ENVIRONMENTAL INFLUENCES ON THE EVOLUTION OF GROWTH AND DEVELOPMENTAL RATES IN PASSERINES

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Abstract.—The reasons why growth and developmental rates vary widely among species have remained unclear. Previous examinations of possible environmental influences on growth rates of birds yielded few correlations, leading to suggestions that young may be growing at maximum rates allowed within physiological constraints. However, estimations of growth rates can be confounded by variation in relative developmental stage at fledging. Here, we re-estimate growth rates to control for developmental stage. We used these data to examine the potential covariation of growth and development with environmental variation across a sample of 115 North American passerines. Contrary to previous results, we found that growth rates of altricial nestlings were strongly positively correlated to daily nest predation rates, even after controlling for adult body mass and phylogeny. In addition, nestlings of species under stronger predation pressure remained in the nest for a shorter period, and they left the nest at lower body mass relative to adult body mass. Thus, nestlings both grew faster and left the nest at an earlier developmental stage in species with higher risk of predation. Growth patterns were also related to food, clutch size, and latitude. These results support a view that growth and developmental rates of altricial nestlings are strongly influenced by the environmental conditions experienced by species, and they generally lend support to an adaptive view of interspecific variation in growth and developmental rates.

Key words.—Adaptation, aerial foraging, allometry, comparative analysis, development, independent contrasts, nest predation.

A major question in evolutionary biology is to explain why life-history traits vary among species (Roff 1992, 2002; Stearns 1992; Charnov 1993). Most attention has focused on traits such as fecundity, age at first reproduction, survival, and rate of aging. Growth and developmental rates have received less attention even though they are integral components of life-history strategies and vary widely among species. As a result, our understanding of why growth and development varies among species remains unclear.

Life-history theory predicts that individuals should grow and develop at an infinite rate to achieve maximum output of offspring (Stearns 1992). However, this ''Darwinian demon'' ideal is not possible because of basic limits set by physiological constraints on growth rates (Ricklefs 1969b; West et al. 2001). Nevertheless, organisms might be expected to grow and develop at the fastest rate possible within these constraints (Ricklefs 1969b, 1979a; Ricklefs et al. 1998). Such views have been reinforced by an absence of correlations between growth rates and environmental variation in past interspecific examinations (see Ricklefs et al. 1998). On the other hand, benefits of maximum growth rates might be compromised by physiological or environmental costs. For example, fast growth can yield costs to reproductive output (Roff 1992; Stearns 1992), antiherbivore defense (Herms and Mattson 1992), starvation, predation, parasitism, disease susceptibility (Nylin and Gotthard 1998; Lankford et al. 2001), physical performance (Billerbeck et al. 2001), and adult body size (Nylin and Gotthard 1998) based on intraspecific studies of growth in plants, insects, fish, frogs, and lizards (summarized in Arendt 1997; Metcalfe and Monaghan 2001). Con-

sequently, we might expect growth rates to be optimized among species that occupy different environmental conditions that vary in such costs and benefits. A critical question then centers on which selection pressures cause variation in growth rates among species.

Birds are ideal for addressing this question for four reasons. First, data on growth rates are relatively abundant. Second, birds vary widely in growth rates and nestling periods (at least a 30-fold difference from seabirds to small passerines; Ricklefs 1979a, 1983). Third, a rich array of factors has been hypothesized to influence the evolution of growth and developmental rates in birds, with little resolution of the relative importance of these differing factors (see Table 1; summarized in Starck and Ricklefs 1998a). Finally, different theoretical models of avian growth and development differ substantially in their assumptions and predictions. For instance, some predicted a strong relationship between time-dependent juvenile mortality and growth rates (Case 1978), whereas others predicted a very weak one or even the absence of such a relationship (Ricklefs 1969b, 1984). In support of the latter, some comparative studies found no correlation between nest mortality rates and growth rates (Ricklefs 1969b; Ricklefs et al. 1998). In contrast, a negative correlation between nest mortality rates and duration of the nestling period has been consistently observed (Ricklefs 1969b; Bosque and Bosque 1995; Martin 1995; Ricklefs et al. 1998). These contrasting results may suggest that nest mortality rates influence duration of the nestling period, but does not influence rate of growth. However, previous analyses may have been compromised by a confounding between growth rate and duration of the nestling period. In particular, nestlings of species with low mortality remain in the nest longer and generally achieve either a longer period of asymptotic growth or weight re-

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TABLE 1. Summary of factors that were hypothesized to drive the evolution of growth and development in birds together with the conceived direction. A + means higher growth rates and longer nestling periods, a − means slower growth rates and shorter nestling periods, and 0 means no effect.

Factor	Growth	Nestling period
Body size[1]	−	+
Developmental mode (altricial or precocial)[2]	−	−
Clutch size (energetic limitation)[3]	−	+
Sibling competition[4]	+	−
Time-dependent mortality[5]	+ or 0	−
Foraging ecology[6]	−	+
Latitude[7]	+	−
Nutritional limitation[8]	−	+
Growth rate (K)[9]	n/a	−

[1] Ricklefs 1968a; Starck and Ricklefs 1998d.
[2] From altricial to precocial species, that is, slower growth and shorter to lacking nestling period; Ricklefs 1973, 1979a; Starck and Ricklefs 1998c.
[3] Lack 1968; Ricklefs 1986a.
[4] Werschkul and Jackson 1979; Ricklefs 1982; Bortolotti 1986; Royle et al. 1999.
[5] Williams 1966; Lack 1968; Ricklefs 1984 (positive effect), 1969b, 1979a (no effect).
[6] Unpredictability of food, Case 1978; aerial foragers, O'Connor 1978; seabirds, Ricklefs 1979a, 1982.
[7] Ricklefs 1976; Oniki and Ricklefs 1981.
[8] Concerns tropical frugivorous birds, Ricklefs 1983.
[9] We can expect that species growing at higher rates (K) will also fledge earlier.
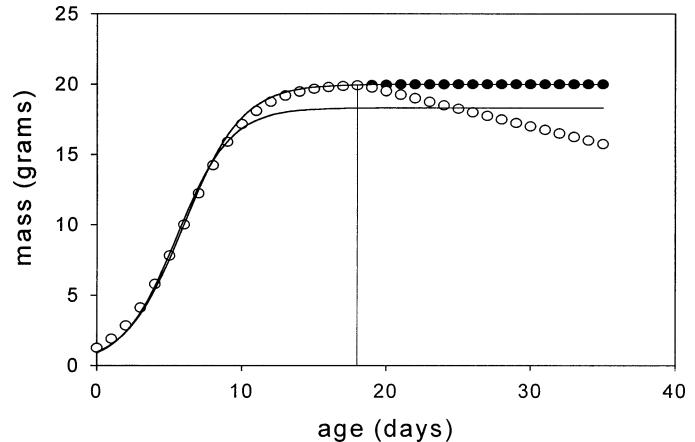

FIG. 1. Schematic depiction of the influence of the pattern of growth data (either with weight recession in later phases of the growth or without it) on the estimation of parameters of the logistic growth curve. Both datasets have the same initial rate of the weight increase up to day 18. The growth curve parameters for the growth data without recession (full circles with growth curve) are: $K = 0.5$, $A = 20$, $ti = 6$. The same parameters for the data with recession (open circles, lower growth curve) are $K = 0.54$, $A = 18.3$, $ti = 5.5$. The difference is caused by the recession data forcing the asymptote of the best fit curve to be lower and K to be higher. Consequently, we get two different values of K for the exact same rate of increase because of differing patterns of development after reaching the maximum weight in the nest (see Fig. 2).

cession than for species that leave the nest earlier. These differences can cause overestimation of growth rate for species that remain in the nest longer (see Fig. 1 and Methods) and, thereby, may obfuscate relationships between growth rates and nest mortality rates.

