The evolution of fledging age in songbirds

D. A. ROFF,* V. REMEŠ† & T. E. MARTIN‡

*Department of Biology, University of California, Riverside, CA, USA
†Laboratory of Ornithology, Faculty of Science, Palacký University, Olomouc, Czech Republic
‡US Geological Survey Biological Resources Discipline, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT, USA

Abstract

In birds with altricial young an important stage in the life history is the age at fledging. In this paper we use an approach proven successful in the prediction of the optimal age at maturity in fish and reptiles to predict the optimal age of fledging in passerines. Integrating the effects of growth on future fecundity and survival leads to the prediction that the optimal age at fledging is given by a function that comprises survival to maturity, the exponent of the fecundity-body size relationship and nestling growth. Growth is described by the logistic equation with parameters, A, K and t_i. Assuming that the transitional mortality curve can be approximated by the nestling mortality, M_n, the optimal fledging age, t_f, is given by a simple formula involving the three growth parameters, nestling mortality (M_n) and the exponent (d) of the fecundity-body size relationship. Predictions of this equation underestimate the true values by 11–16%, which is expected as a consequence of the transitional mortality function approximation. A transitional mortality function in which mortality is approximately 0.3–0.4 of nesting mortality (i.e. mortality declines rapidly after fledging) produces predictions which, on average, equal the observed values. Data are presented showing that mortality does indeed decline rapidly upon fledging.

Introduction

The central equation of life history theory is the Euler or characteristic equation, which comprises the age-schedules of reproduction and mortality and the Malthusian parameter, r, the last parameter being a measure of fitness (Fisher, 1930; Charlesworth, 1994; Roff, 2002). An analysis of the Euler equation shows that an important determinant of fitness is the age at first reproduction (Lewontin, 1965; reviewed in Roff, 1992). The evolution of this trait is the result of the integration of two other classes of traits, namely growth rate parameters and age-specific mortality rates. The importance of age-specific mortality rates on the evolution of the age at first reproduction is obvious. However, the influence of growth rate parameters is indirect, with their effects, in large measure, acting via effects on mortality rates and body size. The latter trait does not itself enter directly into the Euler equation but is important because it typically determines reproductive success, either by increasing mating probability (e.g. dominance/territoriality in either males or females) or by increasing the number of propagules produced (reviewed in Roff, 1992, p. 126–128). A positive covariation between fecundity and body size is well demonstrated within ectotherm species (reviewed in Roff, 1992, p. 126) and has been frequently observed in those mammal species that produce relatively large litters (reviewed in Roff, 1992, p. 127).

Using a model based on the observed growth curve, the fecundity-body size relationship and adult mortality rates, Roff (1984) produced a simple model that predicted with considerable accuracy the age at first reproduction in a wide range of fish species. This model was later successfully extended to turtles, snakes and lizards (Roff, 2002, p. 217–220). All taxa thus far examined are ectotherms and thus the question arises whether this model is also appropriate for endotherms in general or at least for some classes of endotherms. In the present paper we adopt the same modelling approach to address this question with respect to age at maturity and fledging age in passerines. For this purpose we make use of the extensive database compiled by Remeš & Martin (2002)

Correspondence: Derek A. Roff, Department of Biology, University of California, Riverside, CA 92521, USA.
Tel.: 951 827 2437; fax: 951 827 4286; e-mail: Derek.roff@ucr.edu

on the growth characteristics and nestling mortality rates of 107 North American passerines.

The model

Assumptions and database

(1) Following the empirical analyses of Ricklefs (1968), Starck & Ricklefs (1998) and Remeš & Martin (2002), we assume that nestling growth follows the logistic equation

$$W(t) = \frac{A}{1 + e^{-K(t-t_i)}} \quad (1)$$

where $W(t)$ is mass at age t, A is the asymptotic size, K is a measure of 'growth rate' and t_i is the inflection point on the growth curve. Where there were data from multiple populations of the same species, Remeš & Martin (2002) averaged across populations to produce species-specific parameter values. Similarly, where data on both sexes were available, Remeš & Martin (2002) used the average value. Because some species show a weight recession just prior to or after leaving the nest, Remeš & Martin (2002) estimated the growth parameters in two ways: first they fitted the growth function with the data truncated at the maximum nestling mass and, second they estimated parameter values using data truncated at 70% of adult mass. The results presented by Remeš & Martin (2002) did not differ qualitatively between these two estimation approaches, but to ensure that the present analysis is robust to the method of estimation we here present results using both sets of estimates.

The data of Remeš & Martin (2002) shows that fledging mass is approximately 80% of adult mass on average and that the two are highly correlated (Fig. 1, Table 1).
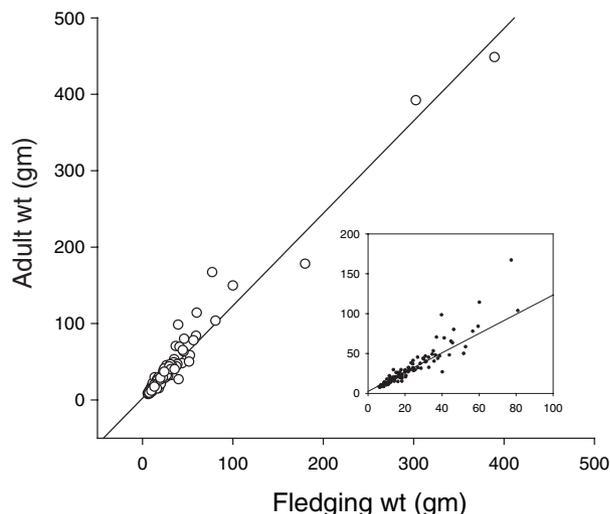

Fig. 1 Plots of adult mass on fledging mass, showing that adult mass is proportional to fledging mass (inset shows data spread excluding the three largest species). Data are from Remeš & Martin (2002).

