

A new view of avian life-history evolution tested on an incubation paradox

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Viewing life-history evolution in birds based on an age-specific mortality framework can explain broad life-history patterns, including the long incubation periods in southern latitudes documented here. I show that incubation periods of species that are matched phylogenetically and ecologically between Argentina and Arizona are longer in Argentina. Long incubation periods have mystified scientists because they increase the accumulated risk of time-dependent mortality to young without providing a clear benefit. I hypothesize that parents of species with low adult mortality accept increased risk of mortality to their young from longer incubation if this allows reduced risk of mortality to themselves. During incubation, songbird parents can reduce risk of mortality to themselves by reducing nest attentiveness (percentage of time on the nest). Here I show that parents of species with lower adult mortality exhibit reduced nest attentiveness and that lower attentiveness is associated with longer incubation periods. However, the incubation period is also modified by juvenile mortality. Clutch size variation is also strongly correlated with age-specific mortality. Ultimately, adult and juvenile mortality explain variation in incubation and other life-history traits better than the historical paradigm.

Keywords: age-specific mortality; life-history evolution; clutch size; incubation period; nest attentiveness; developmental rates

1. INTRODUCTION

A central focus of life-history studies is to understand why life-history strategies vary among species (Lack 1968; Roff 1992; Charlesworth 1994). General theory has suggested that age-specific mortality is a major source of selection on life-history evolution; greater adult mortality favours increased reproductive effort whereas greater juvenile mortality favours reduced reproductive effort (Cole 1954; Williams 1966; Roff 1992; Charlesworth 1994). Empirical studies in fishes, insects, invertebrates and plants have supported this theory (Crowl & Covich 1990; Reznick *et al.* 1990; Roff 1992). By contrast, the longstanding paradigm in avian systems suggests that food limitation is a primary cause of life-history variation (Lack 1954, 1968; Martin 1987). Food limitation explains considerable life-history variation within bird species (Martin 1987), but has been unable to explain most variation among species (Slagsvold 1982; Martin 1995; Owens & Bennett 1995; Martin *et al.* 2000). Here, I suggest that life-history theory based on age-specific mortality (Cole 1954; Williams 1966; Roff 1992; Charlesworth 1994) better explains general avian life-history patterns and can provide new insight into previously unresolved problems.

One unresolved problem concerns developmental periods of birds. Developmental periods are thought to be longer in southern latitudes, where nest predation rates are sometimes greater than in northern sites (Martin 1996). Increased nest predation is thought to favour shorter developmental periods (Lack 1968; Bosque & Bosque 1995; Martin 1995; but see also Ricklefs (1993)). Thus, longer incubation periods in southern areas where predation is greater pose a paradox (Martin 1996). Moreover, long incubation periods are puzzling in general because they increase the risk of time-dependent mortality to eggs,

with no clear benefit (Boersma 1982; Ricklefs 1993). Here, I examine the ability of age-specific mortality to resolve this apparent paradox.

Reducing risk of mortality can have greater fitness benefits than increasing fecundity in species with low adult mortality (e.g. Barbraud & Weimerskirch 2001). Because of such fitness effects, 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). Indeed, parents of passerine species in South America with lower adult mortality were less willing to risk additional mortality to feed their young compared with related species from North America (Ghalambor & Martin 2001). Such effects should also apply to incubation. 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). Indeed, the energy costs of incubation have recently been shown to increase mortality (Visser & 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). Nest attentiveness (percentage of time on the nest) can thereby influence mortality risk for adults and, under the above theory, should be reduced in species with lower extrinsic adult mortality, as appears to occur more commonly in southern regions (Rowley & Russell 1991; Sandercock *et al.* 2000; Ghalambor & Martin 2001; Sanz 2001).

Nest attentiveness influences length of incubation period within species (Haftorn 1983; Lyon & Montgomerie 1985; Moreno 1989) and attentiveness varies among species (Conway & Martin 2000), providing the potential for it to influence interspecific variation in incubation periods

(Boersma 1982). Here, I examine the novel hypothesis that decreased adult mortality in southern species favours reduced nest attentiveness during incubation, yielding longer incubation periods. I also examine the ability of nest predation to explain additional variation and then examine the ability of age-specific mortality to explain clutch size.

2. STUDY AREAS AND METHODS

Study sites in Arizona included 22 high-elevation (2300 m elevation) forest drainages of mixed conifer and deciduous canopy tree species (Martin 1998). Study sites in Argentina included 16 plots in Yungas forest habitat (Martin *et al.* 2000). Plots were searched for nests from May through to July (1988–2000) in Arizona and from October through to December (1997–1999) in Argentina. Incubation periods were measured for nests found during nest-building or egg-laying as the period from the last egg laid to the last egg hatched (usually synchronous hatching in both sites). Nests were checked every 2–4 days in both locations to measure nest predation rates, which were quantified by the Mayfield (1975) method (detailed in Martin (1998)). Nest predation was only estimated for species with data on more than 20 active nests (only applies to Argentina). Nest attentiveness was measured as the percentage of time that birds were on the nest. From 1993 to 2000 in Arizona and 1997 to 1999 in Argentina, birds were videotaped during incubation for the first 6 hours of the day, beginning at 0.5 h before sunrise. This protocol standardized both time of day and sampling duration to provide data on incubation behaviour and nest attentiveness averaged over the first 6 hours of each day (Martin & Ghalambor 1999; Martin *et al.* 2000).

