

2008

# Differential growth of body components among coexisting passerines in response to nest predation risk

Yi-Ru Cheng  
*The University of Montana*

Let us know how access to this document benefits you.

Follow this and additional works at: <https://scholarworks.umt.edu/etd>

---

## Recommended Citation

Cheng, Yi-Ru, "Differential growth of body components among coexisting passerines in response to nest predation risk" (2008).  
*Graduate Student Theses, Dissertations, & Professional Papers*. 320.  
<https://scholarworks.umt.edu/etd/320>

This Thesis is brought to you for free and open access by the Graduate School at ScholarWorks at University of Montana. It has been accepted for inclusion in Graduate Student Theses, Dissertations, & Professional Papers by an authorized administrator of ScholarWorks at University of Montana. For more information, please contact [scholarworks@mso.umt.edu](mailto:scholarworks@mso.umt.edu).

DIFFERENTIAL GROWTH OF BODY COMPONENTS AMONG COEXISTING  
PASSERINE SPECIES IN RESPONSE TO NEST PREDATION RISK

By

Yi-Ru Cheng

Doctor of Medicine, National Taiwan University, Taipei, Taiwan, 2003

Thesis

presented in partial fulfillment of the requirements  
for the degree of

Master of Science  
in Wildlife Biology

The University of Montana  
Missoula, MT

December 2008

Approved by:

Perry Brown, Associate Provost for Graduate Education  
Graduate School

Dr. Thomas E. Martin, Chairperson  
Wildlife Biology Program

Dr. Ken Dial  
Division of Biological Sciences

Dr. Creagh Breuner  
Wildlife Biology Program

Dr. Erick Greene  
Wildlife Biology Program

Dr. John Maron  
Division of Biological Sciences

Differential growth of body components among coexisting passerine species in response to nest predation risk

Chairperson: Dr. Thomas E. Martin

Environmental sources of mortality can exert strong selection pressures on growth strategies across taxa. Studies of growth responses need to consider multiple body components because components can compete for resources during growth in an integrated growth strategy. However, such studies are lacking and little is known about the extent to which body components may differ in their growth responses to environmental selection pressures. Theory predicts that growth of body components with relatively higher advantages for survival should be prioritized. For example, increases in time dependent mortality, like nest predation risk in birds, should favor growth of body features that enhance the ability to leave nests earlier. We studied 12 coexisting species of passerines to specifically test predictions that species with higher nest predation rates would prioritize growth of locomotor components (e.g. tarsi and wings) at the expense of growth of body mass. We also tested the prediction that these altricial birds should develop endothermy earlier to facilitate their ability to leave the warm nest environment. We found species that experience higher nest predation rates exhibited relatively faster growth rates of wing chord, but not tarsus, compared with body mass. Furthermore, species with higher nest predation rates achieved adult-sized tarsi and 60% of adult wing-chord lengths at relatively smaller body mass, further demonstrating the prioritization of wing and tarsus development. Species with higher nest predation risk also developed endothermy earlier at relatively smaller body mass. Thus, our results suggest that growth responses among species to differences in nest predation risk include an integrated strategy across body components to facilitate an ability to escape a risky environment.

## ACKNOWLEDGEMENTS

I could not have completed this project without the assistance of a great number of people. First and foremost, I am very grateful to my advisor, Dr. Tom Martin, for providing me the opportunity to join his lab, as well as for the tremendous effort he has put into my training. As a newcomer to the field of evolutionary biology, I could not possibly have come far as I have without Tom's generous support and confidence. Though it was often a struggle, I gained substantial growth after "wrestling" intellectually with Tom. I know I will always be influenced not only by his methods but also his passionate curiosity and overall philosophy of science.

I am also grateful to the wonderful scientists on my committee — John Maron, Creagh Breuner, Ken Dial, and Erick Greene — whose thoughtful questions and critical thinking set an example I hope to follow in my own career. Special thanks to Creagh for your support and encouragement, and to Ken for opening my eyes in Africa and showing me how to balance my passions for wildlife and science with the demands of ordinary life. I would also like to thank Art Woods for his assistance with physiology and equations, and Doug Emlen for helping with conceptual questions.

As wonderful as Dr. Martin and my committee both were, I also learned a great deal by interacting with my labmates and colleagues. I want to especially thank Dan Barton, the "white board drawer," who was invaluable in editing my thesis, discussing problems and helping me clarify my confusions. Part of my intellectual growth has to be attributed to his generous share of time and knowledge. I would also like to express my gratitude to all the labmates I have been working with: Brian Schwartz, Alina Niklison, Karie Decker, Elena Arriero, Bradley Fedy, Luis Biancucci, Ania Majewska, Amy Stokes, Amy Johnson and Juan Carlos Oteyza. The graduate life would not be so fruitful and joyful without you. Brainstorming sessions with the TEA group were also especially beneficial. Special thanks to Elliot Parsons, Ashley King, Steve Patterson, Rachel Sprague, Julie Beston and Brandon Jackson for providing academic help and being great friends all along.

It has been an honor for me to study in the Wildlife Biology program at University of Montana. I am really amazed how all the people I met collaborated together and tried their best to make our graduate student life easier and more fruitful. I will greatly

miss Vanetta Burton for her constant willingness to help and the way she made me feel at home so far away from my own country. Jeanne Franz has always patiently answered my tedious questions about regulations and made my foreign travel easy even before I was a student here. Lastly, I would like to give my sincere thanks to all the staff in Foreign Student and Scholar Services, especially Effie Koehn and Barb Seekins.

The large amount of data collection in this project would not have been possible without the field crews in Arizona from 2006 through 2008. I would like to give special thanks to Kara Ryf for collecting data on Virginia's Warblers and Brandon Smith for stacking the heavy ladders I used to access Nuthatch nestlings during their monthlong nestling period.

Finally, my dream of being a biologist and studying birds would not have become reality without financial and emotional support from many additional people. Thanks to the Taiwanese government for awarding my scholarship and to the UM Wildlife Biology program for providing me with a teaching assistantship. My friends, T.C. Mou, Ellen Cheng, Adair Kanter and Bruce Barrett generously hosted me as part of their family and absolutely made Missoula a second home for me. Lastly — but perhaps most importantly — I could not possibly have survived living so far away from my beloved home country without the unwavering support of my family in Taiwan. For that, I dedicate this work to my parents, Shin-Tran Cheng and U-Fon Pan and to my beloved sister Chien-Ru Cheng, brother Shi-Fong Cheng and my friend Chun-Yi Lin.

## TABLE OF CONTENTS

Abstract.....	ii
Acknowledgements.....	iii
List of tables.....	vi
List of figures.....	vi
Introduction.....	1
Material and Methods.....	4
Results.....	8
Discussion.....	9
Reference.....	12
Tables.....	16
Figure Legends.....	18
Figures.....	20
Appendices.....	27

## List of tables

Table 1. Phylogeny, scientific name, species code, nest type and daily nest predation rate of study species.....	16
Table 2. Regression analysis of growth variables with nest predation rates and adult body mass using phylogenetically independent contrasts of 12 passerine species.....	17

## List of figures

Figure 1. Diagram of relative growth rate of body components in relation to nest predation rate among species.....	20
Figure 2. Diagram of growth of a locomotor component and body mass in slow (e.g. cavity nesters) and fast growers (e.g. open-cup nesters).....	21
Figure 3A. Growth rate of body mass in relation to nest predation rate.....	22
Figure 3B. Growth rate of wing chord in relation to nest predation rate.....	22
Figure 3C. Growth rate of tarsus in relation to nest predation rate.....	22
Figure 4A. Ratio of growth rates of tarsus to growth rates of body mass in relation to nest predation rates.....	23
Figure 4B. Ratio of growth rates of wing chord to growth rates of body mass in relation to nest predation rates.....	23
Figure 5A. Partial regression of proportion of offspring mass with nest predation rates when species reached 90% of tarsus after controlling for adult body mass.....	24
Figure 5B. Partial regression of proportion of offspring mass with adult body mass when species reached 60% of wing chord after controlling for adult body mass.....	24
Figure 6A. Age of endothermy in relation to nest predation rate.....	25
Figure 6B. Age of endothermy in relation to growth rate of body mass.....	25
Figure 7A. Proportion of offspring mass at age of endothermy in relation of adult body mass.....	26

Figure 7B. Partial correlation of proportion of offspring body mass at age of endothermy with nest predation rates after controlling for adult body mass.....26

**List of appendix**

Appendix 1. Asymptotic mass and growth rates of body mass, tarsus and wing chord estimated from logistic curves.....27

Appendix 2. Age of endothermy and reached mass at age of endothermy for 12 passerine specie.....28



## Introduction

Growth and development are integral components of life history strategies and have critical consequences for survival, reproduction and offspring quality (Roff 1992; Stearns 1992). Change in form and function during postnatal growth results from differential growth of body components and varies extensively among species (Austin and Ricklefs 1977; Ricklefs 1979a; O'Connor 1984; Klingenberg 1998). These body components may compete for resources during growth (Dunn 1976; Ricklefs 1979b; Sacher and Staffeld 1974), and explanations for why species may prioritize different components in their growth strategy remain unclear. The adaptive growth hypothesis predicts allocation of resources to growth of body components should be dictated by environmental selection pressures (O'Connor 1977). Environmental selection pressures, like food limitation and predation, have been found to affect evolution of growth rates of body mass (Arendt 1997; Case 1978). However, mass is only one component of a growth strategy. The ability of environmental selection pressures to explain differential growth of other body components is poorly studied (O'Connor 1977; Irie and Iwasa 2005).