Here we re-examine the potential relationships between growth rates and nest mortality, as well as other potential environmental selection pressures for a sample of 115 North American passerines. We used original data and recalculated growth rates to standardize for analytical approach and to examine the possible interaction of nestling period on growth rate estimates. We controlled for the influence of developmental mode (altricial–precocial spectrum) by including only altricial passerines. Our primary ecological factors of interest were time-dependent nest mortality caused by predation, latitude, and foraging ecology. Foraging ecology was suggested to influence growth and developmental strategies in seabirds (Ricklefs 1979a). So, we examined aerial versus nonaerial foragers because aerial foragers differ from other passerine groups by unpredictability of their food supply over evolutionary time, which seems to influence life-history strategies (O'Connor 1978; Martin 1995). We also examined clutch size, which may influence the per capita rate of food delivery. We use a comparative approach, which cannot test causal hypotheses, but can provide insight into possible selective forces by examining which factors explain variation in growth and developmental rates among species.

METHODS

Dataset

We collected data for as many species of passerines as we could find in the literature (see Appendix 1). Data on growth

rates, latitudes, and nest predation rates are from original sources. We began with data on nestling growth listed by Starck and Ricklefs (1998b), but we checked and reanalyzed all growth rate estimates (see below). In addition, we were able to locate additional data, yielding primary growth data for 183 populations of 115 species of North American passerines. Of these, we were able to locate data on nest predation rates (proportion of nests taken by predators) for 107 species. Data on the duration of nestling period, clutch size, and foraging category (aerial vs. nonaerial foragers) were from Poole and Gill (1992–2002). Data on adult body mass were from Dunning (1993). Where separate data on adult mass are given for males and females, we took the average.

Time-dependent mortality is the only part of nest mortality that can be expected to favor elevated growth and developmental rates (Ricklefs 1969a; Case 1978). Other sources of mortality that do not bear direct relation to the length of nest cycle are not relevant for the evolution of growth rates. Time-dependent mortality of nests can be caused, for example, by inclement weather but its main source is nest predation (Ricklefs 1969a; Martin 1993). Percent of nests lost to predation was the common form of data available from primary sources and they are a compound result of the rate of time-dependent mortality caused by nest predation and the duration of nesting cycle. Thus, we transformed our data on nest predation to daily nest mortality rates by the formula: $dmr = -(\ln S)/T$, where dmr is daily nest mortality rate caused by nest predation, S is proportion of nests that were successful (1—proportion depredated), and T is the duration of the nest cycle (for discussion on this transformation procedure see Ricklefs 1969a; Ricklefs et al. 1998).

Growth rate can be characterized as an increase in body

mass over time, whereas development is characterized by timing of developmental events during ontogeny of an individual. For example, nestlings of species that fledge earlier develop their body functions more quickly than nestlings in later-fledging species (Ricklefs 1967b, 1979b; Austin and Ricklefs 1977). This different rate of maturation of body functions is certainly connected to the demands of life outside the nest, and we tried to analyze which ecological factors might be responsible for timing of nest leaving (i.e., duration of the nestling period), while controlling for the effect of growth rate. In addition, we analyzed relative fledging mass, defined as the ratio of body mass at fledging to adult body mass as an estimate of the relative stage of development at fledging. Body mass at fledging was defined as the average mass of nestlings at the last day in the nest and was taken from the original studies.

Body mass increases in passerines in an S-shaped function, which is expected on theoretical grounds (West et al. 2001). Many S-shaped mathematical curves could potentially fit growth data, but the logistic growth curve is traditionally used (Ricklefs 1967a, 1968a). Although Brisbin et al. (1987) criticized its use and suggested the use of more complex curves that are able to describe shape as well as rate, the advantage of the logistic growth curve is that it produces only three parameters that are readily biologically interpretable. The logistic growth curve has a form of $W(t) = A/\{1 + e^{[-K(t-t_i)]}\}$, 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, e is the base of natural logarithm, 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 1968a).

Estimates of K (growth rate) are problematic for comparative purposes because of a negative correlation between K and A (asymptotic body mass). The most serious problem arises in species with nestlings that remain in the nest longer and experience weight recession in later phases of the nestling period (see Ricklefs 1968b). Here the downward hook of the data, after a maximum value is achieved, forces A to be estimated lower than it would be without this hook, and consequently the estimate of K is artificially inflated (see Fig. 1). Consequently, species with the exact same growth during the initial growth period (illustrated by the vertical line in Fig. 1) yield different estimates of K when they remain in the nest for differing periods of time (Fig. 1; V. Remeš, unpubl. data). Recently, a new modification of the logistic growth curve was developed to deal with this problem in seabirds (Huin and Prince 2000). It has two K parameters, one for mass increase ($K1$) and the other for the rate of mass decrease during weight recession phase ($K2$). However, it suffers from the same shortcoming as the traditional method. Although this new approach fits growth data with weight recession well, the value of $K1$ (which equals K of the traditional model and is of interest to us) still depends on the pattern and extent of weight recession (V. Remeš, unpubl. data).

To overcome these problems and obtain growth estimates that are comparable across different ecological groups of
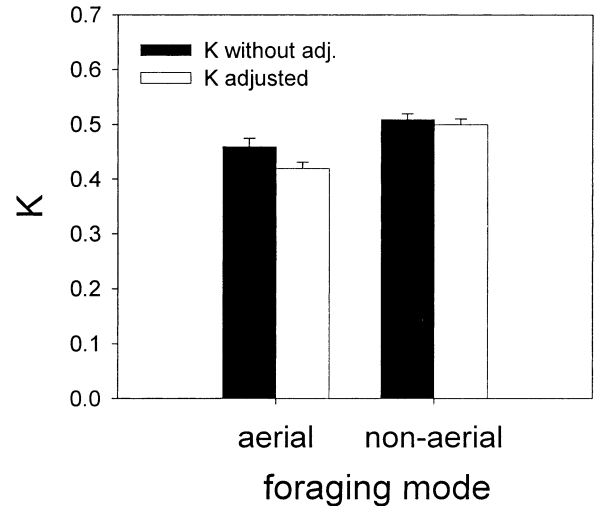

FIG. 2. Estimates of growth rate constant K (mean + SE) for aerial ($n = 20$) and nonaerial ($n = 95$) foragers for raw data and when adjusted for weight recession. In general, K is higher for unadjusted data than when data were truncated at the highest mass reached by the young. This effect was pronounced only in aerial foragers due to their typical growth pattern with strong weight recession in the nest (see also Fig. 1). Paired t-tests: $t_{1,188} = -4.27$, $P < 0.0001$, $n = 190$ for nonaerial foragers; $t_{1,38} = -4.10$, $P = 0.0006$, $n = 40$ for aerial foragers.

birds, we used two approaches. First, we fit the traditional logistic curve to the growth data truncated at the highest mass achieved by nestlings in species that remained in the nest past a maximum mass; truncation was necessary for 61 populations of 39 species, including 15 (of 20) species of aerial foragers, and 24 (of 95) species of nonaerial foragers. The effect of this adjustment on the estimation of K was marked only in aerial foragers, because these have a high incidence of weight recession (see above and Fig. 2). However, even after this adjustment, estimations of K could still be confounded by differences in ages and relative mass at fledging. Consequently, our second approach was to fit the logistic curve to the growth series truncated at 70% of adult body mass. This approach completely standardizes the relative nestling mass over which growth rates are estimated. We chose 70% as a compromise between retaining as much of the growth curve as possible and the maximum number of species possible (some species leave the nest at a lighter mass than 70% of adult body mass and consequently had to be excluded). This procedure led to loss of 18 species but still yielded highly standardized data on 97 species. Both these adjustments yield more standardized and appropriate estimation of K than in previous analyses. Analyses based on K fit to the growth data without either of the two adjustments produced virtually identical results to adjusted data, with exception that the explanatory power of aerial foraging for K was significantly reduced. Given the redundancy of these analytical results, we report only results of the analyses with the two standardized sets of K.

For our analyses we used average K for species. However, growth rate of nestlings can be adversely affected by poor environmental, especially food, conditions during rearing (e.g., Martin 1987; Gebhardt-Henrich and Richner 1998;

TABLE 2. Multiple regression analyses of the constant K of the logistic growth curve in North American passerines in relation to potential ecological factors and covariates. Sample sizes are numbers of species for raw species data (not corrected for phylogenetic relationships) and of phylogenetically independent contrasts for PICs (corrected for phylogenetic relationships). For partial regression and correlation coefficients from the analysis of raw species data, see Figure 3.