Annual adult mortality probabilities were estimated based on intensive banding and re-sighting of breeding adults over 9 years in Arizona and 3 years in Argentina. I used Cormack–Jolly–Seber models run through the program MARK (White & Burnham 1999), holding sex and year constant for survival but allowing them to vary for recapture probability to provide species-level estimates of annual adult survival probabilities (Ghalambor & Martin 2001).

I used data from the literature on incubation period, nest attentiveness, adult mortality, egg temperatures and body mass for North American passerines to examine the generality of patterns found on my study sites. Literature data on nest attentiveness and adult survival were taken from original sources (summarized by Martin (1995) and Conway & Martin (2000)) and supplemented with data from the Birds of North America series (Poole *et al.* 1992–1993; Poole & Gill 1993–2001). The incubation period was obtained from this same series. Egg temperatures were obtained from the appendix of Williams (1996).

Incubation period has been found to increase with egg and body mass (Rahn & Ar 1974; Ricklefs 1993; Ricklefs & Starck 1998), but such analyses were based on comparisons among a variety of avian orders where variation in body mass may be confounded with other factors that may influence length of the incubation period. Little variation is explained among species within orders (Ricklefs & Starck 1998). To control for confounding influences, I restricted analyses to Passeriformes that are less than

100 g and where the female is the sole incubator. Passeriformes were chosen because they represent the most diverse order in Aves and include extensive variation in length of the incubation period, as well as other life-history traits.

I controlled for any phylogenetic effects in cross-species correlations using independent contrasts (Felsenstein 1985; Harvey & Pagel 1991). In addition, a regression approach was used for analysis of covariance (ANCOVA), where I used country as a dummy variable in independent contrasts (Martin 1995). All regressions were forced through the origin (Harvey & Pagel 1991). The phylogenetic hypothesis was based on Sibley & Ahlquist (1990) but modified by subsequent phylogenetic studies as described previously (Martin 1995; Martin *et al.* 2000).

3. RESULTS

(a) *Variation in incubation periods*

Field studies included species paired by phylogeny and ecology between Arizona, USA and El Rey National Park, Argentina (table 1). These pairs of species demonstrated that incubation periods were longer (figure 1), clutch sizes were smaller (Martin *et al.* 2000) and annual adult mortality was lower (Ghalambor & Martin 2001) in Argentina than in Arizona. Thus, species on these sites characterize the typical latitudinal gradient in life-history strategies.

Incubation period is expected to increase with egg mass (Rahn & Ar 1974; Ricklefs & Starck 1998), which is tightly correlated with body mass (Ricklefs & Starck 1998), as I found for the species studied here (species, $r = 0.98$, $p < 0.0001$, $n = 24$; independent contrasts, $r = 0.95$, $p < 0.0001$, $n = 23$). However, incubation period did not increase with body (or egg) mass for Passeriformes in Argentina (species, $p > 0.9$, $n = 19$; independent contrasts, $p > 0.9$, $n = 18$) or Arizona (species, $p = 0.7$, $n = 18$; independent contrasts, $p > 0.9$, $n = 17$). The literature provided data for a larger pool of species of small (< 100 g) North American passerines and also yielded no relationship between incubation period and body mass (species, $p = 0.13$, $n = 97$; independent contrasts, $p = 0.4$, $n = 89$). Finally, body (or egg) mass did not explain differences in incubation periods between regions; incubation differed between regions for the same mass (ANCOVA with mass as a covariate: species, $F_{1,34} = 39.1$, $p < 0.0001$; independent contrasts, $F_{1,34} = 24.5$, $p < 0.0001$). Thus, allometry did not contribute significant variation to the incubation period for the group of species studied here.

Nest predation, on the one hand, explained variation in incubation periods within both Argentina and Arizona, but failed to explain differences between latitudes (figure 2). This result is intuitive because nest predation rates were similar for species paired between Argentina and Arizona (Martin *et al.* 2000) but incubation period was not (figure 1). On the other hand, given that juvenile mortality should interact with adult mortality to influence reproductive effort (Roff 1992; Charlesworth 1994), the similar nest predation rates between regions simplifies the prediction that lower adult mortality in southern species should favour reduced nest attentiveness.

Table 1. Species paired by phylogeny and ecology in a northern mixed forest in Arizona versus a subtropical yungas forest in Argentina for comparative tests.

Arizona	Argentina	figure label
Parulidae (ground nest, foliage- or hover-glean/flush-chase)		
<i>Vermivora virginiae</i>	<i>Basileuterus signatus</i>	Parulid 1
<i>Vermivora celata</i>	<i>Basileuterus bivittatus</i>	Parulid 2
<i>Cardellina rubrifrons</i>	<i>Myioborus bruniceps</i>	Parulid 3
Turdidae (shrub/subcanopy nest, ground forage)		
<i>Catharus guttatus</i>	<i>Catharus dryas</i>	Catharus
<i>Turdus migratorius</i>	<i>Turdus rufiventris</i>	Turdus
Tyrannidae (niche nest, flycatching/hover-glean)		
<i>Empidonax occiden</i>	<i>Lathrotriccus euleri</i> ^a	Empidonax
Emberizidae (shrub nest, ground forage)		
<i>Pipilo chlorurus</i>	<i>Atlapetes torquatus</i>	Emberizid 1
Emberizidae (ground nest, ground forage)		
<i>Junco hyemalis</i>	<i>Arremon flavirostris</i>	Emberizid 2
Troglodytidae (hole nest, ground/branch forage)		
<i>Troglodytes aedon</i>	<i>Troglodytes aedon</i>	Troglodytes

^a Previously placed in the genus *Empidonax*.

