



## AN ABSTRACT OF THE THESIS OF

Suzanne H. Austin-Bythell for the degree of Master of Science in Wildlife Science presented on 16 October 2006.

Title: Growth and Development of Temperate and Tropical Passerines of the New World: A Life History Perspective

Abstract approved:

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Tara R. Robinson

I studied developmental rates in a suite of temperate and tropical passerine bird species from the New World to test the hypothesis that tropical passerines exhibit slower patterns of growth and development than temperate birds. I also investigated how the expression of several developmental rates varied with life history traits including mass and tarsus growth rate as well as nestling period. I present data on the developmental marker of age of eye-opening, and for the first time, relate this characteristic to a suite of life history traits. Additionally, I investigated how differences in the method used to calculate mass growth rate affected correlations to a suite of life history variables. I found that tropical passerines gained mass 17% more slowly than did temperate birds using the conventional means of calculating growth rate; however, there was a 23% difference between temperate and tropical passerines when using a modified logistic growth equation that set a fixed value of the adult mass as the upper asymptotic value ( $A$ ) used to calculate growth rate. Tropical passerines also exhibited a 16% slower rate of tarsus, or long bone, growth.

Other traits, such as nestling period and age at eye-opening, did not differ between temperate and tropical passerines. I found that nestling period is an inappropriate surrogate for growth rate since there is little correlation between these characteristics. Thus, previous studies that have used nestling period instead of growth rate are likely biasing the results. I confirm previous findings on differences in growth and development of passerines between temperate and tropical regions; however, tropical birds appear to exhibit greater variation in developmental characteristics of life histories than do temperate birds, especially among the suboscine passerines.

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**GROWTH AND DEVELOPMENT OF TEMPERATE AND TROPICAL  
PASSERINES OF THE NEW WORLD: A LIFE HISTORY PERSPECTIVE**

by  
Suzanne H. Austin-Bythell

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Suzanne H. Austin-Bythell, Author

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## CONTRIBUTION OF AUTHORS

Dr. Tara Rodden Robinson contributed to all aspects of this thesis. Dr. W. Douglas Robinson assisted with the study design, data collection, funding, and editing of the thesis. Dr. R.E. Ricklefs provided funding, assisted in the study design, and shared resources for analysis of growth rates and age estimation, as well as unpublished data.

## TABLE OF CONTENTS

	<u>Page</u>
CHAPTER 1 – General Introduction: Life history evolution of temperate and tropical songbirds.....	1
LITERATURE CITED.....	6
CHAPTER 2 – Growth and development of temperate and tropical New World passerines: A life history perspective .....	10
ABSTRACT.....	11
INTRODUCTION.....	11
METHODS.....	16
Study sites.....	16
Field methods.....	17
ANALYSES.....	19
Age estimation.....	19
Growth rates.....	20
Life history comparison.....	23
Phylogenetic comparison.....	23
RESULTS.....	24
Growth rates.....	24
Life history comparison.....	26
DISCUSSION.....	35
ACKNOWLEDGMENTS.....	42
LITERATURE CITED.....	43
CHAPTER 3 – Synopsis and Conclusions.....	71
LITERATURE CITED.....	74
TABLES.....	52
FIGURES.....	67
APPENDICES.....	75

## LIST OF TABLES

<u>Table</u>	<u>Page</u>
1: Observed differences in traits of temperate and tropical passerines, and the predicted relationships with growth rate.....	52
2: Results from model selection of nestling mass growth rate in least squares regression on life history traits.....	53
3: Results from model selection of nestling mass growth rate (fixed $A$ ) in least squares regression on life history traits.....	54
4: Results from model selection of nestling period in least squares regression on life history traits.....	55
5: Results from model selection of nestling period in least squares regression on life history traits (using fixed $A$ mass growth rate).....	56
6: Results from model selection of eye-opening in least squares regression on life history traits.....	57
7: Results from model selection of eye-opening in least squares regression on life history traits (without <i>Manacus vitellinus</i> ).....	58
8: Results from model selection of nestling tarsus growth rate in least squares regression on life history traits.....	59
9: Results from model selection of nestling tarsus growth rate in least squares regression on life history traits (using fixed $A$ mass growth rate).....	60
10: Results from model selection of paired species of nestling mass growth rate in least squares regression on life history traits.....	61
11: Results from model selection of paired species of nestling mass growth rate (fixed $A$ ) in least squares regression on life history traits.....	62
12: Results from model selection of paired species of nestling period in least squares regression on life history traits.....	63
13: Results from model selection of paired species of nestling period in least squares regression on life history traits (using fixed $A$ mass growth rate).....	64

## LIST OF TABLES (CONTINUED)

<u>Table</u>	<u>Page</u>
14: Results from model selection of paired species of nestling eye-opening in least squares regression on life history traits.....	65
15: Results from model selection of paired species of nestling eye-opening in least squares regression on life history traits (using fixed <i>A</i> mass growth rate).....	66

## LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1: Tarsus length (mm) and natural log-transformed tarsus length of blue-gray tanagers nestlings of known age throughout the nestling period (d).....	67
2: Frequency histogram of mass growth rate (K) by region.....	68
3: Frequency histogram of tarsus growth rate (K) by region.....	69
4: Frequency histogram of mass growth rate (K), fixed $A$ , by region.....	70

## LIST OF APPENDICES

<u>Appendix</u>	<u>Page</u>
1: Summary of life history characteristics of temperate and tropical passerines.....	75
2: Age estimation models for a subset of passerine bird species.....	79
3: Developmental markers of feather development in nestlings of known and estimated ages.....	80
4: Mass (conventional and fixed $A$ ) and tarsus growth rate ( $K$ ).....	82
5: Phylogeny of temperate and tropical passerines based on Sibley and Ahlquist hypothesis (1990).....	89
6: Summary growth curves of temperate and tropical passerines.....	90
Suboscine: Thamnophilidae.....	90
Suboscine: Tyrannidae (manakins).....	92
Suboscine: Tyrannidae (flycatchers).....	93
Oscine: Crown Corvida.....	99
Oscine: Sylvioidea.....	100
Oscine: Muscicapoidae.....	103
Oscine: Passeroidea.....	108
7: Summary growth curves of closely related pairs of temperate and tropical passerines.....	119

# **LIFE HISTORY EVOLUTION OF TEMPERATE AND TROPICAL SONGBIRDS**

## **CHAPTER 1**

### **General Introduction**

Suzanne H. Austin-Bythell

Temperate and tropical passerine birds differ in numerous life history characteristics (Lack 1947, 1948, and 1968; Ricklefs 1980; Martin et al. 2000; Ricklefs and Wikelski 2002; Martin et al. 2006). On average, tropical passerines exhibit smaller clutch size (Moreau 1944; Skutch 1949 and 1985), longer incubation period (Ricklefs 1969b), longer duration of post-fledging care (Russell et al. 2004), and are thought to have slower nestling growth rates (Ricklefs 1976) than do temperate passerines. Recent studies, however, have questioned this temperate-tropical dichotomy in passerine life histories calling for a reevaluation of our understanding of previously accepted patterns (Geffen and Yom-Tov 2000). These recent studies have tended to rely on reanalysis of published data, which may be subject to biases associated with different approaches to data collection.

Two primary advances have led to challenges to the latitudinal gradient of life history variation. One has been the acquisition of new, larger datasets, which allow broader comparisons to be made. Early studies, for example, found that a few Neotropical passerines have higher annual survival than most temperate passerines (Snow and Lill 1974). More extensive data collected over several years analyzed by Karr et al. (1990) found no difference in survivorship and broadly

overlapping distributions of survival estimates for temperate and tropical passerines. Additional new studies with more data have concluded that tropical species do indeed have higher rates of adult annual survivorship and live longer, on average (Johnston et al. 1997; Ricklefs 1997).

A second advance is statistical adjustment for the non-independence of species as sampling units. Phylogenetic comparative methods have revealed that some life history traits thought to differ between temperate and tropical birds are not actually significantly different. Geffen and Yom-Tov (2000) found little support for the idea that tropical birds have longer nestling periods. Thus, the understanding of patterns in avian life history traits is moving forward as more data and new analytical methods are generated.

A prevailing hypothesis of life history evolution in birds suggests that limiting resources regulate reproductive capacity (Lack 1947, 1948, and 1968). Lack (1947 and 1948) suggested birds only produce as many offspring as they are capable of rearing successfully. This can be regulated by clutch size or through later reductions in brood size. The size and number of offspring are directly linked to parental investment and resource availability (Lack 1968; Stearns 1992). For example, a clutch size of two represents, on average, the maximum number of offspring that tropical birds can successfully rear while their temperate counterparts are capable of raising more young per breeding attempt. Hence, selection should favor an optimum clutch size based on resource availability during the breeding season. Resources can be unpredictable and birds may lay more eggs than might be optimal for bad years thereby precipitating later reduction



of the brood (Stoleson and Beissinger 2001). Asynchronously laid clutches and brood reduction may represent additional adaptive measures in birds that rely on unpredictable resources by focusing effort on older, larger chicks at the cost of younger, smaller birds when resources are limited (Stoleson and Beissinger 2001).

Over time, the hypothesis that birds rear the maximum clutch size has been rejected through the use of brood manipulation studies that show tropical birds are able to rear more nestlings per brood than they typically produce (Young 1996), at least to fledging (Styrsky et al. 2005). Styrsky et al. (2005) found that spotted antbirds (*Hylophylax naevioides*) could successfully rear artificially enlarged broods during the nestling period, but after fledging the additional nestling invariably disappeared within the first week after leaving the nest. As a caveat, these antbirds have developed a system of brood division during the post-fledging period, which may have a unique set of constraints (Styrsky et al. 2005).

There are multiple modifications to the hypothesis of the Lack clutch to account for the observed phenotypic differences in life history traits, including: predation pressure (Skutch 1949; Skutch 1985; Martin et al. 2000), lifespan and annual survivorship trade-offs optimizing reproductive investment (Williams 1966), and population-level pressures associated with competition and seasonality (Ashmole 1963; Ricklefs 1980; Yom-Tov and Geffen 2002). Generally, life history hypotheses have focused on fitness trade-offs of valuing self and future reproductive potential over the current reproductive event. This is an underlying assumption of the previously held doctrine of *r* and *K*-selected species.

Deviations in average clutch size occur frequently, for instance in cavity-nesting birds, which are exposed to less predation pressure generally produce a greater number of offspring than do open-cup nesting species in the same habitat (Lack 1947, 1948, and 1968). This has led some to postulate that predation pressure, rather than food availability, is the selective mechanism of clutch size and other life history traits (Ricklefs 1969a; Ghalambor and Martin 2001; Martin et al. 2000; Skutch 1985). Skutch (1949, 1985) proposed that the higher nest predation rates observed in the tropics have favored a smaller clutch size to reduce the loss per reproductive event (Skutch 1949, 1985). This is similar to Williams' (1966) hypothesis, which suggests that differences in life expectancy would cause birds to optimize their reproductive effort to increase adult survivorship. In tropical passerines, adults re-nest frequently after nest failure (Lack and Moreau 1965; Styrsky et al. 2005) and have a longer lifespan, on average (Snow and Lill 1974); thus, selection should favor reducing the energetic investment in each clutch to minimize the cost of each loss on adult survival (Skutch 1949 and 1985; Williams 1966; Martin et al. 2000). There is a paradox in tropical passerines, who experience higher predation rates than do temperate birds, as a breeding system that is selected to reduce costs associated with predation would be expected to have shorter incubation and nestling periods in order to limit cost (and exposure time) during the most vulnerable portions of an organism's life cycle (Martin et al. 2000). Nestling periods of tropical passerines do not differ from those in the temperate region yet growth rate is thought to be slower (Geffen and Yom-Tov 2000; Ricklefs 1976; but see Oniki and Ricklefs 1981).

Life history theory predicts that if predation was the primary driving mechanism for the selection of traits, like clutch size or incubation and nestling periods, organisms would adapt to limit the exposure period to this risk (Lack 1968; Stearns 1992; Remes and Martin 2002; Martin et al. 2006). Implicit is the assumption that fast growth rates are correlated to short nestling periods. Thus, as with incubation and nestling periods, nest predation should impose directional selection on nestling growth rate by indirectly favoring the survival of birds that grow quickly allowing early fledging to escape high nest predation (Lack 1968; Remes and Martin 2002). Tropical birds should be under strong selection for higher growth rates than temperate birds. Recent studies of nest predation have found higher rates, on average, in the tropics; however, in ‘good’ years nest predation rates may be similar to the temperate zone (Robinson et al. 2000).

Natural selection on growth rate must act within the physiological limits of the nestling (Starck and Ricklefs 1998). Selection favoring slowed or accelerated growth will be bounded by constraints on quantity of quality food provided to the nestling, the ability of the nestling to assimilate nutrients, and the rate of cellular division in growing tissues (Starck and Ricklefs 1998). Thus, growth phenotypes are the result of physiological and ecological influences, which maximize the fitness of the parent-offspring unit (Ricklefs 1996).

Reproductive effort is optimized at both the organismal and population level meaning phenotypic plasticity of traits varies among individuals and between populations (Stearns 1992). Thus, understanding the limits on individual fitness between temperate and tropical birds provides insights into other aspects of avian

life history evolution, such as differences in developmental rates. Elucidation of ecological or physiological limits will increase our understanding of how different life history strategies evolved. However, data are limited on many life history traits, or have been analyzed without accounting for phylogeny. Thus, many current ideas associated with temperate-tropical differences in life history evolution should be revisited in the light of phylogeny. This study reassesses perceived differences in developmental rates between tropical and temperate passerines in the context of phylogeny and life history.

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## **CHAPTER 2**

### **GROWTH AND DEVELOPMENT OF TEMPERATE AND TROPICAL PASSERINES OF THE NEW WORLD: A LIFE HISTORY PERSPECTIVE**

Suzanne H. Austin-Bythell, Tara Rodden Robinson, W. Douglas Robinson,  
and Robert E. Ricklefs

Key words: growth rates, nestling development, life history evolution, logistic growth equation, Passeriformes, Aves.



***ABSTRACT:***

1. We studied developmental rates in a suite of temperate and tropical passerines of the New World to determine if tropical birds exhibit slower patterns of growth than temperate birds. We also explored how a suite of life history traits vary with developmental characteristics.
2. We investigated two estimates of mass growth rate as well as tarsus growth rates, and duration of the nestling period. Additionally, we present data on the developmental marker of age of eye-opening, and for the first time, relate this characteristic to a number of life history traits.
3. Tropical birds grew in mass 17% more slowly than temperate birds when conventional means of calculating growth rates were used and 23% slower using a new method that adjusted for adult mass. Growth of the tarsus length differed by 16% while other developmental rates, such as nestling period duration and age at eye-opening, did not differ among passerines from different latitudes. Additionally, we found that nestling period is an inappropriate surrogate for nestling mass growth rate.
4. This study confirms previous research that suggested a regional difference in passerine growth and development; however, we note that tropical passerines exhibit a greater variation in the expression of life histories than do temperate birds, especially among the suboscine passerines.

***INTRODUCTION:***

Life histories of temperate and tropical passerines differ along a latitudinal gradient (Lack 1947, 1948; Lack and Moreau 1965; Skutch 1949, 1985; Snow and Lill

1974; Ricklefs 1976; Russell et al. 2004; Martin et al. 2006). Tropical passerines are thought to exhibit a slower pace of life than temperate birds, which is linked to differences in seasonal fluctuations in productivity between regions (Ricklefs and Wikelski 2002; Wikelski et al. 2003). Traits affecting survival and reproduction vary considerably across latitudes with selection favoring individual survival over reproduction in the tropics (Ricklefs and Wikelski 2002; Tieleman et al. 2006). This trade-off between reproduction and survival is thought to influence other aspects of life history phenotypes, causing similar responses to variation, or syndromes, within life histories (Ricklefs and Wikelski 2002). Reproduction, in particular, is expected to respond to changes in adult survival (Ricklefs 1969b; Stearns 1992). The relatively high adult survival rates exhibited in tropical passerines (Johnston et al. 1997; Ricklefs 1997; but see Karr et al. 1990) should be associated with relatively low values for a suite of reproductive characteristics (Ricklefs and Wikelski 2002), such as clutch size (Moreau 1944), nestling growth rate (Ricklefs 1976), incubation period (Geffen and Yom-Tov 2000), nestling period (Ricklefs 1968a but see Geffen and Yom-Tov 2000), and post-fledging period (Russell et al. 2004) that reflect a syndrome of a slower pace of life. Temperate birds should show the reverse pattern, with selection favoring reproduction over individual survival (Ricklefs and Wikelski 2002; Martin 1996).

Recent findings suggest that reproduction is also influenced by resource availability and predation pressure (Martin et al. 2000; Ghalambor and Martin 2001; Wikelski et al. 2003). Nest predation is thought to be higher in the tropics compared to the temperate region (Martin 1987; Robinson et al. 2000). In one study, nest predation was found to be 23% higher in the tropics than in the temperate zone (Robinson et al.

2000). Nest height and location may play a role in mitigating impacts of nest predation on reproductive success by reducing predation pressure on enclosed or cavity nests or those placed at greater heights (Robinson et al. 2000; Martin 1987). Typically, cavity or enclosed nesting species experience lower predation rates (Robinson et al. 2000). Growth and developmental rates of altricial birds have also been positively correlated to predation rates, with birds that experience high nest predation rates growing faster than those with lower predation rates (Remes and Martin 2002, but see Ricklefs 1969b and 1973). This is thought to reduce the duration of risk exposure in the nest (Remes and Martin 2002, but see Ricklefs 1969b and 1973).

Nestling growth rate is a phenotypic character that directly affects reproduction and survival of individual birds (Ricklefs 1969b; Stearns 1992; Starck and Ricklefs 1998; Blount et al. 2006). Considerable variation in this trait exists among orders, families, and species, which likely reflects different reproductive strategies at work (Starck and Ricklefs 1998). Past studies have documented a positive correlation between nestling growth rate and duration of time required to produce a successful brood (Ricklefs 1969b; Starck and Ricklefs 1998), meaning that growth, associated with the duration of the nestling period, dictates fecundity through the number of broods potentially produced per season (Ricklefs 1969b). Tropical passerines (<100g) were found to grow 23% slower than temperate birds and have longer periods of parental care, thereby limiting reproductive output (Ricklefs 1976; Russell et al. 2004). Life history theory suggests that a by-product of the higher survival rates of life of adult tropical birds is higher adult investment in each nestling, and thus, higher quality fledglings that are better able to compete for resources upon reaching independence (Russell et al. 2004; Robinson et al.

2000; Stearns 1992). However, a recent study found that adult provisioning rate did not differ in two subspecies of house wren, while field metabolic rate of the adults was lower throughout the nestling period in the tropical subspecies (Tieleman et al. 2006); post-fledging care and total parental investment in nestlings was not assessed. Thus in this study, total investment in reproduction effort was not measured as, generally, post-fledging care typically lasts much longer in the tropics (Russell et al. 2004).

Ecological and life history influences on nestling growth are limited by physiological constraints such as the quantity of quality food resources delivered to the nestling, the rate at which chicks assimilate nutrients, and rates of tissue deposition during growth (Starck and Ricklefs 1998; Ricklefs 1996). These constraints limit the plasticity of growth, and likely other aspects of life history syndromes, leading to limits in the variation of overall life history strategies (Ricklefs 1996; Starck and Ricklefs 1998; Ricklefs and Wikelski 2002). Few have studied how growth rate of body mass, and other developmental characteristics like nestling period and long bone growth, correlate with life history traits.

Ricklefs (1976) suggested that differences in growth exhibited between temperate and tropical regions were influenced by the inclusion of many tropical species of slow-growing suboscines and tanagers in his analyses. Other studies on development, like nestling period, found that phylogeny muted the effect by reducing statistical significance of latitude on nestling period (Geffen and Yom-Tov 2000). Further research is needed on developmental characteristics in passerines to account for phylogeny, to increase sample sizes used to construct growth curves, and to expand the number of species in both regions available for comparison. Additionally, few have performed a comparative study

on nestling period separately from growth rate using the same suite of species even though nestling period has been used as a surrogate for growth rate (Bosque and Bosque 1995; Tieleman et al. 2006).

Another issue that has received renewed interest recently is how modifications to the parameters used in the logistic growth equation affect the estimates of growth rate, and thus, the relationships among other life history and life table variables (Remes and Martin 2002). We briefly describe and assess two means of approximating growth rate and the impacts that these estimates have on correlational analyses of life history traits.

Our objectives were: 1) to determine if differences in developmental rates observed between temperate and tropical regions occurred when phylogeny was controlled, 2) to quantify correlations between nestling growth rate, nestling development, and other life history traits, and 3) to assess if the parameters of the logistic growth equation are sufficient to describe regional differences in growth rate. We hypothesized that tropical birds exhibit slower growth rates compared to temperate birds, as found by Ricklefs (1976). Additionally, we hypothesized that reproductive traits vary with growth; thus, factors favoring selection of slow growth should also produce similar variation in other reproductive and life history characteristics. For instance, we hypothesized that if birds have slow growth rates then they should also have long incubation periods. We summarize the observed differences in reproductive life history traits and our predictions for correlations with growth in Table 1.

## ***METHODS***

### **Study sites:**

We collected data on nesting passerines at three sites, two temperate (Michigan and Oregon, USA) and one tropical (Panama province, Republic of Panama), between 2003 and 2006.

Michigan (42°N 85°W): We quantified reproductive traits and growth rates of temperate birds at Lux Arbor Reserve and Kellogg Biological Station (KBS) in southwestern Michigan. Lux Arbor is a 1323-ha mosaic of agricultural fields, deciduous forest, Christmas tree plantations, wetlands, meadows, and second growth adjacent to a large shallow lake (<http://lter.kbs.msu.edu/>). Average annual precipitation is 89 cm y, and mean annual temperature is 9.7°C (<http://lter.kbs.msu.edu/>). KBS is a parkland habitat located approximately 17-km south of Lux Arbor. Data collection began May 1 and ended August 1, covering the peak of the breeding season. To collect nestling measurements for cavity-nesting species, such as house wrens (*Troglodytes aedon*), black-capped chickadees (*Poecile atricapilla*), tree swallows (*Tachycineta bicolor*), and eastern bluebirds (*Sialia sialis*), we used nest boxes. Boxes were anchored to metal posts without predator guards, and were located in various habitats to attract target species.

Oregon (44°N 123°W): To increase sample sizes of north temperate cavity-nesting species, we collected additional data in rural Benton County, Oregon. This site consists of a network of public and private pasturelands, working organic farms, and oak savanna within a 24-km radius of Corvallis, Oregon. Average annual rainfall for the region is 103 cm y and the mean annual temperature is 11.5°C (<http://www.ocs.oregonstate.edu/>). Nest boxes were placed on posts, trees, and telephone poles with the intent of attracting target species, including western bluebirds (*Sialia*

*mexicana*), tree swallows, violet-green swallows (*T. thalassina*), and white-breasted nuthatches (*Sitta carolinensis*). Predator guards were not used. Data collection occurred between April and early September, encompassing the majority of the breeding season for target species.

Panama province (9°N 79°W): Fieldwork was conducted in, and adjacent to, Soberania National Park in central Panama province. Soberania consists of 22,000 hectares situated 30-km north of Panama City. Our primary study site was in and around the small town of Gamboa, which is situated at the confluence of the Chagres River and Panama Canal. The site consists of lowland second growth rainforest and parkland habitats in suburban Gamboa. Average rainfall is 260 cm y (Robinson et al. 2000), and average annual temperature is about 25°C (Tieleman et al. 2006). No nest boxes were used due to low occupancy. Fieldwork occurred from March through July annually to capture the peak of the breeding season.

### **Field Methods:**

We conducted generalized nest searches for passerine species nesting in second growth habitats. We made efforts to include regionally distinct species, such as wrentits (*Chaemea fasciata*), warblers (*Dendroica petechia*), chickadees (*Poecile atricapilla*), antbirds (*Myrmeciza* spp.), manakins (*Pipra* and *Manacus* spp.), and antshrikes (*Thamnophilus doliatus*), to determine if these species exhibited different growth patterns than those that were phylogenetically similar in both temperate and tropical regions. To increase the resolution of our study, we also collected information on pairs of phylogenetically matched species from both regions. Some pairs were chosen *a priori*; however, most were assigned after data collection had begun based on availability of

nests and growth data. Degree of relatedness varied among the species pairs from the same species at both sites (*T. aedon*) to more distantly related pairings based on the Sibley-Ahlquist hypothesis (1990). Therefore, we used phylogenetic comparative methods during statistical analyses.

We gathered information on life history traits, including clutch size, incubation period, nestling period, and nestling growth rate by monitoring nests throughout the breeding cycle (Appendix 1). We collected measurements of the length of the incubation and nestling periods from nests where age was known and averaged these values. Fresh egg masses and clutch sizes in nests found early in incubation were measured and then averaged. For nestling growth, we measured mass ( $\pm 0.1$  g), tarsus length ( $\pm 0.01$  mm), bill length ( $\pm 0.01$  mm), and unflattened wing chord ( $\pm 0.5$  mm) of individually-marked nestlings. We visited nests every 2-3 days, and within each nest we marked nestlings by coloring a metatarsus with a non-toxic felt marker to facilitate individual identification. Nestlings were weighed to the nearest 0.1 g (Acculab PocketPro 60g Electronic Balance; Salter Brecknell Electronic Pocket Balance). We measured tarsus length from the notch in the metatarsus to the opened pad of the foot and bill length from the distal end of the nares to the tip of the bill using electronic calipers (Mituyo Digimatic). Measurements of the unflattened wing chord were taken with a wing ruler. Additional growth data were supplied by R.E.R. or taken from published values in the literature; data on wrentits (*C. fasciata*) were provided by PRBO Conservation Science. We measured nestlings until the risk of causing premature fledging became too great, after which we discontinued measurements of growth.



We also assessed developmental milestones of feather growth and eye-opening. Developmental milestones by age included: first eye-opening, approximate primary feather length (5-mm categories), and condition of feather (pin or broken sheath) (Appendix 3). These milestones were used as a rough gauge of nestling maturity (O'Connor 1977), and as a confirmation of age estimation in nests for which hatch dates were unknown. Additionally, we measured nest heights (m), and documented nest type (cavity, open-cup, or enclosed-cup). Nest height was simplified for analyses as low (0-1m), medium (1-3m) and high (>3m). Adult morphometrics, for comparisons and analyses, were taken from our own unpublished data or from the literature. For type of parental care, we collected data from the literature and our own observations. We classified the categories as 'uni' when one parent reared the nestlings or 'bi' when two or more adults reared the nestlings.

## ***ANALYSES:***

### **Age Estimation:**

To increase our sample sizes in analyses of mass growth rate, we created models that enabled us to predict age; this allowed us to include nestlings where hatch date was not known. We used model selection (adjusted  $R^2$ ) in general least squares regression using age as the response variable and tarsus length, bill, and wing chord as the explanatory variables in order to find the best description of nestling age for each species based on data from nestlings where age was established by direct observation of hatching (Appendix 2). Nests where status had been checked the day prior to finding nestlings or where we observed pipping were also considered to be of known age. Distribution of morphometric measures were generally curvilinear in shape; thus, we log-transformed the morphometric variables (Figure 1). Log-transformation was sufficient to correct the non-

linearity of most data, except in species with long nestling periods. Because non-linearity was not always corrected at the end of the nestling period, we manually checked and corrected age estimates of nestlings based on ages calculated for the same individual earlier in the nestling cycle (when the growth curve was linear). This was based primarily on the timing between nest checks. We then cross-referenced these estimated ages with developmental markers of nestlings of known age.

Sample sizes of known-age nestlings followed to fledging were small for some species. To increase sample sizes, we included nestlings whose hatch date was not exactly known if we could estimate age based on developmental progress. For external development, we considered developmental milestones of estimated-age nestlings that were matched to within 1 to 2 days of ages known to be correct estimates (Appendix 3). The age of each developmental milestone was assigned by determining when 50% of the individuals in the sample exhibited the trait.

### **Growth Rates:**

We analyzed growth rates with nonlinear regression using the logistic equation for growth (PROC NLIN, SAS Institute) (Oniki and Ricklefs 1981; Ricklefs 1983). The formula for logistic growth is:

$$M_t = \frac{A}{1 + e^{-K(t-i)}}$$

where  $t$  is time;  $M_t$  is the mass at age  $t$ ;  $A$  is the asymptote of the growth curve where mass is at its highest point (or adult weight);  $i$  is the inflection point of the growth curve where  $M_t = A/2$ ; and  $K$  is the growth rate constant (Ricklefs 1967a). We calculated  $K$ ,  $i$ , and  $A$  for all species for which we had sufficient growth data. Several species in this study experienced a weight gain that exceeded adult mass prior to a period of weight

recession. Weight recession occurred primarily in species from the family Hirundinidae, as has been previously observed (Ricklefs 1968c). When weight recession occurred, we truncated the data at the peak weight.

Nestlings that experience a weight plateau yet do not approach adult weight prior to fledging have not stopped growing. This plateau has been attributed to changes in body composition, specifically the water index (lean dry mass/water), that nestlings undergo while growing (Ricklefs 1967b; Ricklefs 1968c; Starck and Ricklefs 1998). The changes in water index of tissues, such as feathers and muscle mass, has been credited with problems associated with descriptions of species growth curves with asymptotic masses well-below the adult value and weight recession (Ricklefs 1967b; Ricklefs 1968c; Starck and Ricklefs 1998). The remaining period of growth to adult size has not been characterized owing to the difficulty in measuring nestlings after fledging.

A lack of post-fledging data may lead to biased growth rate estimates. A steep slope in the growth curve at the time of fledging may be associated with birds that have not stopped growing and/or nestlings that fledge at the beginning of the upper asymptote. Bias may arise due to inaccurate calculations of parameters within the logistic growth model. The parameters of the logistic growth model are calculated in non-linear regression simultaneously with  $A$  being inversely related to  $K$ . Inaccurate calculations of  $A$  can lead to biased growth rates,  $K$ . In species that fledge early,  $A$  can be overestimated (exceeding adult measures) thereby leading to an estimate of  $K$  that is biased low, or in species that fledge well-below adult mass (as in robins or doves),  $A$  may be underestimated and conversely  $K$  would be biased high because the full growth curve was not used to calculate the growth rate constant in non-linear regression. To determine if

these potential biases were impacting our analysis, we included the variable of the proportion of  $A$  to adult mass. This variable will determine the impact of size at fledging has on our analyses, and whether accepted patterns in growth rate, like the regional difference observed among passerines, may be an artifact of the parameterization of the logistic growth equation. If this ratio is found to be significantly correlated to growth, we will include estimates of nestling mass growth rate calculated using a fixed  $A$  of adult mass.

When data were limited (e.g.,  $n < 3$ ) or when there were large gaps in the growth curve, we used a fixed asymptote to estimate  $K$  (Appendix 4). These values were perceived as potentially biased compared to more complete growth curves; thus, life history comparisons did not include these growth constants. Additionally, we used a fixed  $A$  of adult mass when the estimated asymptote was biased (e.g., estimated  $A$ , not associated with weight recession, exceeding adult mass by greater than 5 grams). This only occurred with one species included in the life history analyses, the song sparrow (*Melospiza melodia*).