	K [1]							
	Raw species data ($n = 107$)				PICs ($n = 103$)			
	Full model		Best model [2]		Full model		Best model [2]	
	t	P	t	P	t	P	t	P
Adult body mass	−6.50	<0.0001	−6.54	<0.0001	−2.34	0.0214	−2.39	0.0188
Clutch size	−1.14	0.2587	—	—	−0.16	0.8764	—	—
Dmr [3]	4.49	<0.0001	5.11	<0.0001	4.53	<0.0001	4.48	<0.0001
Foraging mode [4]	−1.90	0.0604	−1.97	0.0515	0.49	0.6257	—	—
Latitude	1.69	0.0940	—	—	0.94	0.3509	—	—

[1] Fit to the growth data that were truncated at the highest mass reached by the young in the nest.
[2] Selected by the backward selection procedure in the multiple regression model of SPSS.
[3] Dmr is daily nest mortality rate caused by nest predation.
[4] Foraging mode is aerial foragers (coded 1) and nonaerial foragers (coded 0).

Schew and Ricklefs 1998). As a result, we repeated analyses with maximum K for species, which might better reflect evolutionary responses of growth rates than average values. Nevertheless, results of these two analyses did not differ. Consequently, only the results of the analyses with average values of K are reported because we used average values for all other variables.

Phylogenetic Analyses

We analyzed raw species data, but also employed the method of phylogenetically independent contrasts to control for possible phylogenetic influences (Felsenstein 1985; Harvey and Pagel 1991) based on the CAIC software package (Purvis and Rambaut 1995). We analyzed the independent contrasts in a phylogenetic regression framework (Grafen 1989), in which contrasts computed by CAIC (CRUNCH algorithm) were analyzed with standard multiple linear regressions forced through the origin (see Garland et al. 1992).

For analyses adjusting for phylogenetic relationships, we used a working phylogeny depicted in Martin and Clobert (1996), which is based on Sibley and Ahlquist's (1990) DNA-DNA hybridization phylogenetic hypothesis, and supplemented it with more recent molecular phylogenetic information (details are available from the authors upon request).

We did not have consistent estimates of branch lengths and so we used equal branch lengths (Garland et al. 1993). Previous analyses comparing equal branch lengths versus variable ones found little effect on results (Martins and Garland 1991). Estimation of branch lengths is an empirical issue and their performance should be statistically tested (Garland et al. 1992). We checked the performance of equal branch lengths by plotting the absolute values of the standardized contrasts against their standard deviations (Garland et al. 1992). In all cases, performance of equal branch lengths was good and much better than that of another option, Grafen's (1989) branch lengths.

Statistics

Logistic growth curves were fit in nonlinear regression in SPSS (1996). We used the Levenberg-Marquardt estimation method, sum of squared residuals loss function, and no pa-

rameter constraints. The ability of various factors to explain interspecific variation in the growth rate constant K, duration of nestling period, relative fledging mass, and premature fledging was tested by multiple linear regressions in SPSS. The best models were selected by the backward selection procedure. Our P-to-enter and P-to-remove values were 0.05 and 0.1, respectively (Sokal and Rohlf 1995). Selection of the final model in backward selection procedure depends in part on these P-values. Thus, we also validated the models by the means of Akaike's information criterion (AIC), which is computed as $n\ln(SSE/n) + 2p$, where n is the number of observations, SSE is the sum-of-squares error, and p is the number of model parameters. This is a general criterion for choosing the best number of parameters to include in a model. We chose a model with the minimum number of parameters from the set of models for which the difference between AIC(i) and AIC(min) was lower than two, where AIC(i) is AIC of the particular model and AIC(min) is minimum AIC of all the possible models (see Anderson et al. 2000). Marginal means for raw species data were estimated by ANCOVAs in SPSS. Phylogenetic regressions were performed on independent contrasts as ordinary multiple linear regressions forced through the origin.

Relative fledging mass was distributed normally. Other variables were transformed to meet the assumption of normal distribution. Adult body mass, clutch size, K, latitude, and premature fledging were log_{10} transformed and daily mortality rates caused by nest predation were square-root transformed.

RESULTS

Growth Rate (K)

Growth rates (K) fit to the data truncated at the highest mass achieved by nestlings were significantly correlated with adult body mass and daily nest predation rates (full model: R^2 adj. $= 0.45$, $F_{5,101} = 18.07$, $P < 0.0001$; reduced model: R^2 adj. $= 0.44$, $F_{3,103} = 28.81$, $P < 0.0001$). The influence of foraging mode was only marginally significant (Table 2, Fig. 3). Results were essentially the same for phylogenetically independent contrasts, with the exception that foraging mode was dropped from the model (Table 2).
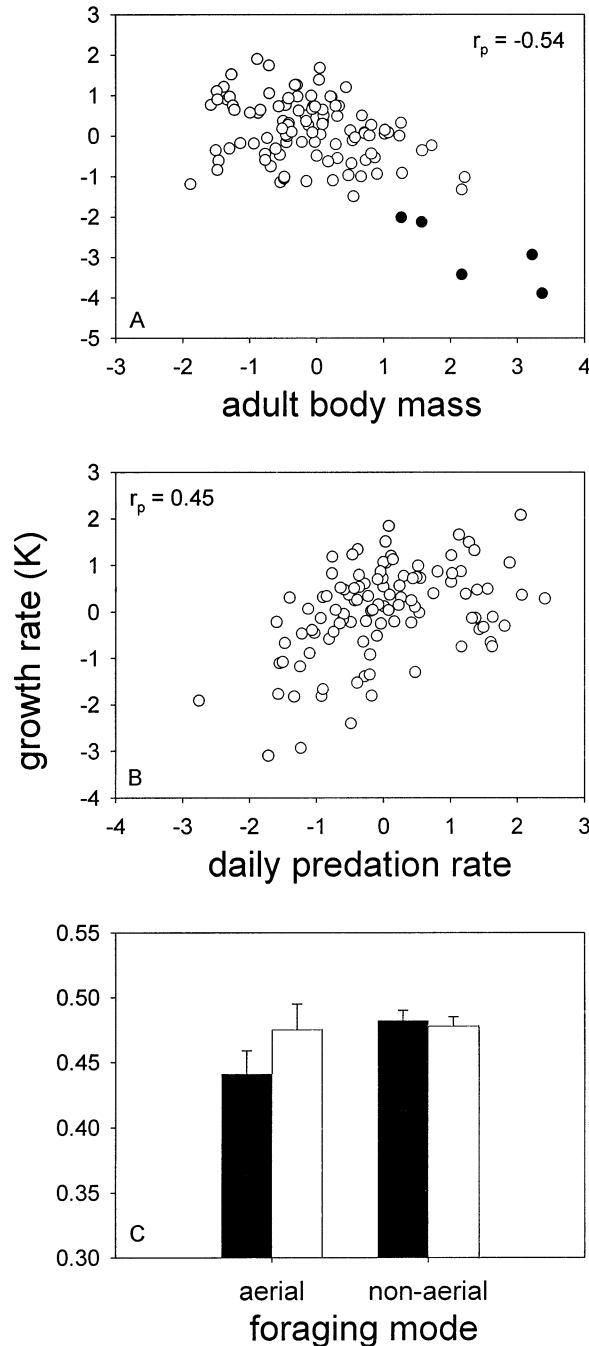
FIG. 3. Scattergrams of the standardized residuals from the multiple regression model of raw species data for K fit to the growth data that were truncated at the highest mass reached by the young in the nest (see Table 2). (A) K versus adult body mass (full circles, Corvidae; open circles, others), both corrected for daily predation rates and foraging mode; (B) K versus daily predation rates, both corrected for adult body mass and foraging mode; and (C) marginal means for foraging mode (black bars, all species; white bars, without four species of *Empidonax*), adjusted for adult body mass and daily predation rates. K relates to adult body mass, daily predation rates, and foraging mode (coded as nonaerial foragers = 0 [n = 89], aerial foragers = 1 [n = 18]) by the equation: $\log(K \text{ [day}^{-1}]) = -0.256 \ (0.040) - 0.128 \ (0.020) \log(\text{body mass [g]}) + 0.976 \ (0.191) \text{ square root } (dpr \text{ [day}^{-1}]) - 0.039 \ (0.020) \text{ foraging mode.}$ Parameters are partial regression coefficients (SE). r_p-values are partial correlation coefficients.