Table 1 Summary of regressions relating observed adult mass, observed fledging mass, and two asymptotic masses (A_1 is the maximum mass achieved in the nest, A_2 is 70% of adult mass).

Response variable	Predictor variable	r^2	n	Intercept (SE)	Slope (SE)
Adult mass	Fledging mass	0.96	115	2.55 (1.33)	1.21 (0.02)
Adult mass	A_1	0.96	115	0.80 (1.30)	1.18 (0.02)
Adult mass	A_2	0.98	97	−1.29 (1.09)	1.17 (0.02)
A_1	Fledging mass	1.00	115	1.47 (0.27)	1.02 (0.005)
A_2	Fledging mass	0.98	97	1.83 (0.87)	1.00 (0.015)

However, the regression slopes (i.e. 1.18 and 1.17) of adult mass on the asymptotic mass parameters (see Table 1) indicate that these parameters are not direct estimates of adult mass but are proportional to it. The regression slopes of asymptotic mass parameters on fledging mass are very close to, and not significantly different from, unity (1.02 and 1.00), indicating that these parameters estimate the asymptotic mass at fledging not adult mass. The difference in slopes between adult mass vs. asymptotic mass on fledging mass implies that growth subsequent to fledging is not simply a continuation of the nestling logistic growth function.

(2) Survival during the nestling period can be specified as

$$e^{-\int_0^{t_f} M(x)\,dx} = e^{-M_n t_f} \quad (2)$$

where $M(x)$ is the age-specific nestling mortality rate and t_f is the age of fledging. Because of the limitations of the available data, we shall assume that this mortality can be reasonably approximated by a constant instantaneous mortality rate of M_n (Fig. 2: Note that an increase in M_n, as indicated by dotted line in Fig. 2, will favour a decreased fledging age, as already observed by Remeš & Martin, 2002). Being unable to fend for itself and avoid predators during early development, the mortality rate of the chick that leaves the nest, M_0, exceeds the mortality rate of a chick that remains within the nest. Initially, the survival rate of an altricial hatchling displaced from the nest is zero (i.e. $M_0 = \infty$), but as development proceeds, chicks become increasingly capable of mobility outside the nest and more likely to evade predation away from the nest than within the nest. At some age, t_f, the mortality rate inside the nest exceeds that outside the nest and selection favours fledging. The rate of mortality declines following the fledging to an adult instantaneous mortality rate of M_a (Deevey, 1947; Sullivan, 1989; Anders *et al.*, 1997; Perkins & Vickery, 2001; Gardali *et al.*, 2003).

(3) At some age t_a 'adult' mass is achieved and no further growth takes place. The age of adult mass consists of the time to fledging, t_f, and the time from fledging to t_a, denoted as t_0 (Fig. 2): hence $t_a = t_f + t_0$. No data are available on t_a but, following from the assumption/
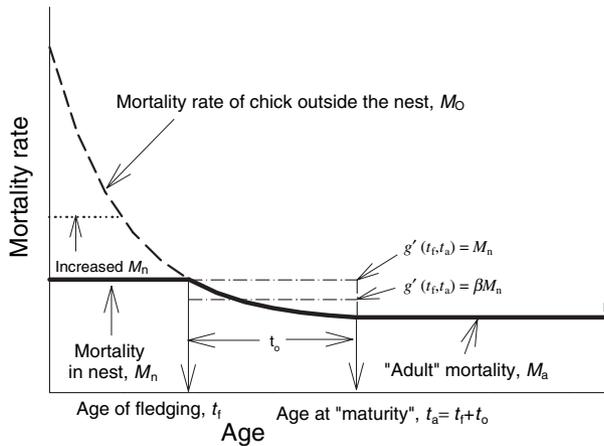
Fig. 2 A schematic plot of the relationship between the mortality rate within and outside the nest as a function of the age of the nestling. The mortality curve for chicks outside the nest is hypothetical and simply illustrates the assumption that, for altricial birds, leaving the nest cannot be achieved until development has proceeded to the point at which the chicks have reasonable mobility and thermoregulatory ability. Dotted line illustrates that the effect of increasing nest mortality is to decrease fledging age. The dot-dashed lines show the two transitional mortality functions used as approximations to the declining function indicated by the solid line.

observation that adult mass is proportional to fledging mass (Table 1), we can write the mass at age t_a, $G(t_a)$ as

$$G(t_a) = CW(t_f) = \frac{CA}{1 + e^{-K(t_f - t_i)}} \qquad (3)$$

where, as described above, $W(t)$ is the nestling growth function and C is the proportionality constant.

