2002, 2004, 2015, Martin et al. 2015a). Greater nest predation favors shorter incubation periods to reduce risk and may do so both through increased parental effort in warming eggs and through intrinsic trade-offs (Martin 2002, Fontaine and Martin 2006, Martin et al. 2007, 2015a, LaManna and Martin 2016). However, responses to nest predation should be modified by extrinsic adult mortality. High extrinsic adult mortality may also favor high parental effort that manifests as warm egg temperatures and cause embryos to develop at their physiological maximum (Figure 5), such that further warming has minimal effects (Ton and Martin 2017). By contrast, the longer incubation periods of many tropical birds exist despite commonly higher nest predation compared with north temperate species (Martin 1996). This seeming conundrum may reflect selection from lower extrinsic adult mortality in the tropics acting through the 2 mechanistic pathways (Figure 5; Martin 2002, Martin et al. 2007, 2015a). Lower extrinsic adult mortality may favor strategies that benefit parents over offspring, such as reduced parental effort to reduce intrinsic costs to residual reproductive value, while causing lower egg temperatures and longer incubation periods. Simultaneously, lower extrinsic adult mortality may favor physiological programs that require longer incubation periods to enhance phenotypic quality and delay the onset of senescence. The pathway involving parental effort and egg temperature appears to explain ~60% of the variation in incubation periods among species, while intrinsic programs explain residual variation (Figure 5; Martin et al. 2007, 2011, 2013, 2015a, Ton and Martin 2017). Ultimately, denying the roles of either of these 2 factors obscures understanding of the causes and consequences of variation in incubation periods and broader incubation strategies that include parental effort and egg size (Figure 5).

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