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COMMENTARY

The adaptive significance of variation in avian incubation periods

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ABSTRACT

In spite of strong selection by time-dependent mortality on the length of the embryo development (incubation) period, time to hatching varies substantially among species, independently of body size. One view, strongly supported by the work of Thomas Martin and his colleagues, maintains that this variation reflects parental strategies to minimize their own mortality risk at the nest—strategies that influence egg temperature and embryo growth rate. A second, not incompatible, view maintains that variation in the incubation period reflects a trade-off between the growth rate of the embryo and its subsequent quality as a free-living individual. We evaluate several lines of evidence relating nest attendance by adults and the quality of the immune system to the length of the incubation period. Particularly important is the role of sibling competition in selecting for rapid embryo growth and early hatching, and the fact that many species with prolonged incubation periods are raised either as single chicks or in broods with staggered hatching, which predetermines the outcome of sibling competition.

Keywords: development rate, embryo, life history, parent–offspring conflict, time-dependent mortality

El significado adaptativo de la variación en los períodos de incubación de aves

RESUMEN

A pesar de una fuerte selección por la mortalidad dependiente del tiempo de la duración del período de desarrollo del embrión (incubación), el tiempo de incubación varía considerablemente entre especies. Un punto de vista, fuertemente apoyado por el trabajo de Thomas Martin y sus colegas, sostiene que esta variación refleja las diferentes estrategias de los padres para minimizar el riesgo de mortalidad en el nido, que influyen en la tasa de crecimiento temperatura del huevo y el embrión. Por el contrario, mantenemos que la variación en el período de incubación puede representar un compromiso entre la tasa de crecimiento del embrión y la calidad del neonato. Aquí evaluamos varias líneas de evidencia relativa asistencia nido por los adultos y la calidad del sistema inmune a la longitud del periodo de incubación. Particularmente importante es el papel de la competencia de hermanos en la selección para un rápido crecimiento del embrión y la eclosión temprana, y el hecho de que muchas especies con periodos de incubación prolongados, ya sea se plantean como polluelos individuales o en crías con sombreado de escalonado, que predetermina el resultado de la competencia de hermanos.

Palabras clave: embrión, historia de vida, los conflictos entre padres e hijos, mortalidad dependiente del tiempo, tasa de desarrollo

INTRODUCTION

Among species of birds that lay eggs of similar size, the time required for embryo development and hatching varies by a factor of >2 (Rahn and Ar 1974). Part of this variation in the incubation period is related to the degree of development (precocity) of the hatchling, with the self-sufficient (precocial) neonates of such birds as ducks and chickens requiring more time to develop than the dependent (altricial) neonates of songbirds and others (Starck 1993, Starck and Ricklefs 1998). This variation partly reflects the general inverse relationship between rate of growth and functional maturity documented in birds (Ricklefs 1979, Ricklefs et al. 1994). However, even among altricial species that have similar functional capacity at hatching, the log-transformed length of the incubation period for eggs of the same size has a standard deviation of 0.093 $\log_{10}$ units, corresponding to a factor of 1.24; the range between 2 standard deviations on either side of the mean incubation period for a given egg size, which includes ~95% of the species, represents a factor of 1.53, or a 53% increase of the longer period over the shorter period (Ricklefs 1993). Considering the high mortality rates of eggs caused by predation, weather, and other

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factors, why some species of birds with similar neonates take longer to hatch their eggs than others requires explanation.

Avian biologists have proposed a range of hypotheses to account for this variation in incubation periods. Certainly, time-dependent mortality—caused by weather and predators—favors more rapid development, all else being equal (Ricklefs 1969, 1984, Remeš and Martin 2002). Møller (2005) suggested that parasites in the nest might have a similar effect. To ensure rapid development, avian embryos must be maintained by the incubating parent within a narrow range of elevated temperatures. This creates a conflict for the parent between incubation of the eggs and self-maintenance. The primary consideration regarding variation in the duration of incubation is the degree to which adults control embryo development time by their incubation behavior; additional variation in development time might also reflect intrinsic growth programs of embryos. Thomas Martin and his colleagues have argued that variation in the incubation period reflects the proportion of time that parents incubate their eggs (Martin 1996, 2002, Martin et al. 2007, 2011, 2013, 2015). Accordingly, low nest attentiveness would represent primarily a strategy to reduce parental exposure to causes of adult mortality at the nest, simply by the parents not being there, what Cresswell (2008) and Lima (1998) have referred to as the nonlethal effects of predation. The time required for embryo development is inversely related to the temperature at which the egg is maintained, which depends on the incubation behavior of the parents.