In the analyses of raw species data, the relationship between K and daily predation rate was curvilinear (Fig. 3B), as indicated by a significant nonlinear quadratic term ($t_{1,104}$ = −3.44, P = 0.0008), when effects of adult body mass and foraging mode were controlled. No such effect was apparent in the analyses of phylogenetically independent contrasts when adult body mass was controlled ($t_{1,101}$ = −0.02, P = 0.9807).

Although foraging mode was marginally significant in the analysis of raw species data (Table 2), this influence was due to four species of the genus *Empidonax* (see Fig. 3C), and after adjusting for phylogenetic effects it disappeared (Table 2). A strong phylogenetic effect was also apparent in the scaling of growth rate with adult body mass due to the influence of the family Corvidae (see Fig. 3A). After accounting for the effects of phylogeny, the influence of adult body mass on growth rate was much smaller (Tables 2, 3). Moreover, when the contrast between Corvidae and Vireonidae was excluded, the effect of adult body mass on growth rate completely disappeared ($t_{1,100}$ = −0.99, P = 0.3257, r_p = −0.10) and daily predation rate became the best predictor ($t_{1,100}$ = 4.69, $P < 0.0001$, r_p = 0.43).

Very similar results were obtained from the analyses of growth rates (K) fit to the data truncated at 70% of adult body mass. The difference was that both clutch size and latitude also entered the model in both raw species data (full model: R^2 adj. = 0.44, $F_{5,83}$ = 13.23, $P < 0.0001$; reduced model: R^2 adj. = 0.44, $F_{4,84}$ = 16.52, $P < 0.0001$) and phylogenetically independent contrasts (Table 3).

Nestling Period

Adult body mass, daily nest predation rates, foraging mode, and K were significantly related to the length of the nestling period when estimates of K were fit to the data truncated at the highest mass achieved by the nestlings (R^2 adj. = 0.72, $F_{5,101}$ = 56.15, $P < 0.0001$; Table 4, Fig. 4). The same results were found when analyses were performed on phylogenetically independent contrasts (Table 4). When the covariate K was based on data truncated at 70% of adult body mass, the analyses of factors influencing length of the nestling period yielded virtually identical results.

Premature Fledging

We also examined the extent to which nestlings were willing to fledge prematurely, defined as duration of the normal nestling period minus duration of the nestling period when nestlings fledge prematurely. The extent of premature fledging decreased with daily predation rates ($t_{1,30}$ = −3.93, P = 0.0005, n = 33) after accounting for the effect of adult body mass ($t_{1,30}$ = 3.70, P = 0.0009, n = 33; Fig. 5; whole model: R^2 = 0.43, $F_{2,30}$ = 13.16, $P < 0.0001$). This was the same for phylogenetically independent contrasts. Neither clutch size nor the growth rate constant K entered these models.

Relative Fledging Mass

Relative fledging mass (± SE, n), defined as the ratio of the mass at fledging to adult body mass, averaged 0.819 (± 0.015, 115) over all species. Both daily predation rates

TABLE 3. Multiple regression analyses of the constant K of the logistic growth curve in North American passerines in relation to potential ecological factors and covariates. Sample sizes are numbers of species for raw species data (not corrected for phylogenetic relationships) and of phylogenetically independent contrasts for PICs (corrected for phylogenetic relationships).

	K[1]							
	Raw species data ($n = 89$)				PICs ($n = 85$)			
	Full model		Best model[2]		Full model		Best model[2]	
	t	P	t	P	t	P	t	P
Adult body mass	−5.78	<0.0001	−5.76	<0.0001	−3.86	0.0002	−3.90	0.0002
Clutch size	−2.57	0.0121	−2.59	0.0114	−2.19	0.0317	−2.20	0.0307
Dmr[3]	2.41	0.0181	2.81	0.0061	2.15	0.0342	2.17	0.0327
Foraging mode[4]	−0.70	0.4885	—	—	0.08	0.9374	—	—
Latitude	3.13	0.0024	3.18	0.0021	2.45	0.0163	2.47	0.0157

[1] Fit to the growth data that were truncated at 70% of adult body mass.
[2] Selected by the backward selection procedure in the multiple regression model of SPSS.
[3] Dmr is daily nest mortality rate caused by nest predation.
[4] Foraging mode is aerial foragers (coded 1) and nonaerial foragers (coded 0).

and foraging mode were significantly related to relative fledging mass, with adult body mass controlled (Table 5, Fig. 6; whole model: R^2 adj. = 0.46, $F_{3,102} = 30.24$, $P < 0.0001$). Examination of phylogenetically independent contrasts, with adult body mass controlled, still yielded significant effects of daily predation rates, but foraging mode was dropped from the stepwise selection procedure (Table 5).

Relative fledging mass was curvilinearly related to daily predation rate, as reflected by a significant nonlinear quadratic term ($t_{1,103} = 2.46$, $P = 0.0154$), when the effects of adult body mass and foraging mode were controlled (see Fig. 6B). However, no such term was apparent in phylogenetically adjusted data, when the effect of adult body mass was taken into account ($t_{1,100} = 0.86$, $P = 0.3928$). All analyses of the relative fledging mass were performed without the strongly outlying *Leucosticte tephrocotis* (relative fledging mass = 1.54; see also Appendix 1).

DISCUSSION

Previous comparative studies of variation in growth rates found little in the way of environmental correlates (see Ricklefs et al. 1998). In direct contrast, we found very strong effects of predation, with smaller but significant contributing effects of foraging mode, clutch size, and latitude on both growth rate and developmental strategies. These results show that growth and development of altricial nestlings are shaped by extrinsic environmental forces.

Daily predation rates scaled positively with growth rates and negatively with duration of the nestling period (after controlling for growth rates; Tables 2–4; Figs. 3B, 4B). Furthermore, species with higher nest predation fledged at lighter relative mass (Table 5, Fig. 6B). These results suggest that multidimensional aspects of the growth strategies of altricial nestlings are strongly influenced by risk of nest predation. Such results are in line with theoretical arguments made by Lack (1968) and Case (1978), and with empirical studies of Kleindorfer et al. (1997) and Hałupka (1998).

However, the benefits of growing faster and shortening the nestling period may reach a point of diminishing returns. Indeed, the curvilinear relationship between nest mortality versus growth rates (Fig. 3B; Results) and relative fledging mass (Fig. 6B; Results) could arise if costs (ecological: Martin 1992; Martin et al. 2000a,b; physiological: Metcalfe and Monaghan 2001) of even faster growth exceed the benefits. Alternatively, leveling off of growth rates could be caused by reaching the maximum growth rate possible within cellular and physiological constraints (see Ricklefs 1969b). More-

TABLE 4. Multiple regression analyses of the duration of the nestling period in North American passerines in relation to potential ecological factors and covariates. Sample sizes are numbers of species for raw species data (not corrected for phylogenetic relationships) and of phylogenetically independent contrasts for PICs (corrected for phylogenetic relationships). For partial regression and correlation coefficients from the analysis of raw species data, see Figure 4.