(4) In ectotherms fecundity is typically an allometric function of size, with an exponent of approximately 3 for linear body measures and 1 for mass measures (Roff, 1992, p. 126). Data for passerines is complicated by the general observation that egg mass increases with female size, both within and among species (Christians, 2002; Martin *et al.*, 2004). The reasons for this increase are unknown, though a larger egg produces a larger hatchling, which probably increases both pre- and post-fledging survival (Magrath, 1991; Roff, 1992, p. 350; Williams, 1994; Barbraud *et al.*, 1999). This does not explain why egg size should covary with body size. However, because of this covariation, the total clutch mass increases with body size (Saether, 1987; Visman *et al.*, 1996; Barbraud *et al.*, 1999; T.E. Martin, unpublished data). We shall assume that increased clutch mass effectively increases fecundity by increasing the survival probability of chicks, and that this 'effective fecundity' is an allometric function of adult body size

$$F(t_a) = cG(t_a)^d = c[CW(t_f)]^d \qquad (4)$$

where c is a constant, characteristic of the population or species. We shall assume that the exponent d lies

between 0.75, the exponent obtained from an interspecific analysis (Visman *et al.*, 1996) and also the exponent for metabolic rate and productivity (Charnov, 2000), and 1.00, which is the value typically observed for ectotherms and can be justified on geometric considerations (Roff, 1984, 1992).

(5) We assume that population size is stable, in which case the appropriate measure of fitness depends upon how density-dependence acts (Charnov, 1993; Charlesworth, 1994; Mylius & Diekmann, 1995; Benton & Grant, 2000; Roff, 2002). Provided that there is no genetic variation for the characteristics that favour survival through the period during which density-dependence acts, or that the traits under study are genetically uncorrelated with such characteristics, the appropriate fitness measure is the expected lifetime fecundity of a female, R_0. Even in the absence of these conditions being met, R_0 may often be a reasonable measure (Benton & Grant, 2000). In the absence of sufficient information to include density-dependent functions, we shall assume that one or both of the foregoing conditions hold and use R_0. If this measure is inappropriate then prediction should be compromised.

Analysis

Under the above scenario, and assuming an equal sex ratio, we have

$$R_0 = 0.5cG(t_a)^d e^{-M_n t_f - g(t_f, t_a)} \int_0^\infty e^{-M_a x} dx \qquad (5)$$

where x is adult age scaled to commence at the age at first reproduction, and $e^{-g(t_f, t_a)}$ is the survival between t_f and t_a (the period labelled t_0 in Fig. 2), which is a function of the 'M_0' curve. Note that this age is here set to the point at which growth ceases. In most cases there will be a period during which ecological conditions, such as winter, do not favour reproduction and do not permit further growth: these periods affect all life histories equally and hence can be ignored in this analysis. We are interested in determining the optimal value of t_a. Because terms involving t_a do not enter into the integral, we can write fitness, w, as

$$w(t_a) = 0.5G(t_a)^d e^{-M_n t_f - g(t_f, t_a)} = 0.5cG(t_a)^d e^{-h(t_a)} \qquad (6)$$

To find the optimal value of $t_a = t_f + t_0$ we differentiate with respect to t_a and find the value at the differential equals zero (see appendix), which is when

$$h'(t_a) = \frac{dG'(t_a)}{G(t_a)} = \frac{dW'(t_a)}{W(t_a)} \qquad (7)$$

where $W'(t_f) = \frac{\partial W(t_f)}{\partial t_f}$ and $h'(t_a) = \frac{\partial h(t_a)}{\partial t_a}$. In the absence of data on the transition function for mortality upon fledging to a constant adult mortality rates we shall assume, as a first approximation, $g(t_f, t_a) \approx M_n t_0 =$

$M_{\mathrm{n}}(t_{\mathrm{a}} - t_{\mathrm{f}})$, from which we obtain $h'(t_{\mathrm{a}}) = M_{\mathrm{n}}$. This 'step' function will overestimate the transitional mortality rate (Fig. 2). We can more closely approximate the transitional mortality by $g(t_{\mathrm{f}}, t_{\mathrm{a}}) \approx \beta M_{\mathrm{n}} t_0 = \beta M_{\mathrm{n}}(t_{\mathrm{a}} - t_{\mathrm{f}})$, where β is a proportionality factor that is population- or species-specific. Assuming this, we have $h(t_{\mathrm{a}}) = \beta M_{\mathrm{n}} t_{\mathrm{a}} + M_{\mathrm{n}} t_{\mathrm{f}}(1 - \beta)$. Because t_f is much smaller than t_a, we can use the approximation $h(t_{\mathrm{a}}) \approx \beta M_{\mathrm{n}} t_{\mathrm{a}}$, from which we obtain $h'(t_{\mathrm{a}}) = \beta M_{\mathrm{n}}$. In the absence of estimates of β we shall use a single value. In doing this we merely imply that the distribution of β values is not very wide: if this assumption is incorrect it should not be possible to find a value of β that improves the fit between predicted and observed ages at fledging.

Substituting the appropriate values in eqn 7 and rearranging gives

$$t_{\mathrm{f}} = \frac{1}{K}\ln\left(\frac{B(\mathrm{d}K - M_{\mathrm{n}})}{M_{\mathrm{n}}}\right) = t_i + \frac{1}{K}\ln\left(\frac{\mathrm{d}K}{M_{\mathrm{n}} - 1}\right), \quad (8)$$

where $B = e^{Kt_i}$. Predictions for the alternate transitional mortality rate are obtained by substituting βM_n for M_n. The above equation predicts the optimal age at fledging and hence also the optimal age at first reproduction, excluding any time period, such as the winter, when growth and reproduction are ecologically unfavourable.

