

Avian growth and development rates and age-specific mortality: the roles of nest predation and adult mortality

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Abstract

Previous studies have shown that avian growth and development covary with juvenile mortality. Juveniles of birds under strong nest predation pressure grow rapidly, have short incubation and nestling periods, and leave the nest at low body mass. Life-history theory predicts that parental investment increases with adult mortality rate. Thus, developmental traits that depend on the parental effort exerted (pre- and postnatal growth rate) should scale positively with adult mortality, in contrast to those that do not have a direct relationship with parental investment (timing of developmental events, e.g. nest leaving). I tested this prediction on a sample of 84 North American songbirds. Nestling growth rate scaled positively and incubation period duration negatively with annual adult mortality rates even when controlled for nest predation and other covariates, including phylogeny. On the contrary, neither the duration of the nestling period nor body mass at fledging showed any relationship. Proximate mechanisms generating the relationship of pre- and postnatal growth rates to adult mortality may include increased feeding, nest attentiveness during incubation and/or allocation of hormones, and deserve further attention.

Introduction

Growth and development rates are an essential component of the life history of every species. Moreover, they vary widely among species and many hypotheses have been advanced to explain this variation (Starck & Ricklefs, 1998). One hypothesis states that high mortality of juveniles selects for rapid growth (Williams, 1966; Lack, 1968; Ricklefs, 1969b; Case, 1978). In birds it is now well supported empirically: high nest predation covaries with rapid nestling growth and short incubation periods (e.g. Bosque & Bosque, 1995; Martin, 1995; Remeš & Martin, 2002).

Life-history theory predicts that high adult mortality selects for high parental investment into the current brood at the expense of future reproductive bouts. Parents of species with high extrinsic mortality are

expected to provide more resources to their offspring (Williams, 1966; Charlesworth, 1994; Roff, 2002). Thus, development characteristics that are sensitive to the amount of resources supplied by parents should covary with adult mortality rates. Age-specific mortality has been shown to drive the evolution of life histories in other taxa (e.g. Reznick *et al.*, 1990). However, the application of this approach in bird studies lagged behind because of the traditional emphasis on food limitation (Lack, 1954, 1968; Martin, 1987). Thus, it seems timely to apply this theoretically well-supported approach to birds as an important model in evolutionary research (see Martin, 2002).

High parental investment may be connected with juvenile growth by several proximate pathways. First is obviously food: growth rate of songbird nestlings depends on the amount of food brought by parents (Martin, 1987). Consequently, high supply of food by parents may lead to rapid growth. Secondly, parents with elevated death rates may brood nestlings more often and in this way save their thermoregulatory energetic costs. Saved resources may be channelled to growth. These are

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proximate relationships and reflect phenotypic plasticity of growth (Schew & Ricklefs, 1998). However, they provide the opportunity for the evolutionary response and for the fixation of the relationship between adult mortality and juvenile growth rate on the interspecific scale.

The proximate link between parental investment and prenatal development rate (inverse of the incubation period duration) is more obvious. Egg development is sensitive to temperature (Webb, 1987). Parents investing more time into nest attentiveness (time spent on the nest incubating) achieve higher incubation temperature. This leads to shorter incubation periods (Martin, 2002). Moreover, females put androgens into egg yolk. Although the evidence is mixed, at least in some species more yolk androgens lead to more rapid growth or more vigorous begging (reviewed in Groothuis *et al.*, 2005). If higher levels of maternally derived androgens translate into higher circulating levels in nestlings, this may also lead to more rapid growth because high circulating levels of testosterone are related to more vigorous begging (Goodship & Buchanan, 2006).

On the other side, developmental traits that are less sensitive to parental investment need not be related to adult mortality rates. Timing of nest leaving is related to nest predation rate, i.e. short nestling periods are related to high nest predation as predicted by a life-history model (Roff *et al.*, 2005). However, nestlings are able to leave the nest even several days before normal fledging time (Remeš & Martin, 2002). This decision seems to be related to immediate danger of nest predation and thus cannot be easily related to the level of parental investment. As body mass of the young at fledging also depends on the timing of nest leaving, the argument is similar also for this developmental trait. On the other side, there are developmental processes the rate of which depends on the amount of resources supplied by parents and have direct bearing to timing of nest leaving (e.g. development of feathers). Thus, there could be a relationship between adult mortality, parental investment and timing of nest leaving.