We calculated growth rates for tarsus length as with nestling mass; however, because bone growth is more linear at the tail of the growth curve there was a tendency for the asymptotic value to exceed adult tarsus length. Thus, curves were fit using the peak nestling tarsus length as a fixed asymptote. To avoid overanalyzing the data for tarsus growth, we used only known-age birds. In several species, tarsus length data were limited or unavailable; thus, datasets for tarsus and mass growth rates differ. We could not analyze paired species for tarsus growth rate for this reason.

### **Life History Comparison:**

We compared mass growth rate, tarsus growth rate, nestling period, and the developmental marker eye-opening to region using one-way ANOVA. We then compared these same variables in a separate analysis of life history traits using adjusted  $R^2$  model selection in general least squares regression. Criteria for inclusion and retention in the model were p-values of 0.1 and 0.05, respectively; these limits were chosen *a priori*. Variables included in the model were: region (temperate vs. tropical; 0 vs. 1, respectively) incubation period, nestling period, clutch size, nest height, nest type, egg mass, type of parental care, and adult morphometrics. We included region in the models in order to determine how this variable might vary with other life history traits. Non-linearity was present, so all continuous variables (excluding clutch size and age at eye opening) were natural log-transformed to adjust the distributions. Categorical variables were converted to indicator (dummy) variables (parental care: uni=0, bi=1; region: temperate=0, tropical=1; nest type: cavity=0, cup=1). When a category had three classes, as in nest height, codes were low (0), medium (0.5), and high (1). Many variables co-varied with adult mass; thus, we controlled for adult mass by regressing natural log-transformed egg mass, adult tarsus length, and adult wing length against adult mass, separately (Harvey and Pagel 1991; Stearns 1992). Residual values from these regressions were used in the remaining analyses (Harvey and Pagel 1991; Stearns 1992).

### **Phylogenetic Comparison:**

Related species may have similar life histories due to common ancestry (Harvey and Pagel 1991). Thus, in conventional analyses where species' values are equally weighted, results may be biased (Harvey and Pagel 1991; Felsenstein 1985). To account for phylogenetic effects, we created phylogenetically independent contrasts (PIC)

(Felsenstein 1985) in the PDTREE module (Garland et al. 1992) of Mesquite (Maddison and Maddison 2004) using the Sibley and Ahlquist hypothesis (1990) (Appendix 5).

Modifications to this tree from recent phylogenies were included when possible (Barhoum and Burns 2002; Barker et al. 2002; Cibois and Cracraft 2004; Carson and Spicer 2003; Klicka et al. 2000; Van der Meij et al. 2005; Klicka et al. 2005; Jonsson and Fjeldsa 2006). Branch lengths were natural log-transformed to improve the fit of the standardized contrasts (Garland et al. 1992). PICs for each trait were analyzed as before in general least squares regression; slopes were forced through the origin (Garland et al. 1992; Garland et al. 1993).

## **RESULTS:**

### **Growth Rates and Development:**

Mass and tarsus growth rates ( $K$ ) for all species are reported in Table 4. Similar to previous findings (Ricklefs 1976), we found that there was a temperate and tropical regional difference in nestling growth rate ( $F_{1,44} = 12.57$ ,  $R^2 = 0.22$ ,  $P = 0.0009$ ; PIC,  $F_{1,44} = 16.24$ ,  $R^2 = 0.27$ ,  $P = 0.0002$ ). We found that the median mass growth rate was 17% slower than in temperate species (Figure 2). This value is slightly less than Ricklefs' (1976) original estimate of 23%. Median mass growth rates differed from 0.371 in tropical birds to 0.467 in temperate birds. Interestingly, the tropics had species that represented the extreme values of mass growth with  $K$ -values of 0.233 (*Tyrannus melancholicus*) and 0.631 (*Myrmeciza exsul*) while temperate passerines ranged from 0.365 (*Progne subis*) to 0.528 (*Pipilo erythrophthalmus*).

The tarsus growth rate also differed ( $F_{1,38} = 6.76$ ,  $R^2 = 0.14$ ,  $P = 0.0132$ ; PIC  $F_{1,38} = 0.00$ ,  $R^2 < 0.00$ ,  $P = 0.9485$ ) with tropical birds growing a median difference of 16% more slowly than temperate species (Figure 3). However, phylogenetic controls impact

this result substantially, which may be related to several factors. First, dummy variables describing region may have been insufficient to describe this relationship. Contrasts generated from dummy variables often had branch lengths that were insufficient to approximate the variables regardless of the transformation used (personal observation) or long bone growth may be highly constrained among groups. This would mean that levels of ossification and size of the cartilaginous zones were fairly consistent among related species; however, much variation exists among passerines suggesting that this is not the case (Starck and Ricklefs 1998). Temperate birds had a median tarsus growth rate of 0.393 while tropical passerines had a value of 0.330. When compared in a least squares regression this was found to be positively significantly correlated to nestling mass growth rate ( $F_{1,38} = 39.37$ ,  $R^2 = 0.51$   $P < 0.0001$ ). This correlation was apparently influenced by phylogeny since the relationship was no longer significant when PICs were used ( $F_{1,38} = 0.32$ ,  $R^2 = 0.01$ ,  $P = 0.5775$ ). Tarsus growth rate varied in tropical species from 0.215 (*Euphonia lanirostris*) to 0.440 (*Arremonops conirostris*) and from 0.270 (*Tachycineta bicolor*) to 0.572 (*Melospiza melodia*) in temperate passerines.

Similar to Geffen and Yom-Tov (2000), we found that there was no regional difference in nestling period ( $F_{1,44} = 0.03$ ,  $R^2 < 0.00$ ,  $P = 0.86$ ; PIC,  $F_{1,44} = 2.48$ ,  $R^2 = 0.05$ ,  $P = 0.1223$ ) and a significant difference in incubation period between temperate and tropical passerines ( $F_{1,44} = 15.24$ ,  $R^2 = 0.26$ ,  $P = 0.0003$ ; PIC,  $F_{1,44} = 12.74$ ,  $R^2 = 0.2245$ ,  $P = 0.0009$ ). Additionally, we found that the developmental milestone of eye-opening was relatively consistent amongst passerines in this study ( $F_{1,44} < 0.01$ ,  $R^2 < 0.00$ ,  $P = 0.978$ ; PIC,  $F_{1,44} = 0.47$ ,  $R^2 = 0.01$ ,  $P = 0.4978$ ). There was one outlier, *Manacus*

*vitellinus*, which had no effect on results when removed ( $F_{1,43} = 0.28$ ,  $R^2 = 0.01$ ,  $P = 0.5995$ ; PIC,  $F_{1,43} = 0.52$ ,  $R^2 = 0.01$ ,  $P = 0.4761$ ).

### **Life History Comparison:**

#### *Mass Growth Rate:*

When growth rate was compared to a number of life history characteristics there were significant negative correlations with region, nest type, nestling period, and the ratio of the upper asymptotic value (from the logistic growth equation) and adult mass ( $A$ :Adult mass) ( $F_{6,39} = 8.44$ , Adj.  $R^2 = 0.50$ ,  $P < 0.0001$ ) (Table 2). Mass growth rate decreased as the duration of the nestling period increased. Fast growth rate was linked to cavity nesting species, which is contrary to previous studies that indicate slow growth in cavity nesting species. This correlation is likely influenced by the large number of slow-growing open-cup nesting suboscines in the tropics, and the lack of tropical cavity nesting species. Additionally, the age of eye-opening and the residuals of the adult wing length had marginal negative correlations with mass growth rates when adult morphometrics and egg mass were corrected for mass. Also, mass growth rate tended to be slower in passerines that fledged near adult mass (i.e. had a ratio of  $A$ :Adult mass approaching or above 1). When phylogeny was controlled using PIC, significant negative correlations were found with region,  $A$ :Adult mass, residuals of the adult wing length, and age of eye-opening ( $F_{8,37} = 6.85$ , Adj.  $R^2 = 0.51$ ,  $P < 0.0001$ ) (Table 2). This suggests that birds with slower growth rates tended to have longer adult wing length and opened their eyes later than those with faster mass growth rates. Nestling period and nest height, in addition to the residuals of egg mass and the adult tarsus length, were included in the PIC model but were not significantly correlated to mass growth.



The inclusion of the ratio of the asymptotic mass to the adult mass has important implications on further analyses. This variable was initially added to address concerns that differences in mass growth rate between regions was an artifact of how the logistic growth equation was fitted to the data. The significant correlation of this ratio with growth rate suggests that the use of a floating asymptote (calculated concurrently with the inflection point,  $i$ , and growth rate,  $K$ ) may be somehow biasing the growth rates of birds that leave the nest before the growth curve is fully quantified. For instance, temperate birds that we've found to have a faster growth rates yet similar nestling periods to tropical birds may not actually be growing more quickly, but instead may be growing at a similar rate based on the proportion of adult mass that they've reached. When calculating  $K$ , we typically don't quantify the entirety of the growth curve causing inherent biases in the estimate. Temperate birds appear to fledge at a mass closer to adult size compared to tropical passerines that leave the nest at a lighter relative mass than do temperate birds causing the growth rate calculated by conventional means to be biased. These biases, in both directions, likely have some impact on our understanding of interspecific developmental rates. The consistent correlation of this variable to growth rate in the best fitting models appears to lend merit to this concern. As previously discussed, using a fixed asymptote of adult mass in the logistic growth equation may be a means of circumventing issues caused by differences in relative mass at the upper asymptote as well as indirectly accounting for physiological changes in body composition. Here, we present data using growth rates calculated using conventional calculations in nonlinear regression of  $A$ ,  $i$ , and  $K$  in the logistic growth equation as well as growth rates fitted similarly but with a fixed asymptote of adult mass (unless mass exceeded adult mass in

which case the peak nestling mass is used to calculate  $A$ ). We will hereafter specify use of the latter method by stating that the asymptote was fixed.

In least squares regression, the natural log-transformed growth rate (fixed  $A$ ) differed between region ( $F_{1,44} = 12.5$ ,  $R^2 = 0.22$ ,  $P = 0.0001$ ) The median difference between regions for this growth rate estimate was 23% with tropical birds growing at a slower rate than temperate birds (Figure 4). Phylogeny appeared to have some effect on this association with a moderately significant correlation when this factor was controlled ( $F_{1,44} = 3.64$ ,  $R^2 = 0.08$ ,  $P = 0.0629$ ). When compared with other life history traits, we found significant negative correlations to nest type and adult wing length (residuals) ( $F_{7,38} = 7.59$ , Adj.  $R^2 = 0.51$ ,  $P < 0.0001$ ) (Table 3). Hence, in this estimate of growth rate, the direction of variation is similar for these traits as with conventional growth analyses. While not significant, incubation period was also correlated to mass growth rate (fixed  $A$ ). After controlling for phylogeny, adult wing length (residuals) was retained in the model and significant negative correlations with eye-opening and incubation were added ( $F_{5,40} = 5.66$ , Adj.  $R^2 = 0.34$ ,  $P = 0.0005$ ) (Table 3). Thus, birds with slow growth tended to open their eyes later in development. Nest height was included in the model as was egg mass (residuals); however, neither variable was significant.

#### *Tarsus Growth:*

Nestling tarsus growth rate was positively correlated with mass growth rate (fixed  $A$ ) and tarsus growth rate ( $F_{1,38} = 13.32$ ,  $R^2 = 0.26$ ,  $P = 0.0008$ ; PIC  $F_{1,38} = 5.84$ ,  $R^2 = 0.13$ ,  $P = 0.0206$ ). Interestingly, the correlation remained significant after phylogeny was

controlled unlike when the conventional means of calculating nestling growth rate was used.

Tarsus growth rate had significant negative correlations with clutch size, incubation period, and residuals of egg mass ( $F_{6,33} = 29.81$ , Adj.  $R^2 = 0.82$ ,  $P < 0.0001$ ) (Table 8). Thus, increases in the length of the incubation period, the clutch size, and the egg mass (residuals) were corresponded to decreases in the rate of tarsus growth. Mass growth rate was also found to positively vary with tarsus growth rate resulting in songbirds with a general pattern of fast or slow growth. While only marginally significant, the positive correlation between the residuals of adult wing length is interesting suggesting that birds with long wings have relatively fast tarsus growth rates. Contrasts for tarsus growth reduced significant variables to region nest type, nestling period, and residuals of the adult wing length, adult tarsus length, and egg mass ( $F_{8,31} = 75.21$ , Adj.  $R^2 = 0.94$ ,  $P < 0.0001$ ) (Table 8). Though not significant, nestling period and type of parental care were moderately related to tarsus growth rate after phylogeny was controlled. When this analyses was conducted nestling mass growth rate (fixed  $A$ ), we found that region, nest height, and residuals of egg mass had significant negative correlations while mass growth rate (fixed  $A$ ) and residuals of the adult tarsus length had significant positive correlations to tarsus growth rate ( $F_{8,31} = 17.66$ , Adj.  $R^2 = 0.77$ ,  $P < 0.0001$ ) (Table 9). Species with slow rates of tarsus growth also exhibited slow mass growth rates. Meanwhile, species with relatively long tarsi length for their body mass had fast tarsus growth rates. Again, controls for phylogeny muted some of these effects and only region, nest type, and adult tarsus length (residuals), adult wing length (residuals), and egg mass (residuals) were significantly correlated to tarsus growth rate ( $F_{7,32} =$

83.11, Adj.  $R^2 = 0.94$ ,  $P < 0.0001$ ) (Table 9). Thus, this is very similar to the results when conventional means of generating nestling growth rate was used; however, nestling growth rate (fixed  $A$ ) was never considered in the current model. This suggests that mass growth calculated using a fixed  $A$  of adult mass may remove an underappreciated effect that nestling period may have had on mass growth rate. Hence, this method may be a better means of assessing growth rates among passerines species that fledge at different stages of completion of the growth curve.

#### *Nestling Period:*

We compared nestling period as with the growth rates. We found that nestling period had a strong negative correlation with nest type and conventional mass growth rates as well as significant positive correlations with incubation period, nest height, and residuals of the egg mass ( $F_{6,39} = 31.42$ , Adj.  $R^2 = 0.80$ ,  $P < 0.0001$ ) (Table 4). Increases in nest height, incubation period, and investment in eggs are correlated to increases in nestling period. Using mass growth rates (fixed  $A$ ), the significant variables in the previous model did not differ, but the growth rate (fixed  $A$ ) was no longer included ( $F_{5,40} = 33.47$ , Adj.  $R^2 = 0.78$ ,  $P < 0.0001$ ) (Table 5). When phylogeny was controlled, negative correlations included nestling mass growth rates, nest type, and residuals of the adult wing chord ( $F_{6,39} = 7.68$ , Adj.  $R^2 = 0.47$ ,  $P < 0.0001$ ) (Table 4). Significant positive correlations occurred with incubation period, the residuals of the adult tarsus length, and marginally, to eye-opening. This suggests that passerines with long relative adult tarsus length have short nestling periods while those with long wings relative to their body mass tend to have longer nestling periods. When mass growth rates were replaced with the fixed  $A$  estimates of

nestling growth rate, nest type and incubation remained significant, eye-opening became significant, and positive correlations with nest height and residuals of the egg mass were suggestive ( $F_{5,40} = 7.4$ , Adj.  $R^2 = 0.42$ ,  $P < 0.0001$ ) (Table 5). Additionally, species with short incubation periods generally had short nestling periods. Large egg masses, while not significant, occurred in species with long nestling periods.

#### *Eye-opening:*

Eye-opening was positively correlated to nestling period ( $F_{2,43} = 8.03$ , Adj.  $R^2 = 0.24$ ,  $P < 0.0011$ ; PIC,  $F_{1,44} = 4.75$ , Adj.  $R^2 = 0.08$ ,  $P = 0.0347$ ) (Table 6); however, there was an influential point (golden-collared manakin). Analyses were run with and without this point. When golden-collared manakins were excluded from the dataset, nestling period remained significant suggesting that passerines with long nestling periods opened their eyes later, and though not significant, incubation period was added to the model ( $F_{2,42} = 11.77$ , Adj.  $R^2$ ,  $P < 0.0001$ ;  $F_{1,43} = 7.98$ , Adj.  $R^2 = 0.14$ ,  $P = 0.0071$ ). (Table 7). Birds with short incubation periods tended to open their eyes later in the nestling period. When fixed A was used in the model, the results did not differ from the previous analyses for the conventional least squares regression; however, when phylogeny was controlled nestling period and fixed A growth rate had significant negative correlations with eye-opening (PIC:  $F_{4,40} = 3.77$ , Adj.  $R^2 = 0.20$ ,  $P = 0.0108$ ) (Table 7). Passerine species with later eye-opening also had slow mass growth rates.

#### **Paired Comparisons:**

##### *Mass Growth Rates:*

Limiting the dataset to pairs of closely related species allowed us to simplify the analyses and assess pair-level differences in region. We approached these analyses in two ways. First, we conducted a paired comparison of mass growth rates in two-way ANOVA to assess the effect of pairs and region. PICs could not be analyzed in this manner owing to the need to use indicator variables to generate the contrasts. Next, we compared developmental characteristics of the paired species to other life history variables in conventional least squares regressions estimates as well as phylogenetically independent contrasts. In paired comparisons of nestling mass growth rate, we found that region was significantly correlated while the pairs themselves had little effect on growth rate ( $F_{11,10} = 2.76$ ,  $R^2 = 0.75$ ,  $P = 0.0603$ ). However, the model was not significant owing to the inclusion of the pair variable in the analysis. Vireos, sparrows, and wrens tended to grow quickly while the tyrannids were at the slower end of the distribution. Paired species tended to be similar between regions with more closely related having similar growth and life histories (i.e. vireos, wrens, and robins); however, the suboscine passerines were consistently outliers. Indeed, when one pair of flycatchers was removed, based on outlier analyses, another set replaced it as an outlier. This had no effect on the overall significance of the variables in the paired comparisons. Similarly, paired comparisons using the modified growth rate estimate found the effect of pairs to be more significant than the effect of region ( $F_{11,10} = 5.45$ ,  $R^2 = 0.86$ ,  $P = 0.006$ ). This suggests that the values of the pairs are influencing the patterns of growth rate more so than region.

When paired species' mass growth rates were analyzed with life history traits in adjusted  $R^2$  model selection, significant negative correlations were found with region, nest type, and nestling period ( $F_{5,16} = 13.03$ , Adj.  $R^2 = 0.74$ ,  $P < 0.0001$ ) (Table 10).

Short nestling periods were linked to fast mass growth rates. Marginal negative relationships were found with  $A$ :Adult mass and the residuals of the adult wing chord. Contrasts limited the significant correlations to region,  $A$ :Adult mass and residuals of the adult wing chord ( $F_{4,17} = 10.65$ , Adj.  $R^2 = 0.66$ ,  $P = 0.0002$ ) (Table 10). This suggests that growth rate decreases with adult wing chord length as well as with latitude. When fixed  $A$  estimates of growth rate were compared, we found significant negative correlations with nest type, incubation period, residuals of the adult wing length and residuals of the egg mass, and a positive relationship with residuals of the adult tarsus length ( $F_{6,15} = 6.75$ , Adj.  $R^2 = 0.62$ ,  $P = 0.0013$ ) (Table 11). An increased number of correlations were found using this method. There was also a suggestive correlation to nest type. PICs limited significant negative correlations to incubation period and residuals of the egg mass and adult wing length ( $F_{7,14} = 4.04$ , Adj.  $R^2 = 0.50$ ,  $P = 0.0127$ ) (Table 11). Additionally, nestling period and nest height were found to be marginally correlated to this estimate of nestling growth rate. Species with fast growth rates (fixed  $A$ ) also exhibited short incubation periods and smaller relative egg sizes.

#### *Nestling Period:*

Tropical and temperate birds did not differ in nestling period or the timing of eyes opening. Nestling period was found to have significant negative correlations to region, nest type, and nestling growth rate as well as a positive correlation to incubation period ( $F_{6,15} = 33.68$ , Adj.  $R^2 = 0.90$ ,  $P < 0.0001$ ; PIC,  $F_{6,15} = 6.00$ , Adj.  $R^2 = 0.59$ ,  $P = 0.0023$ ) (Table 12). These models suggest that nestling period is longer in tropical passerines than in temperate birds. However, the inclusion of region for this subset of

species is somewhat confusing and is contrary to previous results. We suggest that this result is influenced by the long nestling periods of several suboscines that are largely frugivorous for instance, *Elaenia flavogaster* and *Elaenia chiriquensis*. We removed the pairs that included the *Elaenia* spp and found that this region was no longer correlated to nestling period; however, nest type and nestling growth rate had negative significant correlations while egg mass (residuals) was positively correlated to duration of the nestling period ( $F_{4,13} = 26.94$ , Adj.  $R^2 = 0.86$ ,  $P < 0.0001$ ) (Table 12). When estimates of fixed  $A$  growth rates were used, nest type and incubation period varied with nestling period ( $F_{5,16} = 21.62$ , Adj.  $R^2 = 0.83$ ,  $P < 0.0001$ ) (Table 13). This suggests that duration of the nestling period increased with the length of the incubation period.

#### *Eye-opening:*

There were no significant correlation between the developmental milestone of eye-opening and other life history variables for paired species ( $F_{4,17} = 2.42$ , Adj.  $R^2 = 0.21$ ,  $P = 0.0889$ ; fixed  $A$ ,  $F_{3,18} = 2.72$ , Adj.  $R^2 = 0.20$ ,  $P = 0.0751$ ) (Table 14). However, once phylogeny was controlled, eye-opening was significantly correlated to clutch size and residuals of the adult tarsus length when conventional growth rate estimates were included in the model ( $F_{5,16} = 1.63$ , Adj.  $R^2 = 0.13$ ,  $P = 0.2095$ ) (Table 14). This suggests that age at eye-opening is earlier in passerines with smaller clutches and later in songbirds with longer tarsi (once adult mass is controlled). Only residuals of the adult tarsus length were correlated to eye-opening when fixed  $A$  growth was included in the model ( $F_{4,17} = 1.71$ , Adj.  $R^2 = 0.12$ ,  $P = 0.1946$ ) (Table 14).



## ***DISCUSSION:***

Past comparative studies have found differences between nestling growth rate in temperate and tropical birds, and our findings continue to support this trend among passerines providing further evidence that the pace of life differs between regions (Ricklefs and Wikelski 2002). This element was significant when a fixed asymptote of adult mass was used, thus, suggesting that other variables were more important in explaining the variation of this trait. Although distributions of growth rates of passerine birds in temperate and tropical regions overlapped, mean growth rates across our samples of species were slow in tropical birds. On average, tropical species grew at a rate of 17% slower than their temperate counterparts (Figure 2) and 23% slower using the modified method of estimating nestling growth rate (Figure 4). Additionally, we found that nestling period did not differ between regions indicating that growth rate is not likely influenced by a latitudinal gradient in nestling period.

We found that the ratio of the asymptotic value (calculated concurrently with  $K$ ) to the adult mass was consistently correlated to the mass growth rate using the conventional means of calculating the estimate. This suggests that while tropical birds do not have a longer nestling period they do have a tendency to fledge at a lower proportion of adult mass than do temperate birds. As is evident from the analyses using both estimates of growth rate compared to a subset of life history traits, the asymptotic value used in calculating the growth rate estimate has important implications in our understanding of the latitudinal variation of growth as well as its relationships with other life history traits. The inclusion of the ratio ( $A$ :Adult mass) in the best fit regression suggests that this is a significant effect which has potential impacts on the interpretation

of the results. Additional research is needed to determine which means of estimating nestling growth rate best describes the entire process of postnatal growth. Until this is resolved, we suggest presenting growth data using both means of estimation. We suggest that other methods of calculating growth using truncated data at a standardized proportion of adult mass may be biasing growth estimates by limiting the information used to calculate nestling growth rates (Remes and Martin 2002; Ferretti et al. 2005). Though standardizing the calculations of growth rates is appealing, all efforts should be made to quantify the entirety of the growth curve.

Comparisons between nestling period and mass growth rate with other life history characteristics generated different results of nestling period with mass growth rate; however, there were general syndromes amongst these developmental variables. For instance, birds with long relative wing lengths tended to have long nestling periods, and slow mass and tarsus growth rates. Additionally, birds that had long nestling periods also tended to open their eyes later. Those with smaller eggs relative to their body size tended to have faster tarsus growth rate while those with large eggs had longer nestling periods; however, phylogeny played some role in the expression of egg mass limiting these correlations when controlled. Many of these relationships are well-established in the literature.

Though nestling period and growth rate are interrelated, our results indicate that these are not interchangeable measures of development. Several prominent studies have been published which use nestling period instead of growth rate, likely due to the availability of information on nestling period (Bosque and Bosque 1995; Tieleman et al 2006). Studies that use nestling period as a surrogate for mass growth rate are probably

producing biased results. A negative correlation between growth rate and nestling period was found in our study; however, the correlation coefficient was very low suggesting that nestling period does not adequately describe nestling growth rate (natural log-transformed  $F_{1,44} = 10.16$   $R^2 = 0.19$ ,  $P = 0.0026$ ; fixed  $A$  growth estimate,  $F_{1,44} = 1.68$ ,  $R^2 = 0.04$ ,  $P = 0.2021$ ). Furthermore, natural selection is likely acting slightly differently on nestling period and mass growth rate with growth being more limited by physiology than nestling period.

Similar to mass growth, tarsus growth was 16% slower in the tropical passerines (Figure 3). Tarsus growth rate should not be affected by the method of calculation of the asymptotic value in the logistic growth equation because almost all passerines in this study fledged at or slightly above the adult value (Austin unpublished data). This suggests that there may be some underlying constraint such as calcium availability imposing a limit on tarsus growth rate, and indirectly mass growth (Dawson and Bidwell 2005). Recent studies of tree swallows (*T. bicolor*) have confirmed that calcium supplementation of nestlings increases the growth rate and the tarsus length (Dawson and Bidwell 2005). Other studies have suggested that mass growth rate may be limited by growth of the most constrained tissues (Starck and Ricklefs 1998). Starck (1993) suggested that the limiting tissue may be the long bones, however, later studies have produced conflicting results (Starck and Ricklefs 1998). Long bone growth is largely dictated by the size of the cartilaginous proliferation zone and the level of ossification of the bone at hatching in altricial nestlings; this tends to vary widely among species (Starck 1993; Starck and Ricklefs 1998). Yet we find a consistent difference between the temperate and tropical regions. This suggests that regional differences in reproductive

strategies or nutrient availability are present and acting on a physiological level across phylogenies.

Length of the nestling period varied with this trait with birds that had short nestling periods typically experiencing the fastest tarsus growth rates. Similar to previous studies, we find that the adult size of the tarsus is correlated to the tarsus growth rate, when mass wasn't controlled ( $F_{1,38} = 6.25$ ,  $P = 0.0168$ ) (Starck 1993). Generally, birds with long adult tarsi also have fast tarsus growth. We didn't find that mass growth is closely related to tarsus growth once phylogeny was controlled, as has been previously suggested (Starck 1993). Tarsus growth rate does tend to have a lower rate than mass growth, which suggests that this character may be imposing some limit on other developmental characteristics. Other important factors associated with tarsus growth were nest type, residuals of the egg mass, and residuals of the adult wing length. Interestingly, when fixed  $A$  growth rate was included instead of conventional nestling growth rates were used, birds that nested closer to the ground tended to have faster tarsus growth and shorter nestling periods than species that nested higher in the understory. Previous studies have suggested a relationship between predation rate and nest height, which may be influencing nestling growth rates of birds that nest lower to the ground (Remes and Martin 2002; Martin 1987). However, we did not investigate the impacts of predation on growth rate here. Additionally, since most species that nest near or on the ground in this study were closely related the effect was removed when PICs were used in the analyses. Additional study, using a broader subset of ground nesting birds from a number of superfamilies, is needed to confirm this result.

Though rate of growth differed between regions, we did not find a similar correlation with clutch size as might be expected. Only when region was removed was clutch size significantly correlated to growth consistently. Phylogeny reduced significance of this effect except when paired species were analyzed. This suggests that region is a better indicator of growth rate (tarsus and both mass estimates) than is clutch size; hence, differences in clutch size have little impact on growth rate at this coarse resolution of analyses.

Unlike tarsus and mass growth, there was no difference between temperate and tropical passerines in the timing of eye-opening in nestlings. Delayed eye-opening in altricial nestlings has generally been considered an indicator of slower maturation of the eyes (Fontanesi et al. 1993; Starck and Ricklefs 1998). However, this is not a well-studied characteristic, with most work being conducted on pigeons or embryonic chickens (Fontanesi et al. 1993). One study found that functioning in the Wulst region of the brain, the visual cortex center in mammals, did not occur until after the eyes open (Khayutin 1985; Starck and Ricklefs 1998). Subsequent studies found that development of the eye in an altricial bird species, the domestic pigeon, occurs during postnatal development with the maturation of the retina being near completion at the age of eye-opening (Fontanesi et al. 1993). In this study, we found that bird species with eyes that open later in the nestling period spend more time within the nest. Age at eye-opening is a precursory attempt to compare a morphological marker of sensory development to life history traits of passerines, and to the best knowledge of the authors, has never been reported in this context. We found that this milestone of post-natal development was influenced by nestling period; however, the correlation from the model was low,

suggesting a poor fit, and when only closely-related paired species were examined, there were no significant correlations until phylogeny was controlled. When phylogeny was controlled using paired species, only clutch size and residuals of the adult tarsus length were significantly related to age of eye-opening.

There appears to be some flexibility in the expression of this trait with some birds opening their eyes later in development. However, there are only two birds in this study that open their eyes prior to three days of age, both were antbirds. Most birds in this study do not open their eyes before 4 days of age. Birds that nest in cavities appeared to open their eyes slightly later than open-cup nesting birds. Two tropical species represented the extreme ages of this developmental milestone. Barred antshrikes (*Thamnophilus doliatus*) opened their eyes on their hatch day while golden-collared manakins (*Manacus vitellinus*) were not observed with their eyes open until 9 days of age. Why these two suboscines would be so different in average age of eye-opening is not readily apparent to the authors, and further research regarding interspecific differences in this developmental milestone should be conducted. Generally, the antbird species included in this study opened their eyes earlier than other species, with white-bellied antbirds at age 2 d and chestnut-backed antbirds at age 3 d. Skutch (1969) noted that nestlings of great antshrikes (*Taraba major*), had eyes open by 2 days of age; however, other antbird species (Thamnophilidae) were documented to open their eyes between days 5 and 7 (*Thamnophilus atrinucha* and *Gymnopithys leucaspis*; Skutch 1969). The variation in this trait exhibited by antbirds is interesting given the similarities in foraging mode and many life history traits.

Research has focused primarily on a temperate-tropical divergence in the expression of life history phenotypes, and our data continues to support this trend in both mass and tarsus growth. However, we feel that another aspect of the temperate-tropical dichotomy should be explored, namely differences in the variation in these traits between regions. Generally, we found that temperate passerine species tended to exhibit less variability for many nestling characteristics compared to their tropical counterparts, which included passerine species at the extremes of life history phenotypes (Figure 2). This suggests that the diversity of life histories occurring among passerines in the tropics is greater than in the temperate zone. Differences in variation of life histories between regions may provide insight into how the ecological characteristics of each region influence the physiological limits of passerines, and thus, the evolution of life histories.

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Table 1: Observed differences in traits of temperate and tropical passerines, and the predicted relationships with mass and tarsus growth rate ( $K$ ).