If growth of different body components has differential fitness consequences for species under differing environmental selection pressures, then species should evolve growth strategies that integrate across these body components. Predation, in particular, is thought to exert strong selection on growth rates across taxa (Arendt 1997; Case 1978). This source of selection is thought to be particularly important for birds, where nest predation is a primary source of mortality (Martin 1992) and can strongly influence rate of mass growth (Remeš and Martin 2002). Mass, however, should not be the only body component that is influenced by predation risk. Body components

such as locomotor modules and development of endothermy also may be sensitive to nest predation risk (see next). Yet, no study has examined the differential responses of multiple body components as an integrated response to varying risk of predation.

Increased nest predation risk should favor growth of body components that facilitate an ability to leave the risky nest environment earlier. Past work has focused on growth of mass in response to predation (e.g., Remeš and Martin 2002), but locomotor function and endothermy should be particularly critical for leaving the nest. In particular, locomotor components are important for escaping predators. Hindlimbs (tarsi in birds) are important for running to escape predators at early ages (YC and TEM, pers. obs.) and may be a growth priority in species with higher predation risk. Partially developed wings can assist running, even up vertical surfaces, to aid escape from predators (Dial 2003a, b; Dial et al. 2006) and thereby also be a priority in growth strategies relative to predation risk. Finally, these altricial young need to be able to thermoregulate on their own once they leave the nest environment in which parents provide warmth. Thus, species with higher nest predation risk should be under selection to prioritize growth of locomotor components (e.g. tarsi and wings) and endothermy. Different body components can compete for resources and influence the growth of each other (Ricklefs 1968, 1973, 1979a; Dunn 1975a; Nijhout and Emlen 1998). Prioritization of locomotor and endothermy components may come at the expense of body mass in such cases, whereas if resource competition is not an issue then they may not be related (fig. 1). Whether species relatively prioritize growth of such components even at the expense of growth of body mass (fig. 1), to facilitate their ability to leave the risky nest environment is untested, and that is our goal here.

Endothermy represents a particularly interesting character with respect to such prioritization issues. Larger body mass can enhance endothermy because of the

thermal inertia provided by larger mass. Indeed, rate of development of endothermy is often highly correlated with the rate of mass growth across species of altricial birds (Dunn 1975b; Olson 1992). Yet, development of endothermy entails a maintenance cost that could reduce resources allocated to growth and constrain overall growth rates (Ricklefs 1973). Consequently, if endothermy is achieved at relatively smaller sizes in species with higher predation risk, such results would provide strong evidence of growth prioritization of competing body components relative to predation risk.

Anecdotal evidence provides some hints that differential growth of body components among species may be related to predation risk. For example, Redfern (1994) found that open-cup-nesting birds started growing wings at relatively smaller body mass than cavity-nesting birds. Open-cup nesting birds experience higher nest predation than cavity-nesting birds (Lack 1968; Martin 1995), so these differential growth strategies may reflect responses to predation risk. Yet, these differences could also simply reflect different strategies between nest types. The importance of nest predation can be tested more explicitly by examining variation in growth strategies among species relative to direct measures of nest predation risk. Here we test these ideas.

We investigate the relationship between nest predation risk and differential growth of body components in 12 coexisting passerine species. Nest predation rates of these species vary significantly and were robustly estimated from long term studies (Martin et al. 2007; Martin and Li 1992). This variation in nest predation among species provides a strong basis to test its potential role in growth strategies. Thus, we examined whether growth of locomotor modules (i.e., tarsi and wings) and development of endothermy were increasingly prioritized relative to body mass with increasing nest predation risk.

## Material and Method

### *Study Area and Species*

We studied 12 coexisting species of passerines that breed in a high elevation (~2400m) ecosystem in north-central Arizona (~34°N) (table 1). These 12 bird species represented eight families and 12 genera in Passeriformes and used ground, shrub, niche and cavity nest sites with substantial variation in nest predation risk (Fontaine et al. 2007; Martin and Li 1992). Our study plots were located in snowmelt drainages where the dominant canopies were white fir (*Abies concolor*), Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*) and quaking aspen (*Populus tremuloides*). The understory species included canyon maple (*Acer grandidentatum*), Gambel's oak (*Quercus gambellii*), and New Mexican locust (*Robinia neomexicana*) (Martin 2007).

### *Nest Work*

We searched for and monitored fate of nests from early May to late July from 1988-2005 to obtain robust estimates of nest predation rates (Martin et al. 2007). Nests were monitored every other day to determine fate and hatch dates (Martin and Geupel 1993). Growth rates and development of endothermy were measured from nests studied from 2006-2008.

### *Growth Measurement*

We measured body mass, tarsus length, and wing chord length of nestlings in the afternoon at approximately the same time every other day after hatching. We measured mass using an Acculab PP2060D scale ( $\pm 0.001$ g) and lengths using Mitotoyu Corp. calipers ( $\pm 0.01$ mm). Tarsus was measured as the length of

tarsometatarsal bone and wing chord was measured as distance from the carpal joint to the tip of the longest primary feather (or feather sheath).

### *Age of Endothermy*

We estimated the age of endothermy using the homeothermic index (H). The homeothermic index (H) was measured in a cold stress experiment every other day after hatching immediately following growth measurements (Ricklefs 1968; Dunn 1975b). Nestlings were put in a 10°C cooler for 10 minutes. Initial (Ti) and final (Tf) body temperatures during the cold stress were taken by inserting a thermal probe (Omega Cu-Ni, T type, 36 gauge) into the cloaca, and temperatures were read with a thermometer (Omega HH506A, resolution:0.1°C). The temperature (Ta) of the cooler was the average of temperatures measured in the cooler every 10 seconds during the 10 minute test. The homeothermic index was calculated as  $(Tf-Ta)/(Ti-Ta)$  (Ricklefs 1987), which ranges from 0 to 1. We then estimated the age of endothermy by fitting the H data as a logistic curve as in growth data (see next). The age of endothermy was calculated as the age in days when H achieved 0.9.

### *Data Analysis*

*Growth Estimates.* We estimated growth curves of body mass, tarsus and wing chord for each species using the logistic growth curve  $Y(t) = A / \{ 1 + e^{-K(t-t_i)} \}$ , where Y(t) is the body mass, tarsus length or wing chord length of a nestling at time t, A is the asymptotic value that nestlings approach, K is growth rates, and  $t_i$  is the inflection point of the logistic curve (Ricklefs 1968). This method is commonly used for growth analysis in birds and provides standardized estimates for comparative studies (Remeš and Martin 2002). We estimated the growth rates of body mass with data truncated at

70% of body mass to account for the problem of overestimation from mass recession and different relative fledging masses among species (Remeš and Martin 2002).