Alternatively, Ricklefs (1993) suggested that slow embryo growth reflects a developmental strategy associated with increased quality of the neonate and consequently with the individual's potential life span and lifetime reproductive rate. Both considerations—temperature and individual quality—could influence the length of the incubation period. Here, we argue that the weight of evidence favors incubation strategies that reflect a trade-off between the quality of the individual and its rate of development as an embryo. This issue is important—if the incubation period is related to aspects of individual performance that influence life span and reproductive success, understanding how embryo development affects individual quality could reveal crucial trade-offs governing the evolution of life histories.

The Basic Parameters

(1) All the nutrients required by the embryo are provided in the egg at the time it is laid (Romanoff and Romanoff 1949). However, gas exchange occurs throughout incubation, including inflow of oxygen to support metabolism, and outflow of carbon dioxide and water vapor (Rahn and Ar 1974, Rahn et al. 1979, Ar and Rahn 1980, Rahn and Ar 1980). These processes, including retention of sufficient water in the egg over the incubation period, are critical to embryo development and are adjusted by parental behavior and the quality (including porosity) of the eggshell (Rahn et al. 1977).

(2) The length of the embryo growth period determines the energy efficiency of growth (Romanoff 1960, Ricklefs 1974, 1996) and, therefore, the nutrients that must be provisioned initially to produce a chick. In general, slower growth requires more energy because the embryo's metabolism must be maintained for a longer period. Balancing this, slow growth requires a somewhat lower *rate* of energy consumption, and thus gas exchange—reducing the rate at which water is lost from the egg, although not necessarily the total transpiration over the incubation period (Rahn and Ar 1974).

(3) Embryo growth and development require that the parents warm their eggs. The length of the incubation period is inversely related to egg temperature, as shown by extensive experimentation with artificial incubation (Romanoff 1960, Ricklefs 1987, Deeming and Fergusen 1991, Hepp et al. 2006, Ardia et al. 2009). In some species, both parents incubate the eggs, which they maintain at a high temperature more or less continuously (Skutch 1976, Conway and Martin 2000, Chalfoun and Martin 2007). In other species, only one sex—typically the female—incubates and the eggs go through cycles of heating and cooling corresponding to on and off bouts (Hainsworth and Voss 2002, Martin et al. 2007, 2015).

(4) Species vary in the degree of functional maturity of the neonate (Nice 1962, Starck 1993, Ricklefs and Starck 1998). In general, more mature tissues grow more slowly (Ricklefs et al. 1994, Shea et al. 1995), and chicks with a higher degree of functional maturity at hatching (e.g., precocial species such as ducks and chickens) have longer incubation periods than altricial species such as doves and songbirds.

(5) The length of the incubation period exhibits little genetic variation within populations (e.g., ~3 hr genetic standard deviation in the European Starling [*Sturnus vulgaris*]; Ricklefs and Smeraski 1983). Selection on early postnatal growth rate in chickens and quail has had no effect on the length of the incubation period; nor has selection on the incubation period itself (Siegel et al. 1968, Marks 1979). Thus, although it is clear that the incubation period has undergone evolutionary diversification, this seemingly has required very long periods of divergent unidirectional selection on very conservative traits.

(6) Eggs and their contained embryos are exposed to various mortality factors, many of which, including predation and destruction by storms, are time-dependent (Ricklefs 1969), such that continued exposure increases realized mortality. Thus, any extension of the incubation period increases risk to both the eggs and the parents.