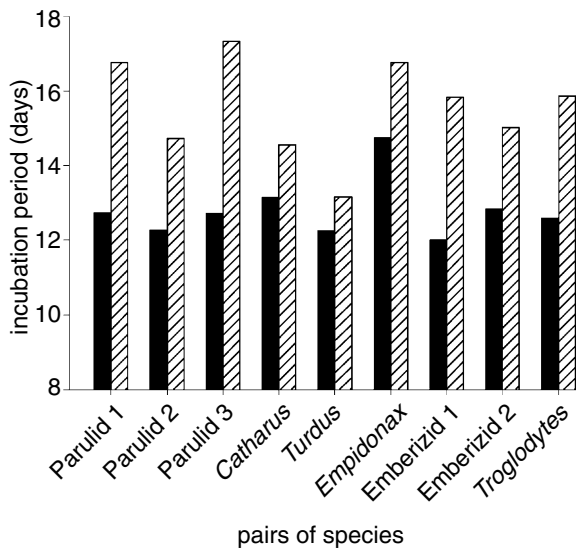


Figure 1. Duration (in days) of incubation periods for species paired by phylogeny and ecology (see table 1 for identifications) between Argentina (shaded bars) and Arizona (black bars) is longer in Argentina (paired $t = 5.7$, $p = 0.001$, $n = 7$, t -test paired by phylogeny where all three parulid species pairs were pooled because individual species were not phylogenetically separated between regions, whereas pairs within Turdidae and Emberizidae were phylogenetically separate (Martin *et al.* 2000).

(b) Adult mortality, attentiveness, and incubation

Nest attentiveness was indeed lower in Argentina (figure 3) and strongly correlated with adult mortality (figure 4a). The North American passerine sample included more species and also showed a strong relationship (figure 4b). Thus, the novel hypothesis that species with lower adult mortality should reduce added risk of mortality to themselves by reducing nest attentiveness was supported both among and within regions (figure 4).

The reduction in attentiveness was predicted to yield longer incubation periods. Lower attentiveness in Argentina (figure 3) was indeed correlated with longer

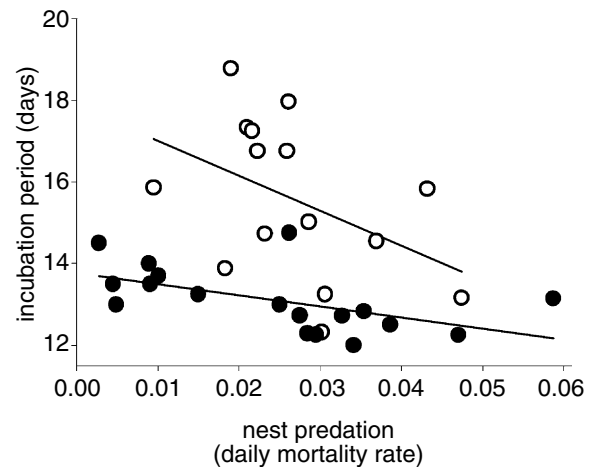


Figure 2. Incubation period differs between Argentina (white circles) and Arizona (black circles) for a given level of nest predation (ANCOVA: species, $F_{1,30} = 30.7$, $p < 0.0001$; independent contrasts, $F_{1,30} = 30.8$, $p < 0.0001$), but decreased with daily probability of nest predation within regions (species, $F_{1,30} = 7.6$, $p = 0.010$; independent contrasts, $F_{1,30} = 4.7$, $p = 0.039$). Nest predation was measured as daily predation rate, which is the daily probability of predation.

incubation periods (species, $r = -0.77$, $p < 0.0001$, $n = 37$; independent contrasts, $r = -0.76$, $p < 0.0001$, $n = 36$), even when controlled for nest predation risk (figure 5a). Nest attentiveness, thus, explained a significant amount of the difference in incubation periods between regions (figure 5a), but also among species within Argentina (figure 5a) and North America (figure 5b). Nest attentiveness is thought to influence incubation by affecting egg temperature and such relationships have been demonstrated within species (Haftorn 1983; Lyon & Montgomerie 1985). I found that such relationships also exist among species (figure 5c).

Attentiveness and its effect on egg temperature and incubation period can be affected by ambient temperature; colder ambient temperatures can yield

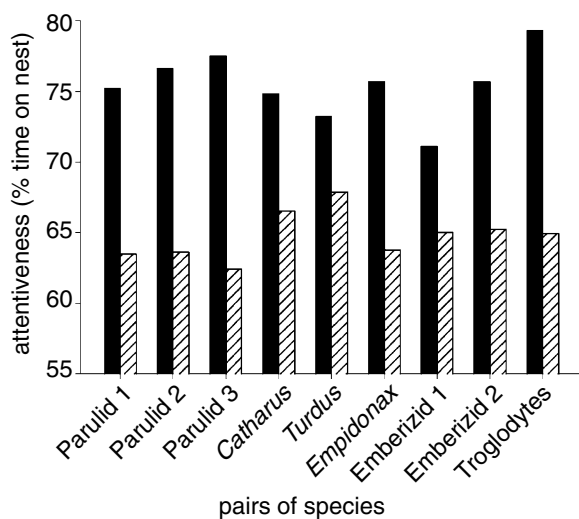


Figure 3. Nest attentiveness (percentage of time on the nest) for species paired by phylogeny and ecology (see table 1 for identifications) between Argentina (shaded bars) and Arizona (black bars) was lower in Argentina ($paired\ t = 7.5$, $p < 0.001$, $n = 7$, t -test paired by phylogeny where all three parulid species pairs were pooled because individual species were not phylogenetically separated between regions, whereas pairs within Turdidae and Emberizidae were phylogenetically separate (Martin *et al.* 2000).