*Predation and Morphological Growth.* Daily nest predation rates during the nestling period were estimated using the Mayfield method (Mayfield 1961) based on data for the same populations from 1988-2005 (Martin et al. 2007). Linear regression analysis was executed to test relationships between nest predation rate and developmental variables of interest. We first examined the relationships between nest predation rates and growth rates (K) of body mass, tarsus and wing chord respectively. Adult body mass was also included in the regression analysis as an explanatory variable to control for scaling effect on growth rates (Remeš and Martin 2002). Adult body mass was  $\log_{10}$  transformed to achieve a normal distribution. We further investigated if species with higher nest predation rates prioritized growth of locomotor components by increasing growth rates of tarsus or wing chord relatively more than body mass (fig. 1). Yet, growth rate did not necessarily reflect the relatively completed proportion of body components. Thus, we further examined the relative prioritization of growth of morphological components by estimating the proportion of adult body mass when species achieved 90% of adult tarsus length and 60% of adult wing chord length (fig. 2). We chose 90% for tarsus and 60% for wing chord because all species reached these minimum proportions before fledging. Adult body mass, tarsus length and wing chord length were averages for species based on long-term banding data collected at the field site since 1993 (Martin, unpublished data). The potential role of nest predation risk on relative sizes of body mass at 90% of tarsus and 60% of wing chord were explored by regressing these characters against nest predation rates.

*Predation and Development of Endothermy.* The potential effect of predation risk

on age of endothermy was examined using linear regression analysis. To investigate if species prioritize development of endothermy over growth of body mass, we tested for a relationship between nest predation rates and the proportion of adult body mass of offspring when the species achieved endothermy (i.e.,  $H = 0.9$ ). We included adult body mass as an explanatory variable in the regression analysis because larger species generally achieve endothermy at a relatively smaller body mass (Dunn 1975b).

*Phylogenetic Analysis.* We also analyzed the data using independent contrasts to control for potential phylogenetic influences using the software package Phylip 3.68 (Felsenstein 1985). We first constructed a working phylogeny based on a published supertree of passerine birds (Jønsson and Fjeldså 2006). We assumed equal branch lengths in the phylogeny and analyzed independent contrasts in linear regression where regressions were forced through the origin (Garland et al. 1992).

## Results

### *Predation and Growth Rates*

Growth rates of offspring body mass, tarsus length and wing chord length were not related to adult body mass among our study species (offspring mass:  $r = 0.125$ ,  $P = 0.699$ ; tarsus:  $r = 0.369$ ,  $P = 0.237$ ; wing chord:  $r = 0.116$ ,  $P = 0.719$ ). Growth rates of body mass and wing chord length increased with nest predation rates among species (figs. 3A, 3B). Growth rates of tarsus were not significantly related to nest predation rates (fig.3C), although a relationship existed when the aerial insectivore (Cordilleran Flycatcher) was excluded ( $r = 0.672$ ,  $P = 0.023$ ). Analyses of phylogenetically independent contrasts showed the same patterns, but the relationship between growth rates of tarsus and nest predation rates disappeared even when the aerial insectivore was excluded (table 2).

### *Relative Growth among Morphological Traits*

Species with higher nest predation rates did not have faster growth rates of tarsus relative to body mass (fig. 4A). In contrast, species with higher nest predation rates showed higher relative growth rates of wing chord to mass (fig. 4B). Independent contrasts showed the same correlations (table 2).

The proportion of adult body mass that species achieved when they reached 90% of adult tarsus and 60% of wing chord lengths demonstrated an allometric effect. Offspring of larger species reached these standardized locomotor appendage dimensions at relatively smaller body mass (tarsus:  $r = -0.789$ ,  $P = 0.002$ ; wing chord:  $r = -0.668$ ,  $P = 0.017$ ). However, the allometric effect disappeared in wing chord when we excluded American Robin, which was the largest species in our study ( $r = -0.435$ ,  $P = 0.181$ ). Nonetheless, we included body mass as a covariate to examine



partial correlations with nest predation rates. Offspring of species with higher nest predation rates reached 90% of adult tarsus length at relatively smaller body mass when controlling for adult body mass (fig.5A). Offspring of species with higher nest predation rates also reached 60% of wing chord at relatively smaller body mass, even when controlling for adult mass (fig.5B). Analyses of independent contrasts showed the same patterns but relationships became marginally significant (table 2).

### *Age of Endothermy*

Endothermy was achieved earlier in species with faster growth rates of body mass (fig. 6A) and higher nest predation rates (fig. 6B). Larger species achieved endothermy at relatively smaller body mass (fig. 7A). Nonetheless, even after controlling for adult body mass, species with higher nest predation rates achieved endothermy at relatively smaller body mass (fig. 7B). These relationships were the same when controlling for possible phylogenetic effects using independent contrasts (table 2).

## **Discussion**

An association between growth rates of body mass and nest predation risk has been described previously among passerine species (Bosque and Bosque 1995; Remeš and Martin 2002). However, growth includes developing body components that potentially compete for resources (Ricklefs 1968, 1973, 1979a; Sacher and Staffeld 1974; McClure and Randolph 1980), and the role of offspring predation risk in influencing the relative growth and development of body components has not been explored. We found that species with higher nest predation risk not only have faster growth of body mass, but also faster growth of wings. Moreover, we found that faster

growth of wings was achieved at smaller relative body mass, suggesting that wing growth was prioritized over mass when predation risk was greater. Locomotor performance is critical for escaping predators and developing wings may be particularly important in birds; partially developed wings can have strong functional significance for escaping predators (Bundle and Dial 2003; Dial 2003a, 2003b). Thus, our results support the hypothesis that body components compete for resources and species with higher nest predation risk prioritize growth of locomotor components that will allow earlier escape from risky nests over growth of mass.

Thermoregulatory independence also is critical for altricial young to survive after leaving their nests without parental brooding. Thermoregulation is energetically costly and can constrain overall growth rates (McClure and Randolph 1980; Olson 1992; Starck and Ricklefs 1998). Yet, we found species with higher nest predation risk developed endothermy earlier and grew their body mass faster. Previous studies also found a positive relationship between growth rates of body mass and development of endothermy, but failed to test ecological selection pressures (Dawson and Evans 1960; Dunn 1975b). Larger body mass can decrease surface-to-volume ratio and help maintain body temperature (Pereyra and Morton 2001). Indeed, larger species achieved endothermy at relatively smaller body mass (also see Dunn 1975). However, we still found species with higher nest predation risk achieved endothermy at relatively smaller body mass even after controlling for adult body mass (fig. 7B). Development of endothermy at relatively smaller body mass might be achieved by earlier maturation of muscular, neural and hormone systems (Starck and Ricklefs 1998; Olson et al. 1999; Marjoniemi 2001). Nonetheless, these results suggest that greater nest predation risk favors prioritization of resources to earlier development of endothermy over body mass.

Nest predation apparently was not a critical factor influencing growth rate of tarsi. Fast growth of tarsi might be important for reasons independent of nest predation. For example, altricial young compete for food from parents by begging before leaving nests (O'Connor 1984) and taller young often obtain more food (Kilner 1995). Consequently, tarsus growth rate may be related to parental feeding strategies and sibling competition. Foraging guild (e.g. ground, arboreal or aerial foraging) might also affect growth of tarsus (Kirkwood et al. 1989), which might explain the relatively slower growth rate of tarsi in the one aerial forager (Cordilleran flycatcher) in our study (fig. 3C). However, a limited sampling of alternative foraging guilds in our study did not allow us to effectively test the possible role of foraging mode.

Food limitation could also influence prioritization of growth of body components at a proximate level (Ashton and Armstrong 2002; Benowitz-Fredericks et al. 2006; Kunz and Ekman 2000). Species with higher nest predation risk have decreased parental feeding (Martin et al. 2000), which may indirectly cause greater food limitation. Therefore, the observed prioritization strategy might be driven by food limitation indirectly resulting from nest predation. Yet, if food limitation is the driver, we should see slower growth rates in species with higher nest predation. On the contrary, we observed faster growth rates in species with higher nest predation risk.

Our study demonstrates that nest predation risk can affect not only overall growth rates but also relative growth of body components. Understanding variation of differential growth trajectories of body components among species can help advance our knowledge of the evolution of growth strategies. Future studies of locomotor performance associated with ontogenetic change can provide new insights into differential growth strategies.