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(7) Selection on the duration of incubation balances costs and benefits to both embryos and parents because offspring success is a component of adult fitness.

The Issues

(1) Incubation periods vary widely among species of birds. In small passerines, the embryo development period can be as short as 11–12 days, or >20 days. In general, more species exhibit prolonged incubation in the tropics than in temperate climates. Martin and his colleagues (Martin 2002, 2004, Martin et al. 2007, 2013, 2015) have argued that most variation in the length of the incubation period reflects parental strategies to reduce their own exposure to time-dependent mortality at the nest. This reduction in parental attendance comes with associated costs expressed in terms of longer incubation periods and reduced nest survival. Because the contribution of an adult's survival to its own evolutionary fitness (its reproductive value) is greater than the contribution of any particular clutch of eggs, parents should generally favor personal survival over clutch survival when the two come into conflict. The nest is assumed to be a dangerous place for parent birds, and they can enhance their own survival by reducing the time spent on the nest each day, with the consequences that the eggs are maintained at a lower average temperature and embryo development is prolonged. Parent birds of some species might also require more time to obtain food for their own needs, which would leave less time for incubation each day among single-sex incubators. Nest (clutch) mortality rates are higher in the tropics than in temperate regions (Ricklefs 1969, Martin 1995, Martin et al. 2007), though overlap does occur (Robinson et al. 2000). And, as mentioned above, incubation periods of many species (though not all) are, on average, longer in the tropics (Skutch 1976, Ricklefs 1993, Conway and Martin 2000).

(2) Time-dependent mortality of eggs is unavoidable, but predation of adults at the nest site is rare, particularly for open-nesting species whose nest sites afford adequate escape routes (Robinson et al. 2005). For example, among ~600 nesting attempts of 2 antbird species (Thamnophilidae) in Panama, mortality of adults at nests was observed in only 2 cases (Rompré and Robinson 2008). Another nesting study on a tropical understory antbird also failed to show any adult mortality (Tarwater 2008). Observations on other species, mostly based on video recording at nests, similarly have reported few instances of predation on adults at the nest. For example, video monitoring of 132 nests of Blackcaps (*Sylvia atricapilla*) in Germany yielded 40 instances of predation by 8 species of predator, with no mention of predation on adults: "When predators approached a nest, adult Blackcaps usually stayed at the nest almost until the predators arrived, leaving at the last second" (Schaefer 2004:172). Similar observations have been reported in multiple studies, including 69 nests of 10 passerine species in grassland habitats, with no mention of adults depredated at the nest, in spite of considerable nest loss (Pietz and Granfors 2000); 142 nests of Black-capped Vireos (*Vireo atricapilla*), with 59 predator visits and 48 nest depredations, but no adult mortality recorded, "although one incubating female narrowly escaped capture by a snake" (Stake and Cimprich 2003:351); no mention of adult mortality at 52 video-monitored nests of Field Sparrows (*Spizella pusilla*) and Indigo Buntings (*Passerina cyanea*) (Thompson et al. 1999); 165 nests of various temperate species monitored with cameras, and with predators identified at 61 of 74 depredated nests, with no mention of adult mortality (Thompson and Burhans 2003); and video monitoring of 182 flycatcher nests and 122 bunting nests in the midwestern United States, recording 144 nest failures but no predation of adult females on the nest (Cox et al. 2014). The general impression from these and similar studies is that parent birds, particularly of open-nesting species, are exquisitely sensitive to the approach of predators to their nests and do not experience undue risk when attending their nests.

Moreover, annual survival of small birds is generally higher, overall, in tropical than in temperate regions (Karr et al. 1990, Ricklefs 1993, Sandercock et al. 2000, Ricklefs et al. 2011), in spite of greater nest mortality rates in the tropics (Ricklefs 1969, Oniki 1979, Skutch 1985), a further indication that adult safety at the nest is not a major contributor to adult survival or to variation in the incubation period. Nest predation rates—although higher, on average, in the tropics—overlap substantially between tropical and temperate locations (Ricklefs 1969, Robinson et al. 2000). Thus, while nest predation undoubtedly exerts a strong influence on avian reproduction, we argue that variation in the length of the incubation period primarily reflects selection on the quality of the neonate, which influences the average life expectancy and lifetime reproductive success of individuals. As in many endeavors, it takes more time to produce a better product.