higher attentiveness, but still lower average egg temperature (White & Kinney 1974; Haftorn 1983). Ambient temperature cannot explain the results here. The average minimum temperatures during the middle (main) month of the breeding season in Argentina (November) and Arizona (June) during 1997–1999 were 11–13 °C and 8–10 °C, respectively. The average maximum temperatures were the same (26–28 °C) in Argentina and Arizona, so temperature differences between sites were small. More importantly, the slightly colder temperatures in Arizona made tests conservative. Colder ambient temperatures yield longer incubation periods (White & Kinney 1974; Haftorn 1983) and if higher attentiveness in Arizona was used simply to offset colder temperatures, then incubation periods should be similar. Instead, the incubation periods associated with higher attentiveness were shorter. The results here represent, to my knowledge, the first demonstration that variation in incubation period is related to nest attentiveness among species and latitudes (figure 5), as has been found within species (Haftorn 1983; Lyon & Montgomerie 1985; Moreno 1989).

(c) Incubation period and age-specific mortality

Nest attentiveness is an extrinsic influence on incubation period. When these extrinsic effects are controlled, remaining variation in incubation period was strongly explained by nest predation within both regions (figure 6a). The faster development favoured by nest predation for a given level of nest attentiveness raises the question: why not always develop faster and have shorter developmental periods for the same parental effort? One hypothesis suggests that faster development may compromise immunocompetence or other physiological processes during development and thereby create adult mortality costs later in life (Ricklefs 1992, 1993). However, the

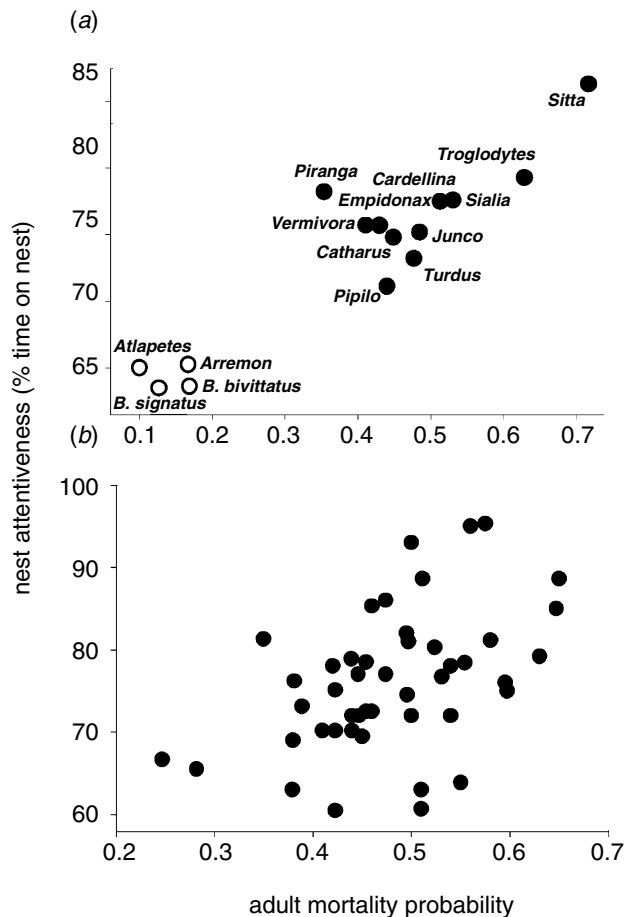


Figure 4. Nest attentiveness relative to adult mortality. (a) Nest attentiveness was greater in species with greater adult mortality between Argentina (white circles) and Arizona (black circles) (species, $r = 0.93$, $p < 0.001$, $n = 15$; independent contrasts, $r = 0.91$, $p < 0.001$, $n = 14$), as well as within regions (ANCOVA with region as a main effect: species, $F_{1,12} = 12.1$, $p = 0.005$; independent contrasts, $F_{1,12} = 6.0$, $p = 0.03$). (b) Nest attentiveness also increased with adult mortality (species, $r = 0.46$, $p = 0.002$, $n = 45$; independent contrasts, $r = 0.42$, $p = 0.004$, $n = 44$) in North American passerines.

mechanistic basis for this hypothesis has not yet been demonstrated. By contrast, a mechanistic basis for the reverse relationship, where extrinsic adult mortality indirectly influences incubation period through attentiveness, was supported here. Moreover, while incubation period was correlated with adult mortality between Argentina and Arizona, there was no correlation within the small samples of either region alone (figure 6b). The larger North American sample also yielded a non-existent or very weak relationship (species, $r = -0.17$, $p = 0.2$, $n = 50$; independent contrasts, $r = -0.29$, $p = 0.039$, $n = 49$). The weak or non-existent relationship between adult mortality and incubation period within regions could result if adult mortality influences incubation period indirectly, as proposed here. Indeed, the links between adult mortality versus attentiveness (figure 4) and attentiveness versus incubation period (figure 5) were much stronger within regions and better explained variation both within and between regions (i.e. figure 6b).