Testing the model

Predicted vs. observed ages at fledging

We test the predictions of the above model by comparing the predicted values of t_f with the observed age at the end of the nestling period using the two sets of parameter estimates (i.e. maximum nestling mass, and 70% adult mass) based on data reported in Remeš & Martin (2002). For both parameter sets there is a highly significant correlation between observed and predicted values, with the fecundity exponent, d, having little effect on the correlation or regression parameters (Fig. 3, Table 2). The percentage deviation between observed and predicted vary from 0.1 to 55.7% across individual species, with a mean ranging from 16 to 17%, a SD of 11% (Table 2) and a SE of 1%. The predictions using the first transitional mortality function $g'(t_{\mathrm{a}}, t_{\mathrm{f}}) = M_{\mathrm{n}}$, are proportional to the observed values but tend to underestimate them by 11–16%. In the first estimate set this underestimation is significant both for the regression model (slope significantly greater than 1, Table 2) and a paired t-test (Table 2), but it is significant only for the paired t-test in the second estimate set (Table 2). The underestimation can be accounted for by the overestimation of the transitional mortality, as shown by slopes obtained using values of β less than unity (Fig. 4). Values of β less than approximately 0.29 produce slopes that overestimate t_f, whereas values of β greater than approximately 0.39 underestimate t_f (Fig. 4). These results predict that there
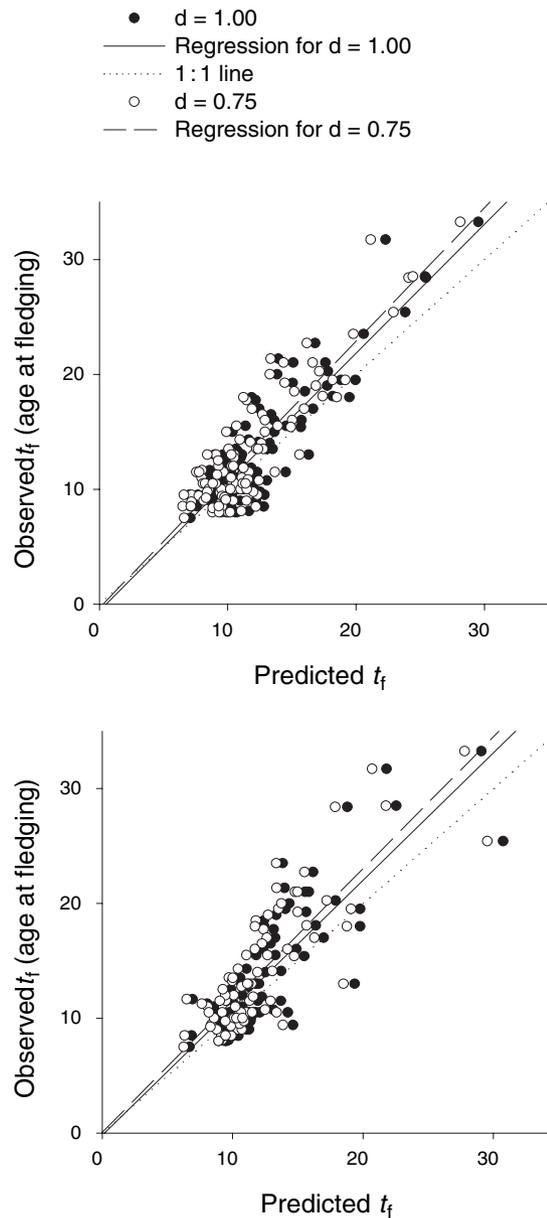

Fig. 3 A comparison of observed and predicted ages at fledging in passerines. The left panel shows results for growth parameters estimated using data truncated at maximum nestling mass. The right panel shows results for growth parameters estimated using data truncated at 70% adult mass.

is a significant decline in mortality rate between fledging and the cessation of growth.

Contributions of parameters to the predicted age at fledging

There are four parameters in the predictive equation (t_i, K, M_n, d), one of which, d, little influences the

Table 2 A comparison of the predicted age at fledging with the observed age at fledging using the first transitional mortality function $g(t_a, t_f) = M_n t_0.$

| Growth parameters estimated by truncation at | d^* | Regression of observed on predicted† | | | |
		Intercept (SE)	Slope (SE)§	r†	Deviation‡
Maximum mass	0.75	−0.33 (0.76)	1.16 (0.06)	0.76	16.7 (10.6)
Maximum mass	1.00	−0.60 (0.77)	1.12 (0.06)	0.78	15.8 (10.6)
70% adult mass	0.75	0.07 (1.08)	1.15 (0.09)	0.67	17.5 (11.8)
70% adult mass	1.00	−0.19 (1.10)	1.11 (0.08)	0.67	17.3 (10.9)

*Exponent of the fecundity function.
†All regressions highly significant ($P < 0.0001$).
‡Deviation = $100 \times$ (Predicted − Observed)/Observed.
§Test of deviation from a slope of 1, from top to bottom: $t_{105} = 2.62$, $P = 0.0100$; $t_{105} = 2.06$, $P = 0.0417$; $t_{87} = 1.72$, $P = 0.0883$; $t_{87} = 1.33$, $P = 0.1882$. Results, from top to bottom, for paired t-test using observed and predicted ages: $t_{106} = 6.26$, $P < 0.0001$; $t_{106} = 3.71$, $P = 0003$; $t_{88} = 5.37$, $P < 0.0001$; $t_{88} = 3.52$, $P = 0.0007$.
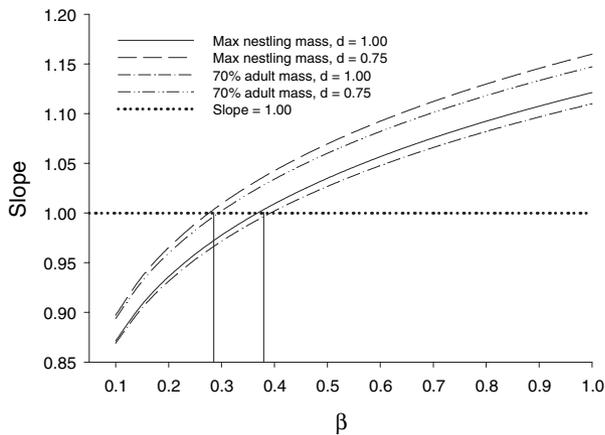SD: standard deviation.