Life History Variable	Temperate	Tropical	Growth Rate
clutch size	larger	smaller	negative
egg mass	smaller	larger	positive
incubation period	shorter	longer	negative
nestling period	similar	similar	negative
parental care (uni vs. bi)	-	-	uni (slower); bi (faster)
nest type (open vs. closed)	-	-	open (faster); closed (slower)
nest height (low, medium, high)	-	-	negative
adult tarsus length	-	-	similar
adult wing length	-	-	negative
age at eye opening	-	-	similar

Table 2: Results from model selection of nestling mass growth rate in least squares regression on life history traits.

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr >  t	Variable: PIC	DF	Parameter Estimate	Standard Error	t Value	Pr >  t
Intercept	1	0.721	0.297	2.430	0.020	nest height	1	-0.089	0.089	-1.010	0.319
region	1	-0.145	0.047	-3.070	0.004	region	1	-0.106	0.046	-2.290	0.028
nest type	1	-0.194	0.069	-2.800	0.008	residuals of ln egg mass	1	-0.317	0.186	-1.700	0.097
ln nestling period	1	-0.363	0.102	-3.550	0.001	ln nestling period	1	-0.154	0.135	-1.140	0.261
eye-opening	1	-0.023	0.017	-1.390	0.173	eye-opening	1	-0.033	0.016	-2.030	0.050
residuals of ln adult wing length	1	-0.118	0.079	-1.490	0.144	residuals of ln adult wing length	1	-0.404	0.125	-3.230	0.003
A:Adult mass	1	-0.355	0.131	-2.700	0.010	A:Adult mass	1	-0.455	0.113	-4.040	0.000
						residuals of ln adult tarsus length	1	0.180	0.109	1.660	0.106

Table 3: Results from model selection of nestling growth rate, using a fixed asymptote of adult mass, in least squares regression on life history traits.

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr >  t	Variable: PIC	DF	Parameter Estimate	Standard Error	t Value	Pr >  t
Intercept	1	1.455	0.604	2.410	0.021	residuals of ln egg mass	1	-0.39657	0.21623	-1.83	0.0741
region	1	-0.074	0.073	-1.010	0.319	residuals of ln adult wing length	1	-0.38313	0.12002	-3.19	0.0027
nest type	1	-0.256	0.103	-2.500	0.017	nest height	1	-0.11663	0.10401	-1.12	0.2688
nest height	1	-0.130	0.106	-1.220	0.229	eye-opening	1	-0.05042	0.02035	-2.48	0.0175
ln incubation period	1	-0.493	0.280	-1.760	0.086	ln incubation period	1	-0.61129	0.28795	-2.12	0.04
ln nestling period	1	-0.292	0.187	-1.560	0.127						
eye-opening	1	-0.027	0.022	-1.230	0.228						
residuals of ln adult wing length	1	-0.293	0.098	-2.990	0.005						

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr >  t	Variable: PIC	DF	Parameter Estimate	Standard Error	t Value	Pr >  t
Intercept	1	0.625	0.374	1.670	0.103	residuals of ln adult wing length	1	-0.25149	0.11035	-2.28	0.0282
nest type	1	-0.354	0.052	-6.760	<.0001	nest type	1	-0.28109	0.09763	-2.88	0.0064
nest height	1	0.182	0.069	2.640	0.012	residuals of ln adult tarsus length	1	0.26682	0.07962	3.35	0.0018
ln incubation period	1	0.712	0.154	4.630	<.0001	eye-opening	1	0.02801	0.01495	1.87	0.0685
eye-opening	1	0.020	0.015	1.270	0.213	ln incubation period	1	0.75972	0.21746	3.49	0.0012
residuals of ln egg mass	1	0.449	0.120	3.730	0.001	ln growth rate	1	-0.25807	0.11202	-2.3	0.0266
ln growth rate	1	-0.263	0.119	-2.210	0.033						

Table 5: Results from model selection of duration of nestling period in least squares regression on life history traits (fixed A nestling growth rate).

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr >  t	Variable: PIC	DF	Parameter Estimate	Standard Error	t Value	Pr >  t
Intercept	1	0.437	0.382	1.140	0.260	residuals of ln egg mass	1	0.31881	0.16285	1.96	0.0573
nest type	1	-0.336	0.054	-6.200	<.0001	nest type	1	-0.33187	0.10166	-3.26	0.0023
nest height	1	0.220	0.070	3.150	0.003	nest height	1	0.14671	0.07856	1.87	0.0692
ln incubation period	1	0.850	0.147	5.760	<.0001	eye-opening	1	0.03742	0.01521	2.46	0.0183
eye-opening	1	0.026	0.016	1.650	0.107	ln incubation period	1	0.77924	0.21397	3.64	0.0008
residuals of ln egg mass	1	0.467	0.126	3.710	0.001						

Table 6: Results from model selection of eye-opening in least squares regression on life history traits.

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr >  t	Variable: PIC	DF	Parameter Estimate	Standard Error	t Value	Pr >  t
Intercept	1	-0.605	1.799	-0.340	0.738	In nestling period	1	2.34557	1.07642	2.18	0.0347
parental care	1	-1.246	0.780	-1.600	0.117	Variable: PIC (model includes fixed A growth rate)	DF	Parameter Estimate	Standard Error	t Value	Pr >  t
In nestling period	1	2.361	0.632	3.740	0.001						
						residuals of ln adult tarsus length	1	-1.04856	0.68291	-1.54	0.1324
						In incubation period	1	-3.02071	2.22087	-1.36	0.1812
						In nestling period	1	2.70643	1.17738	2.3	0.0267
						In growth rate (fixed A)	1	-1.92549	0.93055	-2.07	0.0449

Table 7: Results from model selection of eye-opening in least squares regression on life history traits without the outlier *Manacus vitellinus*.

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr >  t	Variable: PIC	DF	Parameter Estimate	Standard Error	t Value	Pr >  t
Intercept	1	1.181	2.983	0.400	0.694	ln nestling period	1	2.57958	0.91311	2.83	0.0071
ln incubation period	1	-1.612	1.240	-1.300	0.201						
ln nestling period	1	2.817	0.588	4.790	<.0001						



Table 8: Results from model selection of tarsus growth rate in least squares regression on life history traits.

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr >  t	Variable: PIC	DF	Parameter Estimate	Standard Error	t Value	Pr >  t
Intercept	1	1.440	0.348	4.140	0.000	parental care	1	0.2573	0.14865	1.73	0.0934
clutch size	1	-0.064	0.026	-2.460	0.020	region	1	-0.05884	0.04894	-1.2	0.2384
residuals of ln adult wing length	1	0.066	0.049	1.330	0.192	residuals of ln adult tarsus length	1	0.95326	0.0834	11.43	<.0001
residuals of ln egg mass	1	-0.262	0.099	-2.660	0.012	nest type	1	0.33278	0.09311	3.57	0.0012
ln growth rate	1	0.644	0.116	5.550	<.0001	residuals of ln egg mass	1	-0.37357	0.16728	-2.23	0.0329
Region	1	-0.084	0.055	-1.530	0.137	residuals of ln adult wing length	1	0.65105	0.09857	6.61	<.0001
eye-opening	1	-0.017	0.012	-1.360	0.184	ln nestling period	1	0.27796	0.11954	2.33	0.0268
ln incubation period	1	-0.585	0.123	-4.750	<.0001	ln growth rate	1	0.2043	0.145	1.41	0.1688

Table 9: Results from model selection of tarsus growth rate in least squares regression on life history traits (fixed A mass growth rate).

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr >  t	Variable: PIC	DF	Parameter Estimate	Standard Error	t Value	Pr >  t
Intercept	1	0.578	0.360	1.600	0.119	parental care	1	0.27875	0.15012	1.86	0.0726
region	1	-0.102	0.043	-2.380	0.024	region	1	-0.09092	0.04399	-2.07	0.0469
nest type	1	0.130	0.070	1.860	0.072	residuals of ln adult tarsus length	1	0.98097	0.08229	11.92	<.0001
nest height	1	-0.138	0.066	-2.090	0.045	nest type	1	0.32281	0.09425	3.42	0.0017
ln incubation period	1	-0.310	0.166	-1.860	0.072	residuals of ln egg mass	1	-0.41231	0.16752	-2.46	0.0194
ln nestling period	1	-0.201	0.117	-1.720	0.096	residuals of ln adult wing length	1	0.60541	0.09451	6.41	<.0001
ln growth rate (fixed A)	1	0.244	0.086	2.850	0.008	ln nestling period	1	0.20528	0.10949	1.87	0.07
residuals of ln adult tarsus length	1	0.170	0.058	2.960	0.006						
residuals of ln egg mass	1	-0.381	0.131	-2.910	0.007						

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Table 10: Results from least squares regression of nestling mass growth rate on life history traits using closely related paired species.

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr >  t	Variable: PIC	DF	Parameter Estimate	Standard Error	t Value	Pr >  t
Intercept	1	1.177	0.318	3.700	0.002	ln nestling period	1	-0.231	0.164	-1.410	0.177
region	1	-0.183	0.048	-3.800	0.002	residuals of ln adult wing length	1	-0.262	0.117	-2.240	0.039
nest type	1	-0.319	0.074	-4.280	0.001	A:Adult mass	1	-0.326	0.104	-3.140	0.006
ln nestling period	1	-0.576	0.108	-5.310	<.0001	region	1	-0.134	0.042	-3.190	0.005
residuals of ln adult wing length	1	-0.092	0.076	-1.210	0.242						
A:Adult mass	1	-0.203	0.117	-1.740	0.101						

Table 11: Results from least squares regression of nestling mass growth rate (fixed A) on life history traits using closely related paired species.

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr >  t	Variable: PIC	DF	Parameter Estimate	Standard Error	t Value	Pr >  t
Intercept	1	2.373	1.023	2.320	0.035	ln incubation period	1	-2.119	0.701	-3.020	0.009
nest type	1	-0.322	0.104	-3.080	0.008	ln nestling period	1	0.600	0.296	2.020	0.063
nest height	1	-0.350	0.174	-2.010	0.063	nest height	1	-0.411	0.198	-2.080	0.057
ln incubation period	1	-1.147	0.391	-2.930	0.010	clutch size	1	-0.068	0.051	-1.340	0.201
residuals of ln adult tarsus length	1	0.504	0.221	2.280	0.037	residuals of ln adult wing length	1	-0.756	0.256	-2.950	0.011
residuals of ln adult wing length	1	-0.596	0.169	-3.520	0.003	residuals of ln egg mass	1	-2.040	0.580	-3.520	0.003
residuals of ln egg mass	1	-1.647	0.527	-3.130	0.007	residuals of ln adult tarsus length	1	0.514	0.310	1.660	0.120

Table 12: Results from least squares regression of nestling period on life history traits using closely related paired species.

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr >  t	Variable: PIC	DF	Parameter Estimate	Standard Error	t Value	Pr >  t
Intercept	1	0.285	0.594	0.480	0.639	nest type	1	-0.474	0.158	-3.010	0.009
region	1	-0.282	0.092	-3.080	0.008	clutch size	1	-0.081	0.050	-1.600	0.131
nest type	1	-0.476	0.075	-6.390	<.0001	residuals of ln egg mass	1	0.375	0.220	1.710	0.108
clutch size	1	-0.087	0.047	-1.840	0.085	region	1	-0.207	0.084	-2.460	0.027
residuals of ln egg mass	1	0.183	0.164	1.120	0.280	ln incubation period	1	0.882	0.374	2.360	0.032
ln growth rate	1	-0.570	0.158	-3.600	0.003	ln growth rate	1	-0.435	0.162	-2.690	0.017
ln incubation period	1	1.013	0.243	4.160	0.001						

Table 13: Results from least squares regression of nestling period on life history traits using closely related paired species (nestling growth rate using fixed A included in model).

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr >  t	Variable: PIC	DF	Parameter Estimate	Standard Error	t Value	Pr >  t
Intercept	1	-0.304	0.756	-0.400	0.693	nest type	1	-0.392	0.180	-2.170	0.046
region	1	-0.201	0.118	-1.710	0.106	nest height	1	0.130	0.098	1.320	0.205
nest type	1	-0.416	0.096	-4.330	0.001	residuals of ln adult wing length	1	0.209	0.136	1.530	0.146
clutch size	1	-0.108	0.062	-1.740	0.101	residuals of ln egg mass	1	0.646	0.301	2.140	0.049
residuals of ln egg mass	1	0.342	0.208	1.640	0.121	ln growth rate (fixed A)	1	0.237	0.157	1.510	0.151
ln incubation period	1	1.420	0.285	4.970	0.000	ln incubation period	1	1.102	0.419	2.630	0.019

Table 14: Results from least squares regression of eye-opening on life history traits using closely related paired species.

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr >  t	Variable: PIC	DF	Parameter Estimate	Standard Error	t Value	Pr >  t
Intercept	1	4.464	1.890	2.360	0.030	nest height	1	-1.379	0.736	-1.870	0.080
ClutchSize	1	-0.494	0.253	-1.950	0.067	clutch size	1	-0.486	0.229	-2.130	0.049
residuals of In adult tarsus length	1	0.784	0.440	1.780	0.092	residuals of In adult wing length	1	-1.054	1.040	-1.010	0.326
In nestling period	1	1.348	0.811	1.660	0.115	residuals of In adult tarsus length	1	2.012	0.909	2.210	0.042
In growth rate	1	2.289	1.340	1.710	0.106	In growth rate	1	1.212	1.099	1.100	0.286

Table 15: Results from least squares regression of eye-opening on life history traits using closely related paired species (nestling growth rate using fixed A included in model).

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr >  t	Variable: PIC	DF	Parameter Estimate	Standard Error	t Value	Pr >  t
Intercept	1	5.930	0.939	6.320	<.0001	nest height	1	-1.396	0.741	-1.890	0.077
nest type	1	-0.695	0.463	-1.500	0.151	clutch size	1	-0.368	0.203	-1.810	0.088
clutch size	1	-0.311	0.206	-1.510	0.149	residuals of ln adult wing length	1	-1.148	1.043	-1.100	0.287
residuals of ln adult tarsus length	1	0.751	0.392	1.910	0.072	residuals of ln adult tarsus length	1	1.913	0.911	2.100	0.051



Figure 1: Tarsus length (mm) and natural log-transformed tarsus length of blue-gray tanager nestlings of known age through the nestling period. Transformation was applied to improve the distribution of the dataset.

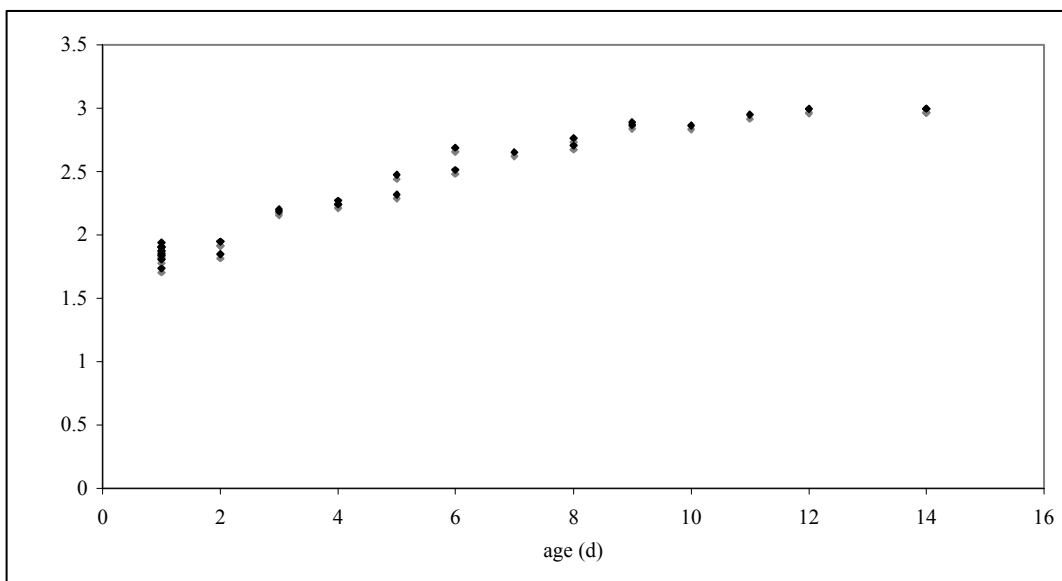
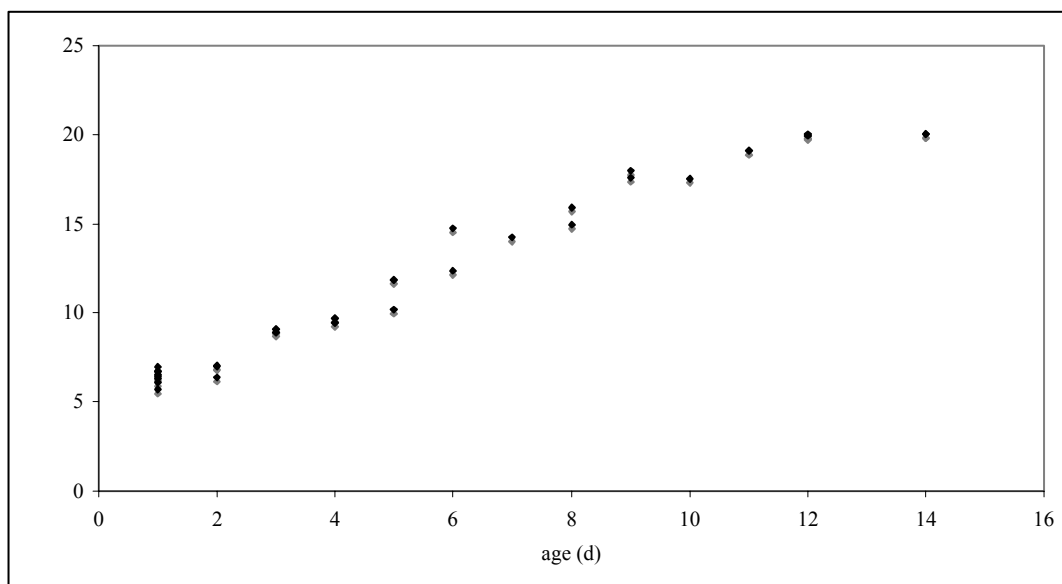


Figure 2: Mass growth rate (K) of temperate and tropical passerines by frequency count.

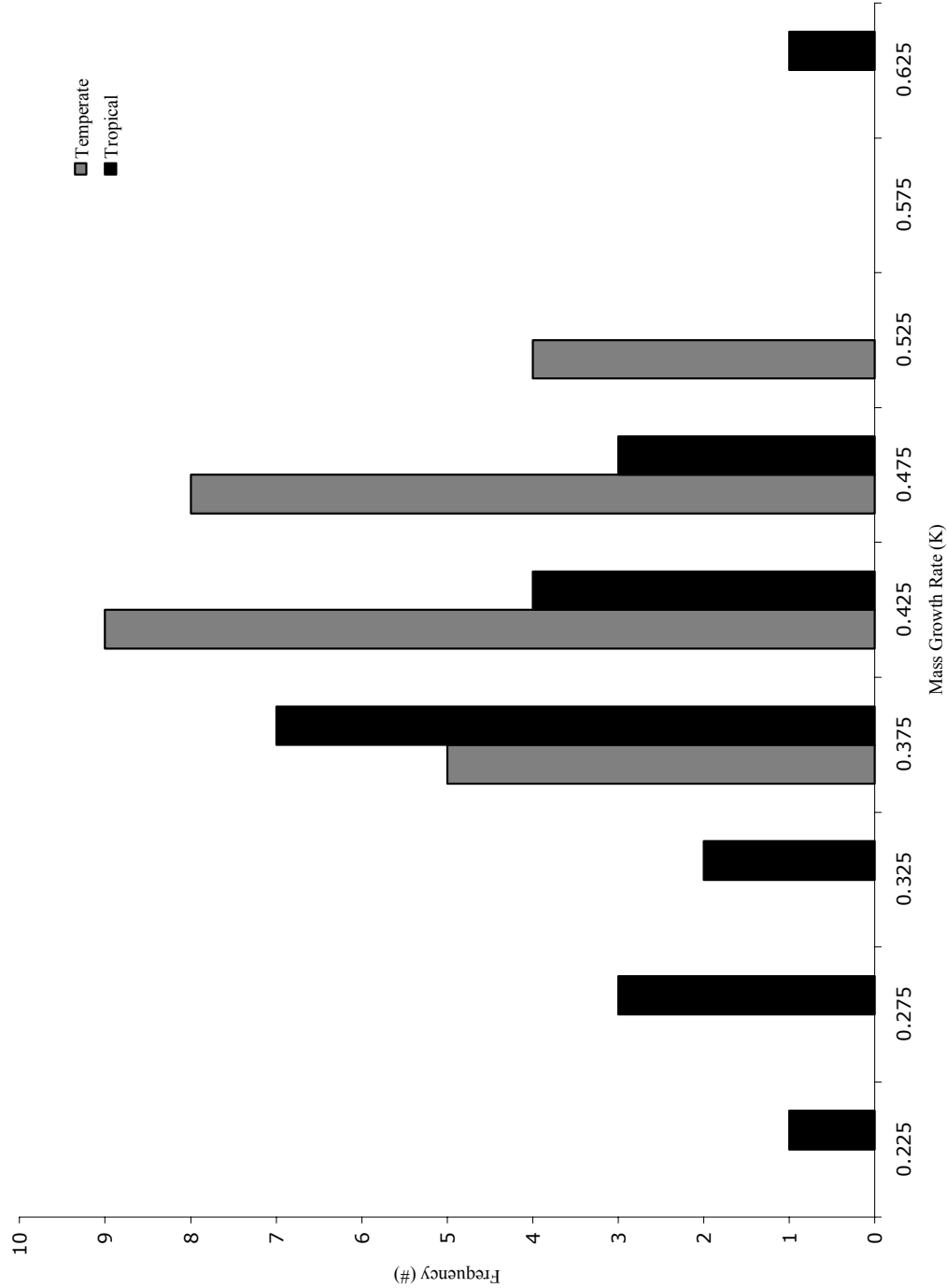


Figure 3: Tarsus growth rate (K) of temperate and tropical passerines by frequency count.

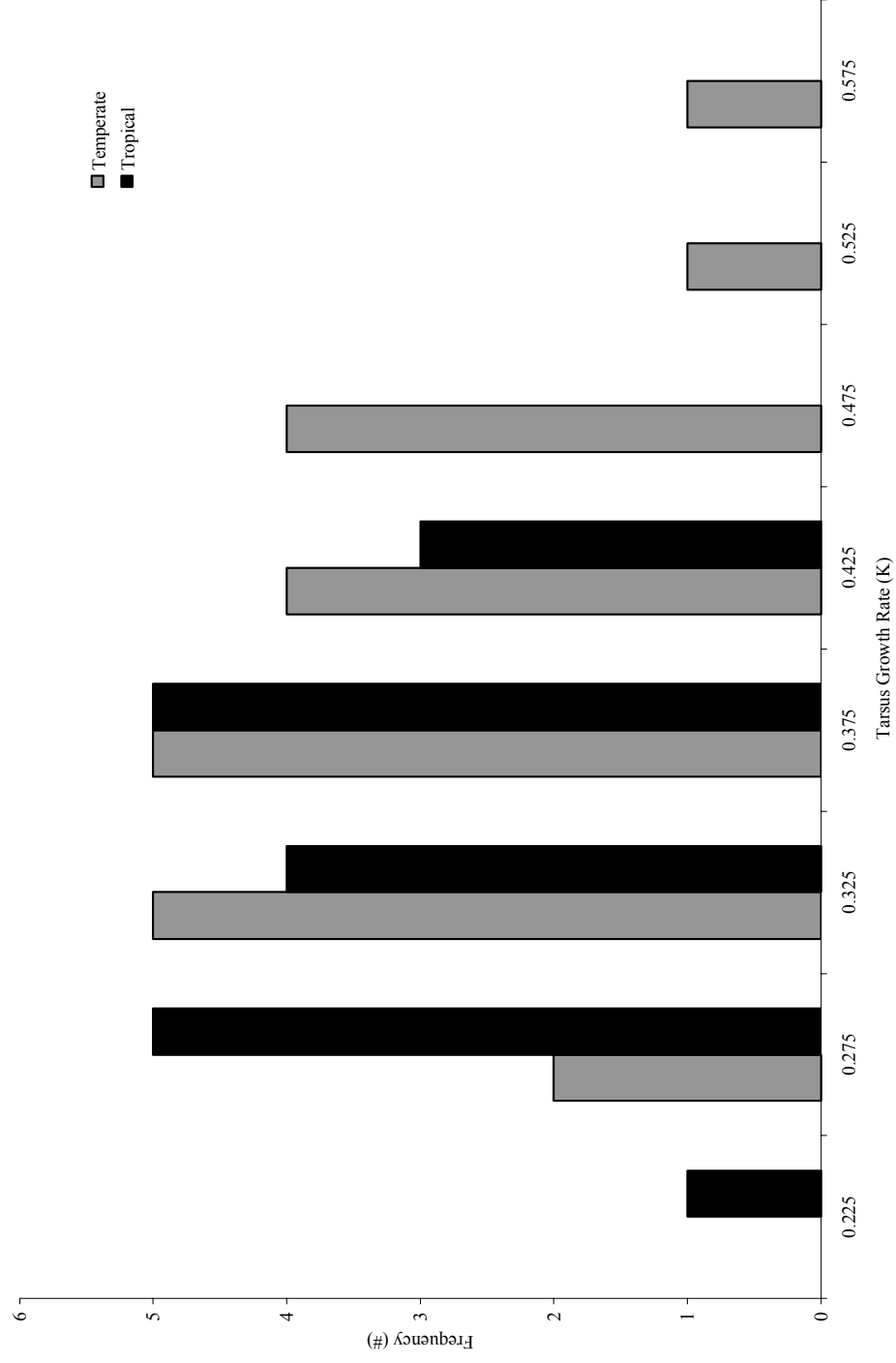
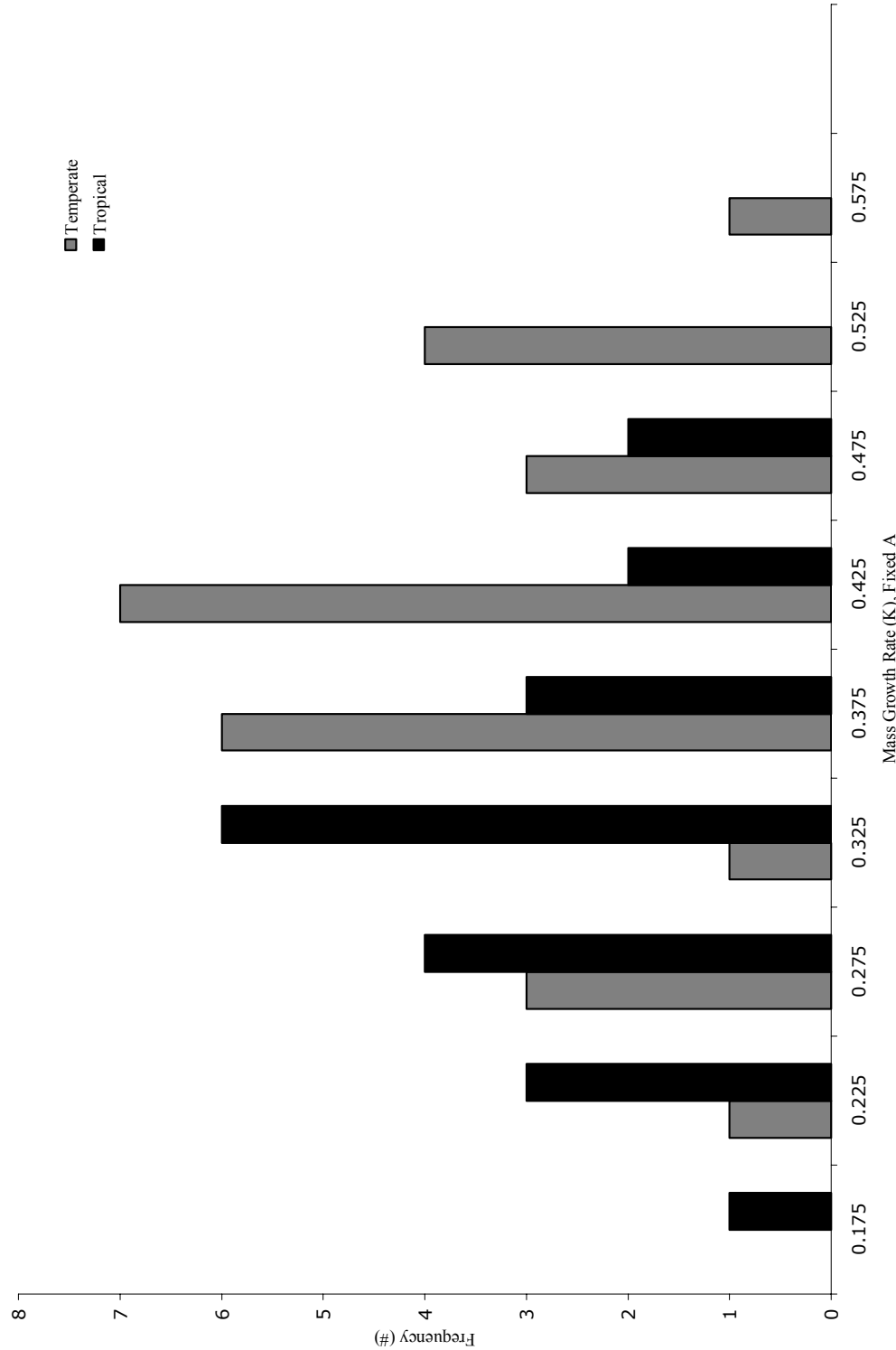


Figure 4: Mass growth rate (K) using the fixed asymptote of adult mass for temperate and tropical passerines by frequency count.



## **Chapter 3: CONCLUSIONS**

### **Life history synopsis**

Suzanne Austin-Bythell

Life history evolution of temperate and tropical passerines has received increased interest recently (Ferretti et al. 2005; Martin et al. 2000; Martin 2004; Martin et al. 2006; Geffen and Yom-Tov 2000; Russell et al. 2004; Stoleson and Beissinger 2001; Ricklefs and Wikelski 2002); however, comprehensive studies of developmental rate have been lacking or have focused on the simplistic measurement of nestling period (Roff et al. 2006; Geffen and Yom-Tov 2000; Bosque and Bosque 1995). Single-species studies documenting growth rate are not uncommon, but not since Ricklefs (1976) has a large-scale comparison of temperate and tropical passerines been conducted. The present study confirms the original result that a temperate-tropical difference in mass growth rates exists among passerine birds. We included other metrics of development by including long-bone growth, neurological development, and nestling period. We also included growth rates for several species that were previously unreported such as: wrenit, white-bellied antbird, rose-breasted grosbeak, golden-fronted greenlet, flame-rumped tanager, and yellow-olive flycatcher. Through the confirmation of temperate-tropical differences, empirical studies can now be crafted to address why growth strategies of passerines might differ between the regions, and potential trade-offs that each strategy may entail.

***Priorities for future research:***

Growth rate data for birds are especially limited in the tropics; thus, researchers conducting reproductive studies on birds in tropical regions should make an effort to collect growth data on several nests per species in order to add to the body of knowledge of growth rates in the tropics. These should be published in peer-reviewed journals. Even among bird species in the temperate zone, which are relatively well-studied, growth data are lacking. Efforts to fill these holes should be made, as developmental rates are vital to

our understanding of the life history strategies of birds (Ricklefs 1996). Collection and publication of both mass and long bone growth rates should become common practice.