I tested these ideas on a sample of 84 North American songbirds and collated published data on nestling growth rate, incubation and nestling period length, and body mass of the young at fledging. As control variables, adult body mass, latitude, clutch size, foraging ecology, and nest predation intensity were used. After controlling for these variables, and the phylogeny of the species, I tested for covariation between annual adult mortality rate and species-specific development characteristics (i.e. nestling growth rate, incubation and nestling period length, and body mass at fledging). It was predicted that nestling growth would covary positively and incubation period duration negatively with adult mortality. I expected no relationship of nestling period duration or fledging mass. These predictions were supported by the comparative analyses made.

Materials and methods

I worked with data from the literature and collated data on growth rates of nestlings from original studies as in Remeš & Martin (2002). Latitude of the growth study was also taken. Growth rate was quantified by the constant K of the logistic growth curve fitted to the growth data truncated at the highest mass achieved by chicks in the nest (see Remeš & Martin, 2002). The logistic growth curve has a form of $W(t) = A/[1 + \exp[-K(t-t_i)]]$, where $W(t)$ denotes body mass of a nestling at time t , A is the asymptotic body mass that the nestling approaches, t_i is the inflection point on the time axis in which growth changes from accelerating to decelerating, \exp represents the exponential function, and K is a constant scaling rate of growth. Because the value of K indexes growth rate independently of absolute time of growth (in time^{-1}), it is a convenient measure for comparative purposes (Ricklefs, 1968). Relative fledging mass was calculated as mass at fledging divided by adult body mass. Adult body mass was taken from Dunning (1993). Data on incubation and nestling period duration, clutch size and foraging ecology was taken from 'The Birds of North America' series (Poole & Gill, 1992–2002). Species were categorized as aerial foragers (species feeding on flying insects) vs. non-aerial foragers (other foraging techniques). Data on nest predation and adult mortality rates were taken from original studies (summarized in Martin, 1995; Remeš & Martin, 2002) and the general reference (Poole & Gill, 1992–2002). Only mortality that accumulates with time is relevant for the evolution of growth rates (Ricklefs, 1969a). Nest predation was available as percentage of nests taken by predators. As it is the product of daily nest predation rate and the duration of the nestling period, I converted it to daily nest predation rate according to: $D_{\text{pr}} = -(\ln S)/T$, where D_{pr} is daily nest mortality rate caused by nest predation, S is proportion of nests that were successful ($1 - \text{proportion depredated}$), and T is the duration of the nest cycle (Ricklefs, 1969a). The parameters most limiting the number of species were growth and adult mortality. I had growth data on 134 species but found adult mortality rates and other relevant factors for 84 of them. Data are summarized in Appendix 1 of Supplementary Material.

Data were analysed by using multiple regression based on previous studies (e.g. Martin, 1995; Remeš & Martin, 2002) for which a set of covariates – adult body mass (g), clutch size (no. of eggs in the clutch), foraging mode (aerial vs. non-aerial foragers) and latitude ($^{\circ}\text{N}$, only in the analysis of K) – were selected and included in the analysis. Against these covariates two mortality factors were tested: nest predation and adult mortality. Response variables were growth rate (K , day^{-1}), incubation period duration (i.e. inverse of prenatal development rate, day), nestling period duration (day), and relative fledging mass (mass at fledging/adult body mass). I selected effects

based on their significance level in a backward stepwise manner.

Common descent of species may cause problems in the analysis of interspecific data. Species are historically related, which causes non-independence of varying strength among data points. This violates assumptions of standard statistical techniques (Harvey & Pagel, 1991). To overcome this problem, the phylogenetic regression of Grafen (1989) was applied. This method is based on generalized least squares and adjusts the statistical analysis for non-independence among species. This method is very flexible and enables fitting of standard statistical models, including interactions and categorical predictors. `PHYREG` macro for `SAS` (SAS Institute, 2005) written by Alan Grafen (Grafen, 2005) available at <http://users.ox.ac.uk/~grafen> was used.