(3) The rate of embryo growth and development varies little within a species; eggs incubated at the same temperature normally hatch within a few hours (e.g., Ricklefs and Smeraski 1983). In experiments with poultry, the incubation period varies inversely with incubation temperature, up to the maximum temperature tolerance of the embryo. Indeed, temperature is the most significant variable to influence the hatching time of a particular egg (Romanoff 1960, Deeming and Fergusen 1991, Deeming 2002). If this growth rate–egg temperature relationship were to apply to all species of birds, incubating adults would have to reach a compromise between maintaining their eggs at high temperatures (thereby reducing development time) and exposing themselves to the risk of predation at the nest site. Presumably, when adults adjust

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this trade-off by spending less time on the nest to reduce their own exposure to risk, average egg temperature is reduced, the embryonic development rate slows, the incubation period lengthens, and the exposure of eggs to time-dependent nest mortality increases.

Considering that daily mortality rates are so much lower for adults than for eggs, reducing adult exposure at the cost of increasing egg exposure most likely produces no overall fitness advantage. In Martin et al.'s (2015) analysis, daily nest mortality rate for open-nesting species at his Venezuela site varied between 0.030 and 0.069 (3–7%) per day. Among these species, annual adult mortality rates varied from 0.1 to 0.4, which corresponds to a range of average daily mortality rates between 0.00029 and 0.0014 (i.e. 2 orders of magnitude lower than egg mortality rates), with little evidence of increased adult mortality on the nest. Even considering that eggs can be replaced, parents seemingly would increase their lifetime reproductive success by reducing the embryo development period of their offspring, as long as neonate quality was unaffected. 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. Recent studies indicate that lower incubation temperatures result in slower nestling growth (Nilsson et al. 2008, DuRant et al. 2013), lower hatchability (Ben-Ezra and Burness 2017), higher nestling metabolism (Ben-Ezra and Burness 2017), lower thermoregulatory performance (DuRant et al. 2013), lower immunocompetence (DuRant et al. 2012), and lower long-term survival (Berntsen and Bech 2016). We argue, instead, that balancing the effects of extrinsic mortality, and independently of temperature effects, embryos are selected to reduce development rate in order to increase neonate quality and extend individual productive life spans as adults.

The Evidence

1. Egg temperature and the length of the incubation period. Resolving the controversy over embryo development rate depends, in part, on the relationship between egg temperature and the length of the incubation period. Experimental work with poultry shows a clear inverse relationship between egg temperature and the duration of incubation (Romanoff 1960, Hepp et al. 2006). The first data available for wild birds were comparative (among species) and nonexperimental. Using published data compiled by J. B. Williams (1996) on egg temperatures of north temperate birds, Martin (2002) reported a significant negative relationship between temperature and incubation period among North American species ($r = -0.49$, $P = 0.018$, $n = 23$; also see Martin et al. 2007). However, in a study on egg temperature and incubation period in New World tropical birds, Tieleman et al. (2004) reanalyzed these data and observed that the full dataset, including European species (and with several typographical errors corrected from the original table), failed to show such a relationship (r [species data] $= 0.06$, $P = 0.73$, $n = 38$). In addition, many of these data were from old sources using different technologies that have produced biased, generally low, egg temperatures. For example, among the measurements in Martin's analysis, those made by Huggins (1941) included an egg temperature for the American Tree Sparrow (*Spizelloides arborea*) of 30.8°C, whereas that for the closely related Field Sparrow (*Spizella pusilla*) was 38.1°C; both species have 11-day incubation periods. Furthermore, among the tropical species included in the field study by Tieleman et al. (2004), egg temperature and incubation period were not significantly related, although the sign of the correlation was consistent with the hypothesis that development rate is inversely related to temperature (r [species data] $= -0.35$, $P = 0.22$, $n = 14$; r [phylogenetic independent contrasts] $= -0.24$, $P = 0.42$, $n = 13$).