Fig. 4 The relationship between the slope of the regression of observed on predicted t_f and β.

prediction within the limits over which it is likely to range (Fig. 4). To examine the potential contribution of the other three parameters we first rewrite eqn 8 as

$$t_f = t_i + \frac{1}{K}(\ln(dK - M_n) + \ln(M_n^{-1})). \qquad (9)$$

The growth parameter K, ranges from 0.22 to 0.74 ($0.165 < dK < 0.74$), with a median value of 0.49, whereas daily nestling mortality rate, M_n, ranges from 0.0009 to 0.05, with a median of 0.016. Consequently, we can write

$$t_f \approx t_i + \frac{1}{K}(\ln(d) + \ln(K) + \ln(M_n^{-1})). \qquad (10)$$

The $\ln(d)$ ranges only from 0 to −0.29, which explains why it has relatively little effect on fledging age. The inflexion parameter t_i varies approximately between 3 and 6, which is similar to the range of $\ln(M_n^{-1})$ (Fig. 5), but the effect of the latter is modulated by the reciprocal

of the growth parameter K, which varies largely within the range 1.5–2.5 (Fig. 5). Fledging age ranges from $7.5d$ to $33.25d$, with a median of $11.5d$, and thus all three parameters can potentially contribute significantly to its variation. This is confirmed by the correlations between each parameter and fledging age: 0.80 for t_i, −0.66 for K and −0.52 for M_n (Table 3).

The effect of asymptotic size on the optimal age at fledging

Asymptotic size does not enter into the optimality solution but this does not mean that this trait cannot influence the optimal age at fledging/maturity. Changing the asymptotic size will change fecundity and very likely will also change survival rates (Saether, 1987, 1988, 1989; Martin, 1995). Further, if the growth parameters are not independent traits, changing one parameter will produce a change in the other parameters. In the present data set all three growth parameters significantly covary (Table 3), which could be a result of independent optimizations that happen to generate covariation, or more likely, and as indicated below, is a consequence of functional constraints among the three traits.

West *et al.* (2001) working from fundamental principles derived a growth curve applicable to a wide range of taxa, including invertebrates, fish, mammals and birds:

$$W(t) = W_{max}\left\{1 - \left[1 - \left(\frac{W_0}{W_{max}}\right)^{0.25}\right]e^{-\frac{at}{4W_{max}^{0.25}}}\right\}^4 \qquad (11)$$

which, like the logistic has just three parameters, W_{max}, which is the asymptotic size, W_0, which is the initial mass, and a parameter 'a', which controls the rate at which the asymptotic value is approached. Unlike the logistic used in the present paper, the asymptotic mass is embedded within the growth equation and is not simply a scaling parameter. The growth curve generated by the above function can be readily fitted by the logistic equation, as illustrated in the case of the robin, *Erithacus*
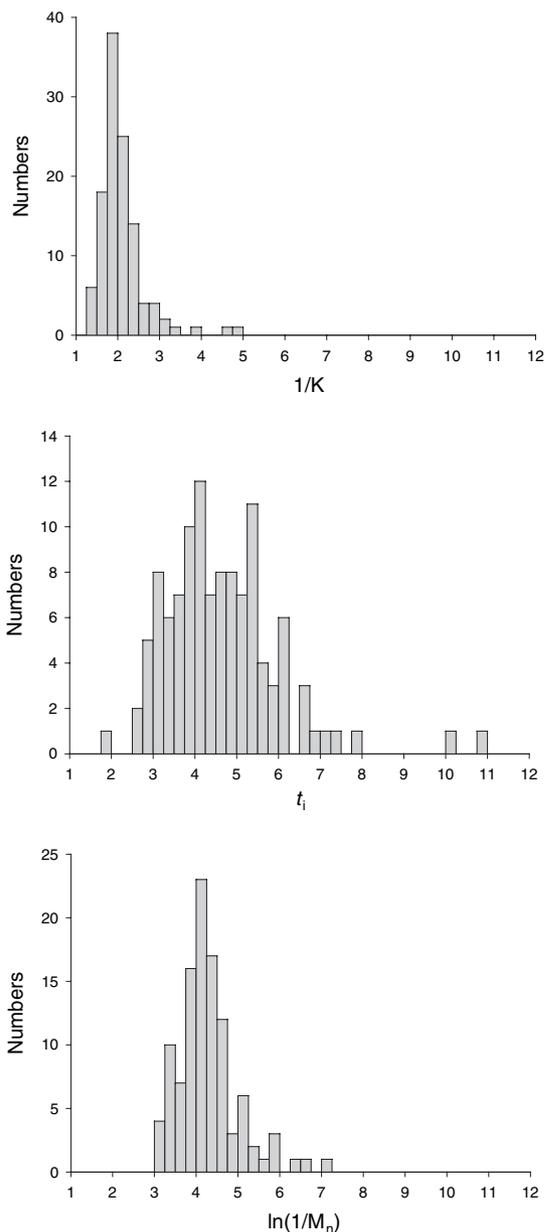
Fig. 5 Distributions of the three parameters, t_i, K and M_n. The latter two are transformed to reflect their contribution to t_f. Parameters estimated using the 'first' data set (maximum nesting mass). One t_i value (15.86) not shown.