Adult and juvenile mortality, thus, can explain substantial variation in incubation period for passerines, but

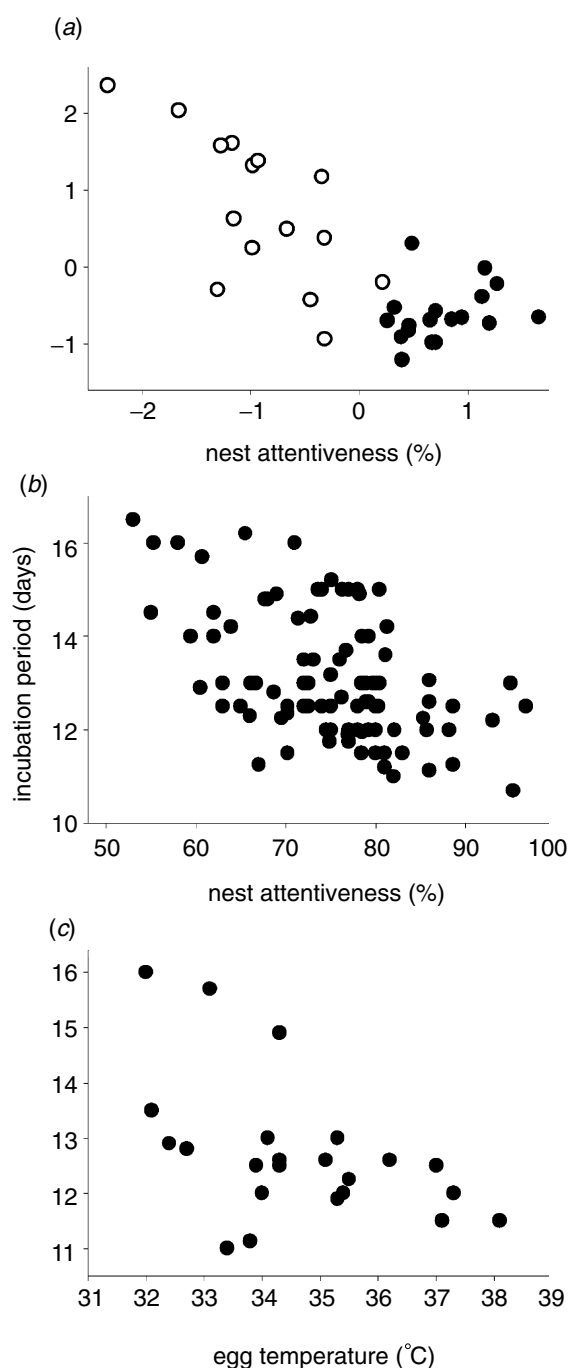


Figure 5. Incubation period relative to nest attentiveness and egg temperature. (a) Incubation period decreases with increasing nest attentiveness while controlling for effects of nest predation across species in Argentina (white circles) and Arizona (black circles) (species, $r_p = -0.78$, $p < 0.0001$, $n = 33$; independent contrasts, $r_p = -0.79$, $p < 0.0001$, $n = 32$). Incubation period decreases with nest attentiveness, while controlling for nest predation, in Argentina (species, $r_p = -0.76$, $p = 0.002$, $n = 15$; independent contrasts, $r_p = -0.75$, $p = 0.002$, $n = 14$), but not Arizona (species, $r_p = 0.34$, $p = 0.2$, $n = 18$; independent contrasts, $r_p = 0.39$, $p = 0.11$, $n = 17$). (b) Incubation period also decreased with increasing nest attentiveness (species, $r = -0.50$, $p < 0.0001$, $n = 89$; independent contrasts, $r = -0.48$, $p < 0.0001$, $n = 81$) for North American passerines in general. (c) Incubation period decreases with increasing average egg temperature (species, $r = -0.49$, $p = 0.018$, $n = 23$; independent contrasts, $r = -0.45$, $p = 0.025$, $n = 22$).