## Reference

- Arendt, J. D. 1997. Adaptive intrinsic growth rates: an integration across taxa. *Quarterly Review of Biology* 72:149-177.
- Ashton, J. C., and D. P. Armstrong. 2002. Facultative prioritization of wing growth in the Welcome Swallow (*Hirundo neoxena*). *Ibis* 144:470-477.
- Austin, G. T., and R. E. Ricklefs. 1977. Growth and development of the Rufous-winged Sparrow (*Aimophila carpalis*). *Condor* 79:37-50.
- Benowitz-Fredericks, Z. M., A. S. Kitaysky, and C. W. Thompson. 2006. Growth and allocation in captive Common Murre (*Uria aalge*) chicks. *Auk* 123:722-734.
- Bosque, C., and M. T. Bosque. 1995. Nest predation as a selective factor in the evolution of developmental rates in altricial birds. *American Naturalist* 145:234-260.
- Bundle, M. W., and K. P. Dial. 2003. Mechanics of wing-assisted incline running (WAIR). *Journal of Experimental Biology* 206:4553-4564.
- Case, T. J. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *The Quarterly Review of Biology* 53:243-282.
- Dawson, W. R., and F. C. Evans. 1960. Relation of growth and development to temperature regulation in nestling Vesper Sparrows. *Condor* 62:329-340.
- Dial, K. P. 2003a. Evolution of avian locomotion: correlates of flight style, locomotor modules, nesting biology, body size, development, and the origin of flapping flight. *Auk* 120:941-952.
- . 2003b. Wing-assisted incline running and the evolution of flight. *Science* 299:402-404.
- Dial, K. P., R. J. Randall, and T. R. Dial. 2006. What use is half a wing in the ecology and evolution of birds? *Bioscience* 56:437-445.
- Dunn, E. H. 1975a. Growth, body components and energy content of nestling Double-crested Cormorants. *Condor* 77:431-438.
- . 1975b. The timing of endothermy in the development of altricial birds. *Condor* 77:288-293.
- . 1976. Development of endothermy and existence energy expenditure of nestling Double-crested Cormorants. *Condor* 78:350-356.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist*

125:1-15.

- Fontaine, J. J., M. Martel, H. A. Markland, A. A. Niklison, K. L. Decker, and T. E. Martin. 2007. Testing ecological and behavioral correlates of nest predation. *Oikos* 116:1887-1894.
- Garland, J. T., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* 41:18-32.
- Irie, T., and Y. Iwasa. 2005. Optimal growth pattern of defensive organs: The diversity of shell growth among mollusks. *American Naturalist* 165:238-249.
- Jønsson, K. A., and J. Fjeldså. 2006. A phylogenetic supertree of oscine passerine birds (Aves: Passeri). *Zoologica Scripta* 35:149-186.
- Kilner, R. 1995. When do canary parents respond to nestling signals of need? *Proceedings of the Royal Society of London Series B-Biological Sciences* 260:343-348.
- Kirkwood, J. K., P. J. Duignan, N. F. Kember, P. M. Bennett, and D. J. Price. 1989. The growth rate of the tarsometatarsus bone in birds. *Journal of Zoology* 217:403-416.
- Klingenberg, C. P. 1998. Heterochrony and allometry: the analysis of evolutionary change in ontogeny. *Biological Reviews* 73:79-123.
- Kunz, C., and J. Ekman. 2000. Genetic and environmental components of growth in nestling blue tits (*Parus caeruleus*). *Journal of Evolutionary Biology* 13:199-212.
- Lack, D. 1968, *Ecological adaptations for breeding in birds*. London, England, Methuen.
- Marjoniemi, K. 2001. Thermogenic mechanisms during the development of endothermy in juvenile birds, University of Oulu, Oulu.
- Martin, T. E. 1992. Interaction of nest predation and food limitation in reproductive strategies. *Current Ornithology* 9:163-197.
- . 1995. Avian life history evolution in relation to nest sites, nest predation and food. *Ecological Monographs* 65:101-127.
- . 2007. Climate correlates of 20 years of trophic changes in a high-elevation riparian system. *Ecology* 88:367-380.
- Martin, T. E., S. K. Auer, R. D. Bassar, A. M. N. Niklison, and P. Lloyd. 2007.

- Geographic variation in avian incubation periods and parental influences on embryonic temperature. *Evolution* 61:2558-2569.
- Martin, T. E., and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* 64:507-519.
- Martin, T. E., and P. Li. 1992. Life history traits of open- vs. cavity-nesting birds. *Ecology* 73:579-592.
- Martin, T. E., P. R. Martin, C. R. Olson, B. J. Heidinger, and J. J. Fontaine. 2000. Parental care and clutch sizes in North and South American birds. *Science* 287:1482-1485.
- Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255-261.
- McClure, P. A., and J. C. Randolph. 1980. Relative allocation of energy to growth and development of homeothermy in the Eastern Wood Rat (*Neotoma floridana*) and Hispid Cotton Rat (*Sigmodon hispidus*). *Ecological Monographs*:199-219.
- Nijhout, H. F., and D. J. Emlen. 1998. Competition among body parts in the development and evolution of insect morphology. *Proceedings of the National Academy of Sciences* 95:3685-3689.
- O'Connor, R. J. 1977. Differential growth and body-composition in altricial passerines. *Ibis* 119:147-166.
- O'Connor, R. J. 1984, *The growth and development of birds*. Chichester & London, John Wiley & Sons.
- Olson, J. M. 1992. Growth the development of endothermy and the allocation of energy in Red-Winged Blackbirds (*Agelaius phoeniceus*) during the nestling period. *Physiological Zoology* 65:124-152.
- Olson, J. M., F. M. A. McNabb, M. S. Jablonski, and D. V. Ferris. 1999. Thyroid development in relation to the development of endothermy in the red-winged blackbird (*Agelaius phoeniceus*). *General and Comparative Endocrinology* 116:204-212.
- Pereyra, M. E., and M. L. Morton. 2001. Nestling growth and thermoregulatory development in subalpine Dusky Flycatchers. *Auk* 118:116-136.
- Redfern, C. P. F. 1994 Variation in the developmental timing of flight-feather growth in nestling birds. *Ibis* 136:72-78.
- Remeš, V., and T. E. Martin. 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.
- . 1973. Patterns of growth in birds. II. Growth rate and mode of development. *Ibis* 115:117-201.
- . 1979a. Patterns of growth in birds. 5. Comparative-study of development in the Starling, Common Tern, and Japanese Quail. *Auk* 96:10-30.
- . 1979b. Adaptation, constraint, and compromise in avian postnatal-development. *Biological Reviews of the Cambridge Philosophical Society* 54:269-290.
- . 1987. Characterizing the development of homeothermy by rate of body cooling. *Functional Ecology* 1:151-157.
- Roff, D. A. 1992, *The evolution of life histories*. New York, London, Chapman & Hall.
- Sacher, G. A., and E. F. Staffeld. 1974. Relation of gestation time to brain weight for placental mammals - implications for theory of vertebrate growth. *American Naturalist* 108:593-615.
- Starck, J. M., and R. E. Ricklefs. 1998, *Avian growth and development*. New York, Oxford University Press.
- Stearns, S. C. 1992, *The evolution of life histories*. New York, Oxford University Press.

**Table 1.** Phylogeny, scientific name, species code, nest type and daily nest predation rate for study species.

Family	Scientific Name	Common Name	Species code	Nest type	Daily nest predation rate (Mean±S.E.)
Tyrannidae	<i>Empidonax occidentalis</i>	Cordilleran flycatcher	COFL	niche	0.0306±0.0029
Vireonidae	<i>Vireo gilvus</i>	Warbling vireo	WAVI	open cup	0.0236±0.0032
Paridae	<i>Parus gambeli</i>	Mountain chickadee	MOCH	cavity	0.0082±0.0008
Emberizidae	<i>Pipilo chlorurus</i>	Green-tailed towhee	GTTO	open cup	0.0399±0.0063
	<i>Junco hyemalis</i>	Grey-headed junco	GHJU	open cup	0.0382±0.0024
Parulidae	<i>Cardellina rubrifrons</i>	Red-faced warbler	RFWA	open cup	0.0388±0.0037
	<i>Vermivora virginiae</i>	Virginia's warbler	VIWA	open cup	0.0414±0.0035
Turdidae	<i>Sialia mexicana</i>	Western bluebird	WEBL	cavity	0.0065±0.0021
	<i>Turdus migratorius</i>	American robin	AMRO	open cup	0.0331±0.0029
	<i>Cartharus guttatus</i>	Hermit thrush	HETH	open cup	0.0483±0.0051
Sittidae	<i>Sitta carolinensis</i>	White-breasted nuthatch	WBNU	cavity	0.0056±0.0013
Troglodytidae	<i>Troglodytes aedon</i>	House wren	HOWR	cavity	0.0044±0.0006



**Table 2.** Regression analysis of growth variables in relation to nest predation rates and adult body mass when controlled for phylogenetic effects using independent contrasts and forcing the regression through the origin. Simple regression reflects independent tests of nest predation and body mass, while partial regression reflected simultaneous testing of nest predation and body mass ( $r$ : Pearson correlation coefficients;  $P$ : P value).