Further research should be conducted on the progression of neurological development among altricial birds. This study is the first to address how the developmental milestone of eye-opening differs among passerine species, as well as how it relates to other life history characteristics. However, our study was merely a preliminary step. Measuring other rates of neurological development that could be conducted easily in the field would assist in our general understanding of avian development patterns. With the increase in programs like MARK, which require accurate estimates of nestling age in order to assess predation rates, understanding and providing measures of growth and age of developmental milestones will become more important. Thus, we have taken a first step by providing our models of age estimation based on morphological measures, as well as the ages of developmental milestones, to assist others working in the temperate and tropical regions in their research. We hope this study will encourage others to pursue understanding in developmental characteristics in the context of life history and phylogeny.

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Appendix 1: Life history traits of temperate and tropical passerines. Length of the incubation period (d) (mean length from raw data, and median value from literature if a range was given), length of nestling period (d) (same procedure as incubation period), and age of nestlings when eyes open. Data from this study unless otherwise specified.

Species	region	incubation period	nestling period	eyes open	references
black-striped sparrow <i>Arremonops conirostris</i>	trop	15	14	3	
cedar waxwing <i>Bombicilla cedorum</i>	temp	12	15.5	3.5	Witmer et al. 1997
northern cardinal <i>Cardinalis cardinalis</i>	temp	11	9	4	Halkin and Linville 1999
American goldfinch <i>Carduelis tristis</i>	temp	13	12	4	Middleton 1993
house finch <i>Carpodacus mexicanus</i>	temp	13.5	12	3	Hill 1993
wrentit <i>Chamaea fasciata</i>	temp	14.9	14.6	6	Geupel and Balliard 2002
yellow warbler <i>Dendroica petechia</i>	temp	11.9	9	3	Lowther et al. 1999
gray catbird <i>Dumetella carolinensis</i>	temp	12.9	10.5	4	Cimprich and Moore 1995
lesser elaenia <i>Elaenia chiriquensis</i>	trop	15	16	4	
yellow-bellied elaenia <i>Elaenia flavogaster</i>	trop	16.1	17.3	3.5	Weeks 1994; Skutch 1960
willow flycatcher <i>Empidonax trailii</i>	temp	14.8	13.8	3.5	Sedgewick 2000
thick-billed euphonia <i>Euphonia lanirostris</i>	trop	14	19	4	
red-throated ant- tanager <i>Habia fuscicauda</i>	trop	14	10	6	
golden-fronted greenlet <i>Hylophilus aurantiifrons</i>	trop	-	-	4	
golden-collared manakin <i>Manacus vitellinus</i>	trop	18	12	9	
song sparrow <i>Melospiza melodia</i>	temp	13	9	4	Arcese et al. 2002

Species	region	incubation period	nestling period	eyes open	references
brown-headed cowbird <i>Molothrus ater</i>	trop	11	12	4	Lowther 1993
shiny cowbird <i>Molothrus bonariensis</i>	temp	11	10.5	2	
streaked flycatcher <i>Myiodynastes maculatus</i>	trop	16	20	6	
chestnut-backed antbird <i>Myrmeciza exsul</i>	trop	16	11	3	
white-bellied antbird <i>Myrmeciza longipes</i>	trop	16	10	2	
house sparrow <i>Passer domesticus</i>	temp	11	14	3	Lowther and Cink 2006
rose-breasted grosbeak <i>Pheucticus ludovicianus</i>	temp	12	10	-	Wyatt and Francis 2002
eastern towhee <i>Pipilo erythrophthalmus</i>	temp	12	10.5	4	Greenlaw 1996
blue-crowned manakin <i>Pipra coronata</i>	trop	16	10	4	Skutch 1969
red capped manakin <i>Pipra mentalis</i>	trop	20.8	12.6	4	
black-capped chickadee <i>Poecile atricapilla</i>	temp	12.5	16	6	Starck and Ricklefs 1998; Smith 1991; Smith 1993
gray-breasted martin <i>Progne chalybea</i>	trop	15	28	7	
purple martin <i>Progne subis</i>	temp	16.5	28.5	6	Brown 1997
crimson-backed tanager <i>Rhamphocelus dimidiatus</i>	trop	13	12	5	
flame-rumped tanager <i>Rhamphocelus flammigerus</i>	trop	13	12	3	
buff-throated saltator <i>Saltator maxinus</i>	trop	14	13	5	
eastern phoebe <i>Sayornis phoebe</i>	temp	16	16	5	Murphy 1981

Species	region	incubation period	nestling period	eyes open	references
western bluebird <i>Sialia mexicana</i>	temp	13.7	21	7.5	unpub. Austin and Robinson; Guinan et al. 2000
eastern bluebird <i>Sialia sialis</i>	temp	14	18.8	5	Gowaty and Plissner 1998
white-breasted nuthatch <i>Sitta carolinensis</i>	temp	13	26	9	Pravosudov and Grubb 1993
chipping sparrow <i>Spizella passerina</i>	temp	11	10.5	4	Middleton 1998
field sparrow <i>Spizella pusilla</i>	temp	11.5	7.5	3	Carey et al. 1994
variable seedeater <i>Sporophila americana</i>	trop	12.5	10	5.5	
mangrove swallow <i>Tachycineta albilinea</i>	trop	17	18	4	Moore 1997; Dyrce 1984; Weeks 1994; eyes open estimated from tree swallow and bahama swallow data
tree swallow <i>Tachycineta bicolor</i>	temp	14.5	20	4	Robertson et al. 1992
violet-green swallow <i>Tachycineta thalassina</i>	temp	14.5	23.5	8	unpub. Austin and Robinson; Brown et al. 1992
golden-hooded tanager <i>Tangara larvata</i>	trop	13	13	7	Skutch 1954
barred antshrike <i>Thamnophilus doliatus</i>	trop	14	9	1	
blue-gray tanager <i>Thraupis epicopus</i>	trop	14	13	5	Skutch 1969
common tody- flycatcher <i>Todirostrum cinereum</i>	trop	23	16	4	
yellow-olive flycatcher <i>Tolmomyias sulphurescens</i>	trop	17.5	22	7	Skutch 1960
house wren <i>Troglodytes aedon</i>	temp	13	16	4	Johnson 1998
southern house wren <i>Troglodytes aedon</i>	trop	13.5	17	4	
clay-colored robin <i>Turdus grayi</i>	trop	14	10	5	Weeks 1994
American robin <i>Turdus migratorius</i>	temp	13	13	4	Sallabanks and James 1999

Species	region	incubation period	nestling period	eyes open	references
scissor-tailed flycatcher <i>Tyrannus forficatus</i>	temp	14.7	15.4	-	Murphy 1988; Regosin 1998
tropical kingbird <i>Tyrannus melancholicus</i>	trop	15.5	18.5	4	
eastern kingbird <i>Tyrannus tyrannus</i>	temp	15.4	16.5	5	Murphy 1981; Murphy 1988; Murphy 1996
western kingbird <i>Tyrannus verticalis</i>	temp	14	16	4	Murphy 1988; Gamble and Bergin 1996
yellow-green vireo <i>Vireo flavoviridis</i>	trop	14	11	5.5	Skutch 1960
red-eyed vireo <i>Vireo olivaceus</i>	temp	12.8	11	3.5	Southern 1958; Cimprich et al. 2000

## Appendix 2: Age estimation models of passerine species.

Species	n	Adj. R <sup>2</sup>	Model
<i>Arremonops conirostris</i>	6	0.97	age=-7.00714+4.1973*ln(wing)
<i>Cardinalis cardinalis</i>	9	0.95	age=-8.3056+3.36416*ln(bill)+2.61102*ln(wing)
<i>Carpodacus mexicanus</i>	13	0.97	age=-8.36942+1.22192*ln(tarsus)+3.86557*ln(wing) age=-9.47188+3.48861*ln(tarsus)+1.44439*ln(wing)+
<i>Chamaea fasciata</i>	39	0.93	1.9703*ln(wing)
<i>Dendroica petechia</i>	20	0.96	age=-6.24116+1.0455*ln(tarsus)+3.11862*ln(wing)
<i>Dumetella carolinensis</i>	34	0.95	age=-8.80996+1.2329*ln(tarsus)+3.46172*ln(wing) age=-11.1882+3.12063*ln(tarsus)+-1.54885*ln(bill)+
<i>Elaenia chiriquensis</i>	7	0.99	4.32568*ln(wing)
<i>Elaenia flavogaster</i>	15	0.95	age=-15.38816+3.91578*ln(tarsus)+4.78188*ln(wing)
<i>Empidonax trailii</i>	15	0.98	age=-7.80527+1.83857*ln(tarsus)+1.46494*ln(bill)+2.4319*ln(wing) age=-11.63207+1.33756*ln(tarsus)+5.53663*ln(bill)+
<i>Euphonia lanirostris</i>	20	0.95	4.40617*ln(wing)
<i>Manacus vitellinus</i>	5	0.98	age=-13.92428+3.88706*ln(tarsus)+3.86885*ln(wing) age=-7.17506+2.24784*ln(tarsus)+2.19738*ln(bill)+
<i>Melospiza melodia</i>	8	0.93	1.08916*ln(wing)
<i>Molothrus ater</i>	6	0.92	age=-5.38322+-3.08599*ln(bill)+4.70143*ln(wing)
<i>Molothrus bonariensis</i>	4	0.98	age=-9.99295+2.07972*ln(tarsus)+6.85836*ln(bill)
<i>Myiodynastes maculatus</i>	3	0.98	age=-8.88432+-3.63281*ln(tarsus)+8.18907*ln(wing)
<i>Myrmeciza longipes</i>	7	0.93	age=-13.38736+4.0067*ln(tarsus)+-2.4724*ln(bill)+3.16172*ln(wing) age=-7.72098+-2.10995*ln(tarsus)+5.41634*ln(bill)+
<i>Passer domesticus</i>	5	0.97	3.74401*ln(wing)
<i>Pipra mentalis</i>	5	0.98	age=-9.56163+2.83263*ln(bill)+4.63779*ln(wing)
<i>Progne subis</i>	11	0.99	age=-10.77184+6.29868*ln(wing)
<i>Rhamphocelus dimidiatus</i>	22	0.96	age=-9.58321+3.6653*ln(tarsus)+1.95418*ln(wing)
<i>Rhamphocelus flammigerus</i>	2	0.99	age=-3.77576+-3.35503*ln(tarsus)+6.26408*ln(wing)
<i>Saltator maxinus</i>	6	0.98	age=-8.27888+4.66249*ln(wing) age=-11.9355+2.35862*ln(tarsus)+-
<i>Sayornis phoebe</i>	15	0.97	1.54356*ln(bill)+4.73803*ln(wing) age=-8.97314+-0.75956*ln(tarsus)+6.15534*ln(bill)+
<i>Sialia mexicana</i>	37	0.92	3.45206*ln(wing)
<i>Sialis sialis</i>	15	0.98	age=-10.10127+3.26084*ln(bill)+4.13404*ln(wing)
<i>Spizella passerina</i>	20	0.96	age=-5.26831+2.16767*ln(bill)+2.61631*ln(wing)
<i>Spizella pusilla</i>	14	0.96	age=-6.2448+0.99804*ln(tarsus)+2.99816*ln(wing)
<i>Sporophila americana</i>	12	0.92	age=-6.71147+2.28305*ln(tarsus)+2.50536*ln(wing)
<i>Tachycineta bicolor</i>	70	0.97	age=-7.7356+-0.61747*ln(tarsus)+1.82293*ln(bill)+4.68504*ln(wing)
<i>Tachycineta thalassina</i>	48	0.97	age=-8.84148+-0.7181*ln(tarsus)+0.75803*ln(bill)+6.17482*ln(wing)
<i>Thraupis epicopus</i>	10	0.97	age=-10.05151+5.77081*ln(wing)
<i>Todirostrum cinereum</i>	21	0.97	age=-8.47592+3.02018*ln(bill)+5.11905*ln(wing)
<i>Tolmomyias sulphurescens</i>	2	0.97	age=-14.90449+5.08949*ln(tarsus)+3.77502*ln(wing) age=-7.74168+1.36822*ln(tarsus)+0.65863*ln(bill)+
<i>Troglodytes aedon aedon</i>	83	0.95	3.62566*ln(wing) age=-9.75156+1.24078*ln(tarsus)+0.74373*ln(bill)+
<i>Turdus grayi</i>	83	0.91	3.54594*ln(wing)
<i>Turdus migratorius</i>	51	0.96	age=-9.37172+1.701*ln(tarsus)+-0.71672*ln(bill)+3.35542*ln(wing)
<i>Vireo flavoviridis</i>	7	0.97	age=-8.73883+2.3589*ln(tarsus)+3.14289*ln(wing) age=-10.07275+1.00949*ln(tarsus)+-1.51304*ln(bill)+
<i>Vireo olivaceus</i>	3	0.99	4.96303*ln(wing)

Appendix 3: Developmental markers by age (d) of feather development in nestlings for birds of known and estimated ages.

Species	n	Naked	Natal Down	Wing feathers breaking skin	Pin feathers <5mm	Pin feathers 5-15mm	Wing feathers broken	Wing feathers complete
<i>Arremonops conirostris</i>	7		1	3	5	5	9	14
<i>Cardinalis cardinalis</i>	20		1		2	4	7	9
<i>Carpodacus mexicanus</i>	33		1	4	5	5	8	12
<i>Dendroica petechia</i>	55		1		3	6	8	10
<i>Dumetella carolinensis</i>	62		1	3	4	6	8	
<i>Elaenia chiriquensis</i>	7		1		4	7	9	13
<i>Elaenia flavogaster</i>	15		1	4			7	16
<i>Empidonax trailii</i>	26		1		3	6	7	12
<i>Euphonia lanirostris</i>	51		1	6	9	10	13	19
<i>Habia fuscicauda</i>	4		1		4		7	
<i>Hylophilus aurantiifrons</i>	3		1	3		5	8	12
<i>Manacus vitellinus</i>	8		1		4	7	9	
<i>Melospiza melodia</i>	16		1			4	8	
<i>Molothrus bonariensis</i>	5		1		4			
<i>Myiodynastes maculatus</i>	8		1	4	6	7	9	15
<i>Myrmeciza exsul</i>	2			1	2	3		
<i>Myrmeciza longipes</i>	16	1		2		6	7	
<i>Passer domesticus</i>	25	1		2	4	7	10	
<i>Pheucticus ludovicianus</i>	8		1	1	5			
<i>Pipra coronata</i>	1		2	3		6	9	
<i>Pipra mentalis</i>	6		1		5	7	10	
<i>Progne subis</i>	29	1	5	5	10	9	12	18
<i>Rhamphocelus dimidiatus</i>	49		1	3	4	5	8	12
<i>Rhamphocelus flammigerus</i>	4	1	2		4	5	7	12
<i>Saltator maxinus</i>	8	3	1	4	4	6	9	14
<i>Sayornis phoebe</i>	15		1		5	8	11	15
<i>Sialia mexicana</i>	39		1	6	6		10	18
<i>Sialis sialis</i>	22		1	4	6	11	10	16
<i>Spizella passerina</i>	52		1		3	5	7	10
<i>Spizella pusilla</i>	22		1	2	3	5	7	10
<i>Sporophila americana</i>	18		1		4	6	7	
<i>Tachycineta albilinea</i>	8		4		7		10	
<i>Tachycineta bicolor</i>	133		1	6	7	9	10	22
<i>Tachycineta thalassina</i>	91		1	6	8	10	12	20
<i>Tangara larvata</i>	2		2	5			8	14
<i>Thamnophilus doliatus</i>	4	1		5	4		7	

Species	n	Naked	Natal Down	Wing feathers breaking skin	Pin feathers <5mm	Pin feathers 5-15mm	Wing feathers broken	Wing feathers complete
<i>Thraupis epicopus</i>	25		1	3	6	9	9	15
<i>Todirostrum cinereum</i>	43		1		4	7	10	17
<i>Troglodytes aedon aedon</i>	148		1		4		8	18
<i>Troglodytes aedon musculus</i>	13		1	4	5	7	13	13
<i>Turdus grayi</i>	143		1	4		7	9	14
<i>Turdus migratorius</i>	113		1		4	7	9	12
<i>Vireo flavoviridis</i>	16		1	3	7	6	7	12
<i>Vireo olivaceus</i>	3		1		4		7	

Appendix 4: Mass (conventional and fixed  $A$ ) and tarsus growth rate estimates and standard errors for a subset of temperate and tropical passerines, ordered alphabetically by taxonomic name. Parameters are defined as  $A$ , asymptotic value;  $i$ , inflection point; and  $K$ , growth constant.

Species	Parameter	Mass Growth Rate			Mass Growth Rate (fixed $A$ )			Tarsus Growth Rate			References
		$n$	Estimate	SE	$n$	Estimate	SE	$n$	Est	SE	
<i>Arremonops conirostris</i>	$A$	7	35.563	8.704	7	39.700	-	6	26.17	-	
	$i$		6.767	1.531		7.458	0.212		3.234	0.117	
	$K$		0.371	0.076		0.343	0.024		0.44	0.028	
<i>Bombicilla cedrorum</i>	$A$	8	35.071	0.724	-	-	-	-	-	-	Putnam 1949; this study
	$i$		6.51	0.143		-	-		-	-	
	$K$		0.467	0.023		-	-		-	-	
<i>Cardinalis cardinalis</i>	$A$	20	30.461	1.491	20	44.650	-	9	25.4	-	
	$i$		4.508	0.25		6.612	0.084		2.847	0.09	
	$K$		0.512	0.034		0.362	0.012		0.438	0.023	
<i>Carduelis tristis</i>	$A$	194	12.031	0.193	194	12.900	-	194	13	-	Holcomb 1968; this study
	$i$		6.202	0.141		6.773	0.086		2.714	0.103	
	$K$		0.411	0.014		0.370	0.009		0.382	0.026	
<i>Carpodacus mexicanus</i>	$A$	33	21.233	1.062	33	21.4	-	13	17.56	-	
	$i$		5.849	0.304		5.895	0.070		2.87	0.084	
	$K$		0.43	0.027		0.426	0.012		0.411	0.019	
<i>Chamaea fasciata</i>	$A$	26	12.318	0.423	26	14.715	-	26	22.73	-	unpub. PRBO
	$i$		5.469	0.223		6.696	0.067		4.234	0.087	
	$K$		0.388	0.023		0.308	0.008		0.336	0.012	
<i>Dendroica petechia</i>	$A$	55	10.424	0.388	55	9.500	-	20	18.53	-	
	$i$		4.795	0.19		4.347	0.047		2.97	0.077	
	$K$		0.519	0.025		0.580	0.014		0.455	0.021	
<i>Dumetella carolinensis</i>	$A$	62	32.769	1.126	62	39.600	-	34	28.32	-	
	$i$		5.341	0.192		6.423	0.054		3.599	0.061	
	$K$		0.469	0.021		0.389	0.009		0.405	0.012	



Species	Parameter	Mass Growth Rate			Mass Growth Rate (fixed A)			Tarsus Growth Rate			References
		n	Estimate	SE	n	Estimate	SE	n	Est	SE	
<i>Elaenia chiriquiensis</i>	A	7	16.224	2.343	7	16.100	-	7	14.63	-	unpub. White and Ricklefs (in Ricklefs 1976); this study
	i		6.961	1.077		6.905	0.177		2.255	0.125	
	K		0.318	0.043		0.320	0.018		0.367	0.025	
<i>Elaenia flavogaster</i>	A	15	14.495	2.787	15	24.700	-	15	18.69	-	unpub. White and Ricklefs (in Ricklefs 1976); this study
	i		6.27	1.926		12.339	0.569		3.628	0.313	
	K		0.268	0.089		0.161	0.019		0.26	0.023	
<i>Empidonax trailii</i>	A	26	13.653	0.829	26	13.400	-	15	15.73	-	
	i		5.118	0.306		5.027	0.068		2.427	0.082	
	K		0.493	0.033		0.502	0.016		0.398	0.016	
<i>Euphonia lanirostris</i>	A	51	15.178	0.725	51	-	-	20	15.75	-	
	i		10.452	0.471		-	-		5.605	0.156	
	K		0.251	0.013		-	-		0.215	0.009	
<i>Habia fuscicauda</i> <sup>1</sup>	A	4	38.000	-	4	38.000	-	3	21.35	-	
	i		6.892	0.279		6.892	0.279		2.31	0.23	
	K		0.354	0.041		0.354	0.041		0.482	0.058	
<i>Hylophilus aurantiifrons</i> <sup>1</sup>	A	3	9.5	-	3	9.5	-	1	15.06	-	
	i		4.765	0.211		4.7652	0.2111		3.189	0.538	
	K		0.556	0.065		0.5555	0.065		0.366	0.078	
<i>Manacus vitellinus</i>	A	8	13.225	3.036	8	16	-	5	16.1	-	
	i		7.018	1.891		8.6094	0.1911		1.951	0.202	
	K		0.266	0.046		0.2364	0.0106		0.294	0.029	
<i>Melospiza melodia</i>	A	-	-	-	16	20.75	-	8	19.07	-	
	i		-	-		5.2206	0.0681		2.107	0.114	
	K		-	-		0.498	0.0175		0.572	0.055	
<i>Molothrus ater</i> <sup>2</sup>	A	-	-	-	13	43.9	-	6	22.77	-	
	i		-	-		6.7153	0.1393		3.009	0.223	
	K		-	-		0.4907	0.0277		0.489	0.069	

Species	Parameter	Mass Growth Rate			Mass Growth Rate (fixed A)			Tarsus Growth Rate			References
		n	Estimate	SE	n	Estimate	SE	n	Est	SE	
<i>Molothrus bonariensis</i> <sup>2</sup>	A	5	37.27	1.961	5	35.3	-	4	13.54	-	
	i		6.378	0.331		6.0843	0.1331		0.927	0.268	
	K		0.491	0.04		0.5241	0.0287		0.476	0.087	
<i>Myiodynastes maculatus</i>	A	8	32.908	1.874	8	41	-	3	19.33	-	
	i		5.59	0.453		7.4261	0.1989		2.992	0.267	
	K		0.358	0.038		0.2652	0.0156		0.302	0.027	
<i>Myrmeciza exsul</i>	A	4	17.794	1.157	4	26	-	-	-	-	unpub. Oniki and Willis (in Ricklefs 1976); this study
	i		3.914	0.296		5.7988	0.1105		-	-	
	K		0.631	0.08		0.4028	0.0234		-	-	
<i>Myrmeciza longipes</i>	A	16	19.27	2.132	16	28	-	7	27.39	-	
	i		4.208	0.601		6.4411	0.1371		2.595	0.149	
	K		0.444	0.063		0.3205	0.0154		0.43	0.039	
<i>Passer domesticus</i>	A	25	27.215	1.18	25	27.7	-	5	19.61	-	
	i		5.46	0.284		5.5673	0.1076		17.49	0.115	
	K		0.448	0.037		0.4362	0.02		0.382	0.019	
<i>Pheucticus ludovicianus</i> <sup>1</sup>	A	10	45.6	-	10	45.6	-	8	21.58	-	
	i		7.936	0.44		7.9364	0.44		3.271	0.274	
	K		0.36	0.047		0.3601	0.0466		0.356	0.047	
<i>Pipilo erythrophthalmus</i>	A	3-12	25.206	1.683	3-12	40.5	-	3-12	27	-	Barber 1950
	i		4.082	0.337		6.849	0.210		2.814	0.147	
	K		0.528	0.063		0.321	0.027		0.515	0.043	
<i>Pipra coronata</i> <sup>1</sup>	A	1	10.5	-	1	10.5	-	1	12.53	-	
	i		7.012	0.042		7.0122	0.0419		1.637	0.437	
	K		0.29	0.004		0.2904	0.00417		0.391	0.082	
<i>Pipra mentalis</i>	A	6	9.842	0.534	6	15	-	5	13.08	-	
	i		4.918	0.376		8.3232	0.2473		2.105	0.228	
	K		0.426	0.052		0.2413	0.0174		0.331	0.032	

Species	Parameter	Mass Growth Rate			Mass Growth Rate (fixed A)			Tarsus Growth Rate			References
		n	Estimate	SE	n	Estimate	SE	n	Est	SE	
<i>Poecile atricapilla</i>	A	69	11.071	0.277	-	-	-	-	-	-	unpub. Robinson and Robinson; Kluver 1961
	i		6.564	0.185	-	-	-	-	-	-	
	K		0.415	0.024	-	-	-	-	-	-	
<i>Progne chalybea</i>	A	29	41.58	0.923	29	-	-	11	15.15	-	
	i		8.096	0.21	-	-	-		3.785	0.101	
	K		0.36	0.018	-	-	-		0.269	0.009	
<i>Progne subis</i>	A	24	60.529	0.387	24	-	-	-	-	-	unpub. Moss (in Starck and Ricklefs 1998)
	i		8.348	0.054	-	-	-	-	-	-	
	K		0.365	0.005	-	-	-	-	-	-	
<i>Rhamphocelus dimidiatus</i>	A	49	27.722	1.8	49	-	-	22	21.24	-	
	i		6.675	0.396	-	-	-		3.437	0.07	
	K		0.38	0.023	-	-	-		0.37	0.013	
<i>Rhamphocelus flammigerus</i> <sup>1</sup>	A	4	32	-	4	32	-	2	23.03	-	
	i		7.32	0.206		7.3202	0.2063		3.464	0.329	
	K		0.339	0.027		0.3392	0.0273		0.356	0.042	
<i>Saltator maxinus</i>	A	8	35.186	2.15	8	46	-	6	24.67	-	
	i		5.492	0.427		7.4642	0.1638		3.11	0.134	
	K		0.427	0.046		0.3087	0.0155		0.398	0.03	
<i>Sayornis phoebe</i>	A	49-94	18.26	0.342	49-94	19.8	-	49-93	17.73	-	Murphy 1981; this study
	i		5.716	0.133		7.2719	0.3056		3.633	0.084	
	K		0.445	0.019		0.2587	0.0245		0.304	0.009	
<i>Sialia mexicana</i>	A	39	28.646	0.342	39	-	-	31	22.6	-	unpub. Austin and Robinson
	i		6.157	0.092		-	-		4.29	0.047	
	K		0.418	0.013		-	-		0.331	0.006	
<i>Sialia stalis</i>	A	22	35.527	1.613	22	31.6	-	15	22.58	-	
	i		6.972	0.333		6.1804	0.0942		3.912	0.08	
<i>Sialia stalis</i>	K		0.371	0.023		0.4288	0.0152		0.35	0.012	

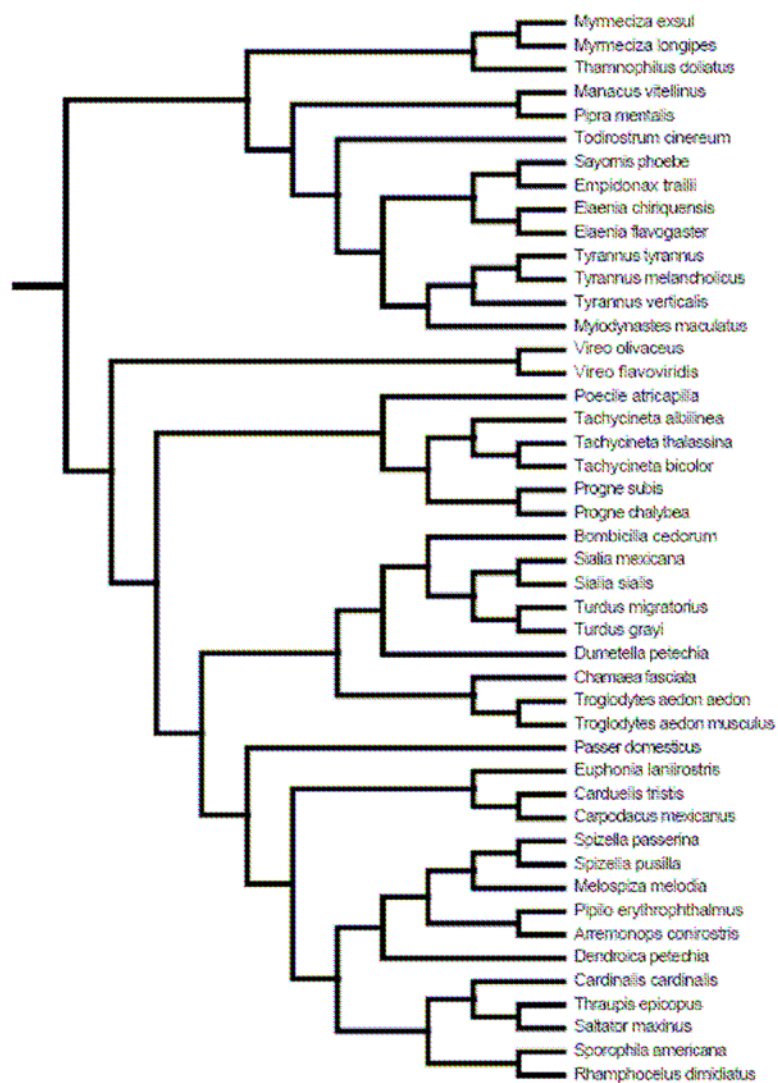
Species	Parameter	Mass Growth Rate			Mass Growth Rate (fixed A)			Tarsus Growth Rate			References
		n	Estimate	SE	n	Estimate	SE	n	Est	SE	
<i>Sitta carolinensis</i> <sup>1</sup>	<i>A</i>	7	21.1	-	7	21.1	-	-	-	-	unpub. Austin and Robinson
	<i>i</i>		9.754	0.305		9.7535	0.3053		-	-	
	<i>K</i>		0.244	0.026		0.2443	0.0258		-	-	
<i>Spizella passerina</i>	<i>A</i>	52	12.767	0.702	52	12.3	-	20	16.28	-	
	<i>i</i>		4.645	0.257		4.4763	0.0489		2.323	0.076	
	<i>K</i>		0.511	0.032		0.5314	0.0155		0.479	0.022	
<i>Spizella pusilla</i>	<i>A</i>	22	13.734	1.801	22	12.5	-	14	18.65	-	
	<i>i</i>		5.073	0.601		4.6494	0.0811		2.718	0.087	
	<i>K</i>		0.498	0.049		0.5345	0.0205		0.493	0.027	
<i>Sporophila americana</i>	<i>A</i>	18	10.04	1.022	18	11	-	12	13.43	-	
	<i>i</i>		5.247	0.57		5.7607	0.0904		2.265	0.136	
	<i>K</i>		0.429	0.042		0.3981	0.0142		0.435	0.039	
<i>Tachycineta albinnea</i>	<i>A</i>	8	15.695	1.142	-	-	-	8	11	-	unpub. White and Ricklefs
	<i>i</i>		5.234	0.412		-	-		1.274	0.974	
	<i>K</i>		0.468	0.123		-	-		0.295	0.062	
<i>Tachycineta bicolor</i>	<i>A</i>	133	23.155	0.282	-	-	-	70	15.27	-	unpub. Austin and Robinson; this study
	<i>i</i>		6.632	0.092		-	-		3.651	0.059	
	<i>K</i>		0.436	0.011		-	-		0.27	0.005	
<i>Tachycineta thalassina</i>	<i>A</i>	91	19.905	0.283	-	-	-	39	12.85	-	unpub. Austin and Robinson
	<i>i</i>		7.326	0.121		-	-		3.041	0.055	
	<i>K</i>		0.367	0.011		-	-		0.282	0.005	
<i>Tangara larvata</i> <sup>1</sup>	<i>A</i>	2	16.2	-	2	16.2	-	2	17.71	-	
	<i>i</i>		7.108	0.142		7.1076	0.1419		3.987	0.295	
	<i>K</i>		0.331	0.017		0.3309	0.0172		0.368	0.044	
<i>Thamnophilus doliatus</i>	<i>A</i>	10	23.552	1.151	10	26.2	-	4	21.42	-	unpub. White and unpub. Morton (in Ricklefs 1976
	<i>i</i>		5.41	0.411		6.3238	0.1873		2.582	0.249	
	<i>K</i>		0.317	0.03		0.2709	0.0174		0.381	0.054	