Table 3 Correlations between growth parameters (estimated using nestling mass up to 70% of adult mass), observed fledging and adult masses, fledging age and nest mortality rate.

	K	A	t_i	t_f	M_n	Adult weight	Fledging weight
K		0*	0	0	0	0	0
A	−0.50		0	0	0.193	0	0
t_i	−0.80	0.75		0	0.001	0	0
t_f	−0.66	0.63	0.73		0	0	0
M_n	0.40	−0.14	−0.34	−0.52		0.456	0.197
Adult weight	−0.47	0.99	0.69	0.55	−0.07		0
Fledging weight	−0.48	0.99	0.71	0.62	−0.13	0.98	

Correlations are shown below the diagonal, probabilities above the diagonal.
*0 Indicates $P < 0.001$.

Further, as shown in Fig. 6, we can predict that A should be negatively correlated with K but positively correlated with t_i, and that K should be negatively correlated with t_i. All three predictions are supported by the data of Remeš & Martin (2002), Table 3.

Discussion

The predictive model for fledging age in passerines developed in this paper is remarkably simple, but produces an excellent correspondence between predicted and observed fledging ages (Fig. 3, Table 2). The first transitional mortality function, $(g(t_f,t_a) = M_n t_0)$, which is a step function that necessarily overestimates the mortality rate during the transitional period (Fig. 2), produces predictions that are 11–16% too small (Fig. 3). To estimate the average change in mortality rate required to eliminate this discrepancy we used an intermediate step function $(g(t_f,t_a) = \beta M_n t_0)$ that requires an additional parameter, β. This analysis indicated that a transitional mortality function in which mortality is approximately 0.3–0.4 of nesting mortality produces predictions which, on average, equal the observed values (Fig. 4). These results suggest that the mortality rate averaged over the nestling period is significantly higher than that immediately following fledging. Support for this hypothesis is given by a comparison of juvenile mortality rates in passerines (data from Saether, 1989) with nestling mortality rates (data from Remeš & Martin, 2002): juvenile mortality rates average 0.003 (SE = 0.0001, $n = 17$), whereas nest mortality rates average 0.017 (SE = 0.0009, $n = 115$), a difference that is highly significant ($t_{122} = 5.92$, $P < 0.001$; Kruskal–Wallis test, $\chi_1^2 = 36.1$, $P < 0.001$). Moreover, studies that tracked young after fledging also indicate a rapid decrease in mortality with age following fledging (e.g. Sullivan, 1989; Anders *et al.*, 1997; Perkins & Vickery, 2001; Gardali *et al.*, 2003). Finally, these results also suggest an interesting relationship that is previously undescribed: selection favours an age of fledging where post-fledging
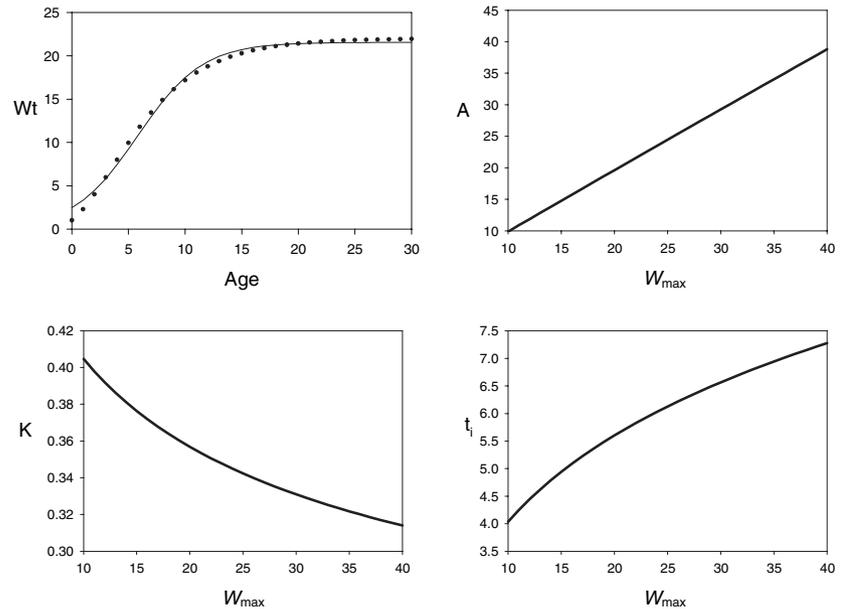
rubecula (Fig. 6). If only the asymptotic value in equation is changed all three fitted values of the logistic equation also change, demonstrating that these components are not completely separate entities (Fig. 6). Thus selection that acted on asymptotic size alone would, according to the model of West *et al.* (2001), create a change in the other growth parameters, which would then induce an evolutionary change in the optimal age at fledging.