		Nest predation		Adult body mass	
		$r$	$P$	$r$	$P$
Simple regression	Growth rate of body mass	0.797	0.002**	0.076	0.813
	Growth rate of tarsus	0.218	0.496	0.316	0.317
	Growth rate of tarsus (w/o cordilleran flycatcher)	0.403	0.220	-	-
	Growth rate of wing chord	0.881	<0.001**	0.194	0.850
	Ratio of growth rate of tarsus to mass	-0.659	0.020**	-	-
	Ratio of growth rate of wing chord to mass	0.707	0.010**	-	-
	Age of endothermy	-0.692	0.013**	-0.187	0.560
Partial regression	Proportion of body mass at 90% of tarsus length relative to adult size	-0.537	0.088*	-0.875	<0.001**
	Proportion of body mass at 60% of wing chord length relative to adult size	-0.566	0.070*	-0.563	0.071*
	Proportion of body mass at age of endothermy relative to adult size	-0.640	0.034**	-0.688	0.019**

\*  $P < 0.1$ , \*\*  $P < 0.05$

Figure 1. Diagram of relative growth rate of body components in relation to nest predation rate among species. Relative growth rate is measured as the ratio of growth rate of locomotor component (e.g. tarsus or wing chord) to body mass for species. Three possible relationships might be generated: a) higher nest predation rates are related to relatively faster growth rates of locomotor components than body mass, b) relative growth rates of locomotor components versus body mass are not related to nest predation rates, or c) higher nest predation rates are related to relatively faster growth rates of body mass than locomotor components.

Figure 2. Diagram of growth of a locomotor component (demonstrated as wing chord here) and body mass in slow (e.g. cavity nesters) and fast growers (e.g. open-cup nesters). A constant proportional size of the locomotor component (i.e., wing chord) allows comparison of proportional mass achieved among species with different rates of growth. In this example, a fast grower has relatively faster growth of wing chord and body mass and reached the constant wing chord at relatively smaller proportion of body mass than the slower grower. **A** represents the proportion of body mass achieved by the fast grower at 60% of adult wing chord and **B** is the proportion of body mass achieved by the slow grower at the same relative size of the wing chord (i.e., 60% of adult size).

Figure 3. Growth rates of A) body mass, B) wing chord, and C) tarsus in relation to daily nest predation rates for 12 altricial species (species codes are from Table 1). Growth rates are estimated from logistic curves following Ricklefs (1968). Growth rates of body mass are estimated from data truncated at 70% of body mass.

Figure 4. Relative growth rates of locomotor components to body mass in relation to daily nest predation rates for 12 altricial species (species codes are from Table 1). Relative growth rate is measured as ratio of growth rate of A) tarsus and B) wing chord to growth rate of body mass.

Figure 5. Standardized residuals from partial regression for proportion of offspring mass when 12 altricial species (species codes are from Table 1) reached A) 90% of tarsus and B) 60% of wing chord in relation to daily nest predation rates after controlling for adult body mass.

Figure 6. Age of endothermy in relation to A) daily nest predation rates and B) growth rates of body mass for 12 altricial species (species codes are from Table 1).

Figure 7. Proportion of offspring mass reached at age of endothermy in relation to A) adult body mass and B) daily nest predation rates when controlling for adult body mass for 12 altricial species (species codes are from Table 1).

Figure 1.

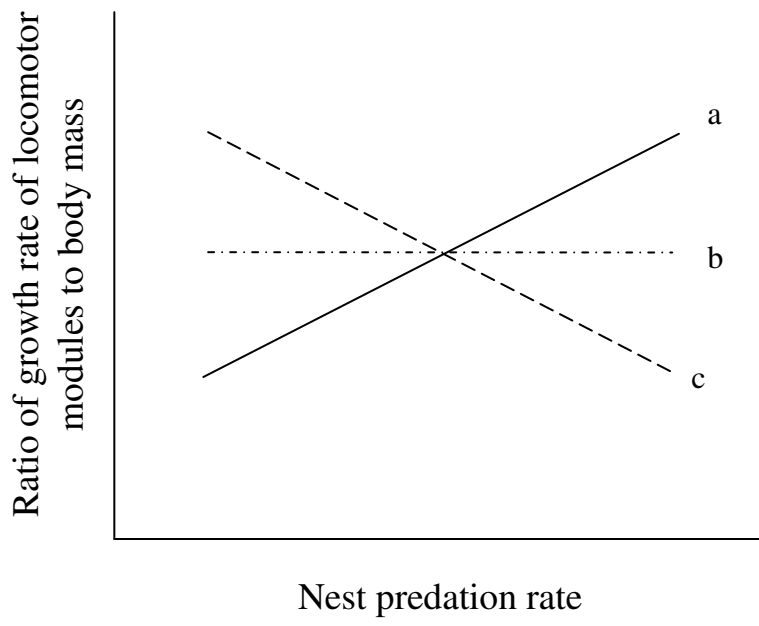


Figure 2.

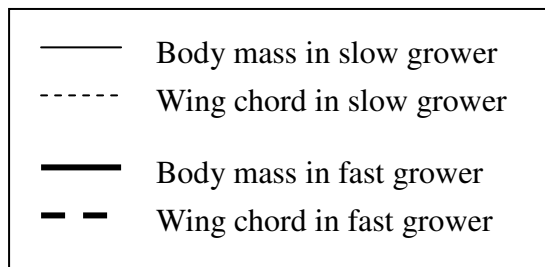
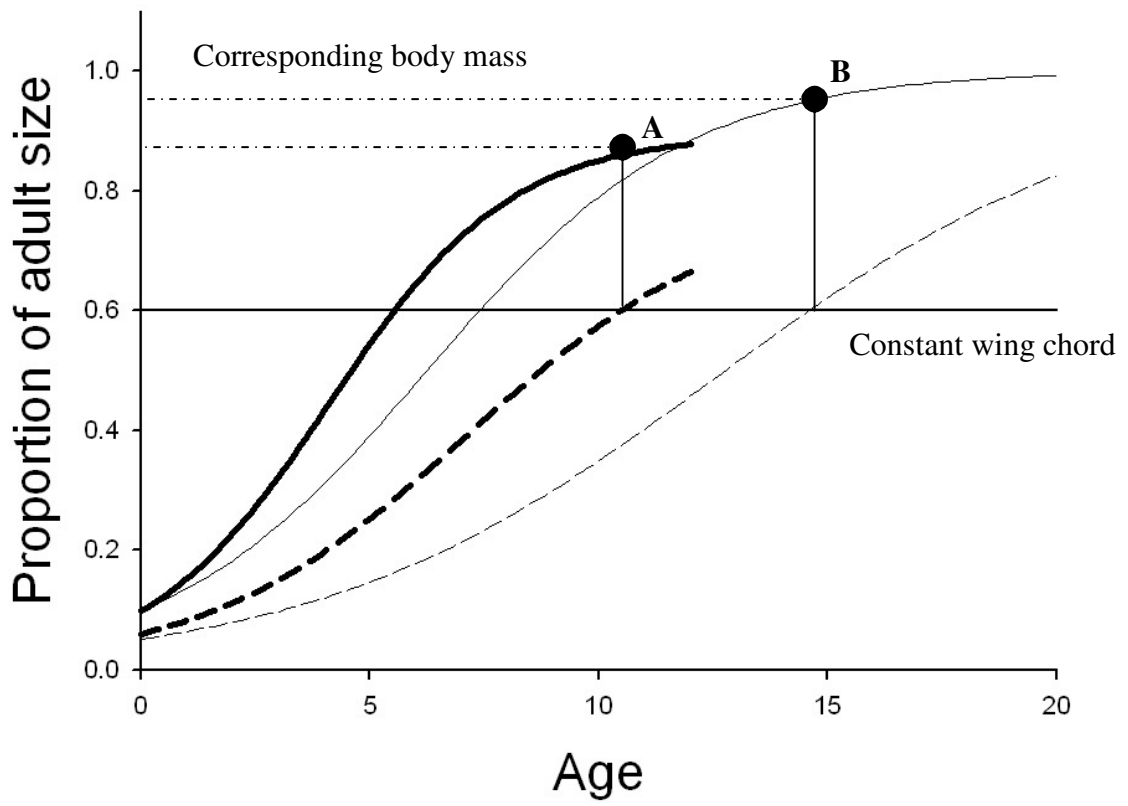


Figure 3.