A working phylogeny of the studied species based on Sibley & Ahlquist (1990), Martin & Clobert (1996) and Remeš & Martin (2002), supplemented by the most recent molecular phylogenies (details are available from the author upon request) was assembled. As the phylogeny was assembled from many sources, I had no consistent estimates of branch lengths. I adopted uniform branch lengths. However, another arbitrary branch lengths option, Grafen's (1989) branch lengths, generated qualitatively identical results.

Results

Growth rate of nestlings increased with both annual adult mortality rate and daily nest predation rate. Other factors were also significant and this model explained 52.3% of variation in growth rate ($F_{6,76} = 13.89$, $P < 0.001$; Table 1; Fig. 1). Incubation period duration decreased with both annual adult mortality rate and daily nest predation rate. Other factors were also significant and this model explained 45.3% of variation in incubation period duration ($F_{4,79} = 16.33$, $P < 0.001$; Table 1, Fig. 1). There was no relationship between either nestling period duration or relative fledging mass and adult mortality. However, both were negatively related to nest predation rate (Table 1). The models explained 61.1% of variation in nestling period ($F_{4,79} = 31.01$, $P < 0.001$

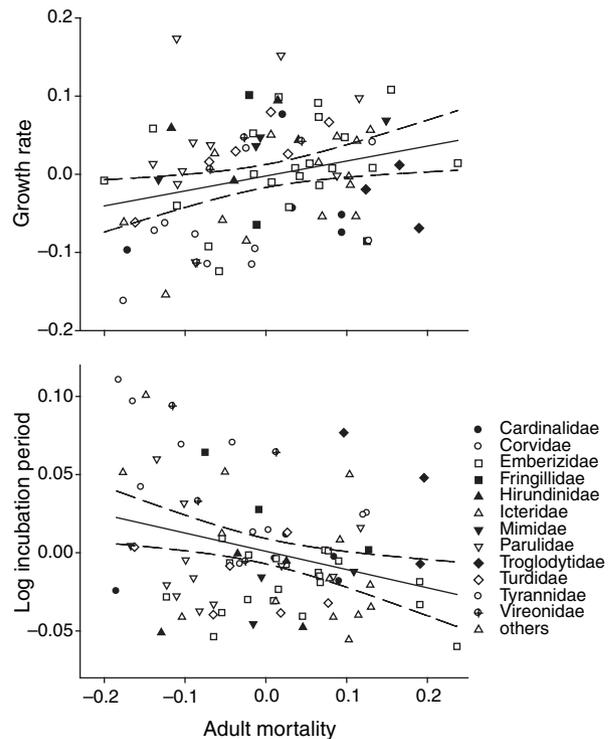


Fig. 1 Relationship between residuals of growth rate (K , day^{-1}) and duration of the incubation period (day), and annual adult mortality rate, adjusted for other factors (see Table 1). Linear regression lines (solid line) with 95% confidence intervals (hatched line) are given. Regression equations are: $K = 0.293(0.082) - 0.075(0.026) \times \text{LOG adult body mass} + 0.004(0.001) \times \text{latitude} - 0.025(0.010) \times \text{clutch size} - 0.032(0.011) \times \text{foraging mode} + 0.847(0.234) \times \text{SQRT daily nest predation rate} + 0.193(0.076) \times \text{annual adult mortality rate}$; $\text{LOG incubation period} = 1.221(0.039) + 0.032(0.014) \times \text{LOG adult body mass} + 0.024(0.006) \times \text{foraging mode} - 0.599(0.118) \times \text{SQRT daily nest predation rate} - 0.117(0.041) \times \text{annual adult mortality rate}$. Foraging mode is coded as 0 (non-aerial foragers) and 1 (aerial foragers). Partial regression coefficients (SE) are given.

and 61.3% of variation in relative fledging mass ($F_{5,78} = 24.73$, $P < 0.001$).