	Nestling period							
	Raw species data ($n = 107$)				PICs ($n = 103$)			
	Full model		Best model[1]		Full model		Best model[1]	
	t	P	t	P	t	P	t	P
Adult body mass	3.95	0.0001	3.73	0.0003	3.91	0.0002	3.80	0.0003
Clutch size	1.92	0.0570	—	—	1.23	0.2220	—	—
Dmr[2]	−3.55	0.0006	−4.34	<0.0001	−2.64	0.0095	−2.88	0.0048
Foraging mode[3]	6.08	<0.0001	5.98	<0.0001	2.54	0.0126	2.61	0.0105
K[4]	−5.74	<0.0001	−5.74	<0.0001	−2.56	0.0121	−2.52	0.0134

[1] Selected by the backward selection procedure in the multiple regression model of SPSS.
[2] Dmr is daily nest mortality rate caused by nest predation.
[3] Foraging mode is aerial foragers (coded 1) and nonaerial foragers (coded 0).
[4] Fit to the growth data that were truncated at the highest mass reached by the young in the nest.
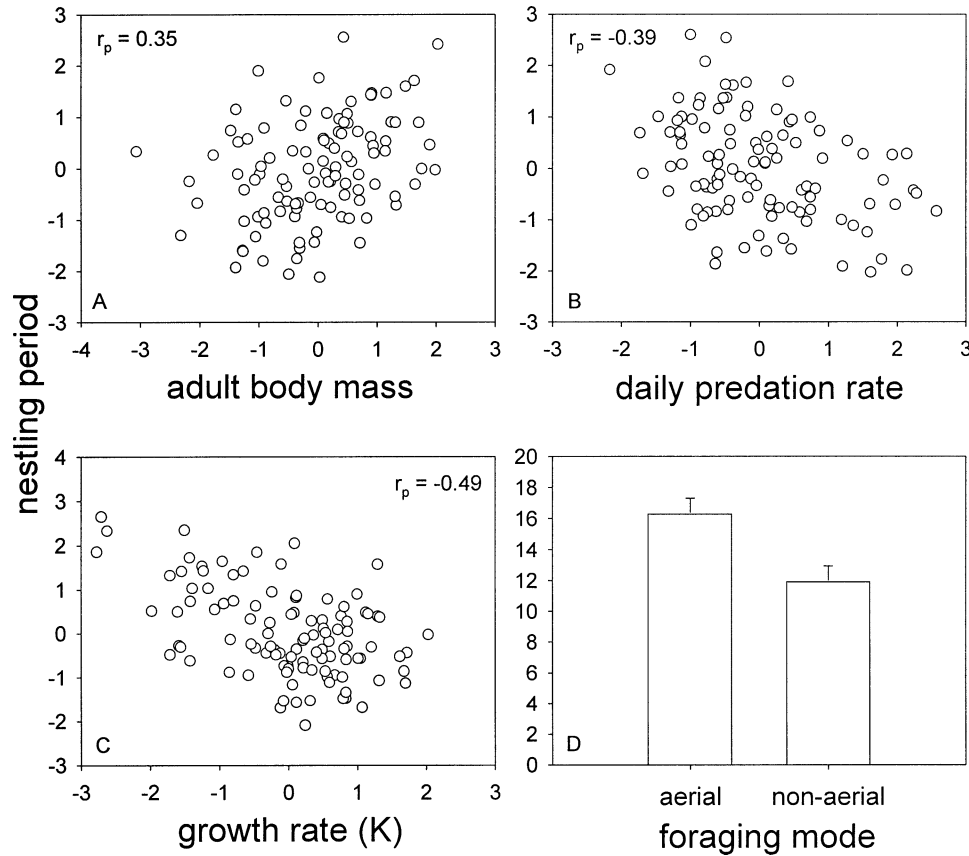
FIG. 4. Scattergrams of the standardized residuals from the multiple regression model of raw species data for the duration of the nestling period, with K fit to the growth data that were truncated at the highest mass reached by the young in the nest (see Table 4). (A) Duration of the nestling period versus adult body mass, both corrected for daily predation rates, foraging mode, and K; (B) nestling period versus daily predation rates, both corrected for adult body mass, foraging mode, and K; (C) nestling period versus K, both corrected for adult body mass, daily predation rates, and foraging mode; (D) marginal means for foraging mode adjusted for adult body mass, daily predation rates, and K. Nestling period relates to adult body mass, daily predation rates, K, and foraging mode (coded as nonaerial foragers = 0 [$n = 89$], aerial foragers = 1 [$n = 18$]), by the equation: log(nestling period [days]) = 0.862 (0.053) + 0.097 (0.026) log(body mass [g]) − 1.038 (0.239) square root (dpr [day^{-1}] − 0.634 (0.110) log(K [day^{-1}]) + 0.135 (0.022) foraging mode. Parameters are partial regression coefficients (SE). r_p-values are partial correlation coefficients.

over, because birds that grow quicker also fledge and mature earlier, the trade-off between growth and maturation could play a role (Ricklefs et al. 1994, 1998; but see Krijgsveld et al. 2001).

Several studies have shown that duration of the nestling period scales negatively with nest predation rates (Lack 1968; Martin and Li 1992; Bosque and Bosque 1995; Martin 1995; Yanes and Suárez 1997). We show that this is true even after accounting for pure growth rates (Table 4, Fig. 4B). Thus, shorter nestling periods result not only from faster growth, but also from earlier timing of nest-leaving at an earlier stage of development. The latter is clearly reflected by the lower relative fledging mass in species with higher predation rates (Table 5, Fig. 6B). However, the precocity of fledging is clearly limited. This limit is evident from the negative relationship between the extent of premature fledging relative to nest predation rates. Whereas species with high predation already leave at an early stage of development and cannot leave many days earlier, species with low predation stay in the nest to a much later stage of development and have the capability of fledging many days earlier than they do (see

Fig. 5). In addition, the reduction in fledging mass when fledging prematurely can be so high and costs connected with it so strong (Lindén and Møller 1989; Magrath 1991; Gebhardt-Henrich and Richner 1998; Lindström 1999) that it can be advantageous to keep this strategy as optional for the circumstances of real predation danger.

Predation was not the only environmental correlate of growth and development. Food limitation has long been proposed to explain the evolution of growth and development of birds through energetic expensiveness of large clutch sizes (Lack 1968), shorter time available for feeding offspring at lower latitudes (Ricklefs 1976), and unpredictability of food supply (O'Connor 1978). Of these three, growth rates were associated with aerial foraging when using K fit to the growth data truncated at the highest mass (Table 2) and with clutch size and latitude when using K fit to the growth data truncated at 70% of adult body mass (Table 3). Nestling period duration differed strongly between aerial and nonaerial foragers (Table 4, Fig. 4D). In contrast, the influence of aerial foraging on relative fledging mass was rather weak in the raw species data (Table 5, Fig. 6C), and disappeared after adjusting for
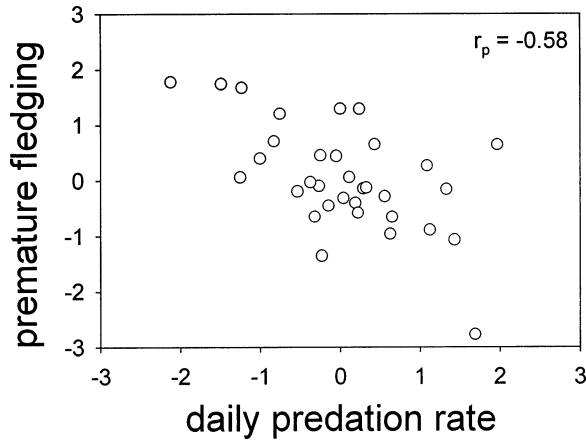
FIG. 5. Scattergram of the standardized residuals of premature fledging (reduction of the duration of the nestling period when fledging prematurely as compared to normal fledging, in days) versus daily predation rates, both corrected for adult body mass, for raw species data. Log(premature fledging [day]) = 0.333 (0.159) − 3.444 (0.876) square root (dpr [day^{-1}]) + 0.336 (0.091) log(body mass [g]), n = 33. Parameters are partial regression coefficients (SE). r_p-value is partial correlation coefficient.

phylogeny (Table 5). This is not surprising, however, because aerial foragers show a high incidence of weight recession (see Methods), and thus rather long nestling periods do not translate to very high mass of fledglings relative to adult body mass.

Aerial foragers seem to be food limited in general (Martin 1987, 1995). Their food supply is temporally unpredictable and there is an ample evidence that adverse climatic conditions can lead on a proximate level to longer incubation and nestling periods and impaired growth, condition, and survival of nestlings (e.g., Bryant 1975; O'Connor 1978; McCarty and Winkler 1999). Nestlings of aerial foragers must survive relatively long periods without parental attendance during inclement weather conditions, whose incidence and duration are unpredictable. Adaptations to sustain these periods include extensive fat deposition and early thermal independence of the nestlings (Ricklefs 1967b; O'Connor 1978). It is possible to speculate that these adaptations aimed at decreasing susceptibility to starvation could also have led to or have been connected with adjustments in growth strategies

of nestlings (O'Connor 1978), including lower growth rates and longer nestling periods. On the other hand, the strongest result concerning aerial foragers (i.e., longer nestling periods) can be explained alternatively—that they must wait in the nest until the maturation of their flight muscles that are critical for their demanding flight life. Thus, results concerning aerial foragers must be interpreted with caution and more analyses are clearly needed, but the positive results found here with relatively low power hold promise for future analyses.