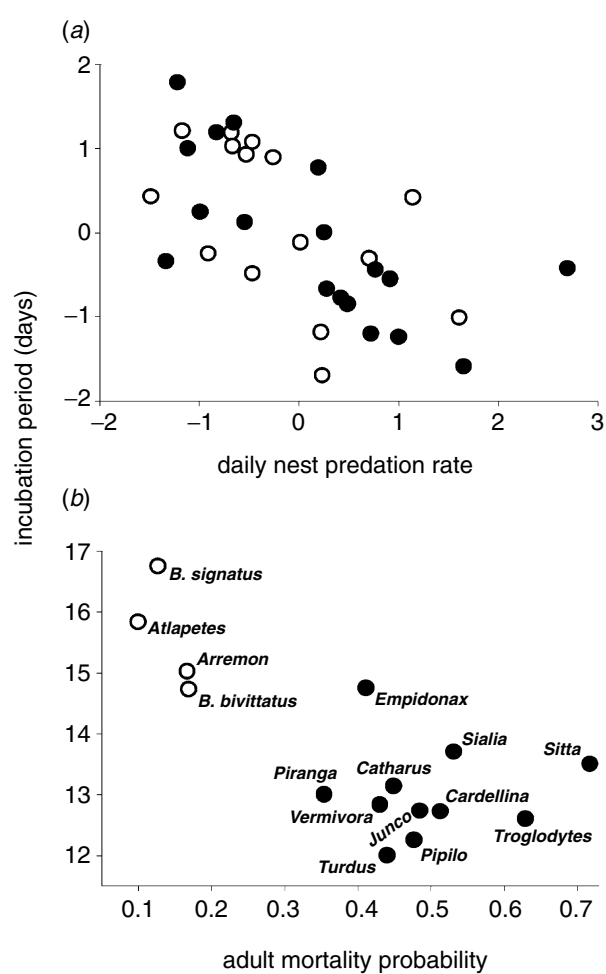


Figure 6. Incubation period relative to age-specific mortality. (a) Incubation period decreases with increased nest predation rate within and across both Argentina (white circles) and Arizona (black circles) (species, $r_p = -0.59$, $p < 0.0001$; $n = 33$; independent contrasts, $r_p = -0.40$, $p = 0.027$, $n = 32$) when nest attentiveness is controlled. (b) Incubation period decreases with adult mortality in Argentina and Arizona (species, $r = -0.75$, $p < 0.001$, $n = 15$; independent contrasts, $r = -0.78$, $p = 0.001$, $n = 14$), but not within each region (ANCOVA with region as a main effect: species, $F_{1,12} = 0.1$, $p = 0.8$; independent contrasts, $F_{1,12} = 0.57$, $p = 0.5$).

incubation periods vary further in other orders and raise additional questions that require exploration. Nonetheless, the results obtained here provide a new perspective on causes of variation in length of the incubation period. They suggest why species with lower adult mortality may accept increased nest predation costs arising from longer incubation periods; parents should accept these added egg mortality costs to current reproductive value when they are less than the gains in residual reproductive value from improved adult survival obtained from reduced parental attentiveness.

(d) Age-specific mortality and clutch size variation

Age-specific mortality also explains variation in clutch size. Earlier analyses showed that nest predation explained variation in clutches within Arizona and Argentina, but not between regions (Martin *et al.* 2000). These analyses did not take into account adult mortality. Adult mortality

explains a considerable amount of the variation in clutch size even when controlling for variation in nest predation (species, $r_p = 0.95$, $p < 0.0001$, $n = 15$; independent contrasts, $r_p = 0.95$, $p < 0.0001$, $n = 14$). Also, nest predation explains a significant amount of the residual variation after correcting for adult mortality both within and among regions (species, $r_p = -0.71$, $p = 0.004$, $n = 15$; independent contrasts, $r_p = -0.69$, $p = 0.006$, $n = 14$).

4. DISCUSSION

Interest in understanding micro-evolution has focused tests in past avian studies on intraspecific variation, which has resulted in tests of phenotypic plasticity rather than evolutionary pathways (Reznick 1985; Martin 1995). As a result, previous tests have not addressed why species have evolved different levels of reproductive effort. Tests of the cost of reproduction have demonstrated such costs (e.g. Visser & Lessells 2001), but have not examined why they favour different levels of reproductive effort among species. Food limitation, a traditional hypothesis, cannot explain much of this variation in reproductive effort among species; many species feed in similar places and on the same foods but have very different clutch sizes (Martin 1995). Of course, food limitation can contribute to life-history variation and even influence attentiveness (Haftorn 1983; Lyon & Montgomerie 1985; Moreno 1989). Consequently, if food was more limited in the south it could explain reduced attentiveness there (i.e. figure 3). Yet food is obtained and brought to young at a higher rate in Argentina than Arizona, suggesting that food is not more limiting in Argentina (Martin *et al.* 2000). Other evidence also suggests that food cannot explain major differences between or within regions (Skutch 1949, 1985; Martin 1995; Magrath & Yezerinac 1997; Martin *et al.* 2000).

More importantly, the idea of greater food limitation in Argentina is difficult to reconcile with the lower adult mortality there. It is difficult to imagine that a reduction in clutch size by one or two eggs, as seen for the paired species studied here (Martin *et al.* 2000), can compensate for greater food limitation and still yield the 50% greater annual adult survival observed between regions (see figure 4a). If such small reductions in clutch size yielded such large payoffs in adult survival, then birds in the northern temperate regions also should be strongly favoured to reduce their clutch sizes similarly. The reason why they do not do so seems easily explained by greater extrinsic adult mortality limiting any survival benefits gained by reductions in clutch size. Even if food limitation is a contributing factor to decreased attentiveness in the south, the decrease in reproductive effort and risk-taking from lower attentiveness is still concordant with mortality theory (Cole 1954; Williams 1966; Reznick *et al.* 1990; Roff 1992; Charlesworth 1994) given the broadly observed decrease in adult mortality in southern regions (Rowley & Russell 1991; Sandercock *et al.* 2000; Ghalambor & Martin 2001; figure 4a). Thus, I propose an age-specific mortality framework to explain life-history evolution in birds.

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 favoured by harsher winters (Rowley &

Russell 1991; Martin 1996; Sandercock *et al.* 2000; Ghalambor & Martin 2001). These differences in extrinsic adult mortality should favour differences in reproductive effort among latitudes (Williams 1966; Charlesworth 1994). The ability of extrinsic adult mortality to drive evolution of reproductive effort has been clearly demonstrated in systems other than birds (Crowl & Covich 1990; Reznick *et al.* 1990; Roff 1992). Lower extrinsic mortality favouring reduced reproductive effort can then explain the broad patterns of higher adult survival and smaller clutch sizes of birds in southern latitudes (Martin *et al.* 2000; Ghalambor & Martin 2001; this study). Extrinsic adult mortality can influence reproductive effort not only in terms of fecundity, but also in terms of parental effort and risk-taking in species caring for altricial young (Williams 1966; Martin 1987; Ghalambor & Martin 2001). Indeed, comparative field experiments between Argentina and Arizona showed that southern parents were less willing to feed their young and risk their own mortality when faced with an adult predator, as expected for species with lower extrinsic adult mortality (Ghalambor & Martin 2001). Similarly, the mortality risks posed by incubation (Visser & Lessells 2001) were ostensibly reduced by reducing nest attentiveness in species with lower adult mortality (figure 4a), as predicted by this theory. Species in other southern locations also show similar patterns of very low nest attentiveness associated with long incubation periods (Frith & Frith 1992, 1995; Mack 1992). Thus, lower extrinsic adult mortality selecting for lower effort and lower risk-taking in southern regions can explain smaller clutch sizes, lower nest attentiveness, longer incubation periods and higher adult survival compared with northern regions (Martin *et al.* 2000; Ghalambor & Martin 2001; this study). Lower adult mortality may even explain the greater incidence of cooperative breeding in southern regions (Arnold & Owens 1999).