Fig. 6 Upper left panel shows the growth curve (•) generated by fitting data from the robin (*E. rubecula*) to equation 11. Parameter values ($W_{max} = 22$g, $W_0 = 1$g, $a = 1.9$) from West *et al.* (2001). The solid line shows the logistic equation fitted by nonlinear least squares regression ($A = 21.557$, $K = 0.3506$, $t_i = 5.824$). The remaining three panels show the changes in the fitted values of A, K and t_i when only W_{max} is varied.

mortality is roughly 0.3–0.4 that experienced in the nest. This relationship encompasses observations that birds fledge at younger ages and developmental stages when nest mortality is greater (i.e. Remeš & Martin, 2002), but provides a more quantitative predictor of the actual age this should occur based on relative rates of pre- and post-fledging mortality.

Mass at fledging is generally less than the adult mass and the nestling growth curve shows that this adult mass cannot be estimated simply by projecting the nestling growth curve. This indicates that there is a significant change in growth following fledging, which, given the radical change in the thermal (i.e. no longer surrounded by warm siblings) and energetic (i.e. increased movement) environment of the fledgling, is not surprising. To further develop the model we require estimates of the change in mass between fledging and the attainment of adult mass. The model predicts the optimal age at fledging based upon the premise that the mass at this age is proportional to the mass at maturity (=cessation of growth). This premise is supported by observation but the lack of data on growth subsequent to fledging hinders theoretical development.

Whereas parental provisioning rate will reduce the likelihood of nestling starvation, nestling mortality due to predation may be largely beyond the control of the parents or chicks. Reduced begging by chicks and reduced provisioning rates may decrease mortality rates from predators that can use such cues, but many predators use alternate modes of detection for which there are few, if any, defenses (Montgomerie & Weatherhead, 1988; Briskie *et al.*, 1999; Martin *et al.*, 2000; Ghalambor & Martin, 2002). A reduction in clutch size

may increase the survival probability of the parent but an increase in provisioning rate may decrease parental survival (reviewed in Roff, 2002, p. 134–139). The optimal evolutionary response will depend upon how these components interact. To illustrate the complexity of this evolutionary response, consider the consequences of a reduction in clutch size at a given age at maturity, t_a. Such a reduction can be modelled by changing the constant, c, in the fecundity eqn 4 (i.e. $F(t_a) = cG(t_a)^d$). Because this coefficient does not enter the optimality equation (e.g. eqn 7), this change per se has no direct effect on the optimal age at fledging/maturity. However, changing c changes fecundity and hence changes the provisioning rate per nestling if total provisioning rate remains unchanged. Such a change would alter the nestling growth rate, which would then favour a change in the optimal age at fledging/maturity. On the other hand the parents might alter their total provisioning rate, which would most likely affect their mortality rate, which would then favour a change in the optimal age at maturity.

Using stepwise multiple regressions Remeš & Martin (2002) found that fledging age to be a function of adult body mass, K, M_n and foraging mode (aerial vs. nonaerial). Rearrangement of the logistic growth eqn 1 gives time to fledging as $t_f = t_i - \frac{1}{K}\ln\left(\frac{A}{W(t_f)} - 1\right)$ and hence in a multiple regression it would not be surprising to find significant contributions by K and by adult mass (which is highly correlated to both A and fledging mass: Table 3). Unlike these growth parameters the entry of M_n is not dictated by any necessary algebraic relationship and its retention in the final regression model is predicted by the model presented in this paper. Further, this model

provides no indication that nest mortality rate should be a function of body size measures, except in as much as they are correlated with the growth parameters. Thus the lowest correlations should appear between nest mortality rate and the three body mass measures, A, adult and fledging mass, which is indeed the case, none even being significant (Table 3).

There remain a number of questions to be addressed in the future: (1) what is the growth function subsequent to fledging, (2) what trade-offs dictate the optimal combination of growth parameters, (3) what is the age-specific mortality curve and what proximate mechanisms generate this trajectory, (4) what is the mortality curve associated with fledging at an earlier age, (5) what is the relationship between clutch mass and body mass, (6) what are the consequences of changes in egg size upon growth and survival? The present analysis highlights the importance of these components of the life history in the evolution of fledging age in passerines and similarly highlights the importance of gathering further data.

Acknowledgments

References

Anders, A.D., Dearborn, D.C., Faaborg, J. & Thompson, F.R., III, 1997. Juvenile survival in a population of neotropical migrant birds. *Cons. Biol.* **11**: 698–707.

Barbraud, C., Weimerskirch, H., Robertson, G.G. & Jouventin, P. 1999. Size-related life history traits: Insights from a study of snow petrels (*Pagodroma nivea*). *J. Anim. Ecol.* **68**: 1179–1192.

Benton, T.G. & Grant, A. 2000. Evolutionary fitness in ecology: comparing measures of fitness in stochastic, density-dependent environments. *Evol. Ecol. Res.* **2**: 769–789.

Briskie, J., Martin, P.R. & Martin, T.E. 1999. Nest predation and the evolution of nestling begging. *Proc. Roy. Soc. Lond. B* **266**: 2153–2160.

Charlesworth, B. 1994. *Evolution in Age Structured Populations*. Cambridge University Press.

Charnov, E.L. 1993. *Life History Invariants*. Oxford University Press, Oxford.

Charnov, E.L. 2000. Evolution of life-history variation among species of altricial birds. *Evol. Ecol. Res.* **2**: 365–373.

Christians, J.K. 2002. Avian egg size: variation within species and inflexibility within individuals. *Biol. Rev.* **77**: 1–26.

Deevey, E.S. 1947. Life tables for natural populations of animals. *Quart. Rev. Biol.* **22**: 283–314.

Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.

Gardali, T., Barton, D.C., White, J.D. & Geupel, G.R. 2003. Juvenile and adult survival of Swainson's thrush (Catherus ustulatus) in coastal California: annual estimates using capture-recapture analyses. *The Auk* **120**: 1188–1194.