Species	Parameter	Mass Growth Rate			Mass Growth Rate (fixed A)			Tarsus Growth Rate			References
		n	Estimate	SE	n	Estimate	SE	n	Est	SE	
<i>Thraupis epicopus</i>	<i>A</i>	25	24.434	0.85	25	32	-	10	20.04	-	
	<i>i</i>		6.158	0.299		8.5255	0.1399		3.743	0.126	
	<i>K</i>		0.367	0.026		0.2537	0.01		0.319	0.015	
<i>Todirostrum cinereum</i>	<i>A</i>	43	7.161	0.131	43	7.3	-	21	18.86	-	
	<i>i</i>		6.437	0.162		6.589	0.0731		5.293	0.082	
	<i>K</i>		0.354	0.014		0.3432	0.00812		0.254	0.006	
<i>Tolmomyias sulphurescens</i> <sup>1</sup>	<i>A</i>	2	16.053	0.443	-	-	-	2	18.05	-	
	<i>i</i>		6.988	0.251		-	-		4.179	0.275	
	<i>K</i>		0.394	0.026		-	-		0.277	0.023	
<i>Troglodytes aedon</i>	<i>A</i>	148	11.712	0.234	-	-	-	83	17.49	-	
	<i>i</i>		5.384	0.115		-	-		3.382	0.045	
	<i>K</i>		0.469	0.012		-	-		0.387	0.008	
<i>Troglodytes aedon musculus</i>	<i>A</i>	17	14.348	0.356	-	-	-	-	-	-	Haverschmidt 1952; this study
	<i>i</i>		5.399	0.156		-	-		-	-	
	<i>K</i>		0.472	0.021		-	-		-	-	
<i>Turdus grayi</i>	<i>A</i>	143	55.852	1.978	143	68	-	82	32.99	-	unpub. White and Ricklefs; this study
	<i>i</i>		6.562	0.238		7.9243	0.0628		4.724	0.057	
	<i>K</i>		0.387	0.018		0.3176	0.00693		0.328	0.007	
<i>Turdus migratorius</i>	<i>A</i>	113	64.104	1.768	113	77.3	-	51	33.91	-	
	<i>i</i>		5.395	0.148		6.4191	0.0434		3.836	0.044	
	<i>K</i>		0.495	0.018		0.4112	0.00739		0.421	0.009	
<i>Tyrannus forficatus</i> <sup>1</sup>	<i>A</i>	4	33.281	0.531	4	43.2	-	4	18.61	-	Murphy 1988
	<i>i</i>		6.87	0.118		8.9144	0.1455		3.76	0.114	
	<i>K</i>		0.382	0.011		0.2741	0.0129		0.339	0.014	
<i>Tyrannus melancholicus</i>	<i>A</i>	5	64.906	12.224	-	-	-	-	-	-	unpub. Ricklefs (in Ricklefs 1976); this study
	<i>i</i>		10.483	1.79		-	-		-	-	
	<i>K</i>		0.233	0.039		-	-		-	-	

Species	Parameter	Mass Growth Rate			Mass Growth Rate (fixed A)			Tarsus Growth Rate			References
		n	Estimate	SE	n	Estimate	SE	n	Est	SE	
<i>Tyrannus tyrannus</i>	<i>A</i>	21	30.949	0.211	21	42.1	-	21	18.26	-	Murphy 1981; this study
	<i>i</i>		5.659	0.052		8.2519	0.2261		2.808	0.154	
	<i>K</i>		0.412	0.007		0.2434	0.0164		0.339	0.019	
<i>Tyrannus verticalis</i>	<i>A</i>	4	37.745	0.591	4	39.6	-	4	19.08	-	Murphy 1988
	<i>i</i>		6.493	0.121		6.8281	0.0764		3.592	0.129	
	<i>K</i>		0.413	0.016		0.3772	0.0106		0.347	0.017	
<i>Vireo flavoviridis</i>	<i>A</i>	16	15.475	1.065	16	15.99	-	7	16.7	-	
	<i>i</i>		5.476	0.403		5.6302	0.1037		3.09	0.171	
	<i>K</i>		0.454	0.043		0.4394	0.02		0.391	0.031	
<i>Vireo olivaceus</i>	<i>A</i>	7	15.645	0.595	7	16.7	-	3	16.55	-	Southern 1958; this study
	<i>i</i>		4.87	0.207		5.2228	0.0603		2.198	0.145	
	<i>K</i>		0.492	0.031		0.4502	0.0132		0.459	0.038	

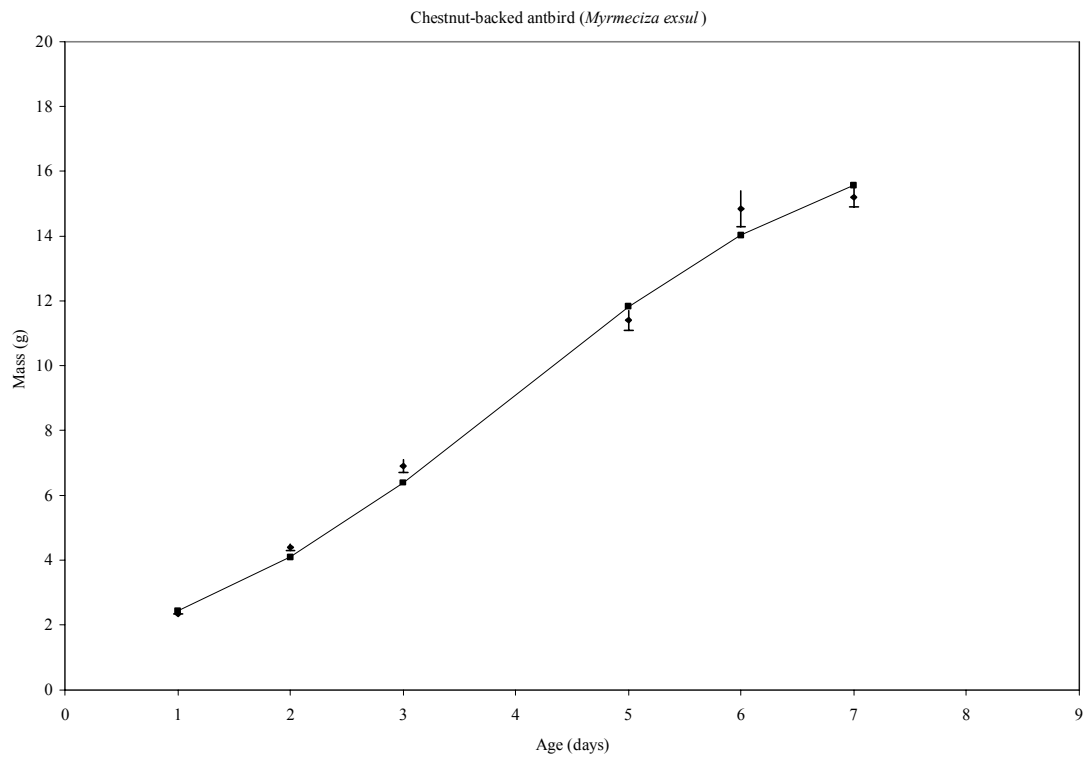
<sup>1</sup> not included in life history analysis due to low sample size, gaps in growth curve, or missing life history variables; <sup>2</sup>Brood parasite not included in life history analysis.

Appendix 5: Phylogeny of temperate and tropical passerines based on Sibley and Ahlquist (1990).

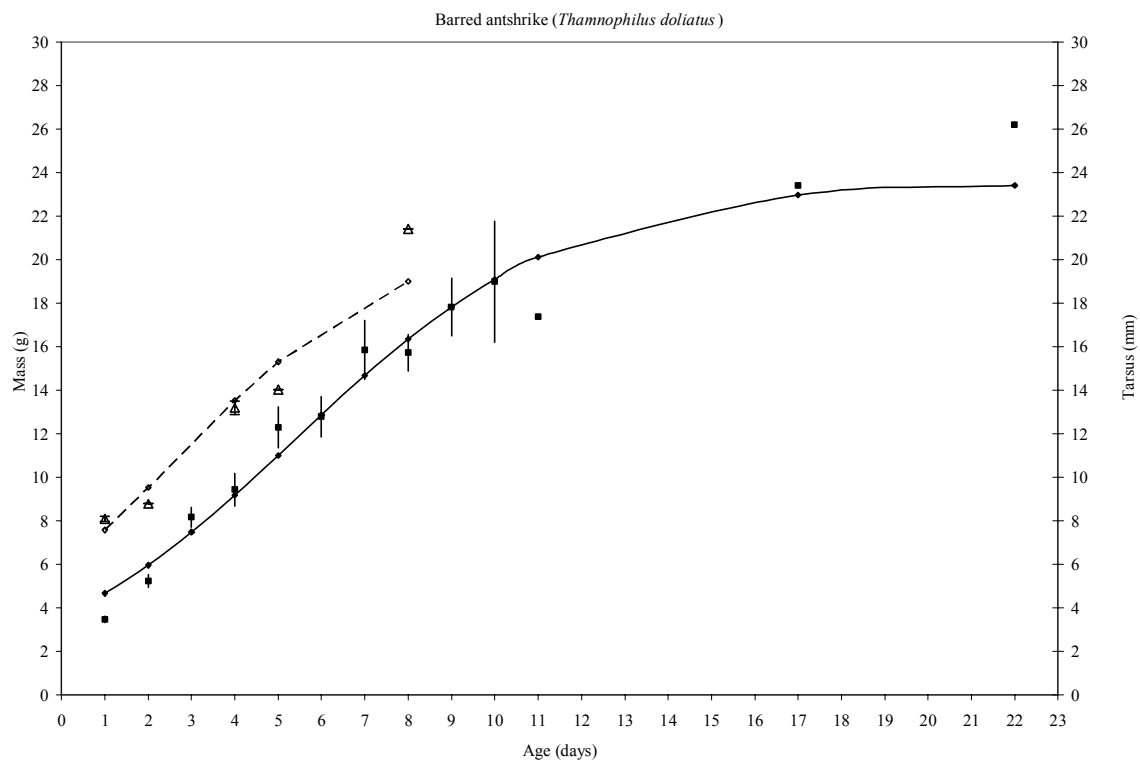
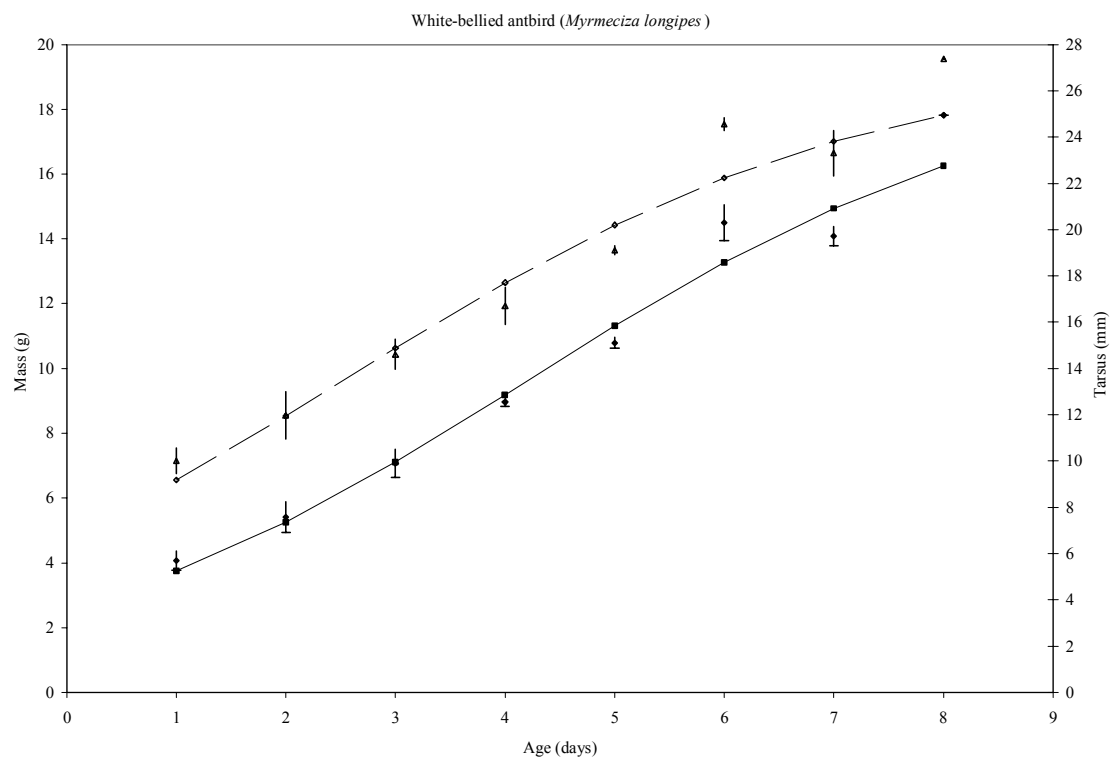


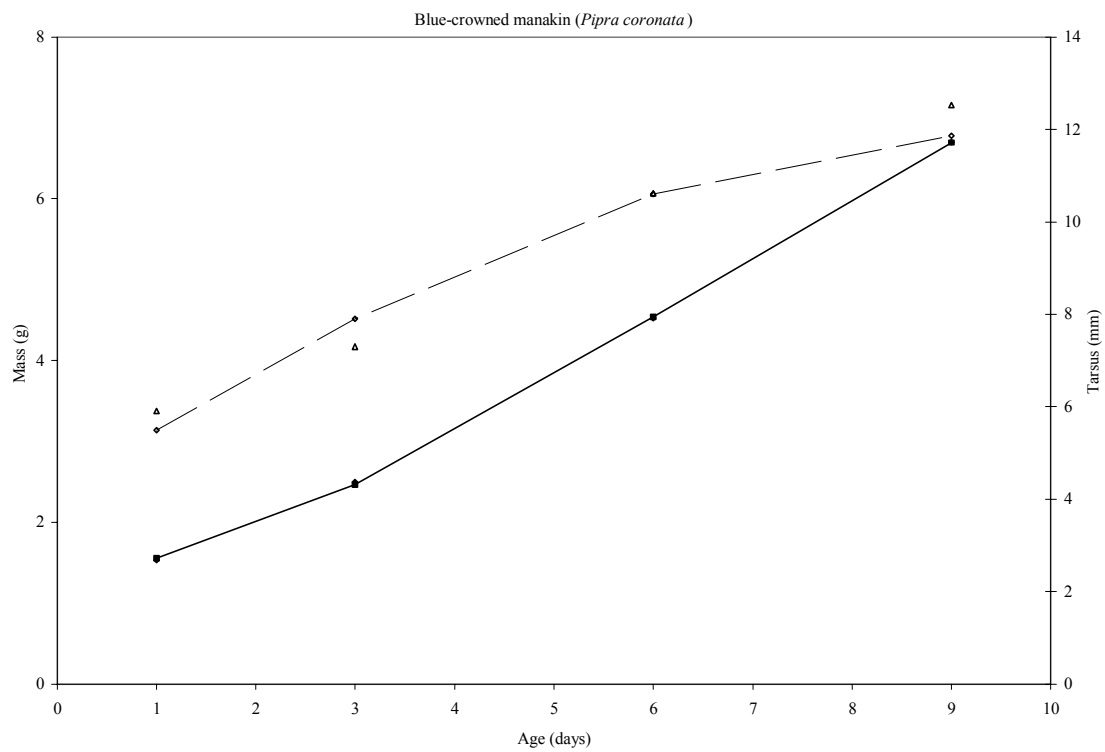
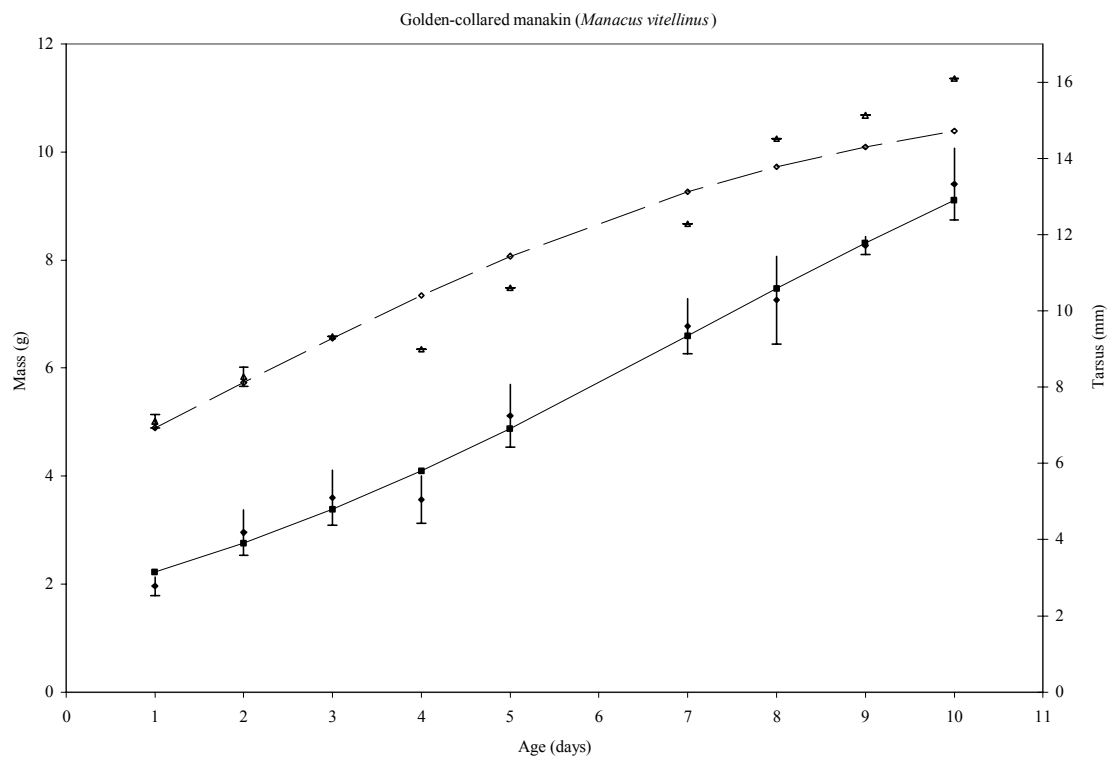
Appendix 6: Summary growth curves of temperate and tropical passerines. Mean mass (g) (black diamond) and tarsus length (mm) (open triangle) and corresponding growth curves of mass (black square and solid line) and tarsus length (open diamond and dashed line). Species are organized alphabetically by Sibley and Ahlquist's (1990) super family classification.

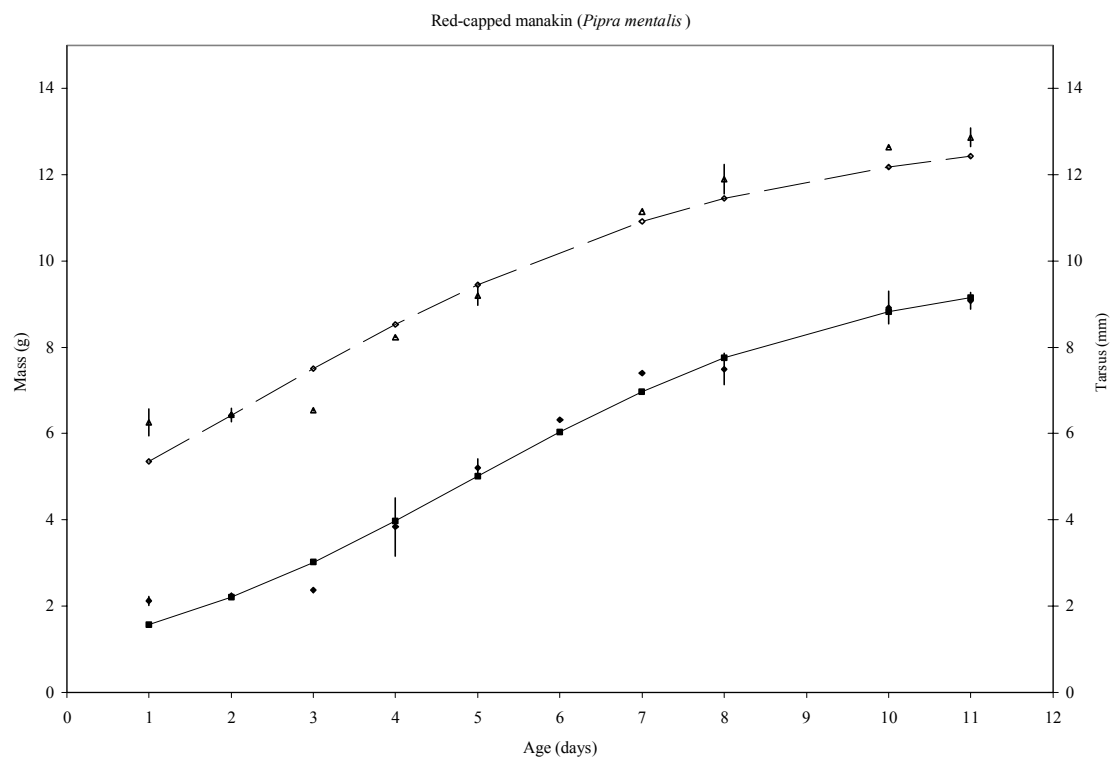
***Suboscine: Thamnophilidae***



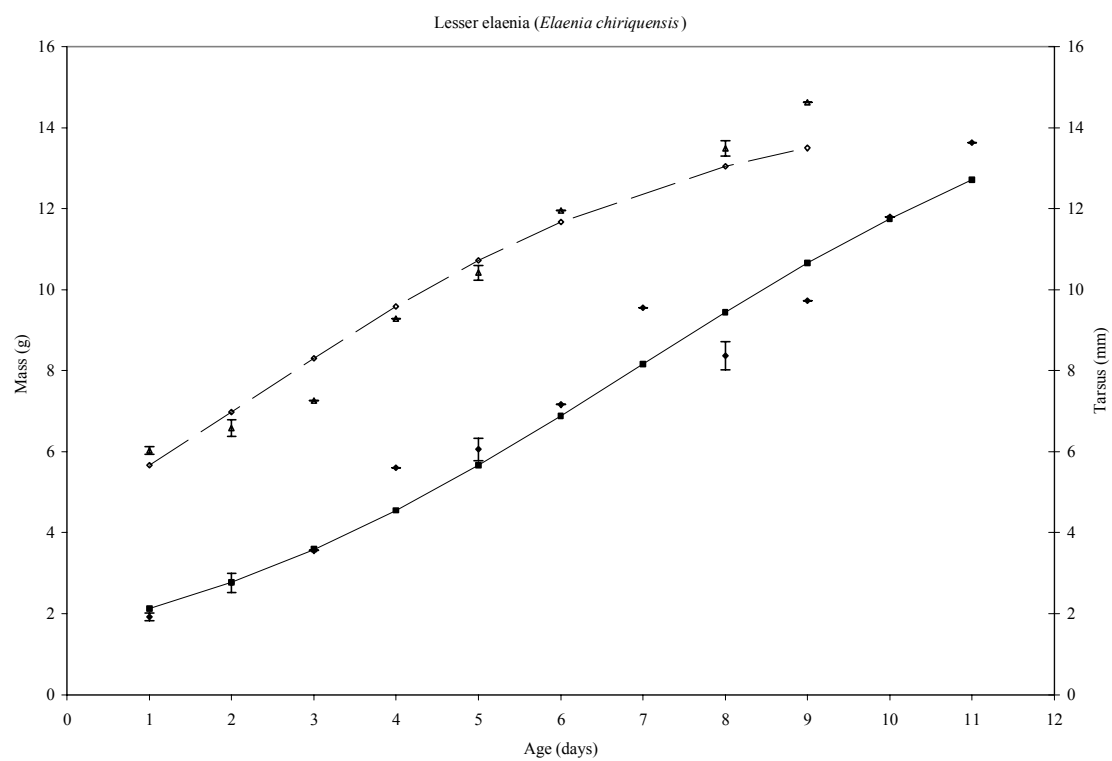


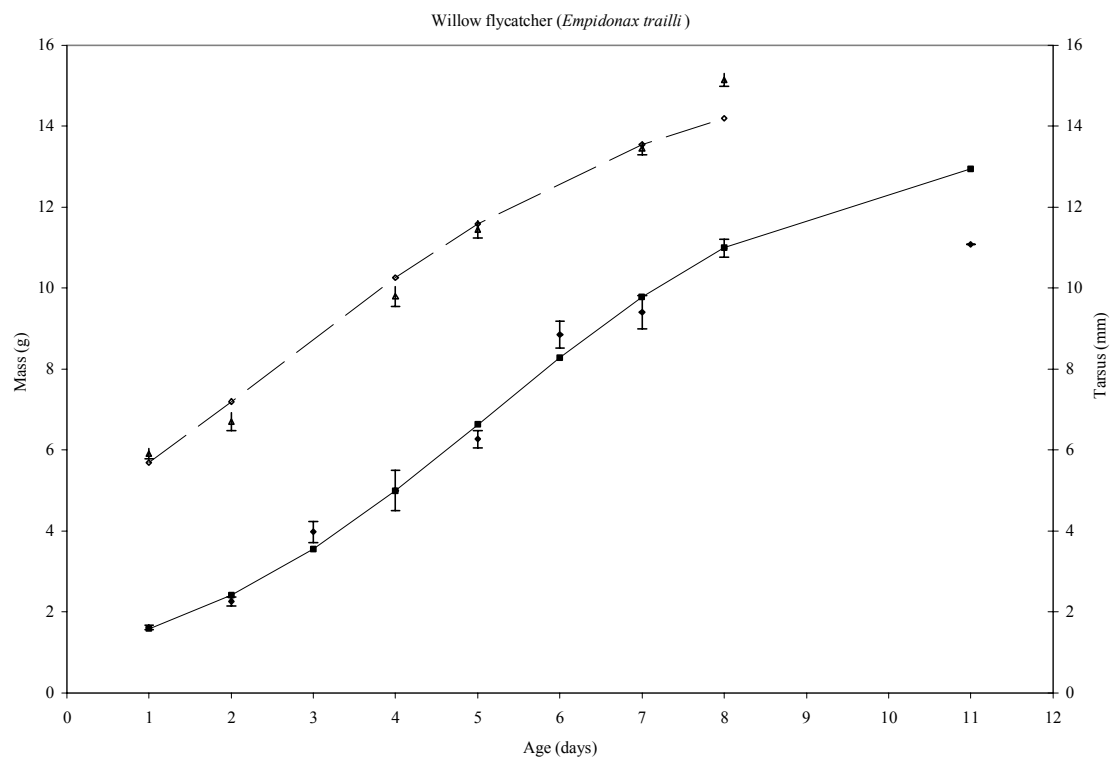
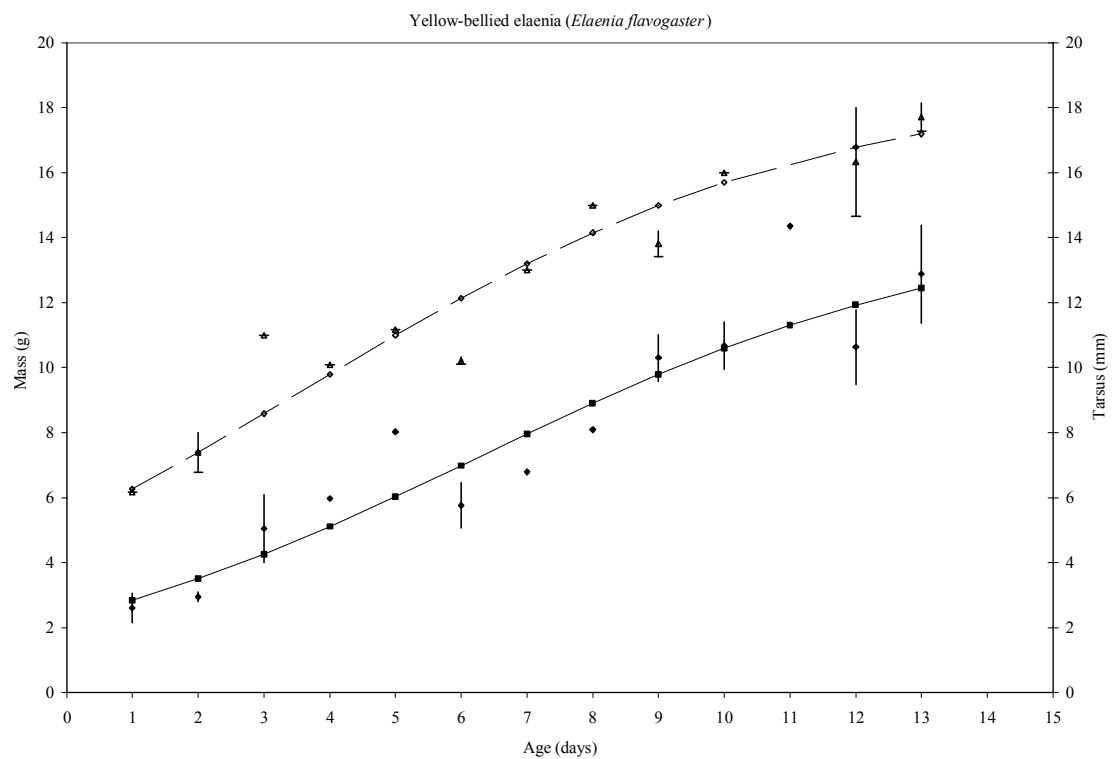