Adult mortality may explain general life-history differences among latitudes, but additional variation exists among species within each region. Adult mortality seems to explain a limited amount of variation within regions (e.g. figures 4 and 6b), while juvenile mortality in the form of nest predation appears to explain more of the variation among species within regions (figure 6a). Indeed, nest predation explained a considerable amount of the inter-specific variation in clutch size and parental care activity within both Argentina and Arizona, but explained little of the variation between regions (Martin 1995; Martin *et al.* 2000) and similar results were found here for incubation periods (figures 2 and 6a). The inability of nest predation to explain latitudinal patterns is not surprising because, unlike adult mortality, nest predation does not vary consistently with latitude (Skutch 1949, 1985; Martin 1996; Martin *et al.* 2000), nor is there any reason to expect it to do so. Indeed, nest predation rates were very similar between Argentina and Arizona (Martin *et al.* 2000). Of course, nest predation can contribute to differences between regions at sites where nest predation is greater in the south. Nonetheless, the constant existence of latitudinal differences in life histories when nest predation is similar (Martin 1996; Martin *et al.* 2000; this study) emphasizes that nest predation is not the primary cause of latitudinal patterns. Instead, adult mortality seems to vary more consistently with latitude and better explain

latitudinal variation in life-history traits, while nest predation varies among nest types (e.g. cavity versus open nests) within a region and explains variation among species within regions.

Historically, avian scientists have focused on understanding variation within a region (e.g. Lack 1968; Martin 1995) and, as a result, missed an entire mode of selection (i.e. adult mortality) that places important bounds on the variation observed within these regions. Age-specific mortality thus seems to exert a hierarchical set of selection pressures to yield the geographical patterns of life history. Historical and continued focus on food limitation in birds may be strongly misplaced and may only reflect a genetic by environmental interaction, whereas new focus on extrinsic sources of adult and juvenile mortality may provide much greater new insight into evolutionary influences on variation in life-history and parental-care strategies among bird species.