Lack (1968) proposed a trade-off between clutch size and growth rate (see also Ricklefs 1968a). Our data illustrate negative covariation among species; species with larger clutch size show slower growth of nestlings for the same adult body mass, nest predation, and latitude. Such a covariation could be merely a correlated response to the same factor—lower nest predation risk may simply favor both larger clutches (Martin 1995) and slower growth (Case 1978) independently. However, because we control for nest predation by multiple regression, it may be that this is cause and effect (i.e., a trade-off). A positive relationship between growth rate of nestlings and latitude was predicted by Ricklefs (1976). Although he suggested this effect to explain slower growth of tropical species, we show that this can be true even on a much smaller geographical scale. However, because both the effect of clutch size and latitude were apparent only when using K fit to the growth data truncated at 70% of adult body mass, they should be taken with caution and be subject to additional analyses.

Adult body mass can have an allometric influence on life-history traits. Because K indexes growth rate independently of body mass (Ricklefs 1968a; Starck and Ricklefs 1998b), however, there is no a priori reason to expect its negative scaling with growth rate. The negative scaling observed here may suggest basic design constraints of large body size (West et al. 2001). Alternatively, slower growth rates and longer nestling periods of larger birds could be a result of lower parental investment in offspring. Larger birds have higher adult survival rates (Sæther 1987, 1988, 1989; Martin 1995), and species with higher adult survival are expected to invest less in progeny (Charnov and Schaffer 1973; Martin 2002). Adult body mass could work here just as a reflection of adult survival rate. To test this hypothesis, comparative studies of

TABLE 5. Multiple regression analyses of the relative fledging mass (fledging mass/adult body mass) in North American passerines in relation to potential ecological factors and covariates. Sample sizes are number of species for raw species data (not corrected for phylogenetic relationships) and of phylogenetically independent contrasts for PICs (corrected for phylogenetic relationships). For partial regression and correlation coefficients from the analysis of raw species data, see Figure 6.

	Relative fledging mass					
	Raw species data (n = 106)		PICs (n = 102)			
	Full and best model[1]		Full model		Best model[1]	
	t	P	t	P	t	P
Adult body mass	−6.01	<0.0001	−4.58	<0.0001	−4.58	<0.0001
Dmr[2]	−5.14	<0.0001	−2.92	0.0043	−2.91	0.0044
Foraging mode[3]	2.62	0.0101	−0.34	0.7383	—	—

[1] Selected by the backward selection procedure in the multiple regression model of SPSS.
[2] Dmr is daily nest mortality rate caused by nest predation.
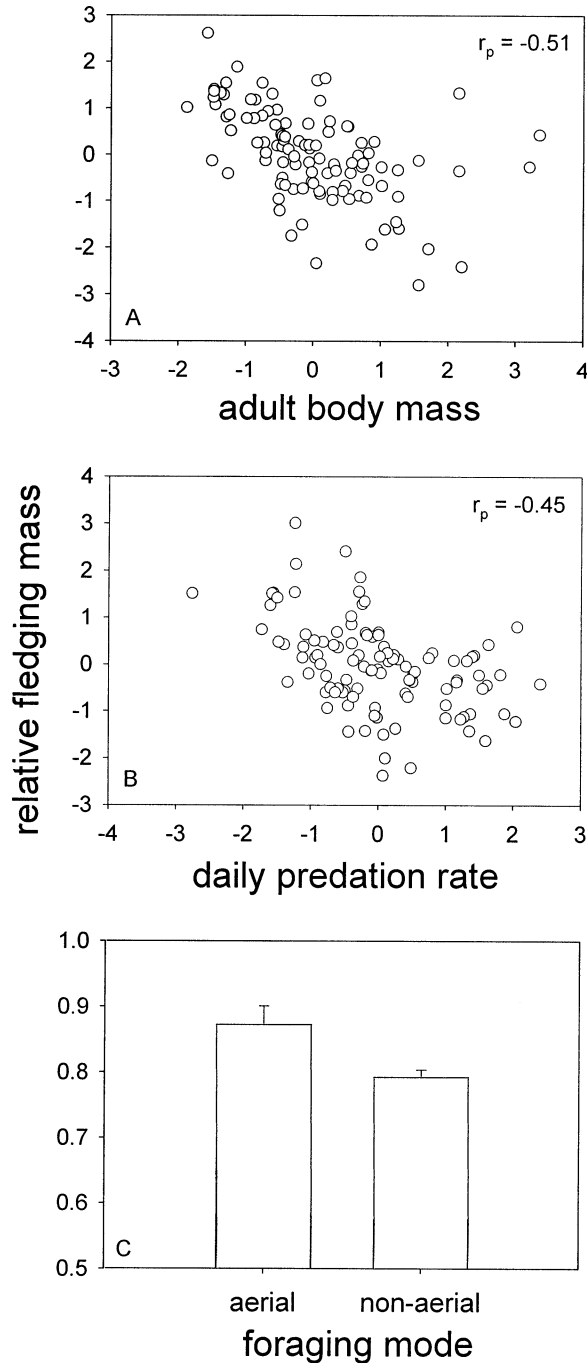[3] Foraging mode is aerial foragers (coded 1) and nonaerial foragers (coded 0).

FIG. 6. Scattergrams of the standardized residuals from the multiple regression model of raw species data for the relative fledging mass (fledging mass/adult body mass; see Table 5). (A) Relative fledging mass versus adult body mass, both corrected for daily predation rates and foraging mode; (B) relative fledging mass versus daily predation rates, both corrected for adult body mass and foraging mode; and (C) marginal means for foraging mode, adjusted for adult body mass and daily mortality rates. Relative fledging mass relates to adult body mass, daily predation rates, and foraging mode (coded as nonaerial foragers = 0 [$n = 88$], aerial foragers = 1 [$n = 18$]) by the equation: relative fledging mass = 1.244 (0.062) − 0.182 (0.030) log(adult body mass [g]) − 1.524 (0.296) square root (dpr [day^{-1}]) + 0.080 (0.031) foraging mode. Parameters are partial regression coefficients (SE). r_p-values are partial correlation coefficients.

growth strategies including adult survival rates and feeding rates are needed.

In sum, we show that growth rates, duration of nestling period, and relative developmental stage at nest-leaving covary in altricial nestlings with nest predation rates, aerial foraging, clutch size, and latitude after taking into account adult body mass and phylogenetic effects. This is in line with the view that growth strategies of altricial nestlings are finely tuned to environmental conditions typical of each species (Lack 1968; Kleindorfer et al. 1997) and lends support to an adaptive view of variation in growth and development (Arendt 1997). Moreover, we show that studies addressing evolution of growth strategies should simultaneously examine both pure growth and timing of developmental events (here, fledging), because these two show independent evolution in relation to extrinsic selective forces.

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APPENDIX 1

Species means used in the analyses for adult body mass (Abm, g), clutch size (Cl, no. of eggs per nest), duration of nestling period (Nstl, days), duration of shortened nestling period when fledging prematurely (Nstl prem, days), growth rate constant K of the logistic curve fit to the growth data truncated at the highest mass achieved by nestlings (K, day^{-1}), data truncated at 70% of adult body mass (K 70%, day^{-1}), body mass at fledging (Fl mass, g), latitude of the study of growth (Lat, °N), number of primary growth series for the species (No. stud), foraging mode (Forag; n, nonaerial; a, aerial foragers), proportion of nests taken by predators (Pred, %), and references for primary sources (Ref).