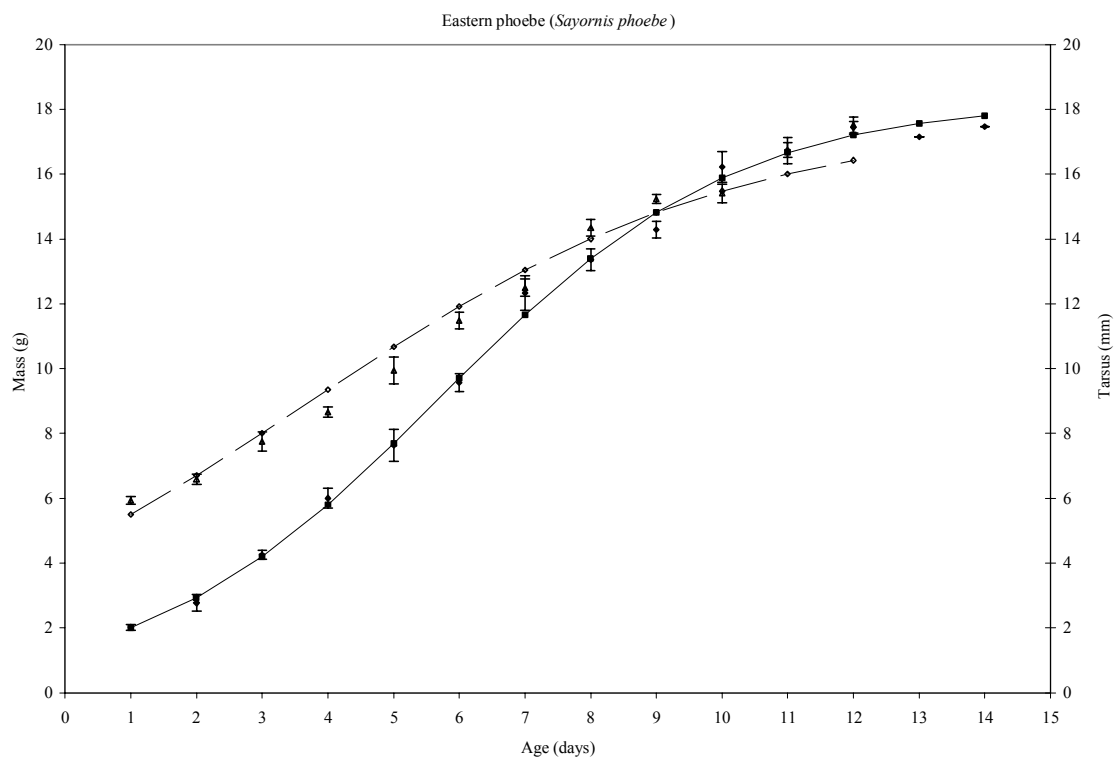
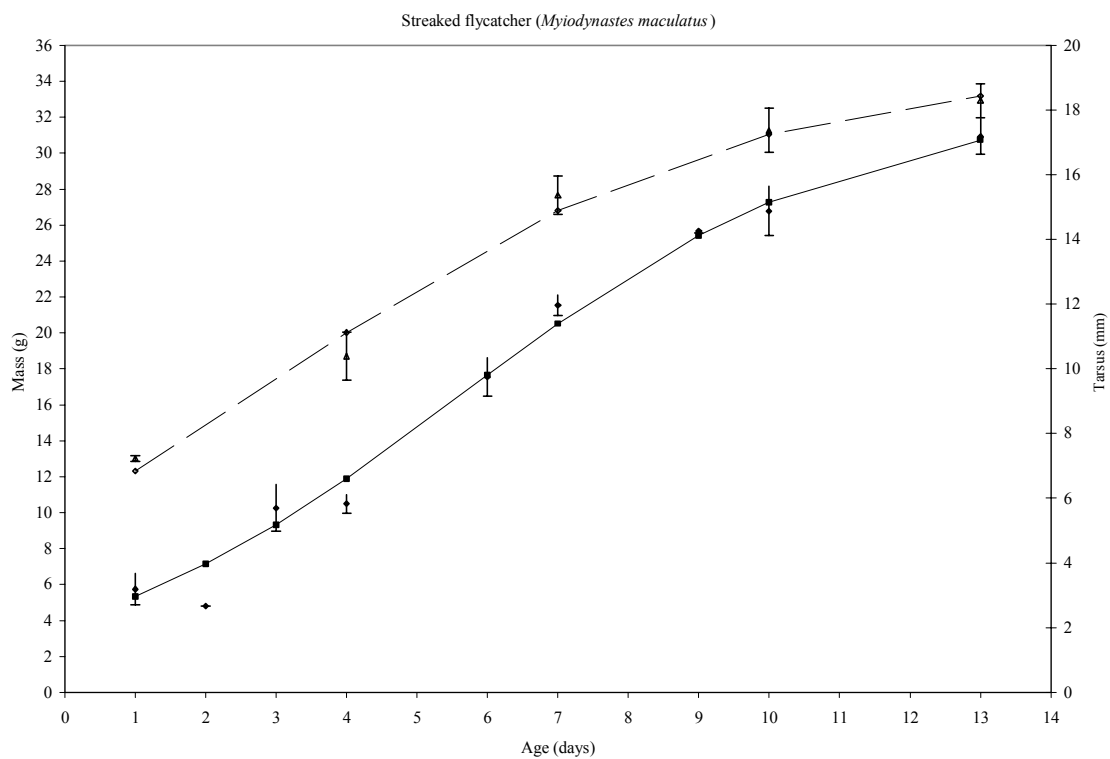
*Suboscine: Tyrannidae, Manakins*

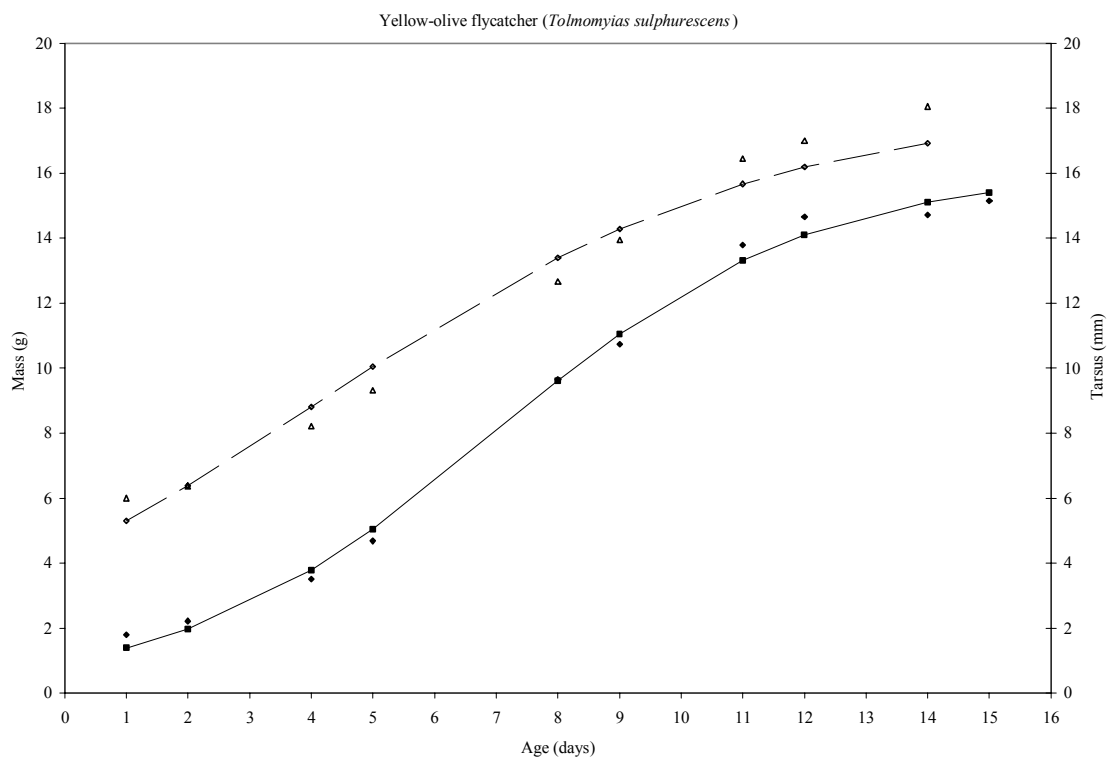
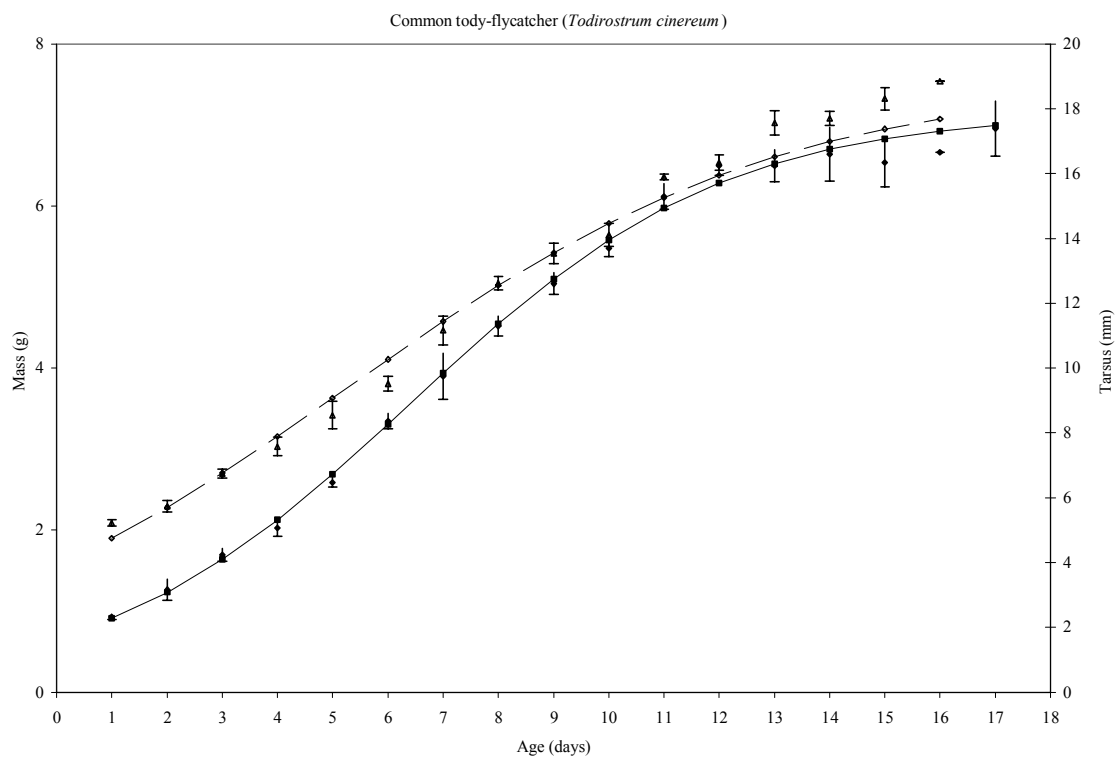


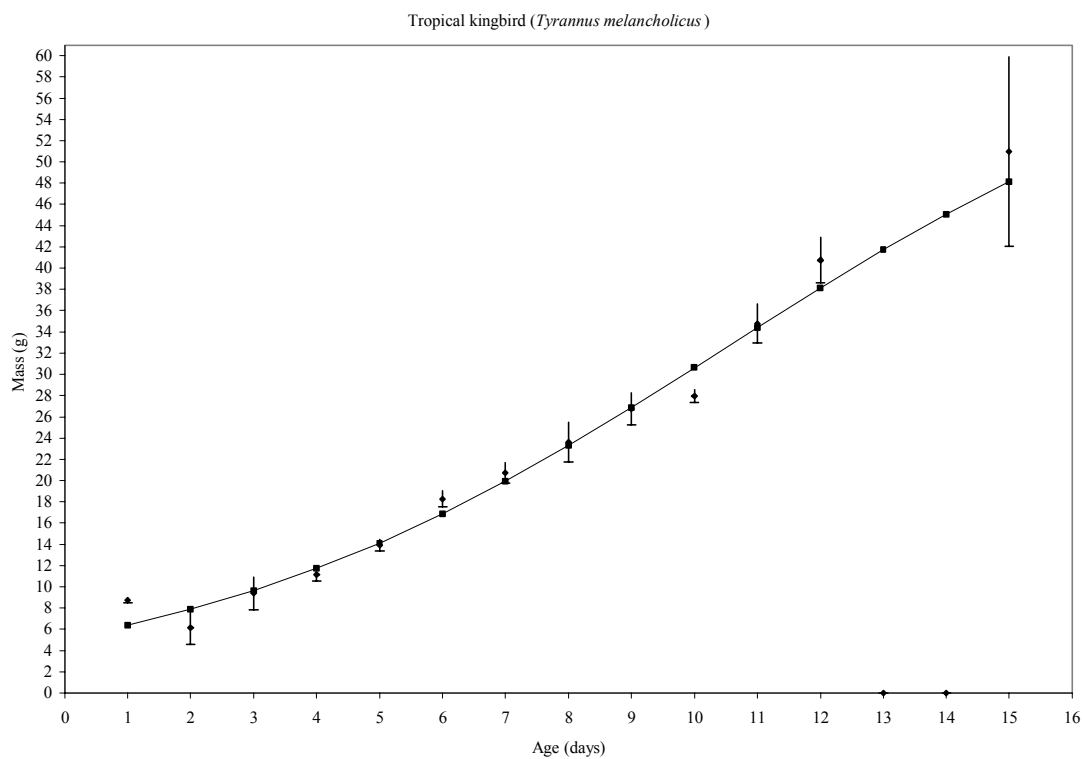
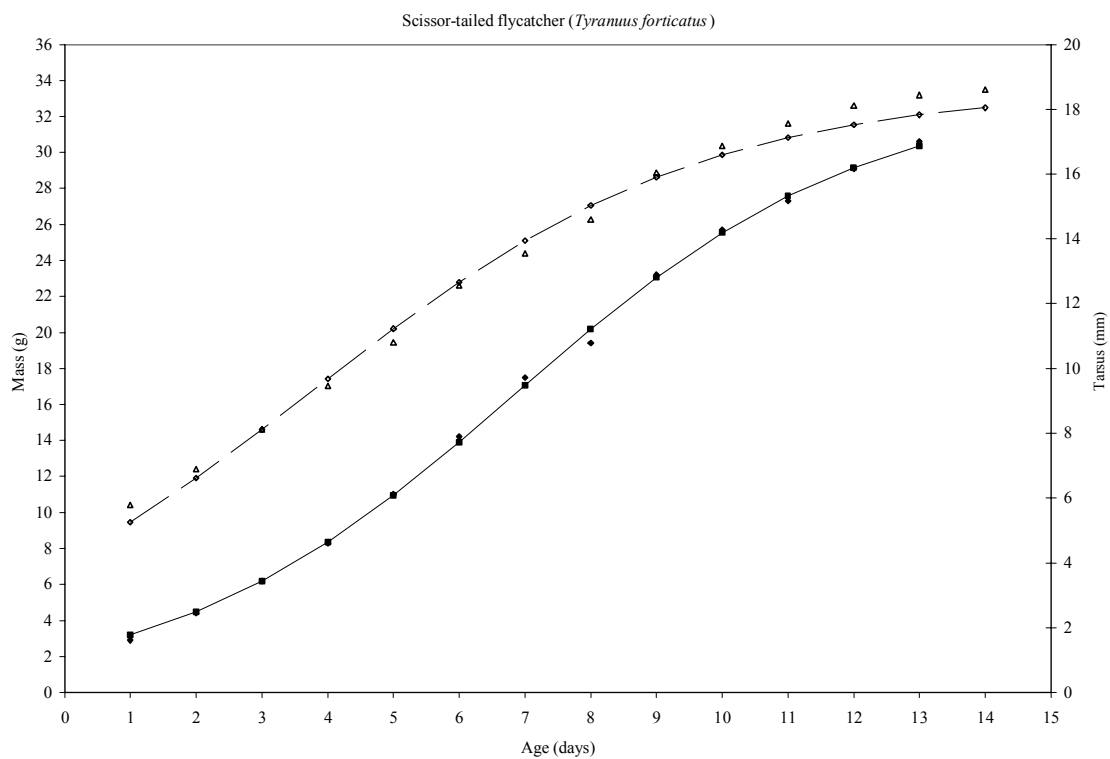
***Suboscine: Tyrannidae, Flycatchers:***

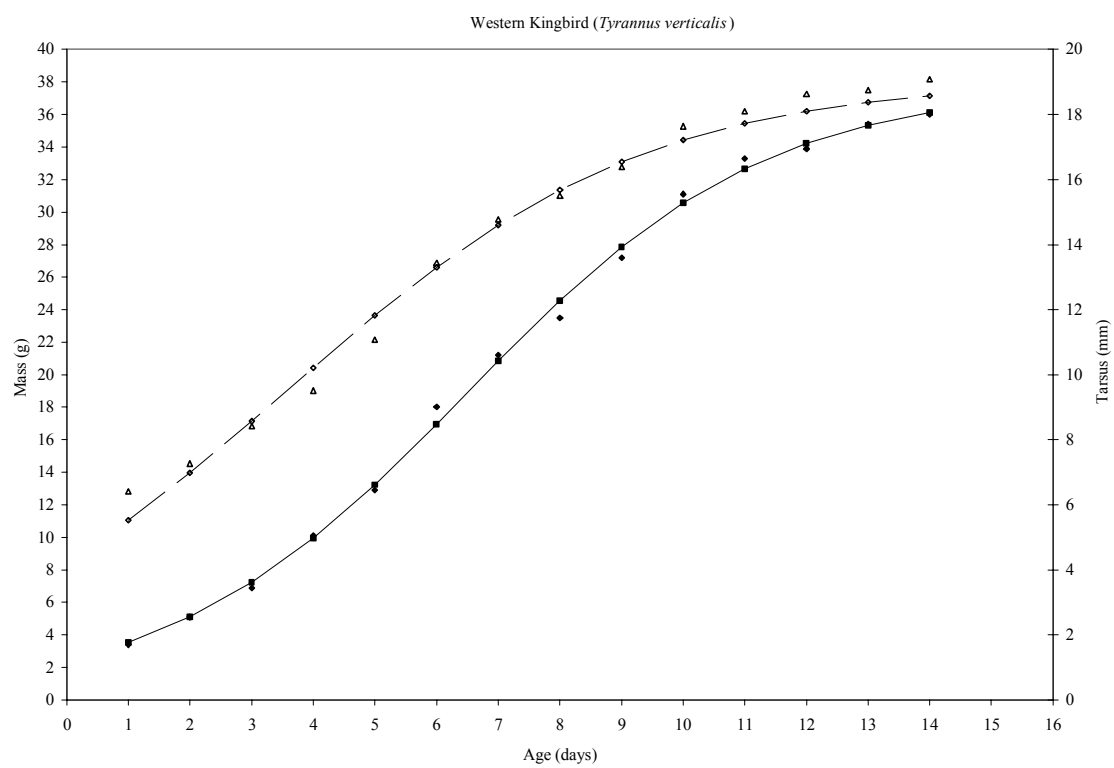
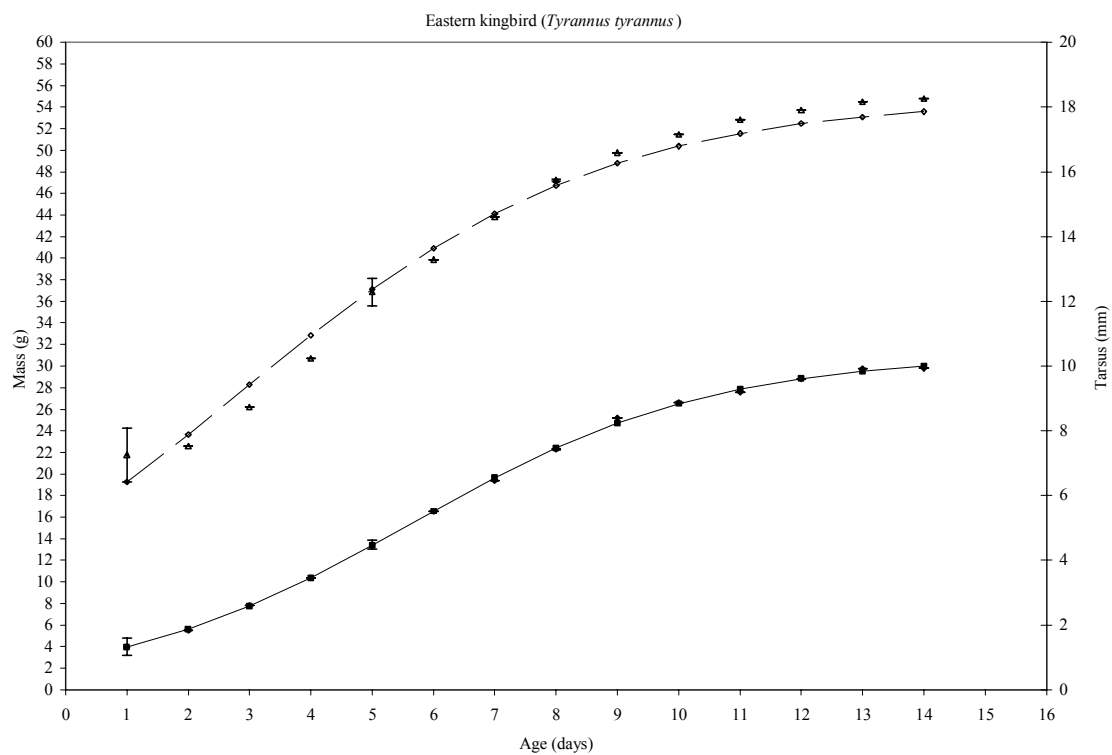






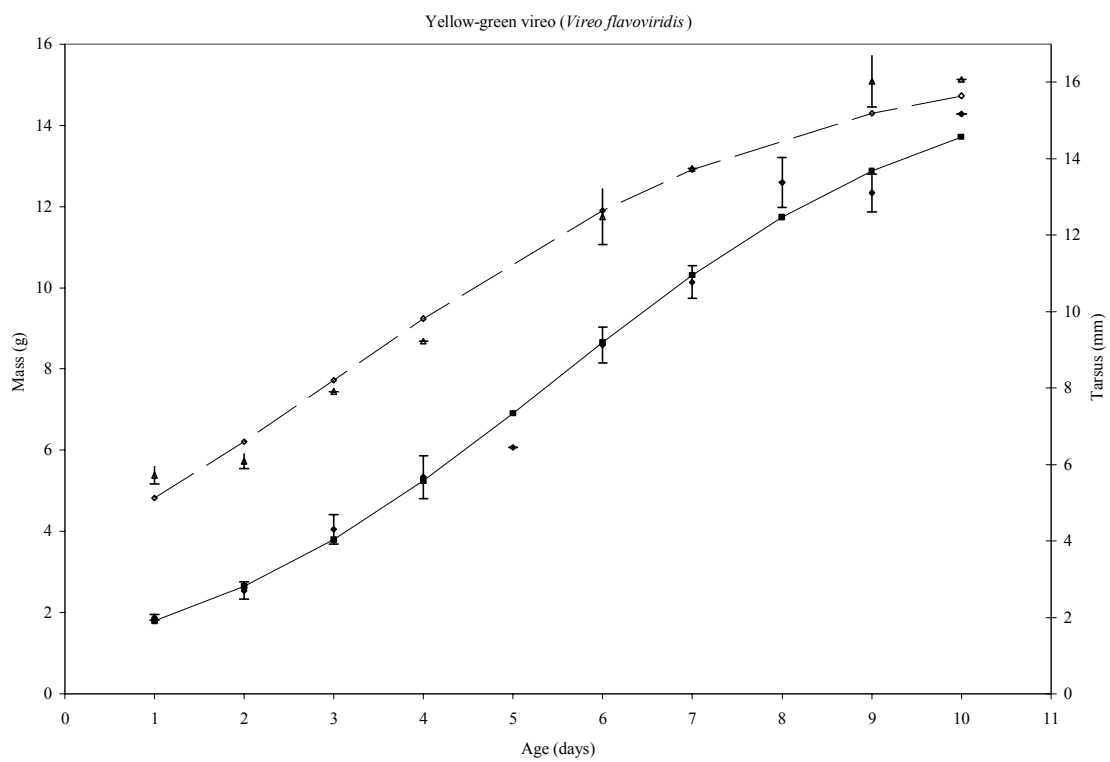
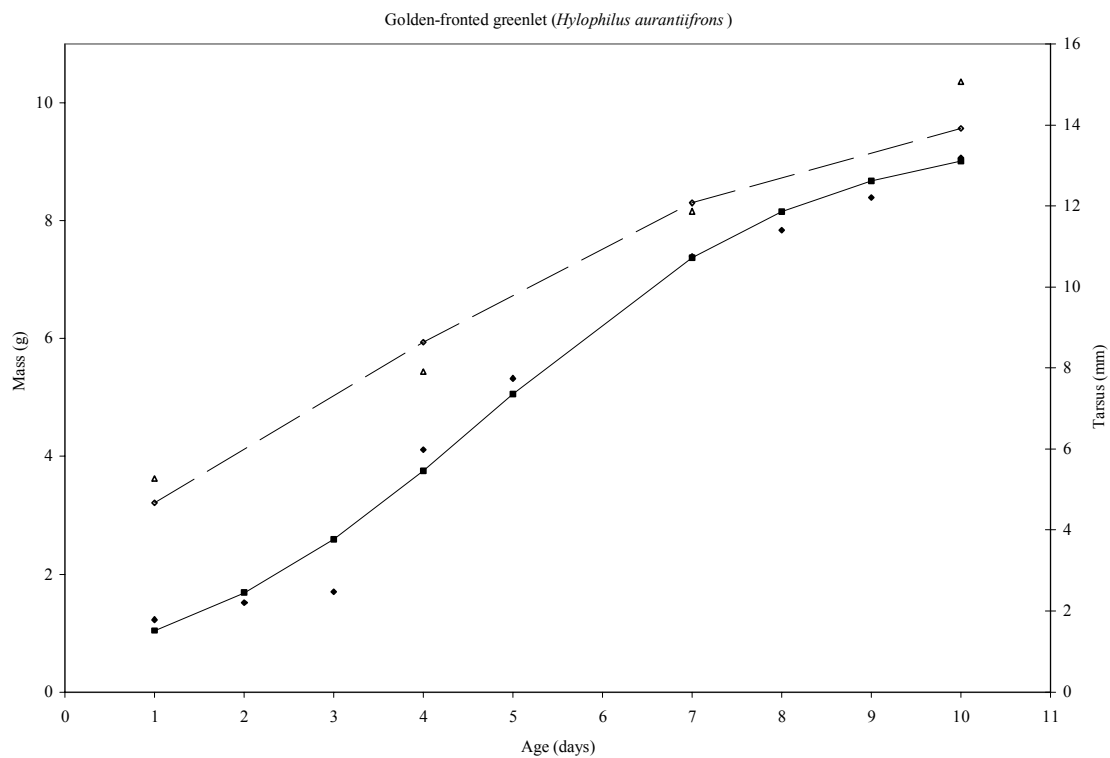