More recently, Martin et al. (2015) analyzed data from 4 study sites (Arizona, Venezuela, South Africa, and Borneo). The data exhibit a strong negative relationship between average egg temperature and the length of the embryo development period (their figure 3). Over the whole sample, the common logarithm of the incubation period (days) decreased by 0.057 $\log_{10}$ units (SE 0.003), a decrease of −12% per degree Celsius in average egg temperature between 32.5°C and 36.5°C, and a factor of 1.7 over the 4°C range ($R^2 = 0.82$, $n = 63$ species). Moreover, egg temperature was positively related to both adult and nest mortality rates, which suggests that higher time-dependent mortality selects higher nest attendance and incubation temperature to reduce the incubation period and exposure to agents of nest mortality (their figure 2).

In the context of the present analysis, our data from Panama provide a useful comparison. Martin et al.'s (2015) Venezuelan data are from a research site at 1,400–2,000 m elevation, where ambient air temperatures are as much as 7–10°C cooler than at our site in Panama at 100 m elevation. Previous studies have shown little influence of elevation below 3,000 m on incubation periods in birds (Skutch 1967, Carey et al. 1982, Carey et al. 1990, León-Velarde et al. 1997, León-Velarde and Monge-C. 2004). In Venezuela, the average 24 hr egg temperature measured in 18 passerine species was 34.6°C (SD 0.95) and the average incubation period was 16.0 days (SD 2.3; range: 12.8–19.9 days). In lowland Panama, the average 24 hr egg temperature measured in 13 passerine species—albeit using somewhat different methods—was 36.9°C (SD 0.83) and the average incubation period was 14.9 days (SD 2.2; range: 12.5–19.0 days; Tieleman et al. 2004). Based on Martin et al.'s (2015) within-site regression, the 2.3°C difference in egg temperature between the Venezuela site

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and our site in Panama would imply a 1.35-fold difference in the incubation periods of birds in the 2 areas, whereas a 1.07-fold difference is observed. Part of the discrepancy might have to do with measurement protocols and the choice of species. Because Martin has not worked at lowland sites in the Neotropics, no direct comparisons are available. However, at our lowland site in Panama, one of the longest incubation periods (18 days) was that of the Spotted Antbird (*Hylophylax naevioides*), which has biparental incubation, an 88% average 24 hr nest attentiveness, and an average 24 hr egg temperature of 36.2°C. By all accounts, the incubation period of this species should be much shorter.

2. Experimental manipulation of incubation temperatures. In an experiment designed to test the effect of natural variation in parental incubation behavior on rate of embryo development, Martin et al. (2007) switched eggs between nests of species with long and short incubation periods. The results showed that incubation periods were shifted, generally by 1–2 days, in the direction of the foster nest, which suggests a role for the incubation behavior of the parent. However, the shifts were considerably smaller than the difference between the natural incubation periods of the donor and foster species.

In a "common-garden" experiment, Robinson et al. (2008) artificially incubated 50 eggs of the House Wren (*Troglodytes aedon*), from 2 populations with differing natural incubation periods (12–13 days [temperate, $n = 27$] vs. 14 days [tropical, $n = 23$]). When placed under identical conditions, eggs from the 2 populations hatched in relation to their natural incubation periods (13.6 vs. 14.9 days, $P < 0.0001$), which suggests that the difference in embryo growth rate between the populations was intrinsic. In a more comprehensive experiment, Robinson et al. (2014) incubated the eggs of a variety of Panamanian birds, with natural incubation periods varying between 12 and 19 days, at a constant temperature of 36.5°C and observed no decrease in the hatching times of the species with the longer incubation periods, and 1- to 2-day increases in those species with the shorter incubation periods.