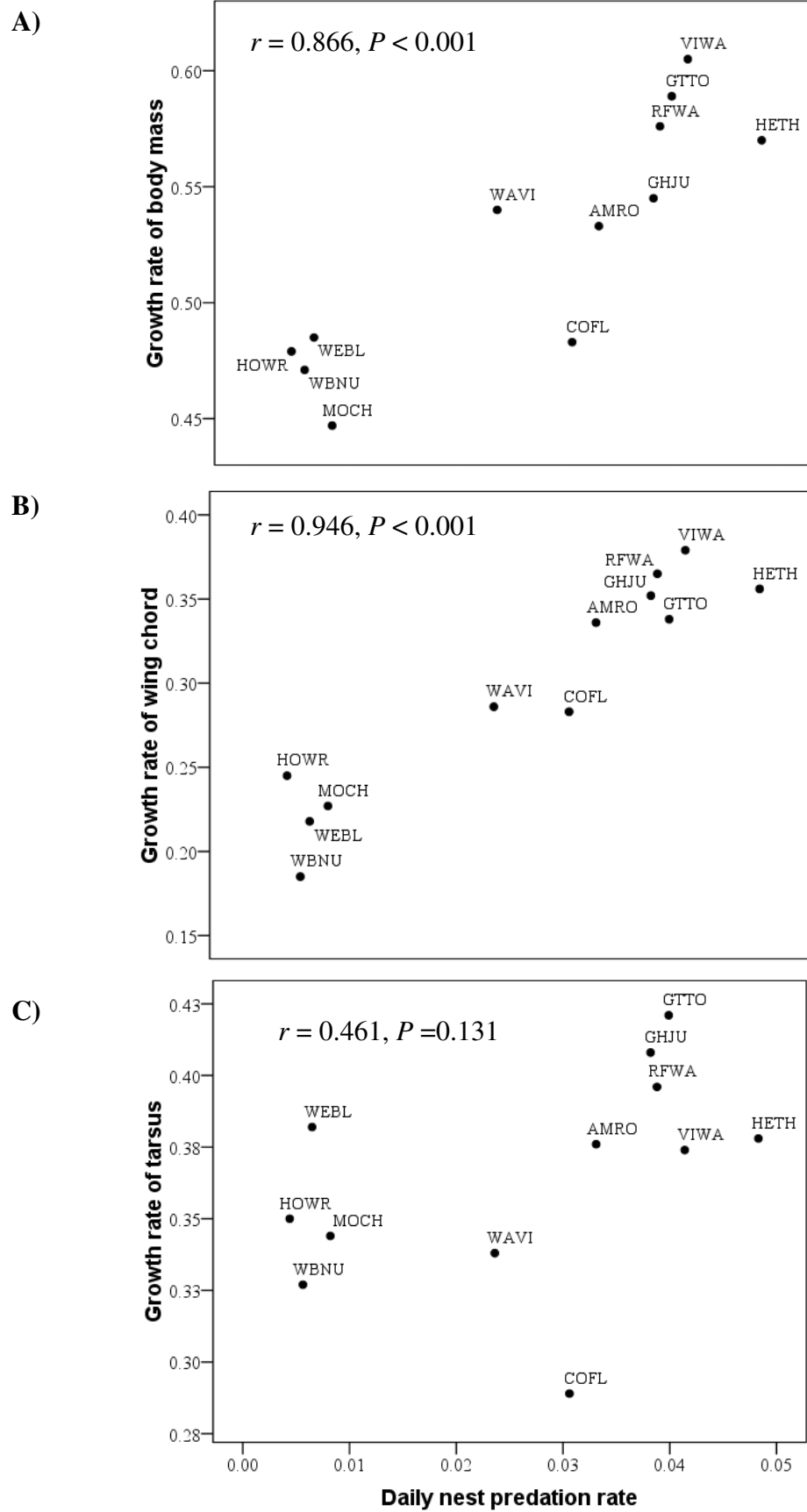


Figure 4.

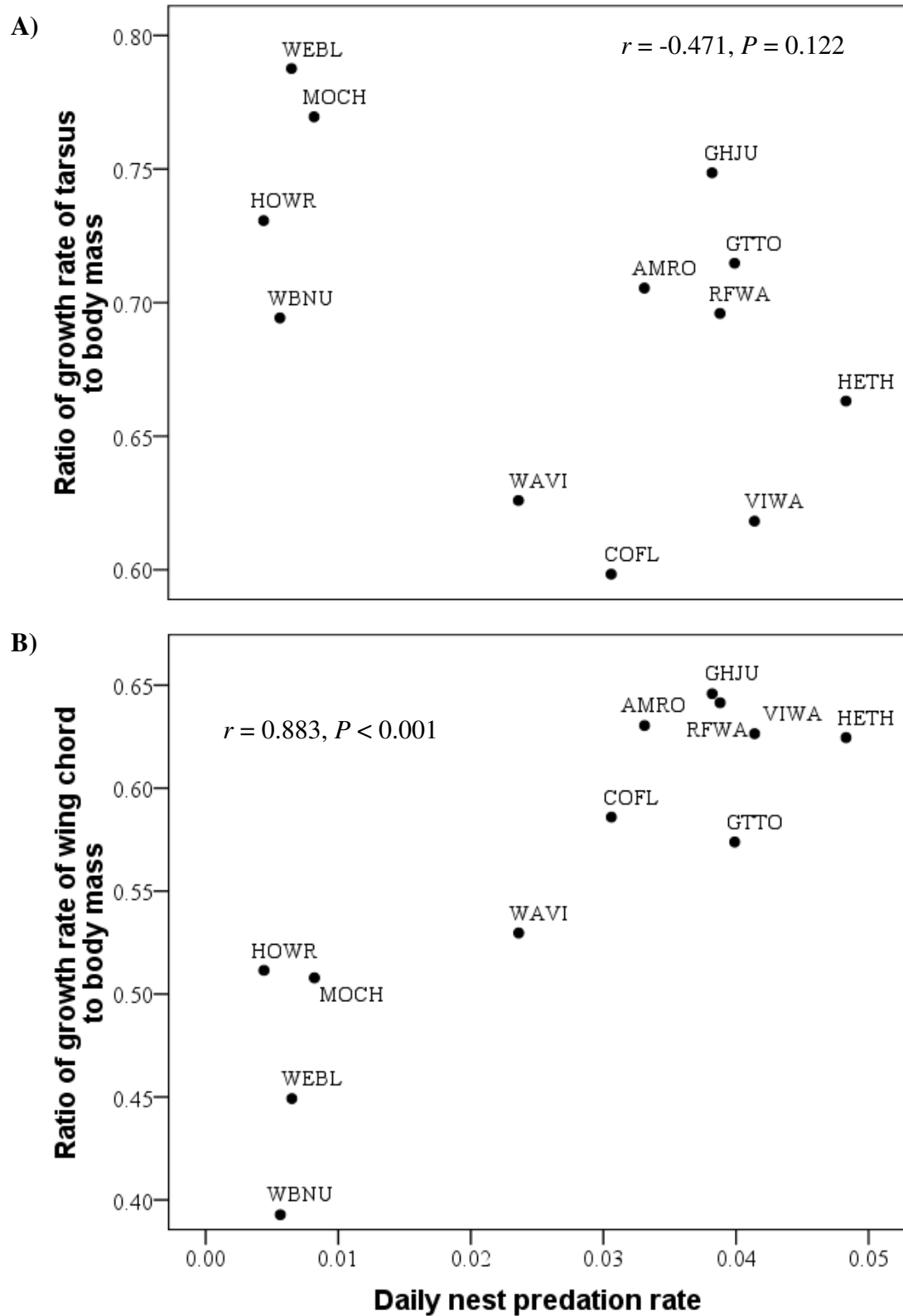


Figure 5.