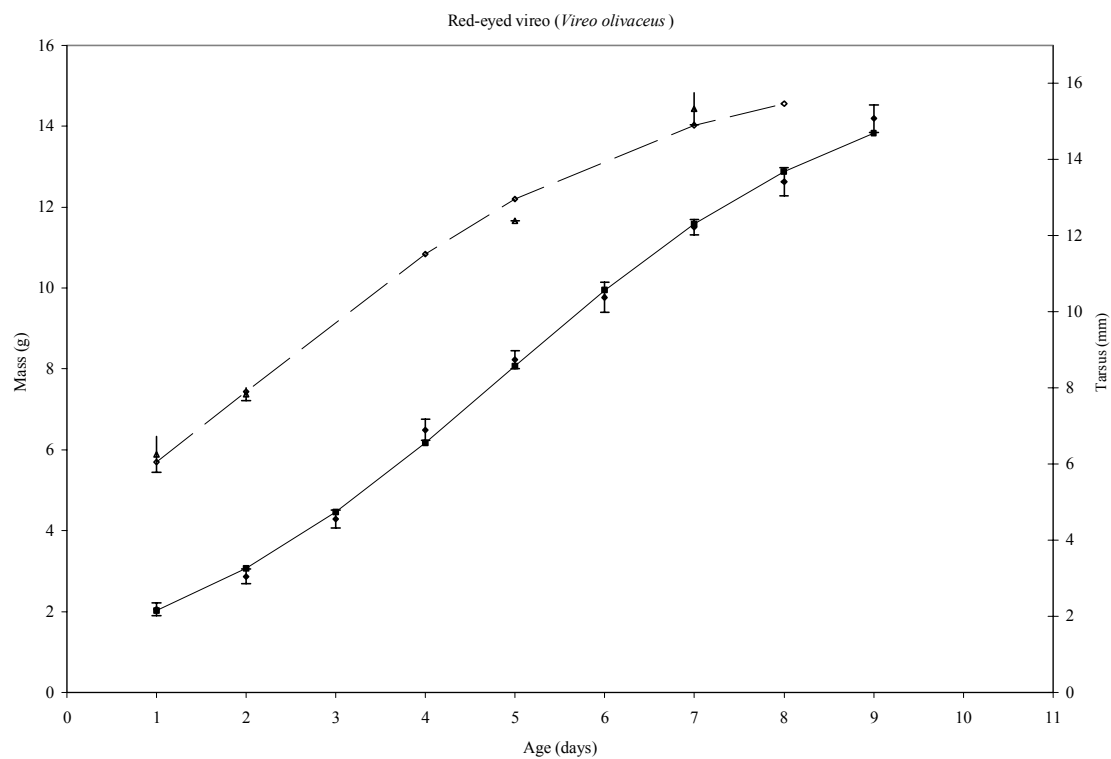




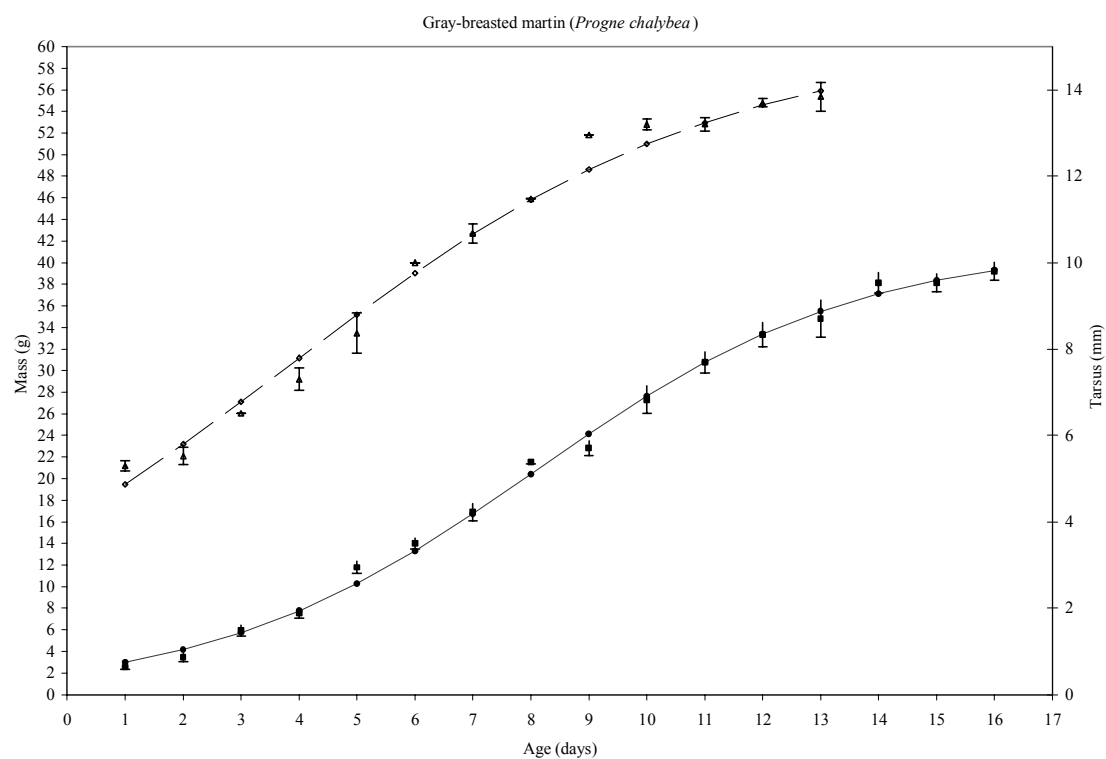


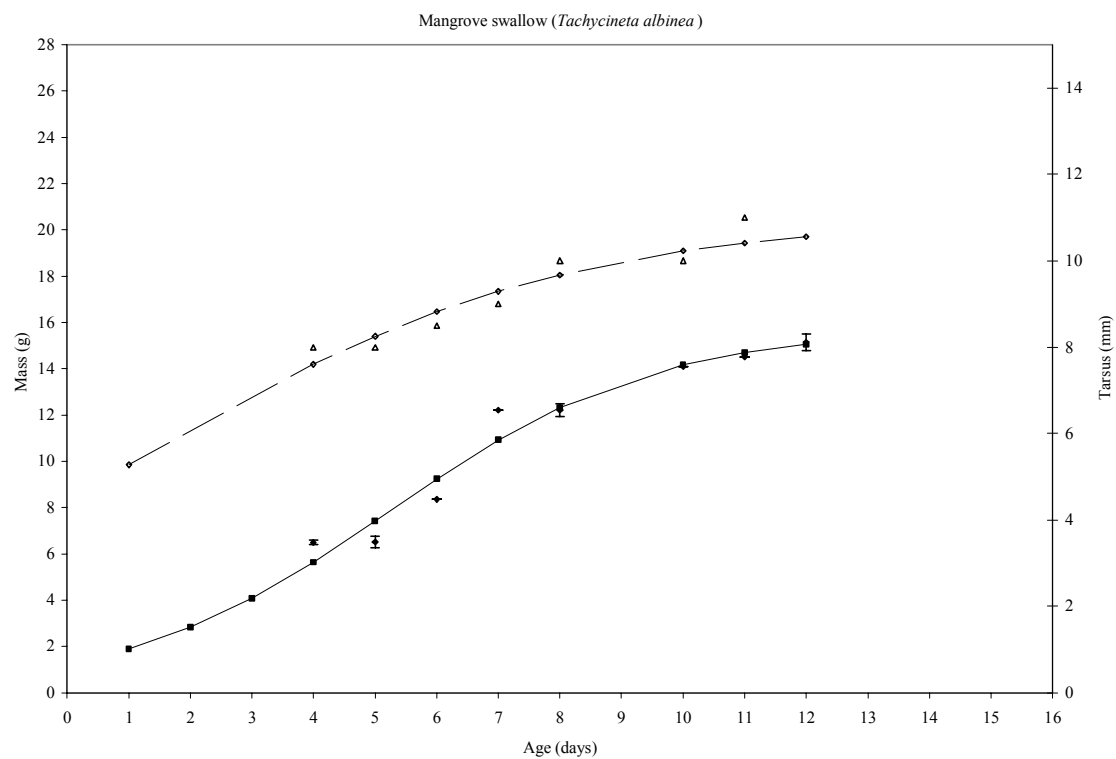
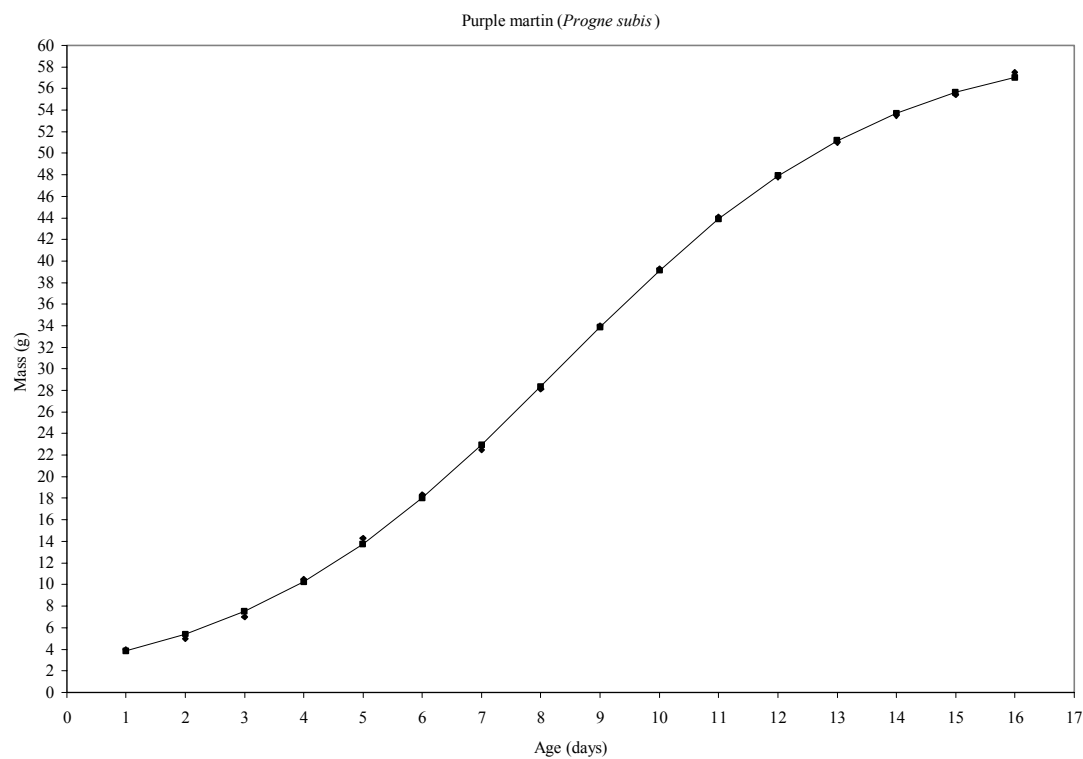
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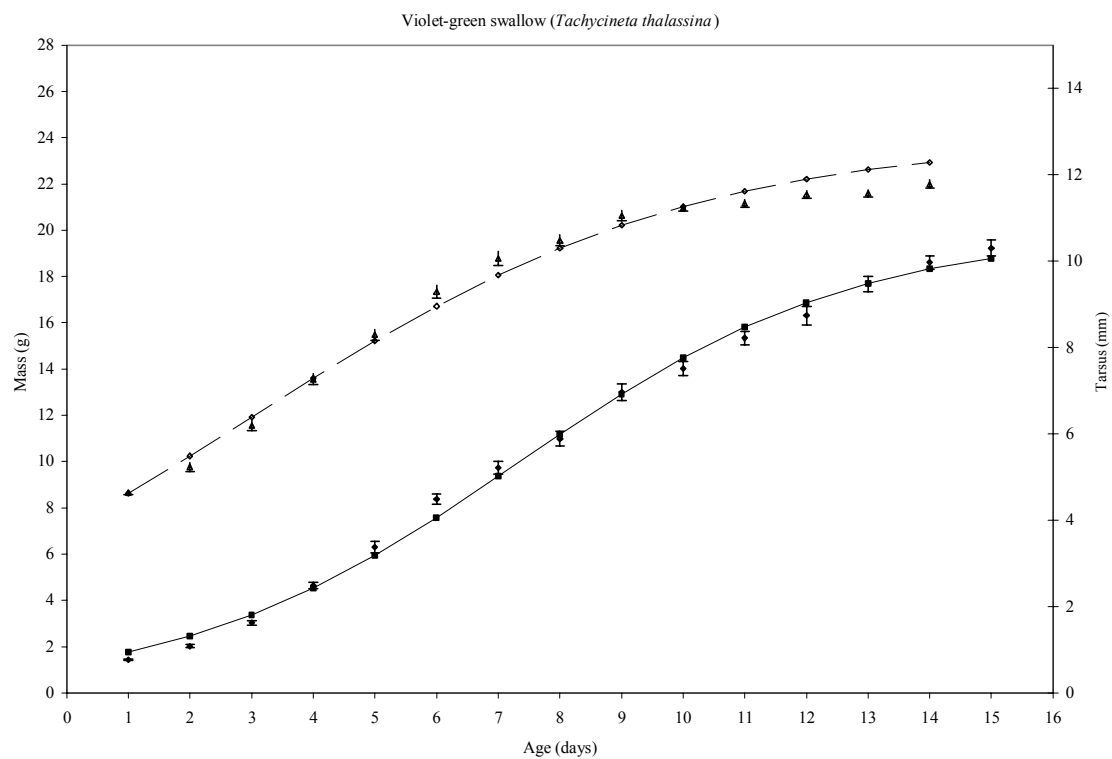
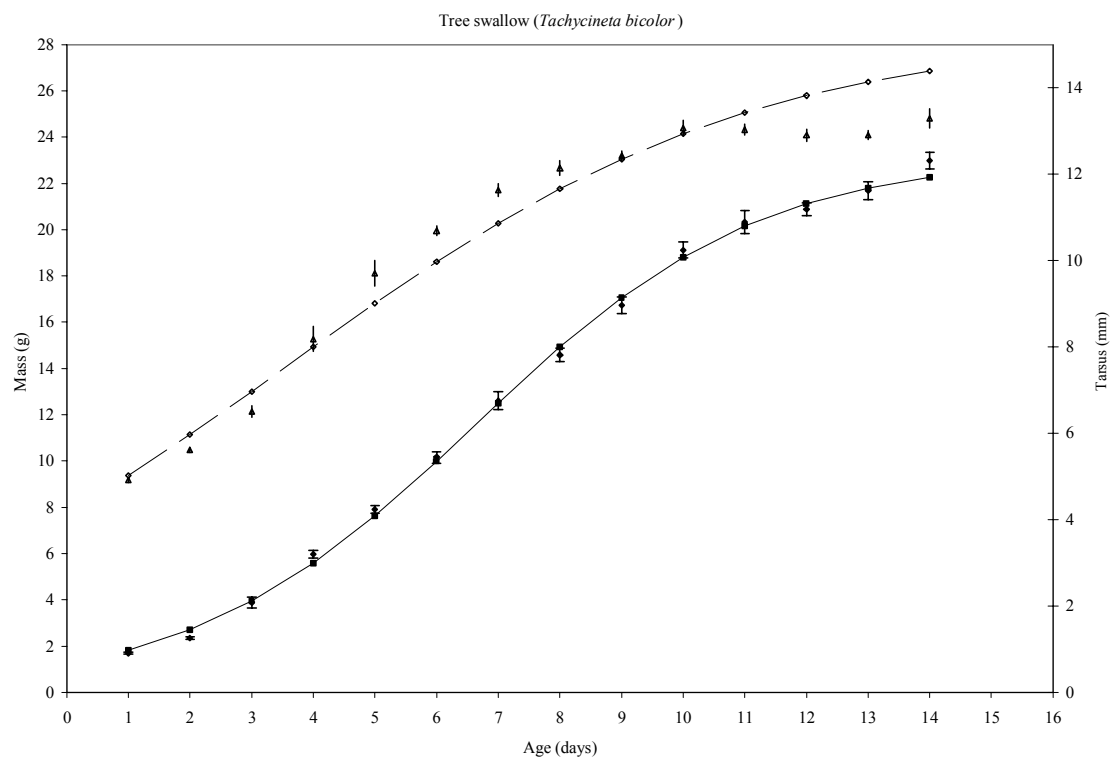


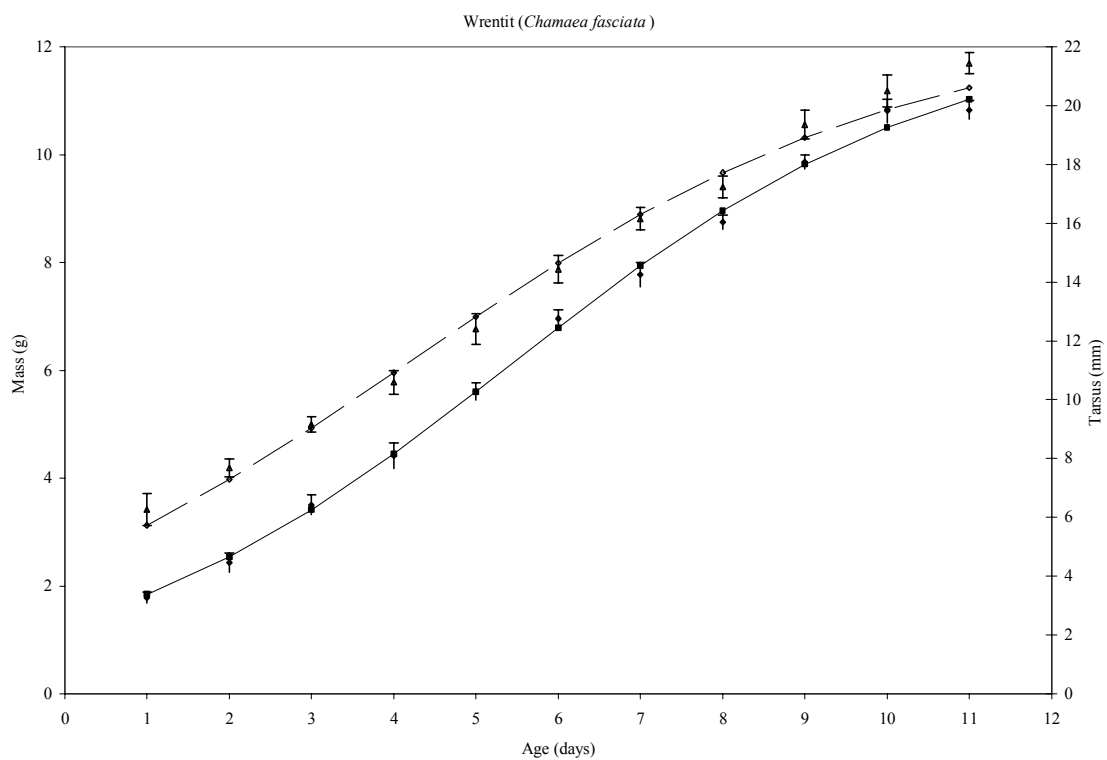
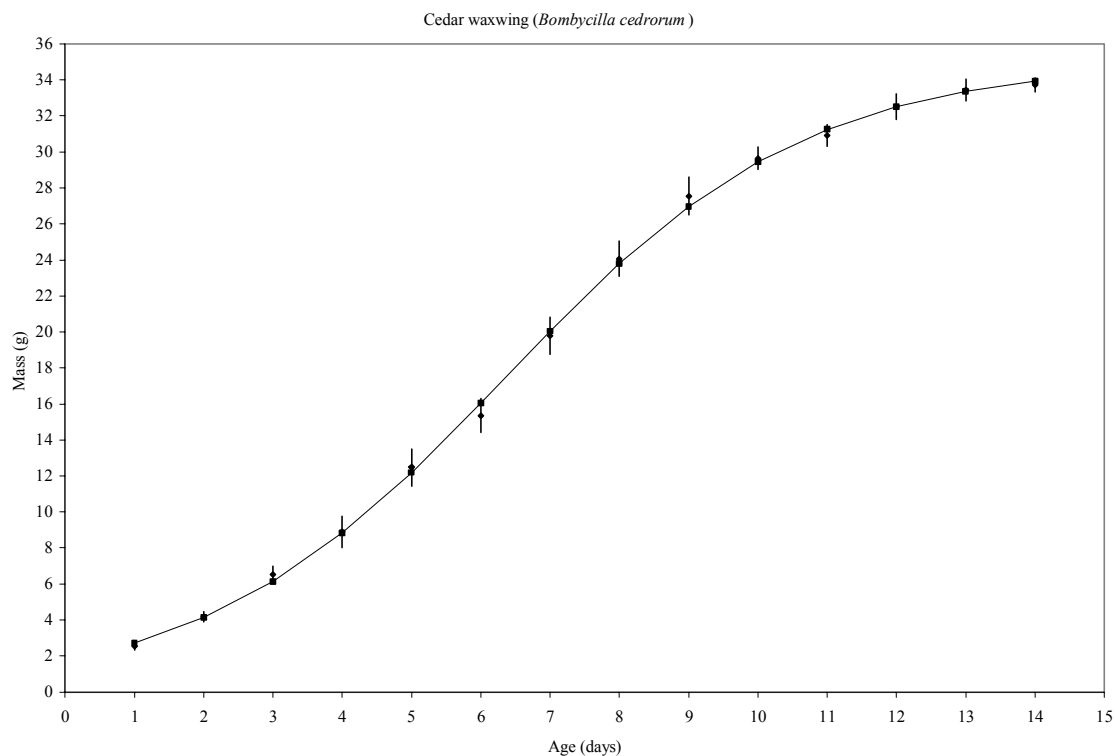


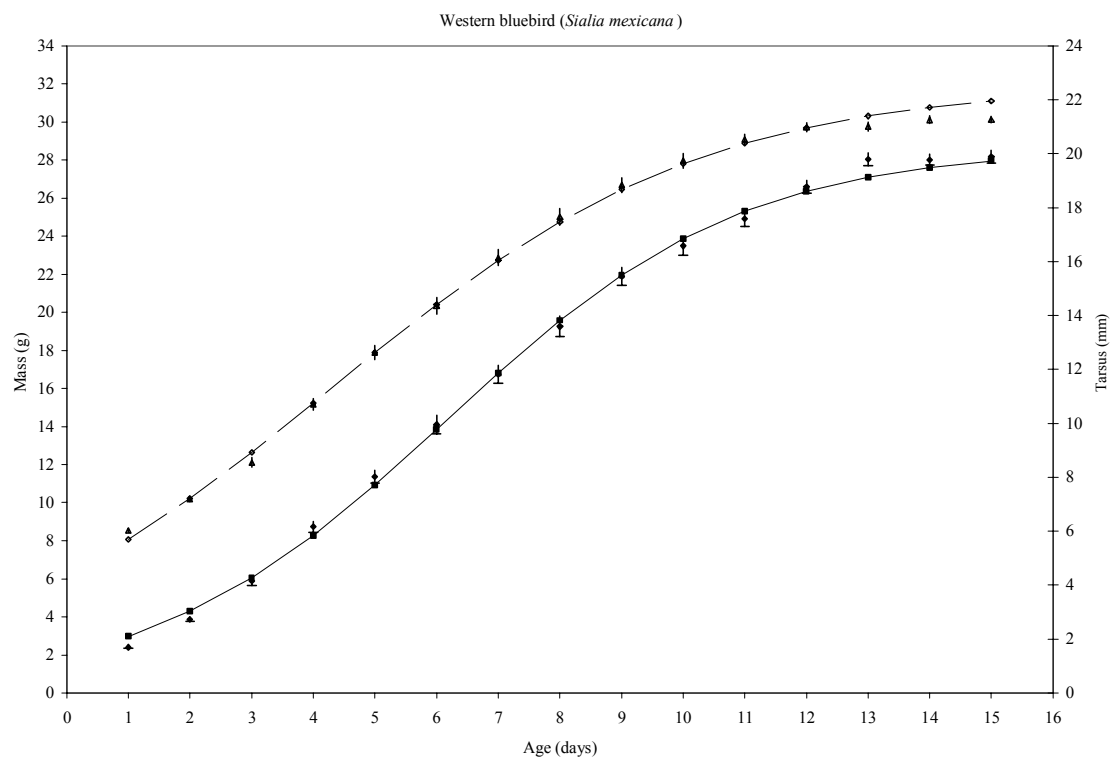
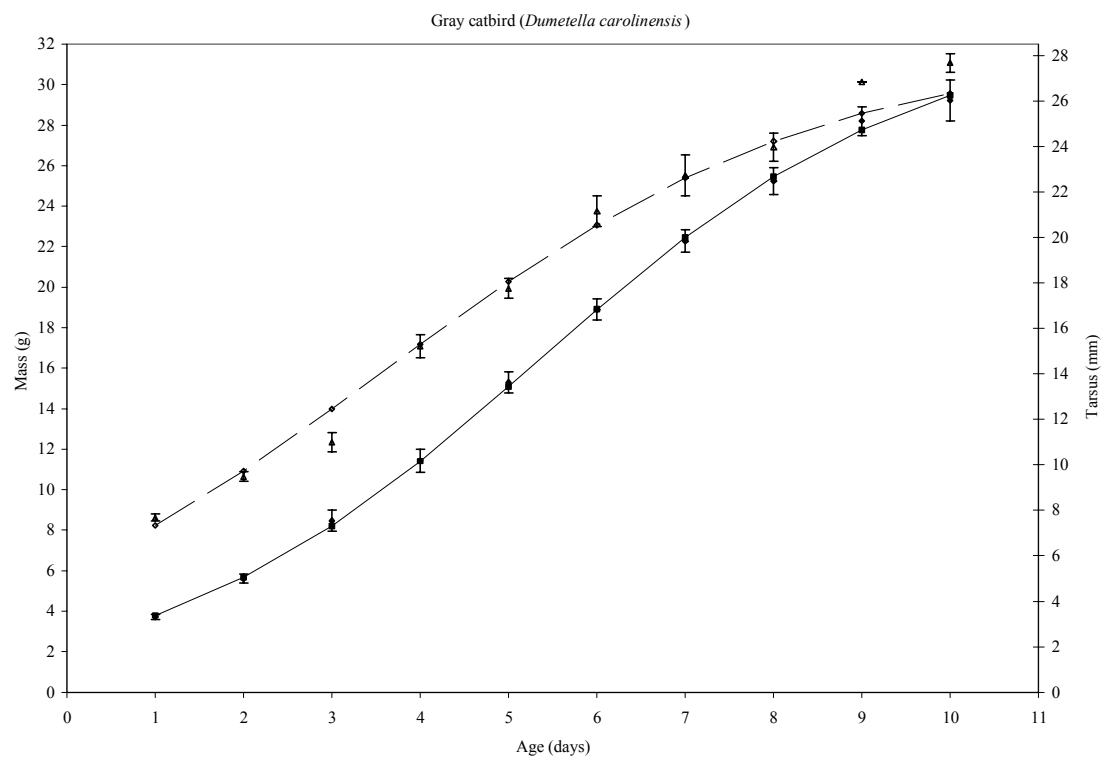
### *Oscine: Sylvioidea*

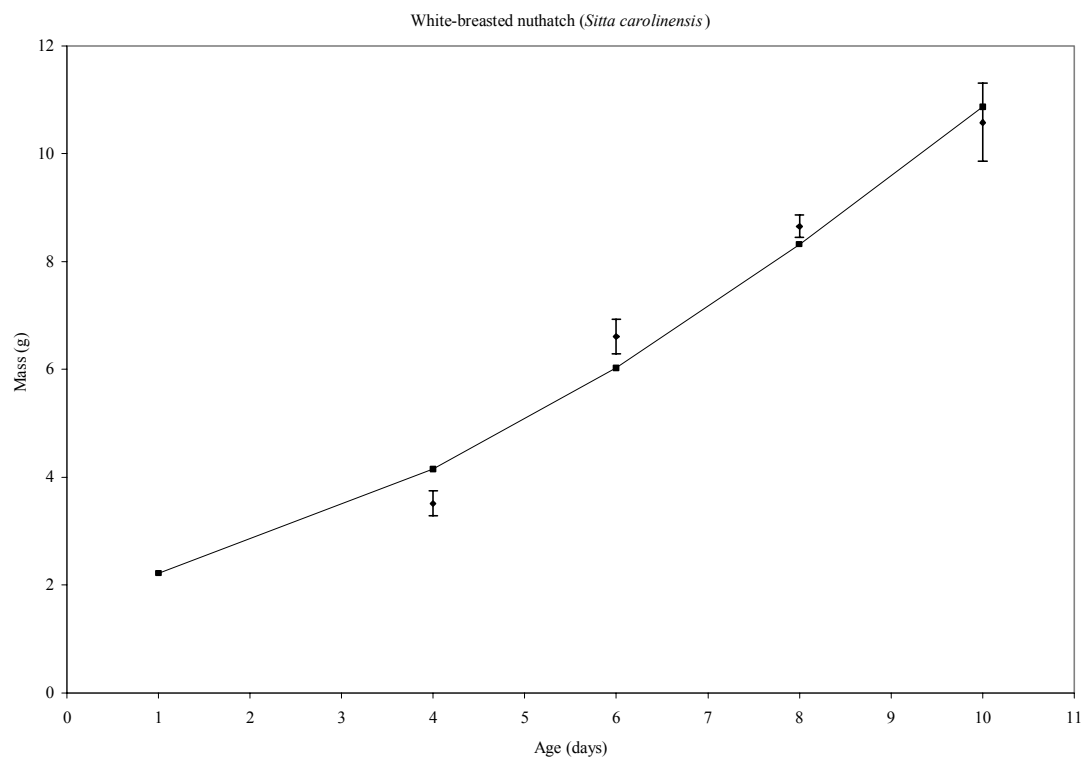
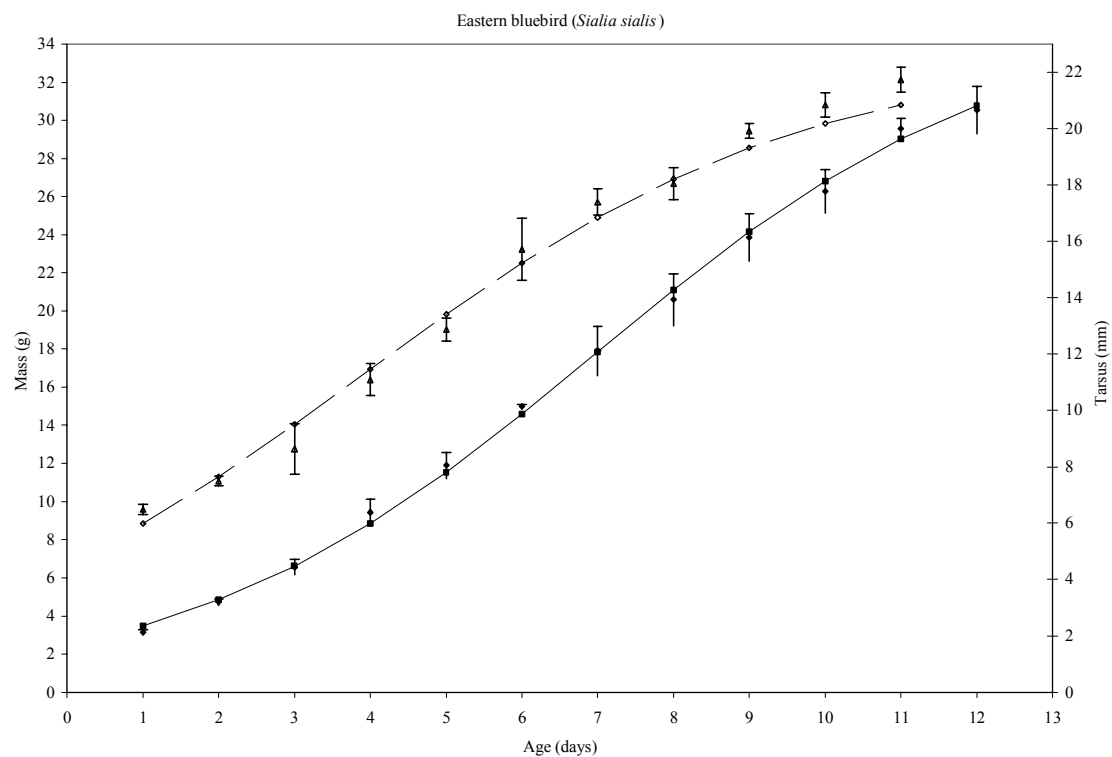


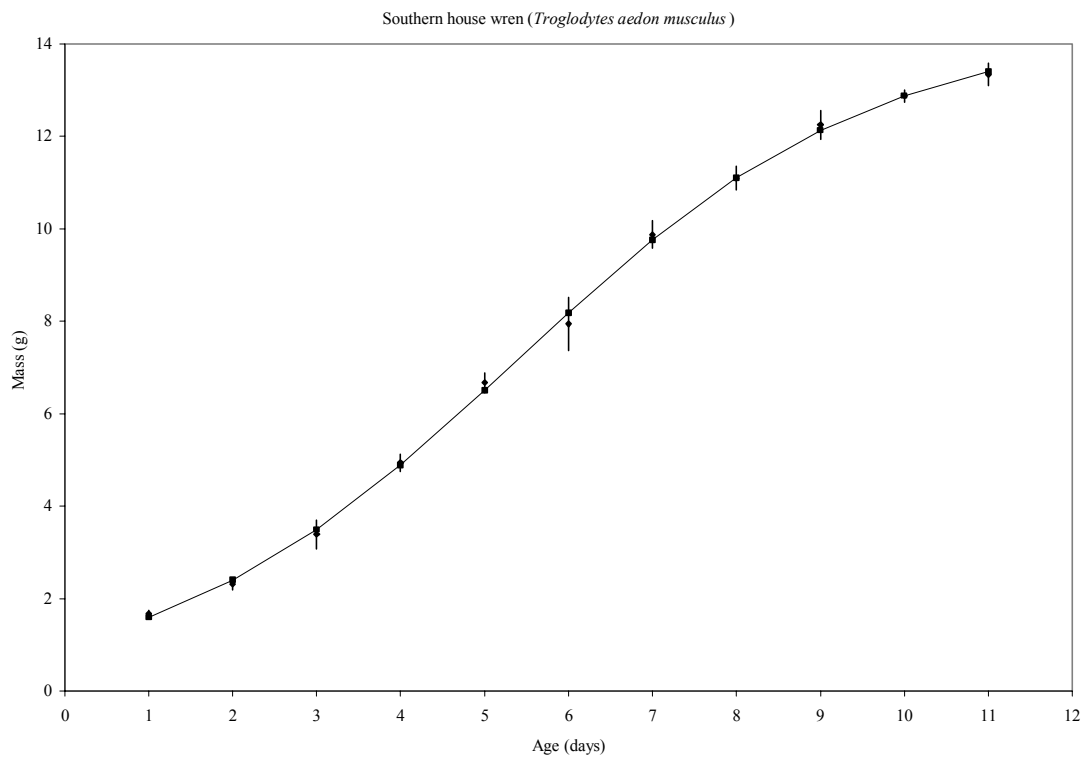
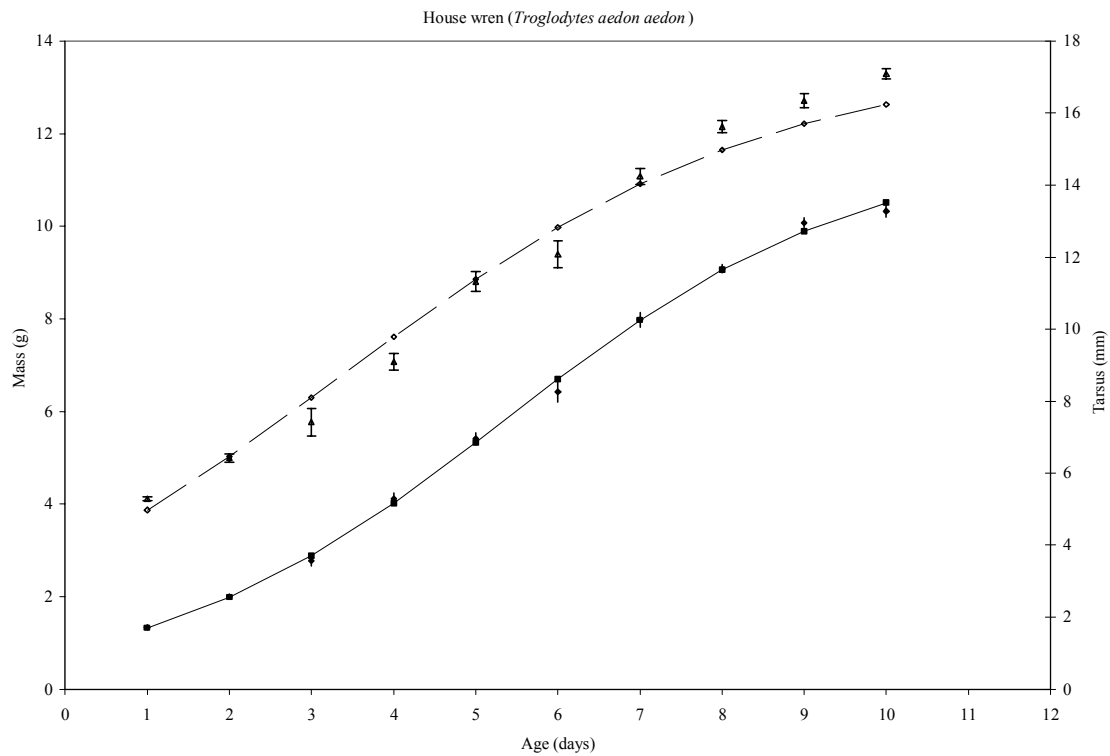