Species	Abm	Cl	Nstl	Nstl prem	K	K 70%	Fl mass	Lat	No. stud	Forag	Pred	Ref
Agelaius phoeniceus	52.6	3.28	11.5	—	0.533	0.585	35.6	41.6	3	n	44.40	1, 4
Aimophila botterii	19.9	3.65	10.0	8.0	0.489	0.484	14.7	31.5	1	n	29.20	5, 6
Aimophila carpalis	15.3	3.80	8.5	—	0.555	0.580	11.9	32.0	1	n	68.00	7
Aimophila cassinii	18.9	3.97	8.0	—	0.515	—	12.0	31.5	1	n	30.77	6, 8
Ammodramus bairdii	17.5	4.33	9.0	—	0.410	0.461	13.6	50.8	1	n	43.00	9, 10
Ammodramus caudacutus	19.3	3.90	9.7	8.0	0.564	0.546	15.4	40.3	2	n	36.20	11, 12
Ammodramus maritimus	23.3	3.39	10.0	8.0	0.579	0.565	16.8	40.3	2	n	24.53	11, 13
Ammodramus savannarum	17.0	4.30	8.0	7.5	0.462	—	10.5	45.0	1	n	58.90	1, 14
Amphispiza bellli	18.9	3.28	95.	—	0.492	0.490	13.9	43.8	1	n	43.20	1, 15
Anthus spinoletta	20.9	4.60	14.1	12.0	0.491	0.448	18.6	45.0	1	n	33.33	16
Anthus spragueii	25.3	4.50	11.2	—	0.515	—	15.5	50.8	1	n	32.75	9, 17
Aphelocoma coerulescens	83.3	3.27	18.0	12.0	0.302	0.296	59.8	27.3	1	n	29.50	1, 18
Auriparus flaviceps	6.8	3.70	19.0	—	0.337	0.463	6.7	33.4	1	n	19.50	19
Bombycilla cedrorum	31.9	4.06	15.5	—	0.439	0.479	33.2	41.6	1	n	21.43	20
Calamospiza melanocorys	37.6	3.80	8.5	7.0	0.456	—	23.6	40.5	1	n	54.14	21
Calcarius lapponicus	27.3	5.25	9.0	—	0.545	0.535	22.1	69.5	2	n	32.40	1, 22
Calcarius mccownii	23.2	3.43	10.0	—	0.480	0.492	18.7	45.7	4	n	38.46	9, 23, 23a
Calcarius ornatus	18.9	4.29	10.0	—	0.511	0.462	14.9	49.0	4	n	44.74	9, 24
Calcarius pictus	26.4	4.08	8.1	—	0.486	0.594	22.0	58.8	1	n	25.32	25
Campylorhynchus bruneicapillus	38.9	3.37	21.0	—	0.396	0.380	31.3	32.2	1	n	28.60	1, 26
Cardinalis cardinalis	44.7	3.00	9.5	7.0	0.598	—	27.1	40.4	2	n	54.00	1, 27, 32
Carduelis flammea	13.6	4.20	11.0	—	0.435	0.548	9.2	59.8	2	n	—	28
Carduelis pinus	14.6	3.80	15.0	12.0	0.375	0.427	18.6	40.8	1	n	—	29
Carpodacus mexicanus	21.4	4.26	15.0	13.0	0.627	—	11.8	46.9	1	n	45.80	1, 30
Catharus bicknelli	28.1	3.53	11.6	—	0.519	0.694	24.8	44.0	1	n	68.53	31
Catharus fuscescens	31.2	4.00	11.0	—	0.646	0.632	24.5	40.9	1	n	55.00	2, 27
Catharus guttatus	31.0	3.46	12.0	—	0.448	0.467	24.8	44.1	2	n	60.10	1, 33
Catharus ustulatus	30.8	3.57	13.0	10.0	0.510	0.518	28.9	44.6	1	n	35.14	34
Chondestes grammacus	29.0	4.09	11.5	7.0	0.675	—	14.0	34.0	1	n	38.70	1, 35
Cinclus mexicanus	57.8	4.30	25.4	—	0.312	0.242	53.0	46.9	1	n	3.80	36
Cistothorus palustris	11.3	4.92	14.0	12.5	0.466	0.487	11.5	44.3	1	n	41.39	1, 37
Cistothorus platensis	9.0	6.59	13.0	11.0	0.408	0.342	7.4	44.0	1	n	22.70	1, 38
Corvus brachyrhynchos	448.0	5.00	33.3	—	0.216	0.236	390.0	45.9	2	n	45.61	39
Corvus caurinus	391.5	4.02	31.7	25.0	0.264	0.272	303.0	49.7	2	n	49.10	1, 40
Dendroica discolor	7.7	3.89	9.4	—	0.507	0.469	6.3	39.2	1	n	61.80	1, 41
Dendroica kirtlandii	13.8	4.63	9.4	8.0	0.547	0.398	12.7	44.0	1	n	40.10	1, 42
Dendroica petechia	9.5	4.27	8.4	—	0.579	0.562	8.9	50.6	4	n	34.20	1, 43
Dendroica striata	13.0	4.32	9.5	—	0.538	0.499	11.3	—	1	n	—	44
Dendroica virens	8.8	4.00	10.0	9.0	0.736	0.566	7.7	45.5	1	n	—	45
Dolichonyx oryzivorus	31.6	5.00	10.5	8.8	0.511	0.511	22.1	43.3	1	n	29.80	1, 46
Dumetella carolinensis	36.9	3.64	10.5	—	0.516	0.495	28.5	45.0	1	n	31.20	1, 47
Empidonax difficilis	10.9	3.30	15.5	—	0.433	0.413	10.5	36.4	2	n	58.90	1, 48
Empidonax minimus	10.3	3.86	14.3	—	0.452	0.474	10.8	50.2	1	a	53.30	1, 49
Empidonax oberholseri	10.4	3.78	17.8	—	0.434	0.394	10.1	37.9	1	a	55.50	1, 50
Empidonax traillii	13.4	3.48	13.5	—	0.388	0.499	12.5	44.6	2	a	44.20	1, 51
Eremophila alpestris	31.4	3.10	9.5	—	0.522	0.559	22.3	48.9	5	n	24.90	1, 9, 52
Euphagus cyanocephalus	62.7	5.13	13.3	—	0.501	0.519	46.0	41.7	1	n	45.50	1, 53
Geothlypis trichas	10.1	4.00	9.8	8.0	0.537	0.598	10.3	43.5	2	n	14.50	1, 54
Gymnorhinus cyanoephalus	103.0	4.00	21.0	—	0.309	0.355	81.3	35.2	1	n	41.20	1, 55
	21.6	3.50	22.7	—	0.442	0.455	20.8	37.9	2	a	13.62	56
Hirundo pyrrhonota	18.6	4.53	20.3	—	0.431	0.429	18.0	43.5	2	a	10.35	23a, 57
Hirundo rustica	47.4	3.25	13.5	—	0.529	0.550	36.7	40.9	1	n	52.50	1, 27

APPENDIX 1

Continued.