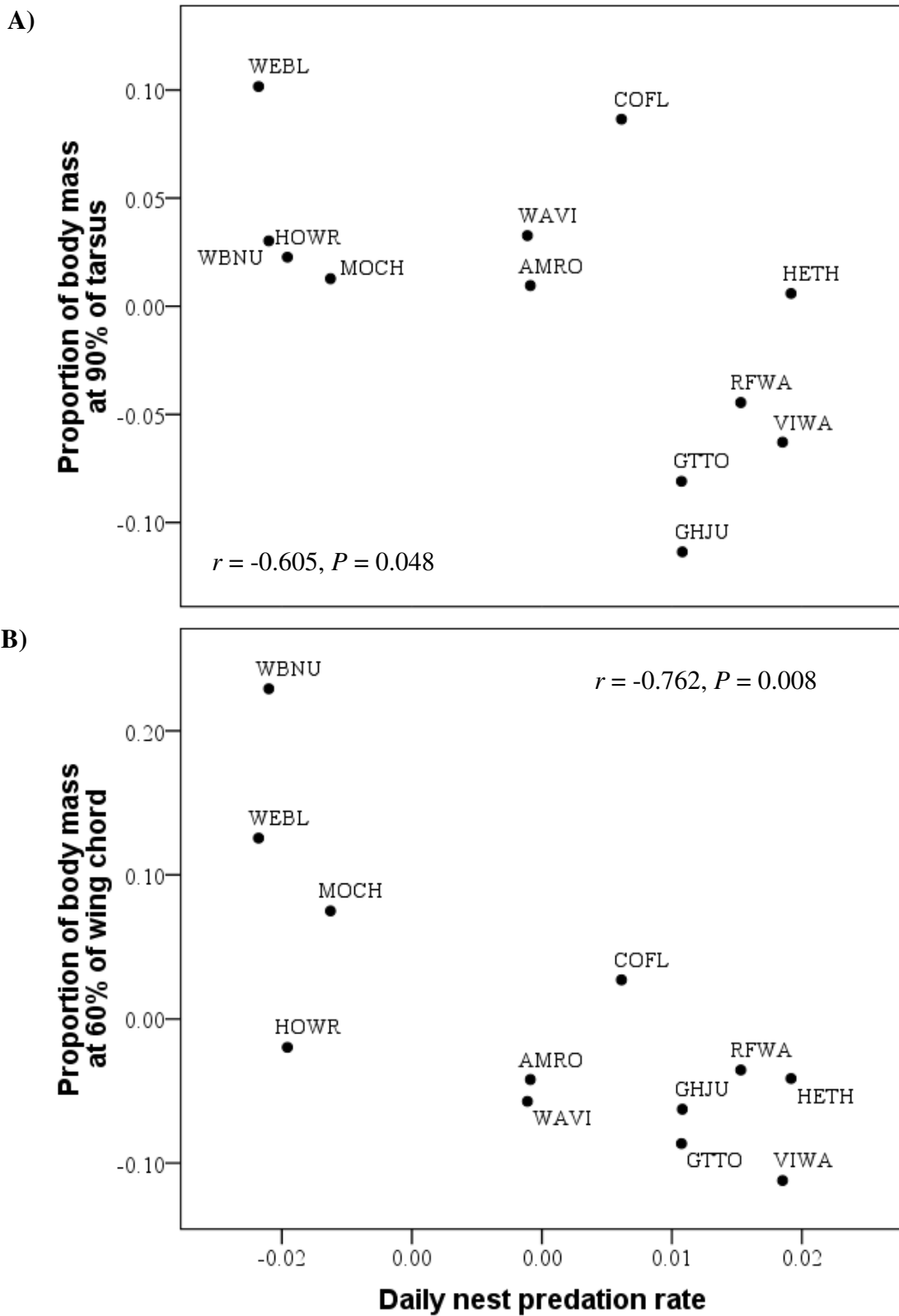
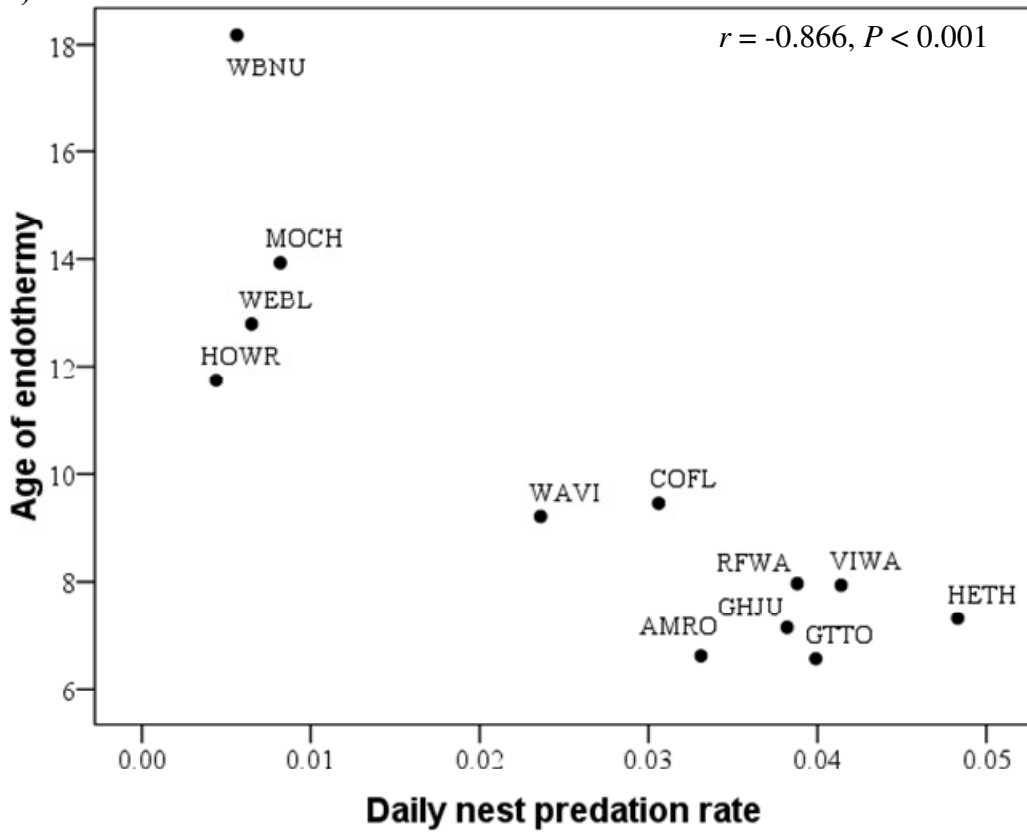




Figure 6.

A)



B)