In the phylogenetic regression, I tested the significance of the two mortality factors while controlling for the

Table 1 Results of the raw species data analyses relating development characteristics to mortality factors (in bold) and relevant covariates among 84 species of North American songbirds.

Factor	Growth rate		Nestling period		Relative fledging mass		Incubation period	
	$F_{1,76}$	P	$F_{1,79}$	P	$F_{1,78}$	P	$F_{1,79}$	P
Body mass	8.51	0.005	12.17	<0.001	57.48	<0.001	5.05	0.028
Latitude	15.12	<0.001	NA	NA	NA	NA	NA	NA
Clutch size	5.82	0.018	n.s.	n.s.	3.81	0.055	n.s.	n.s.
Foraging mode	8.02	0.006	31.63	<0.001	9.19	0.003	14.35	<0.001
Nest predation	13.10	<0.001	51.24	<0.001	31.01	<0.001	25.98	<0.001
Adult mortality	6.46	0.013	1.74	0.191	2.37	0.128	8.05	0.006

NA, not applicable in the particular analysis; n.s., not significant.

covariates. All the relationships between developmental traits and mortalities remained qualitatively the same, including their direction, as in cross-specific analyses without phylogeny: growth rate [adult mortality (AM): $F_{1,76} = 8.55$, $P < 0.0051$; nest predation (NP): $F_{1,76} = 16.94$, $P < 0.001$], incubation period (AM: $F_{1,79} = 7.56$, $P < 0.01$; NP: $F_{1,79} = 11.37$, $P < 0.001$), nestling period (AM: $F_{1,79} = 0.40$, $P = 0.528$; NP: $F_{1,79} = 14.65$, $P < 0.001$), and relative fledging mass (AM: $F_{1,78} < 0.01$, $P = 0.952$; NP: $F_{1,78} = 14.44$, $P < 0.001$). There was no correlation between adult mortality and nest predation rate across species ($r = -0.11$, $P = 0.299$, $n = 84$).

Discussion

Nestling growth rate scaled positively and incubation period length negatively with annual adult mortality rate, even when other relevant factors together with phylogenetic relationships among species were controlled for. This seems to be in accordance with the life-history theory predicting higher parental investment into current offspring when adult mortality is high (Williams, 1966; Charlesworth, 1994; Roff, 2002). On the contrary, there was no relationship between either nestling period duration or relative mass at fledging and adult mortality rates. Timing of fledging is strongly driven by nest predation (Roff *et al.*, 2005). It is still not clear whether parents or offspring determine the length of nestling period on the proximate level (Nilsson & Svensson, 1993; Johnsen *et al.*, 1994; Johnson *et al.*, 2004), but this analysis shows that there is little potential for adult mortality to drive the evolution of this trait.

One possible factor could have confounded this analysis: if parents with high mortality invested more into nest defence, this could lead to lower nest predation rates in these species. Consequently, as nest predation is a strong determinant of nestling growth (Remeš & Martin, 2002), growth could have been slowed in these species. However, as there was no correlation between nest predation and adult mortality (see Results), and effects of adult mortality on development rates were in fact positive, this seems unlikely. Parents either were unable to defend nests effectively or directed their extra investment into other activities. Nest predators may also behaviourally constrain higher investment into the brood. Parental activity around the nest leads to higher risk of nest predation (Martin *et al.*, 2000b; Eggers *et al.*, 2005; Fontaine & Martin, in press). Risk of nest predation shaped evolutionarily both incubation feeding by males (Martin & Ghalambor, 1999) and incubation behaviour of females (Conway & Martin, 2000). Increasing nest attentiveness while reducing activity around the nest may thus be achieved by lengthening on-nest bouts (Conway & Martin, 2000). Similarly, increasing food supply while keeping feeding frequency at low levels may be achieved by increasing food load per feeding trip (e.g. Martin *et al.*, 2000a).