Species	Abm	Cl	Nstl	Nstl prem	K	K 70%	Fl mass	Lat	No. stud	Forag	Pred	Ref
Hylocichla mustelina												
Icteria virens	25.3	3.69	8.9	—	0.528	—	16.3	40.0	1	n	52.90	1, 58
Junco phaeonotus	20.4	3.54	11.5	—	0.457	0.472	17.7	31.9	1	n	26.00	2, 59
Lanius ludovicianus	47.4	5.40	18.1	—	0.370	0.416	44.3	39.5	2	n	19.40	1, 23a, 60
Leucosticte tephrocotis	26.3	4.48	18.5	—	0.363	0.479	40.5	51.5	1	n	16.70	61
Melospiza lincolnii	17.4	4.24	10.5	—	0.574	0.492	14.7	40.5	1	n	42.00	2, 62
Melospiza melodia	20.8	3.88	10.8	—	0.484	0.480	17.8	40.0	1	n	28.10	1, 63
Mimus polyglottos	48.5	3.70	12.0	10.0	0.514	0.504	35.0	28.2	1	n	47.10	1, 64
Myioborus pictus	7.9	3.40	13.0	10.0	0.557	0.478	8.8	36.0	1	n	37.90	65
Myiodynastes luteiventris	46.3	3.42	17.0	—	0.355	0.386	39.0	32.0	1	a	—	66
Oporornis formosus	14.0	4.12	8.5	7.0	0.680	0.530	12.5	38.0	1	n	30.00	1, 67
Oreoscoptes montanus	43.3	3.80	11.9	—	0.480	0.463	38.0	44.0	2	n	32.00	68
Parus atricapillus	10.8	7.00	16.0	12.0	0.402	0.431	11.3	42.4	1	n	19.70	1, 69
Passerculus sandwichensis	20.1	4.13	9.3	8.0	0.519	0.511	15.4	43.3	4	n	43.40	1, 9, 70
Passerina amoena	15.5	3.37	10.0	8.0	0.480	0.604	12.6	42.0	1	n	35.00	71
Pheuticus melanocephalus	44.5	3.40	11.5	—	0.358	0.385	33.0	37.6	1	n	34.00	1, 72
Pica pica	177.5	6.48	28.4	—	0.223	0.324	180.5	49.7	2	n	29.00	73
Pipilo aberti	46.0	2.85	12.5	—	0.497	0.497	31.3	33.6	1	n	63.80	1, 74
Pipilo erythrophthalmus	40.5	3.30	10.5	7.5	0.519	—	0.24.7	39.6	2	n	51.90	1, 27, 75
Piranga olivacea	28.6	3.53	10.0	—	0.431	0.477	20.5	42.5	1	n	32.60	1, 76
Piranga rubra	29.0	3.20	9.5	—	0.704	—	18.2	39.0	1	n	64.00	77
Plectrophenax nivalis	42.2	5.71	12.8	—	0.569	0.556	30.4	71.4	1	n	27.90	1, 78
Pooecetes gramineus	25.7	4.00	10.5	—	0.612	0.600	17.5	43.1	2	n	52.90	1, 79
Progne subis	49.4	4.52	28.5	—	0.306	0.364	52.0	42.3	1	a	6.25	80
Protonotaria citrea	16.2	4.61	10.0	9.0	0.654	0.520	12.7	42.2	1	n	31.00	1, 81
Quiscalus major	166.5	2.77	13.5	—	0.403	—	77.7	28.0	1	n	41.24	82
Quiscalus mexicanus	149.0	3.50	12.0	—	0.422	—	100.5	30.6	1	n	31.08	83
Quiscalus quiscula	113.5	4.80	13.5	—	0.458	—	60.5	40.9	3	n	19.35	84
Riparia riparia	14.6	4.38	19.4	—	0.377	0.277	14.5	42.7	2	a	—	85
Sayornis nigricans	18.7	4.16	19.5	14.5	0.450	0.416	18.7	36.0	1	a	7.29	86
Sayornis phoebe	19.8	4.58	17.0	12.0	0.425	0.414	17.5	39.0	1	a	15.90	1, 87
Seiurus aurocapillus	19.4	4.20	8.5	—	0.473	0.550	13.5	41.6	2	n	24.50	1, 27, 88
Seiurus motacilla	20.3	5.00	10.0	9.0	0.590	0.575	17.1	42.4	1	n	—	89
Setophaga ruticilla	8.3	3.92	9.0	7.5	0.613	0.575	7.7	43.5	1	n	37.80	1, 90
Sialia currucoides	29.0	5.39	19.5	—	0.369	0.541	25.8	46.3	3	a	10.81	91, 92
Sialia mexicana	28.1	5.00	21.4	—	0.487	0.476	25.1	46.0	1	a	29.59	92
Sialia sialis	31.6	4.40	18.0	—	0.463	0.436	27.2	42.5	2	a	48.60	1, 93
Spizella arborea	20.1	4.96	9.0	—	0.543	0.539	16.7	58.5	1	n	—	94
Spizella breweri	10.4	3.27	8.00	—	0.543	0.631	9.6	42.8	3	n	20.50	1, 23a, 95
Spizella pallida	12.0	4.00	8.00	—	0.532	0.497	10.3	53.5	1	n	54.20	1, 96
Spizella passerina	12.3	3.60	10.5	8.0	0.558	0.539	10.6	43.3	4	n	41.20	1, 97
Spizella pusilla	12.5	3.83	7.5	5.0	0.656	0.677	8.9	41.6	4	n	60.40	1, 98
Stelgidopteryx serripennis	15.9	6.25	19.3	—	0.478	0.449	14.1	42.2	1	a	19.00	2, 99
Sturnella neglecta	97.7	5.10	11.0	8.0	0.469	—	40.0	50.8	1	n	46.90	1, 9
Tachycineta bicolor	20.1	5.45	20.0	17.0	0.511	0.491	20.6	45.1	3	a	29.44	1, 100
Tachycineta thalassina	14.2	4.40	23.5	—	0.357	0.589	16.5	48.8	1	a	5.70	101
Toxostoma curvirostre	79.4	3.12	15.0	—	0.403	—	46.6	30.2	2	n	40.20	1, 102
Toxostoma longirostre	69.9	3.75	13.0	—	0.5456	—	37.3	28.2	1	n	62.00	103
Toxostoma rufum	68.8	3.60	10.8	—	0.471	—	41.5	39.0	1	n	29.00	1, 104
Troglodytes aedon	10.9	6.34	17.0	—	0.515	0.471	10.2	49.5	3	n	28.50	1, 105
Turdus migratorius	77.3	3.30	13.0	—	0.519	0.466	56.9	42.4	2	n	40.20	1, 106
Tyrannus forficatus	43.2	4.58	15.4	—	0.382	0.388	30.1	39.0	1	a	25.95	107
Tyrannus tyrannus	39.5	3.40	16.5	—	0.438	0.457	31.8	40.2	3	a	32.70	1, 87, 108
Tyrannus verticalis	39.6	3.89	16.0	—	0.413	0.459	36.0	39.0	1	a	37.60	1, 108
Vermivora peregrina	10.0	5.50	11.5	—	0.654	0.558	7.3	49.8	1	n	40.00	109
Vireo atricapillus	8.5	4.00	10.5	—	0.412	0.357	8.2	32.0	1	n	39.10	110
Vireo belli	8.5	3.40	11.3	—	0.576	0.737	8.1	32.0	1	n	38.50	1, 110
Vireo griseus	11.4	3.74	10.0	—	0.486	0.526	10.4	36.8	1	n	17.02	111
Vireo olivaceus	16.7	3.20	11.0	—	0.554	0.559	13.8	43.5	1	n	24.90	1, 112
Xanthocephalus xanthocephalus	64.6	3.78	10.5	—	0.492	0.495	45.1	42.9	5	n	34.40	1, 113
Zonotrichia albicollis	25.9	4.15	8.5	—	0.513	0.506	20.3	45.8	1	n	41.30	1, 114
Zonotrichia atricapilla	28.8	4.48	9.8	—	0.636	0.557	23.1	55.2	1	n	37.00	115
Zonotrichia leucophrys	28.1	3.90	9.3	7.8	0.564	0.567	20.2	47.9	6	n	51.10	1, 116, 117
Zonotrichia querula	36.3	3.92	9.1	—	0.541	—	24.5	63.7	1	n	30.00	1, 117

APPENDIX 2

Sources of growth rate (G) and nest predation (P) data in Appendix 1 (for sources of other variables, see Methods).

(1) Martin 1995 (P); (2) Conway and Martin 2000 (P); (3) Starck and Ricklefs 1998b (G); (4) Williams 1940, Holcomb and Twiest 1968, Cronmiller and Thompson 1980 in 3 (G); (5) Webb and Bock 1996, no. 216 in 118 (P); (6) Maurer, B. A., E. A. Webb, and R. K. Bowers. 1989. Nest characteristics and nestling development of Cassin's and Botteri's sparrows in southeastern Arizona. Condor 91:736–738 (G); (7) Lowther et al. 1999, no. 422 in 118 (P); Austin and Ricklefs 1977 in 3 (G); (8) Dunning et al. 1999, no. 471 in 118 (P); (9) Maher, W. J. 1972. Growth of ground-nesting passerine birds at Matador, Saskatchewan, Canada. Pp. 85–102 in S. C. Kendeigh and J. Pinowski, eds. Productivity, population dynamics and systematics of granivorous birds. Polish Scientific Publishers, Warszawa (G); (10) Davis, S. K., and S. G. Sealy. 1998. Nesting biology of the Baird's sparrow in southwestern Manitoba. 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