3. Summed brooding time of parents on nests with long and short incubation periods. If absences from nests and resulting low egg temperatures were responsible for the long incubation periods of some birds, one would expect that the adults would benefit from less exposure on the nest over the period required to hatch the eggs. Ricklefs and Brawn (2013) showed that this was not the case for a number of species in Panama, based on automatic recording of the intervals during which parents incubated eggs. In 6 species of lowland, inner-forest flycatchers (Tyrannidae) and antbirds (Thamnophilidae), with natural incubation periods between 17.9 and 23.3 days, the total time that the parents together incubated the eggs varied between 14.2 and 19.5 days. Thus, in tropical species with long incubation periods, parents spent more total time at the nest between laying and hatching the eggs than the overall duration of the incubation periods of many species in the area, which may be as short as 12–14 days (e.g., Clay-colored Thrush [*Turdus grayi*], Red-throated Ant-Tanager [*Habia fuscicauda*], and Yellow-green Vireo [*Vireo flavoviridis*]). Reducing the percentage of time on the nest, to reduce predation risk or increase foraging time, actually increases the total nest attendance time required to hatch the clutch.

Of course, certain times of day or night might be more dangerous at the nest than others, and being away from the nest during such periods might increase adult safety. In one study of forest understory birds in Panama, which used thermistors in the nest to identify the time of clutch predation events, two-thirds of 21 events occurred between 1100 and 1800 hours, and none took place at night (Libsch et al. 2008). Adults of these species incubate continuously through the night, whereas the afternoon period is the low point of adult nest attendance in the daily cycle (Ricklefs and Brawn 2013), but also the warmest part of the day. Nights near the equator are longer than those at higher latitudes during their respective breeding seasons. Because most birds sleep on the nest following the onset of full incubation, one could consider the hours of nighttime darkness as one long on-bout. When this period is considered to offset longer daytime off-bouts in the tropics, the 24 hr constancy of incubating birds exhibits almost no variation with respect to latitude (Álvarez and Barba 2014).

4. Evidence concerning the quality of the hatched chick. Tropical birds typically live longer than temperate birds (Karr et al. 1990, Brawn et al. 1995, Ricklefs 1997, Sandercock et al. 2000, Ricklefs and Shea 2007, Ricklefs et al. 2011, Martin et al. 2015), and this applies especially to tropical species with long incubation periods (Ricklefs 1993). Thus, prolonged embryo development might be associated with lower adult mortality rates in some way, including by delaying the aging process. Possibly relevant to this postulate, among 4 species of birds whose incubation periods ranged from 17 days (Japanese Quail [*Coturnix japonica*]) to 42 days (Leach's Storm-Petrel [*Oceanodroma leucorhoa*]), lipid peroxidation and DNA breakage near the end of embryo growth were inversely related to the length of the embryo development period (Tsunekage 2013, Tsunekage and Ricklefs 2015). Thus, more slowly growing embryos either resisted damage better or repaired damage more readily than more rapidly growing embryos.

Ricklefs and Scheuerlein (2001) characterized the rate of aging in several populations of birds in captivity in relation to body and brain mass, incubation period, postnatal growth rate, and genome size, and found that the logarithm of the Weibull rate of aging (ω; Ricklefs 1998)

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decreased with increasing log-transformed brain mass ($b = -0.285 \pm 0.059$, $r^2 = 0.43$) independently of variation in body size and incubation period. Thus, in that analysis, intrinsic longevity appeared to be unrelated to the rate of embryo growth, although many long-lived birds, such as parrots and albatrosses, also have very long embryo development periods.

In an analysis of data from the literature reporting results of microscopic examination of blood smears, Ricklefs (1992) found that the prevalence of hemosporidian (malarial) parasites is inversely related to the length of the incubation period ([species data] $r^2 = -0.75$). Ricklefs suggested that longer development periods enabled increased resistance to parasites by providing extended time for diversification of the immunoglobulin molecules that are responsible for specific immunity. This hypothesis has not been tested experimentally, or by surveys of the diversity of the immune system response. However, Lee et al. (2008) found a strong positive correlation ([phylogenetic generalized least squares analysis] $P < 0.001$, $r^2 = 0.23$) between the length of the incubation period and constitutive ("natural") antibodies in 70 species of Neotropical birds; other life-history variables were not significantly associated with variation in natural antibodies.