Ghalambor, C.K. & Martin, T.E. 2002. Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. *Behav. Ecol.* **13**: 101–108.

Lewontin, R.C. 1965. In: *Selection for colonizing ability, The Genetics of Colonizing Species* (H. G. Baker & G. L. Stebbins, eds), pp. 77–94. Academic Press, New York.

Magrath, R.D. 1991. Nestling weight and juvenile survival in the blackbird, *Turdus merula*. *J. Anim. Ecol.* **60**: 335–351.

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., Scott, J. & Menge, C. 2000. Nest predation increases with parental activity: Separating nest site and parental activity effects. *Proc. Roy. Soc. Lond. B: Biol. Sci.* **267**: 2287–2293.

Montgomerie, R.D. & Weatherhead, P.J. 1988. Risks and rewards of nest defence by parent birds. *Quart. Rev. Biol.* **63**: 167–187.

Mylius, S.D. & Diekmann, O. 1995. On evolutionarily stable life histories, optimization and the need to be specific about density dependence. *Oikos* **74**: 218–224.

Perkins, D.W. & Vickery, P.D. 2001. Annual survival of an endangered passerine, the Florida Grasshopper Sparrow *Wilson Bull.* **113**: 211–216.

Remeš, V. & Martin, T.E. 2002. Environmental influences on the evolution of growth and developmental rates in passerines. *Evolution* **56**: 2505–2518.

Ricklefs, R.E. 1968. Patterns of growth in birds. *Ibis* **110**: 419–451.

Roff, D.A. 1984. The evolution of life history parameters in teleosts. *Can. J. Fish. Aquat. Sci.* **41**: 984–1000.

Roff, D.A. 1992. *The Evolution of Life Histories: Theory and Analysis*. Chapman and Hall, New York.

Roff, D.A. 2002. *Life History Evolution*. Sinauer Associates, Sunderland, MA.

Saether, B.E. 1987. The influence of body weight on the covariation between reproductive traits in European birds. *Oikos* **48**: 79–88.

Saether, B.E. 1988. Pattern of covariation between life-history traits of European birds. *Nature* **331**: 616–617.

Saether, B.E. 1989. Survival rates in relation to body weight in European birds. *Ornis Scand.* **20**: 13–21.

Starck, J.M. & Ricklefs, R.E. 1998. *Oxford Ornithology Series; Avian growth and development: Evolution within the altricial-precocial spectrum*. Oxford University Press, Oxford, UK.

Sullivan, K.A. 1989. Predation and starvation: age-specific mortality in juvenile juncos (Junco phaenotus). *J. Anim. Ecol.* **58**: 275–286.

Visman, V., Pesant, S., Dion, J., Shipley, B. & Peters, R.H. 1996. Joint effects of maternal and offspring sizes on clutch mass and fecundity in plants and animals. *Ecoscience* **3**: 173–182.

West, G.B., Brown, J.H. & Enquist, B.J. 2001. A general model for ontogenetic growth. *Nature (London)* **413**: 628–631.

Williams, T.D. 1994. Intraspecific variation in egg size and egg composition in birds: Effects on offspring fitness. *Biol. Rev.* **69**: 35–59.

Appendix

Derivation of the optimal ages at maturity and fledging

The fitness function is

$$w = 0.5cG(t_a)^d e^{-M_n t_f - g(t_f, t_a)} \qquad (1)$$

Letting $h(t_a) = M_n t_f + g(t_f, t_a)$ we have

$$\frac{\partial w}{\partial t_a} = dG(t_a)^{d-1} 0.5cG'(t_a)e^{-h(t_a)} - h'(t_a)e^{-h(t_a)} 0.5cG(t_a)^d$$

$$= 0.5cG(t_a)^{d-1}e^{-h(t_a)}(dG'(t_a) - h'(t_a)G(t_a)) \qquad (2)$$

where $G'(t_a) = \frac{\partial G(t_a)}{\partial t_a}$ and $h'(t_a) = \frac{\partial h(t_a)}{\partial t_a}$. To find the optimum value of t_a we set $\frac{\partial w}{\partial t_a} = 0$, which from eqn 2 requires that

$$h'(t_a) = \frac{dG'(t_a)}{G(t_a)} = \frac{dW'(t_f)}{W(t_f)} \qquad (3)$$

Now, if $g(t_f, t_a) = M_n(t_a - t_f)$ then $h(t_a) = M_n t_f + M_n(t_a - t_f) = M_n t_a$. Letting $B = e^{Kt_i}$ we have $W(t_f) = A(1 + Be^{-Kt_f})^{-1}$ and hence $W'(t_f) = AKBe^{-Kt_f}(1 + Be^{-Kt_f})^{-2}$. Substituting in eqn 3 and rearranging

$$M_n = \frac{dW'(t_f)}{W(t_f)} = \frac{dAKBe^{-Kt_f}(1 + Be^{-Kt_f})^{-2}}{A(1 + Be^{-Kt_f}})^{-1}$$

$$= \frac{dKBe^{-Kt_f}}{1 + Be^{-Kt_f}}$$

$$M_n(1 + Be^{-Kt_f}) = dKBe^{-Kt_f}$$

$$e^{-Kt_f} = \frac{M_n}{B(dK - M_n)}$$

$$t_f = \frac{1}{K}\ln\left(\frac{B(dK - M_n)}{M_n}\right) \qquad (4)$$