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REFERENCES

- Arnold, K. E. & Owens, I. P. F. 1999 Cooperative breeding in birds: the role of ecology. *Behav. Ecol.* **10**, 465–471.
- Barbraud, C. & Weimerskirch, H. 2001 Emperor penguins and climate change. *Nature* **411**, 183–186.
- Boersma, P. D. 1982 Why some birds take so long to hatch. *Am. Nat.* **120**, 733–750.
- Bosque, C. & Bosque, M. T. 1995 Nest predation as a selective factor in the evolution of developmental rates in altricial birds. *Am. Nat.* **145**, 234–260.
- Bryant, D. M. 1998 Energetics and lifespan in birds. In *Proc. 22nd Int. Orn. Congr. Durban* (ed. N. J. Adams & R. H. Slotow), pp. 412–421. Johannesburg: Birdlife South Africa.
- Charlesworth, B. 1994 *Evolution in age-structured populations*. Cambridge University Press.
- Cole, L. C. 1954 The population consequences of life history phenomena. *Q. Rev. Biol.* **29**, 103–137.
- Conway, C. J. & Martin, T. E. 2000 Evolution of avian incubation behavior: influence of food, temperature, and nest predation. *Evolution* **54**, 670–685.
- Crowl, T. A. & Covich, A. P. 1990 Predator-induced life-history shifts in a freshwater snail. *Science* **247**, 949–951.
- Deerenberg, C., Pen, I., Dijkstra, C., Arkies, B.-J., Visser, G. H. & Daan, S. 1995 Parental energy expenditure in relation to manipulated brood size in the European kestrel *Falco tinnunculus*. *Zoology* **99**, 39–48.
- Felsenstein, J. 1985 Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.
- Frith, C. B. & Frith, D. W. 1992 Nesting biology of the short-tailed paradigm *Paradigalla brevicauda*. *Ibis* **134**, 77–82.
- Frith, C. B. & Frith, D. W. 1995 Notes on the nesting biology and diet of Victoria's riflebird *Ptiloris victoriae*. *Emu* **95**, 162–174.
- Ghalambor, C. K. & Martin, T. E. 2001 Fecundity-survival trade-offs and parental risk-taking in birds. *Science* **292**, 494–497.
- Haftorn, S. 1983 Egg temperature during incubation in the great tit *Parus major*, in relation to ambient temperature, time of day, and other factors. *Fauna Norv. Ser. C (Cinclus)* **6**, 22–38.
- Harvey, P. & Pagel, M. D. 1991 *The comparative method in evolutionary biology*. Oxford University Press.
- Lack, D. 1954 *The natural regulation of animal numbers*. Oxford: Clarendon Press.
- Lack, D. 1968 *Ecological adaptations for breeding in birds*. London: Methuen.
- Lyon, B. E. & Montgomerie, R. D. 1985 Incubation feeding in snow buntings: female manipulation or indirect male parental care? *Behav. Ecol. Sociobiol.* **17**, 279–284.
- Mack, A. L. 1992 The nest, egg and incubation behaviour of a blue bird of paradise *Paradisaea rudolphi*. *Emu* **92**, 244–246.
- Magrath, R. D. 1988 Hatching asynchrony in altricial birds: nest failure and adult survival. *Am. Nat.* **131**, 893–900.
- Magrath, R. D. & Yezerinac, S. M. 1997 Facultative helping does not influence reproductive success or survival in cooperatively breeding white-browed scrubwrens. *J. Anim. Ecol.* **66**, 658–670.
- Martin, T. E. 1987 Food as a limit on breeding birds: a life-history perspective. *A. Rev. Ecol. Syst.* **18**, 453–487.
- Martin, T. E. 1995 Avian life history evolution in relation to nest sites, nest predation and food. *Ecol. Monogr.* **65**, 101–127.
- Martin, T. E. 1996 Life history evolution in tropical and south temperate birds: what do we really know? *J. Avian Biol.* **27**, 263–272.
- Martin, T. E. 1998 Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology* **79**, 656–670.
- Martin, T. E. & Ghalambor, C. K. 1999 Males helping females during incubation. I. Required by microclimate or constrained by nest predation? *Am. Nat.* **153**, 131–139.
- Martin, T. E., Martin, P. R., Olson, C. R., Heidinger, B. J. & Fontaine, J. J. 2000 Parental care and clutch sizes in North and South American birds. *Science* **287**, 1482–1485.
- Mayfield, H. 1975 Suggestions for calculating nest success. *Wilson Bull.* **87**, 456–466.
- Moreno, J. 1989 Energetic constraints on uniparental incubation in the wheatear *Oenanthe oenanthe* (L.). *Ardea* **77**, 107–115.
- Owens, I. P. F. & Bennett, P. M. 1995 Ancient ecological diversification explains life-history variation among living birds. *Proc. R. Soc. Lond. B* **261**, 227–232.
- Poole, A., Stettenheim, P. & Gill, F. 1992–1993 *Birds of North America*, vol. 1–40. Philadelphia, PA: The Academy of Natural Sciences; Washington, DC: The American Ornithologists' Union.
- Poole, A. & Gill, F. 1993–2001 *Birds of North America*, vol. 41–600. Philadelphia, PA: The Academy of Natural Sciences; Washington, DC: The American Ornithologists' Union.
- Rahn, H. & Ar, A. 1974 The avian egg: incubation time and water loss. *Condor* **76**, 147–152.
- Ricklefs, R. E. 1992 Embryonic development period and the prevalence of blood parasites. *Proc. Natl Acad. Sci. USA* **89**, 4722–4725.
- Ricklefs, R. E. 1993 Sibling competition, hatching asynchrony, incubation period, and lifespan in altricial birds. *Curr. Ornithol.* **11**, 199–276.
- Ricklefs, R. E. & Starck, J. M. 1998 Embryonic growth and development. In *Avian growth and development* (ed. J. M. Starck & R. E. Ricklefs), pp. 31–58. Oxford University Press.
- Reznick, D. A. 1985 Costs of reproduction: an evaluation of the empirical evidence. *Oikos* **44**, 257–267.
- Reznick, D. A., Bryga, H. & Endler, J. A. 1990 Experimentally

- induced life-history evolution in a natural population. *Nature* **346**, 357–359.
- Roff, D. 1992 *The evolution of life histories: theory and analysis*. New York: Chapman & Hall.
- Rowley, I. & Russell, E. 1991 Demography of passerines in the temperate southern hemisphere. In *Bird population studies: relevance to conservation and management* (ed. C. M. Perrins, J.-D. Lebreton & G. J. M. Hirons), pp. 22–44. Oxford University Press.
- Sandercock, B. K., Beissinger, S. R., Stoleson, S. H., Melland, R. R. & Hughes, C. R. 2000 Survival rates of a Neotropical parrot: implications for latitudinal comparisons of avian demography. *Ecology* **81**, 1351–1370.
- Sanz, J. J. 2001 Latitudinal variation in female local return rate in the philopatric pied flycatcher (*Ficedula hypoleuca*). *Auk* **118**, 539–543.
- Sibley, C. G. & Ahlquist, J. E. 1990 *Phylogeny and classification of birds: a study in molecular evolution*. New Haven, CT: Yale University Press.
- Skutch, A. F. 1949 Do tropical birds rear as many young as they can nourish? *Ibis* **91**, 430–455.
- Skutch, A. F. 1985 Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. *Ornithological Monographs* **36**, 575–594.
- Slagsvold, T. 1982 Clutch size variation in passerine birds: the nest predation hypothesis. *Oecologia* **54**, 159–169.
- Visser, M. E. & Lessells, C. M. 2001 The costs of egg production and incubation in great tits (*Parus major*). *Proc. R. Soc. Lond B* **268**, 1271–1277.
- White, F. N. & Kinney, J. L. 1974 Avian incubation. *Science* **186**, 107–115.
- White, G. C. & Burnham, K. P. 1999 Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**, 120–138.
- Williams, G. C. 1966 *Adaptation and natural selection*. Princeton University Press.
- Williams, J. B. 1996 Energetics of avian incubation. In *Avian energetics and nutritional ecology* (ed. C. Carey), pp. 375–416. New York: Chapman & Hall.

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