Several studies have investigated the relationship between the cell-mediated immune response (CMI), as assessed by the phytohemagglutinin (PHA) assay, and both embryo and chick development rate. Tella et al. (2002) found that CMI was positively related to both adult size and the length of the development period across a wide variety of birds. Among small altricial species in their sample, including song birds, body size remained a strong predictor of the PHA response, but the incubation period and postnatal development rate did not. Palacios and Martin (2006) conducted a similar analysis of CMI in small, temperate-zone land birds and found that species with higher blood-parasite prevalence had stronger PHA responses, but that CMI was unrelated, or perhaps weakly inversely related, to the length of the incubation period. Regardless, the CMI data do not address hypotheses based on specific B-cell-related immunity. In a more recent study, Martin et al. (2011) found positive relationships between CMI and a hemagglutination response test for circulating antibodies (Matson et al. 2005), and between CMI and the length of the incubation period adjusted for incubation temperature, representing the "intrinsic" temperature-corrected rate of embryo growth. Clearly, additional analyses of the relationship between immune function and embryo development are needed.

5. Adult control over hatching synchrony and selection for rapid embryo growth. Embryo growth rate is potentially influenced by a number of conflicting selective pressures. If slower embryo development leads to higher chick quality and potentially longer adult life span and reproductive success, selection should favor longer incubation periods. Time-dependent mortality, primarily nest predation, favors shorter incubation periods. However, a potentially stronger selective agent for rapid development is sibling competition for resources. Nestling birds compete for food brought by the parents, and generally the larger (hence older) chick wins the contest (Ricklefs 1965, Lack 1968). Thus, early hatching, as a result of rapid embryonic development, would be strongly selected under these conditions (Werschkul and Jackson 1979, Ricklefs 1993).

(i) Some of the slowest embryo development rates occur in species with single-egg clutches, which therefore do not experience sibling competition. As mentioned above, in species with multi-chick broods, sibling competition is strong and often determines survival in the nest (Lack 1968); the outcome of sibling competition is largely determined by the relative hatching time of the chicks. However, because there is so little genetic variation in hatching time, this becomes important only when (1) chicks tend to hatch synchronously and (2) small heritable differences in development rate influence relative hatching position in the brood (Ricklefs 1992).

(ii) Accordingly, parents can reduce the selective impact of sibling competition by staggering the hatching times of their chicks, which they do simply by initiating incubation early in the laying sequence or varying maternal hormonal deposition in eggs (Gil 2008). Species with multi-egg clutches and long incubation periods tend to have asynchronous hatching or to lack evidence of sibling competition among the nestlings (i.e. all the chicks survive; Ricklefs 1993). However, prolonging the embryo growth period must incur costs for both the parents and the embryos in terms of energy and time-dependent egg mortality. Accordingly, the benefits of slow embryo growth must be substantial.

Conclusions

The time required to incubate the eggs varies among species of birds, but the adaptive significance of this variation is poorly understood. Among single-sex incubators, time away from the nest is needed for individuals to procure food and engage in other maintenance activities. This results in reduced egg temperatures and presumably increases the duration of the incubation period. There is little evidence that nests are dangerous sites for adults or that adult survival is increased by being away from the nest. Indeed, the longer incubation periods of many tropical birds, compared to temperate species, are associated with an increase in the total time parents spend at the nest. In the absence of advantage conveyed to the parent by a long incubation period, we suggest that the advantage belongs to the hatched chick. Species of tropical songbirds with longer incubation periods exhibit higher

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natural antibody levels and lower prevalence of hemosporidian blood parasites, pointing to potential fitness advantages of slow embryo growth. Parental strategies (e.g., early onset of incubation during the egg-laying sequence) that reduce the fitness advantage of rapid embryo growth and early hatching in response to intrabrood competition also suggest that slower development increases individual quality, or at least individual fitness. The relationship between embryo growth rate and lifetime reproductive success clearly warrants additional investigation.

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