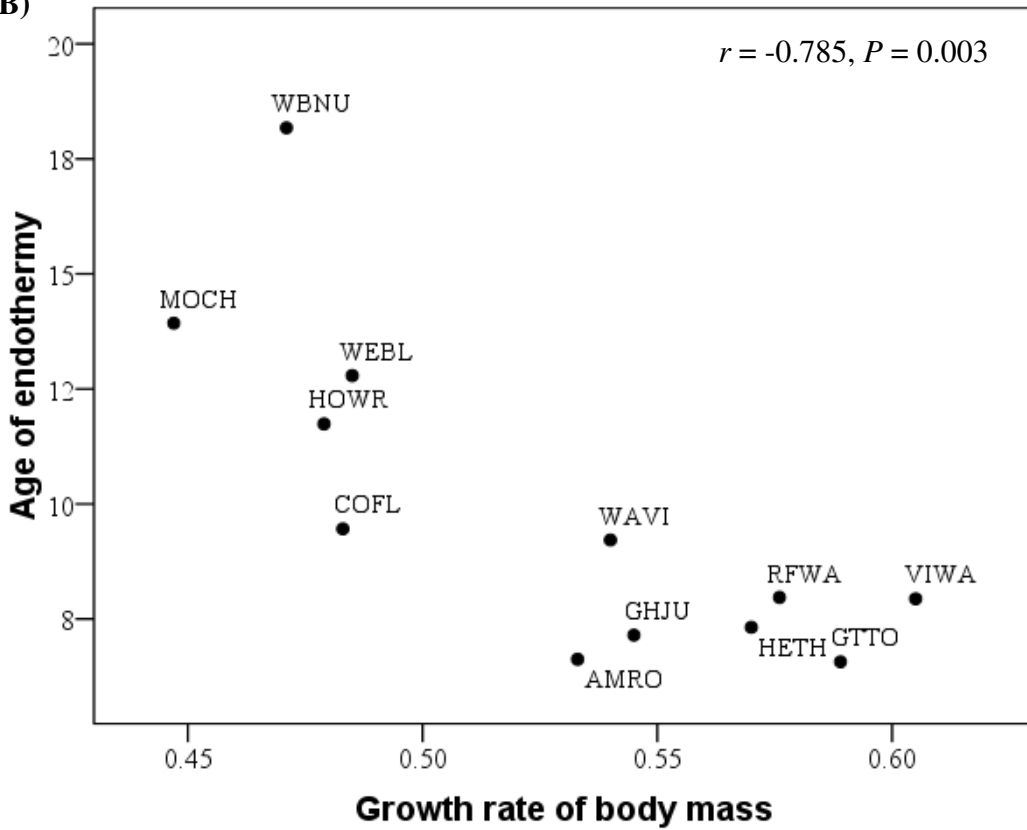
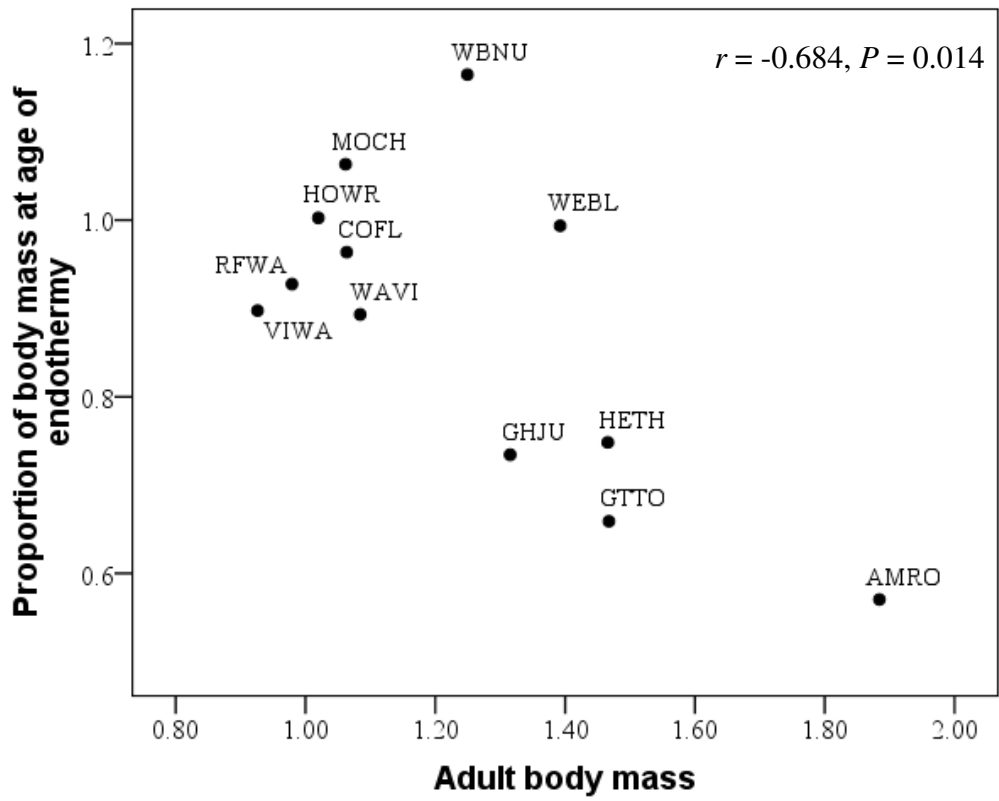
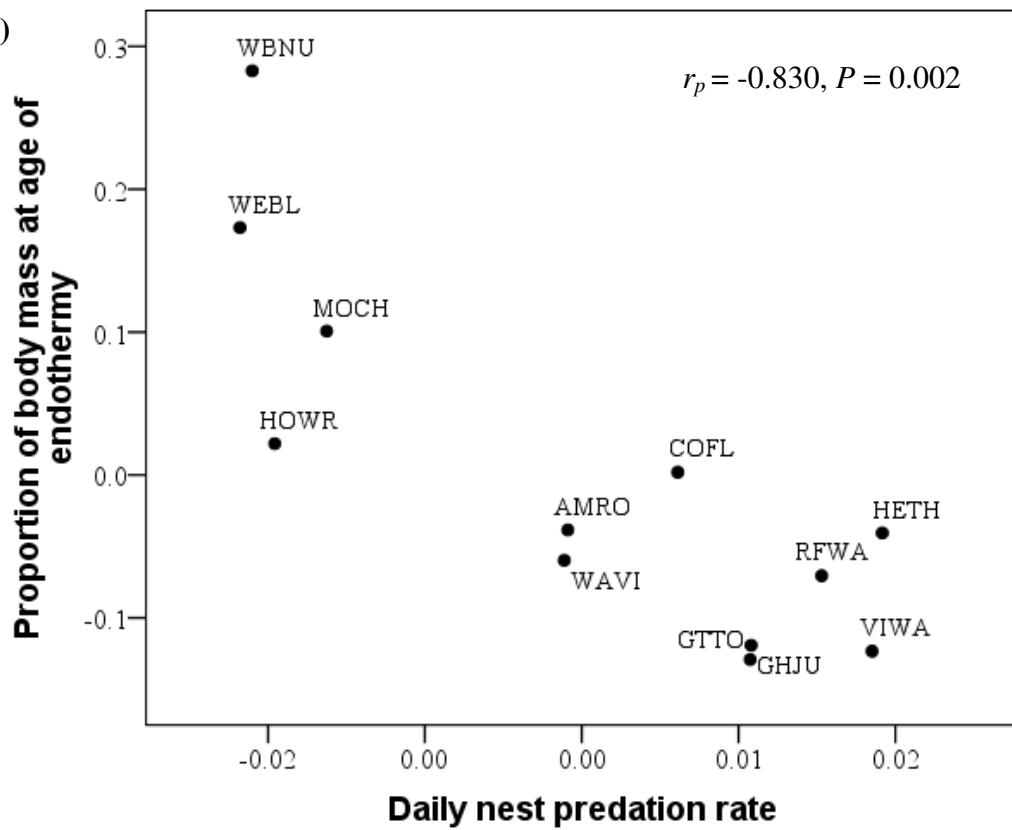


Figure 7.

A)



B)



Appendix 1. Growth characteristics of study species estimated from logistic growth curves, including asymptotes (A) and growth rates (K) of body mass, tarsus and wing chord. (K<sub>70</sub> is growth rate estimated from data truncated at 70% of body mass)

Species	Mass			Tarsus		Wing chord	
	A	K	K <sub>70</sub>	A	K	A	K
Cordilleran flycatcher	12.363	0.456	0.483	17.80	0.29	56.78	0.28
Warbling vireo	11.569	0.491	0.540	18.01	0.34	55.36	0.29
Mountain chickadee	13.069	0.353	0.447	19.18	0.34	66.02	0.23
Green-tailed towhee	24.201	0.515	0.589	26.52	0.42	64.93	0.34
Grey-headed junco	18.477	0.506	0.545	23.06	0.41	62.03	0.35
Red-faced warbler	9.837	0.526	0.576	19.47	0.40	50.96	0.37
Virginia's warbler	8.246	0.543	0.605	18.80	0.37	45.91	0.38
Western bluebird	25.411	0.428	0.485	20.02	0.38	89.16	0.22
American robin	54.123	0.505	0.533	34.35	0.38	92.12	0.34
Hermit thrush	24.594	0.561	0.570	33.05	0.38	69.61	0.36
White-breasted nuthatch	21.564	0.305	0.471	19.10	0.33	90.37	0.19
House wren	10.829	0.476	0.479	17.78	0.35	50.78	0.25

Appendix 2. Mass and proportion of mass when species achieved endothermy, defined as the age in days when homeothermic index was 0.9

<b>Species</b>	<b>Age of endothermy</b>	<b>Mass at age of endothermy (g)</b>	<b>Proportion of mass at age of endothermy</b>
Cordilleran flycatcher	9.46	11.155	0.96
Warbling vireo	9.22	10.843	0.89
Mountain chickadee	13.93	12.254	1.06
Green-tailed towhee	6.57	19.337	0.66
Grey-headed junco	7.15	15.179	0.73
Red-faced warbler	7.97	8.841	0.93
Virginia's warbler	7.94	7.571	0.90
Western bluebird	12.79	24.518	0.99
American robin	6.62	43.695	0.57
Hermit thrush	7.32	21.867	0.75
White-breasted nuthatch	18.18	20.683	1.16
House wren	11.74	10.491	1.00