The effect of adult mortality on prenatal development during incubation may have been mediated by egg yolk hormones. Mother birds allocate androgens into egg yolk during vitellogenesis and these may have positive effects on begging and development of the young (e.g. Schwabl, 1996; Eising *et al.*, 2001; Eising & Groothuis, 2003; Tschirren *et al.*, 2005). Short incubation and nestling periods covary with high levels of egg androgens (Gorman & Williams, 2005). In this way, behavioural constraints imposed by nest predation could also have been avoided. Moreover, if high egg yolk androgen levels translate into high circulating levels in nestlings, this may also lead to rapid growth, as young with high testosterone levels beg more vigorously (Goodship & Buchanan, 2006). However, egg hormones may also have detrimental effects on the young (e.g. Sockman & Schwabl, 2000; Navara *et al.*, 2005).

Comparative analyses of course cannot distinguish between cause and effect. Thus, it is possible that the causality of the correlations revealed in this study is reversed. Incubation periods and chick growth rates may be evolutionarily driven by some hitherto unknown selection pressure. Then, if there is a causal link between these developmental traits and adult mortality, adult mortality may in fact be driven by this selection pressure through the developmental traits. It has been shown that mortality caused by both parasites and pathogens (Møller, 2005) and brood parasitism (Remeš, in press) can influence growth strategies in passerines. Thus, in further analyses it will be important to control also for this factor. However, recent results of comparisons of avian life histories across latitudes suggest that the causal path from adult mortality down to offspring developmental traits is at least an acceptable explanation (Ghalambor & Martin, 2001; Martin, 2002, 2004). Nevertheless, this issue will have to receive more attention in future work.

Besides benefits rapid development can also have its costs, mediated for instance by poorly developed immune system (Ricklefs, 1992, 1993; Tella *et al.*, 2002; Soler *et al.*, 2003; Palacios & Martin, 2006). Slow development with extra energy invested into the maturation of critical physiological functions (e.g. immune or neural system) could bring important advantages later in life (see Ricklefs, 1993; Ricklefs *et al.*, 1998). Thus, the extra resources provided by parents did not necessarily have to be channelled to more rapid growth. Moreover, there are other energetically demanding processes going on during the individual development in the nest. For example, development of feathers could use up the extra energy supplied by parents (Murphy, 1996), which could lead to earlier functional maturation of wings and consequently earlier fledging. However, it seems that neither of these alternatives took place. The first predicts no relationship of any developmental characteristic to adult mortality, whereas the second one, a negative relationship between nestling period and adult mortality. However, there was

a positive relationship between adult mortality and growth rate, but not with either timing of nest leaving or relative fledging mass. It seems that the extra resources were mainly channelled to higher tempo of tissue synthesis and growth, although at least partial channelling into improving some juvenile physiological functions cannot be ruled out. To validate this hypothesis, we will have to analyse potential relationships between adult mortality and juvenile pre- and post-fledging physical and physiological performance.

In sum, I show that both pre- and postnatal growth rates scale positively with adult mortality rates in birds, which accords with life-history theory. More generally, this study shows that life-history theory has the power to predict patterns of relationships between suites of life-history and developmental traits (see also Roff *et al.*, 2005). Developmental traits have recently emerged as an important model system for the investigation of the evolution of avian life histories and provide a new perspective on this attractive issue (Martin, 2002, 2004). Comparative analysis presented here generates a set of questions that should be explored based on both published and new field data. In future work, it will be critical to explore relationships of mortality rate (both of adults and nests) to growth rate, incubation period, feeding frequency, food load per feeding trip, incubation attentiveness and temperature, hormones in egg yolk and blood of nestlings, and physical and physiological performance of offspring (see Martin, 2002; Gorman & Williams, 2005).

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Supplementary Material

The following supplementary material is available for this article online:

Appendix S1. Species mean values used in the analyses for adult body mass, clutch size, duration of incubation and nestling period, growth rate constant *K* of the logistic curve, body mass at fledging, latitude of the study of growth, foraging mode, daily nest mortality rate caused by predation, and annual adult mortality rate.

This material is available as part of the online article from <http://www.blackwell-synergy.com>

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