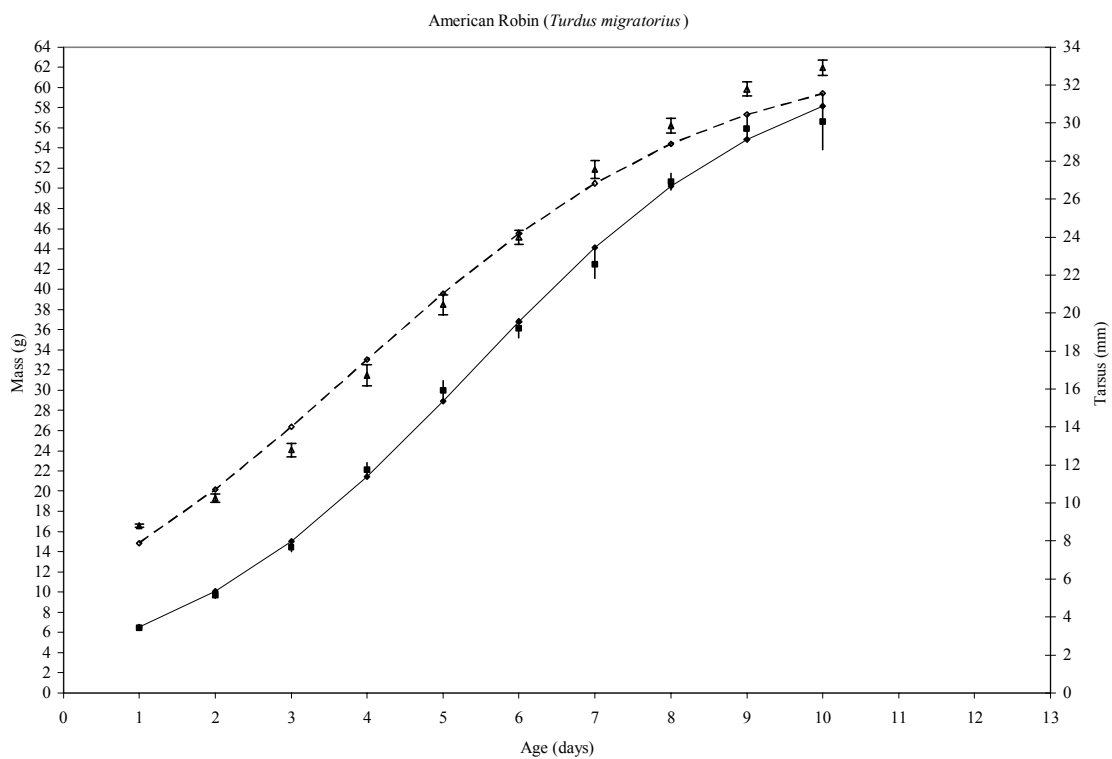
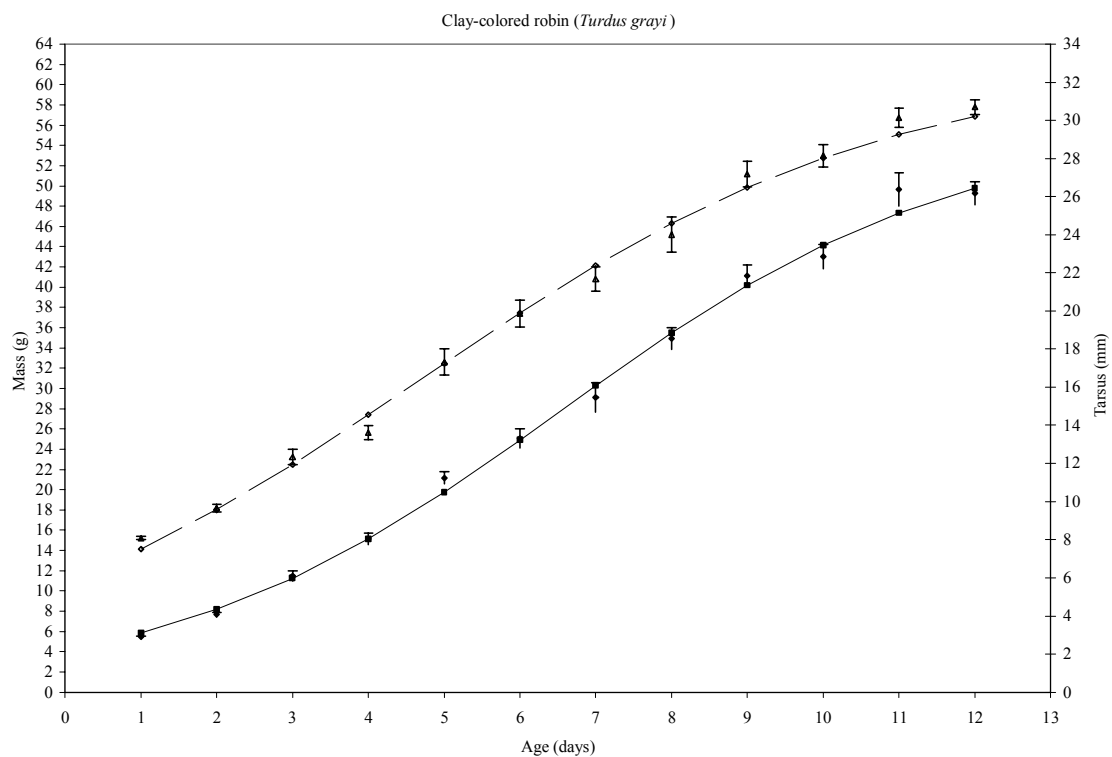
***Oscine: Muscicapoidae***

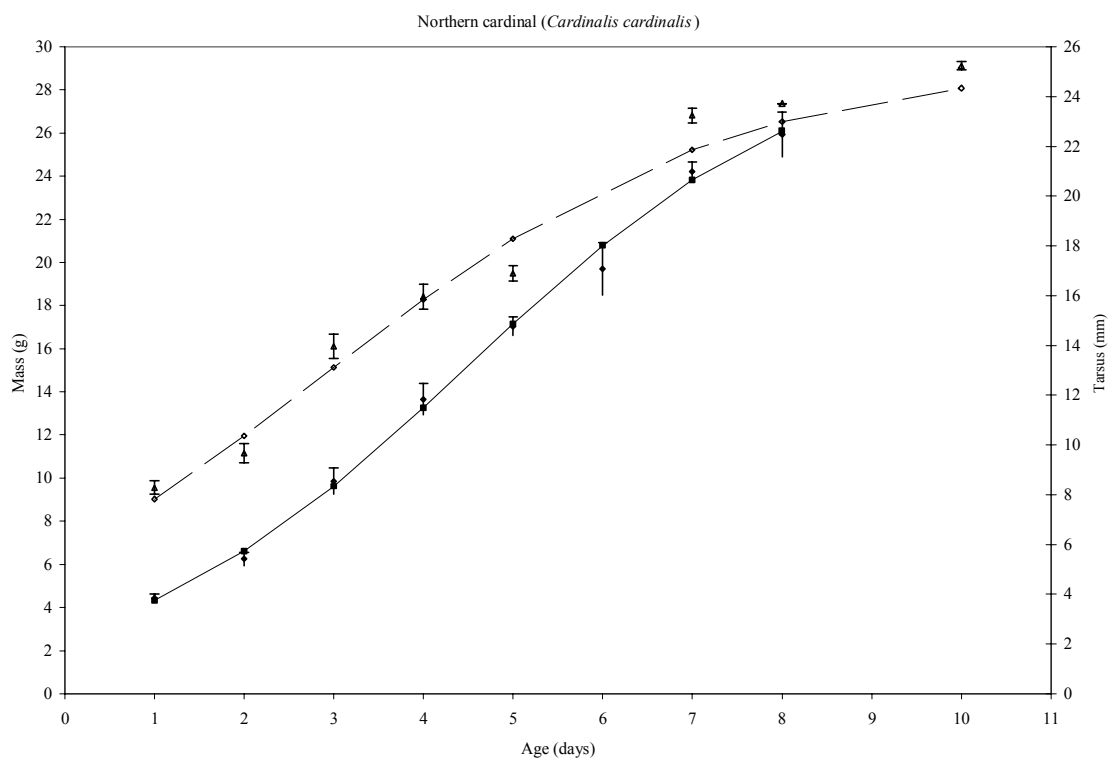
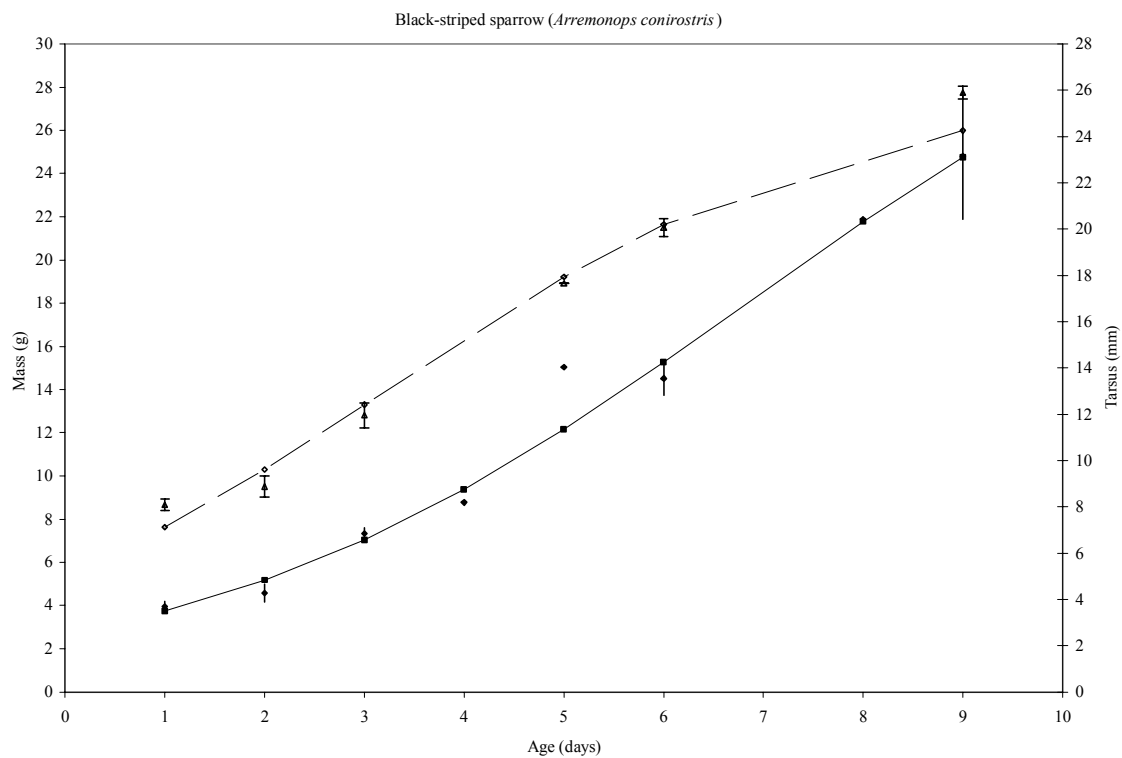


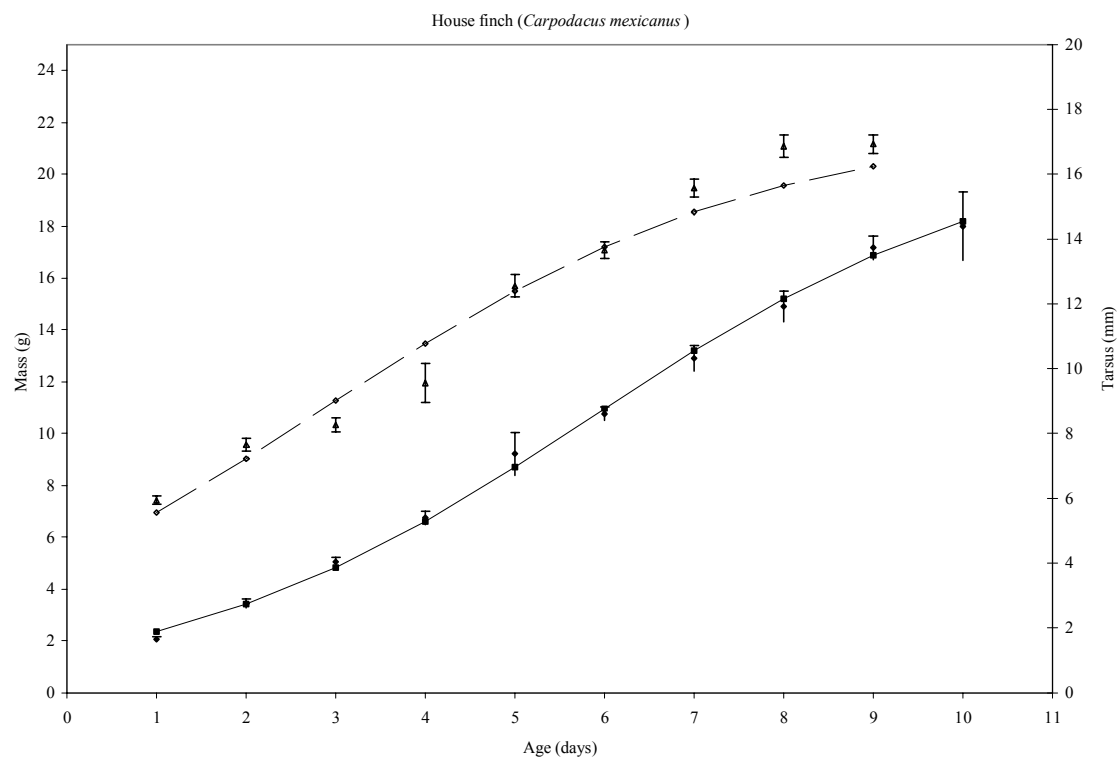
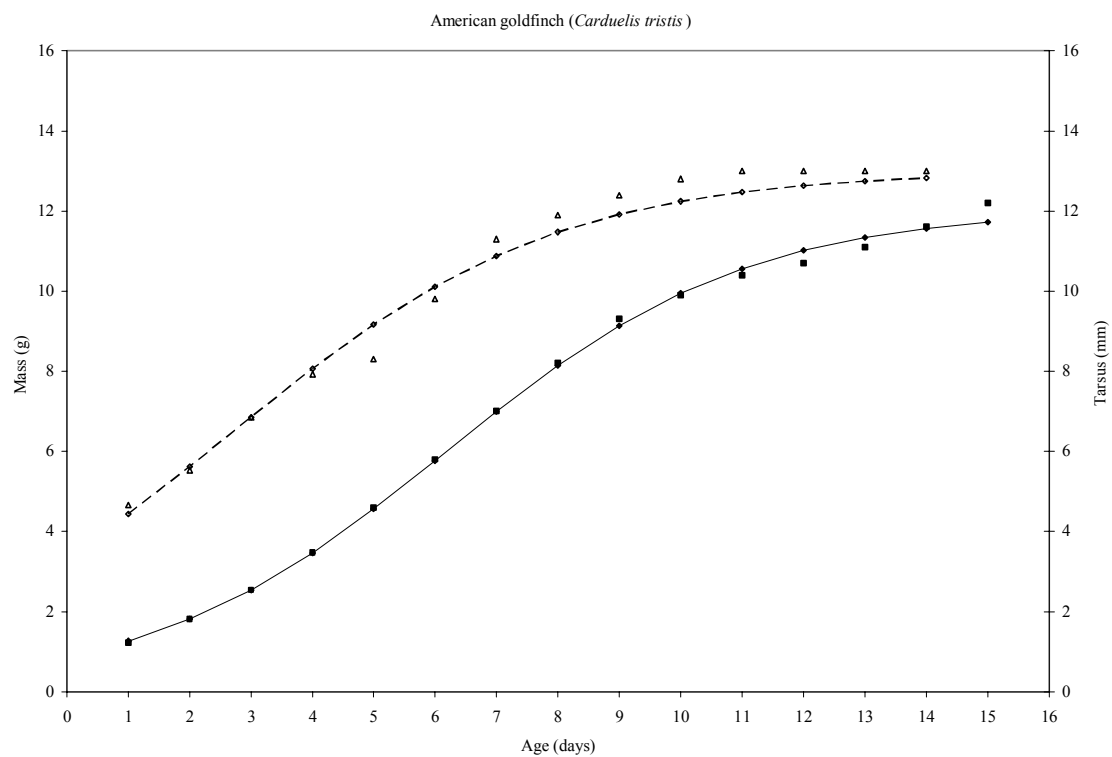


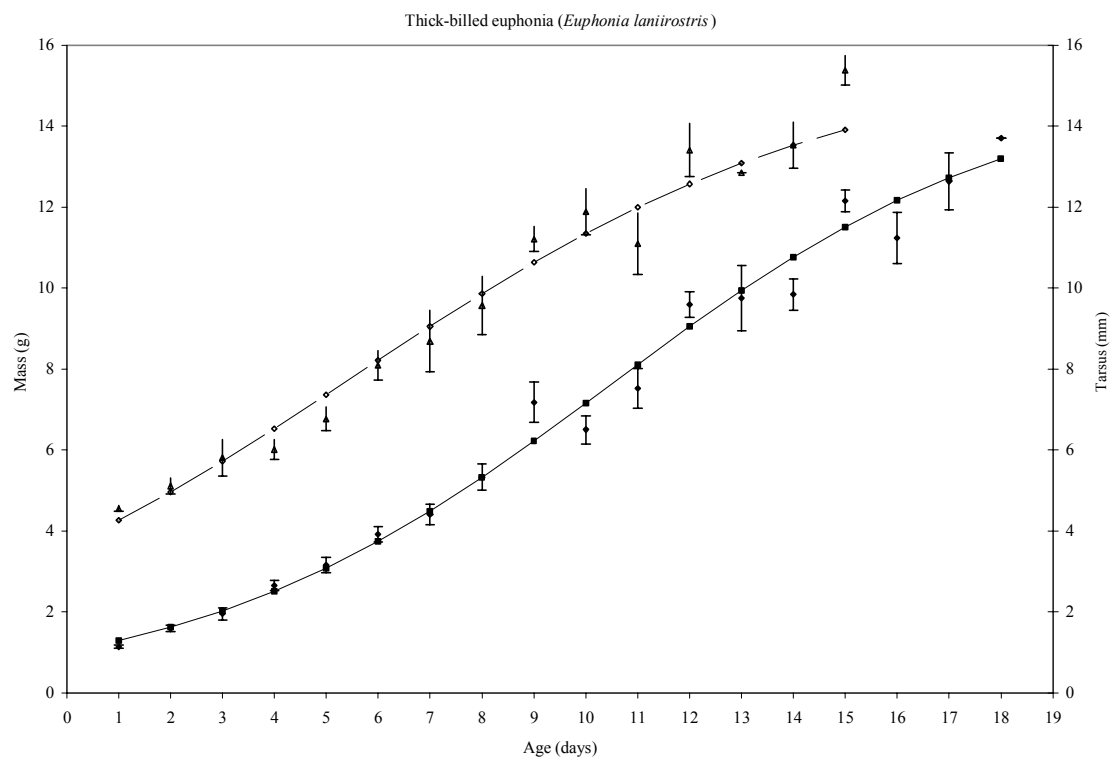
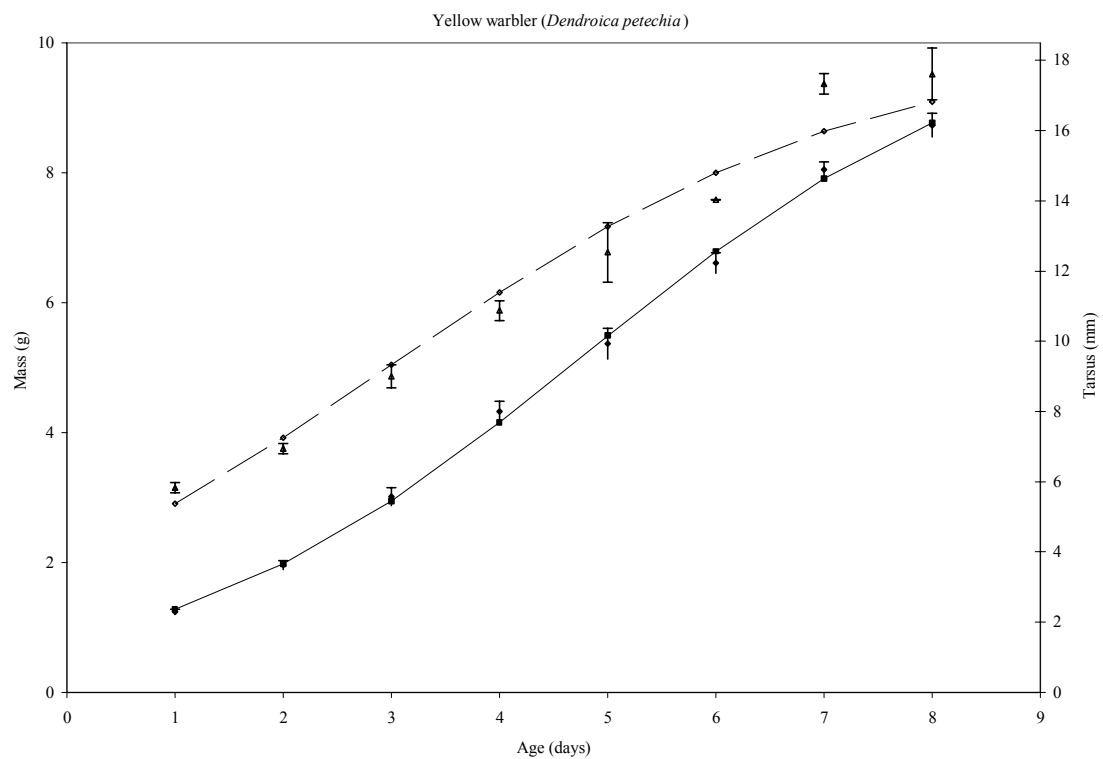


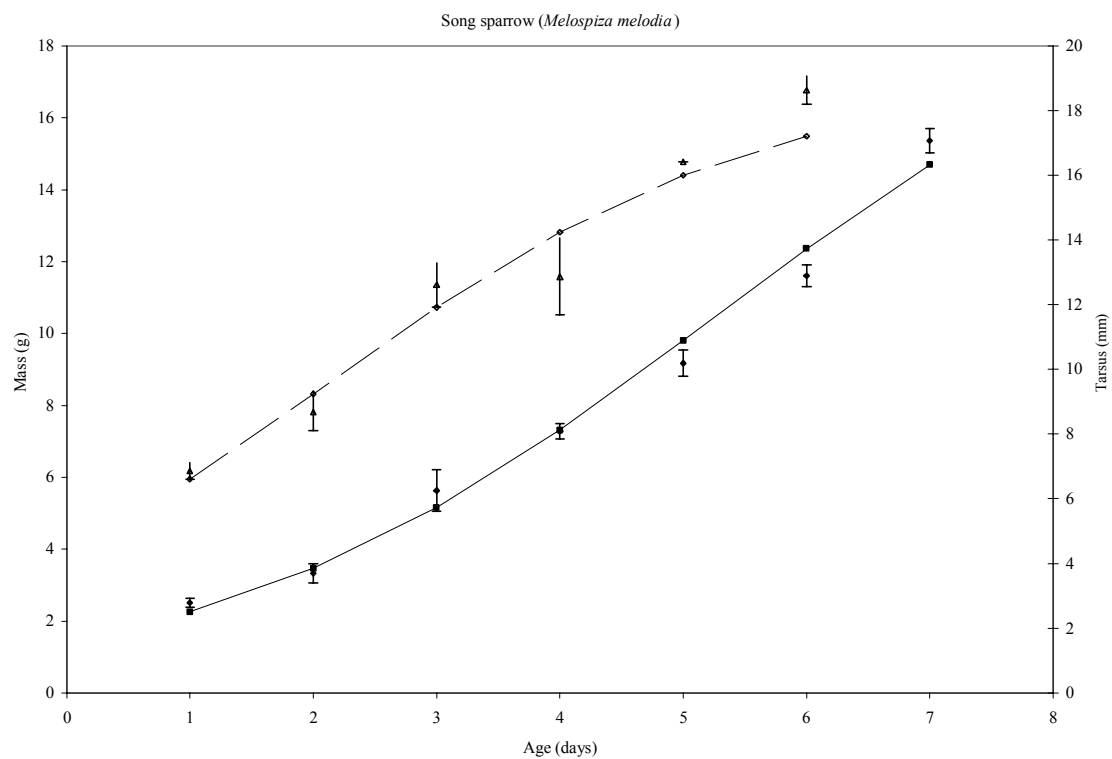
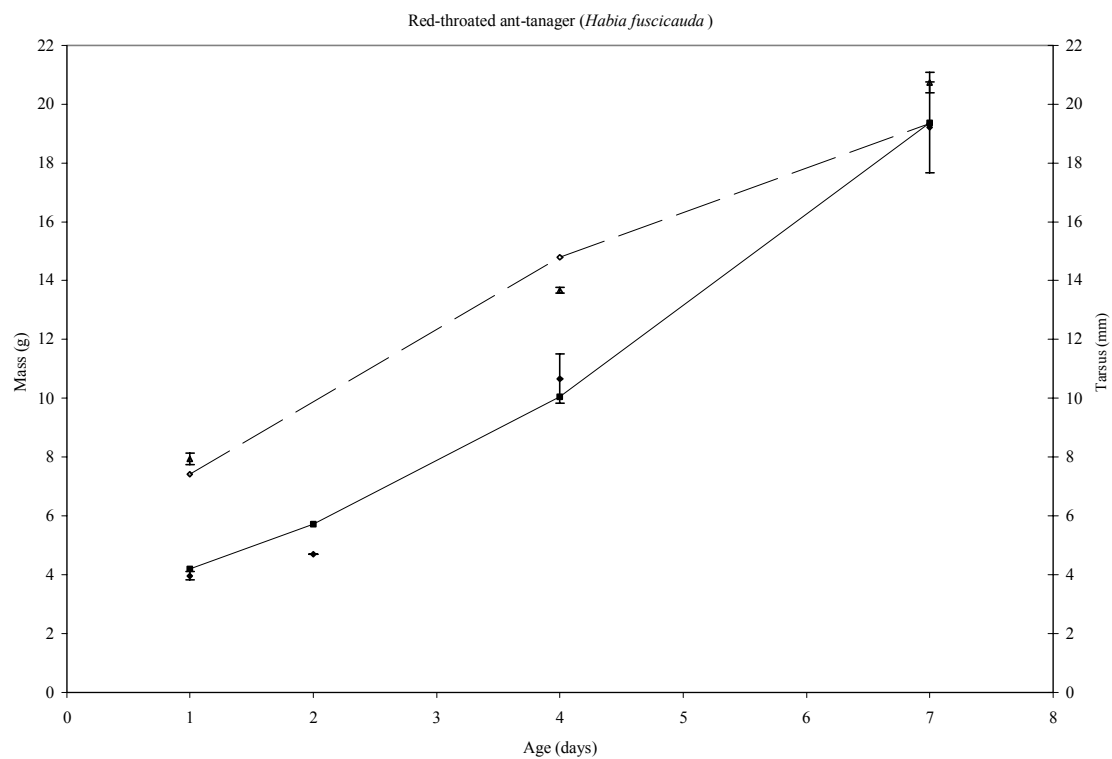


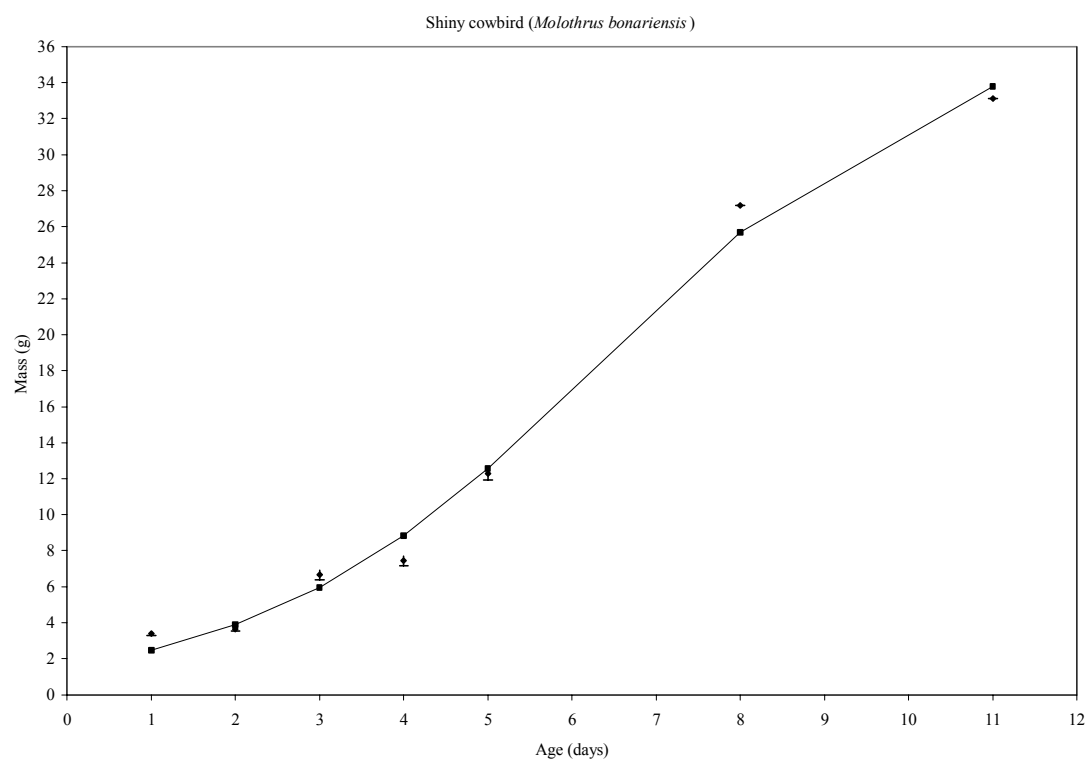
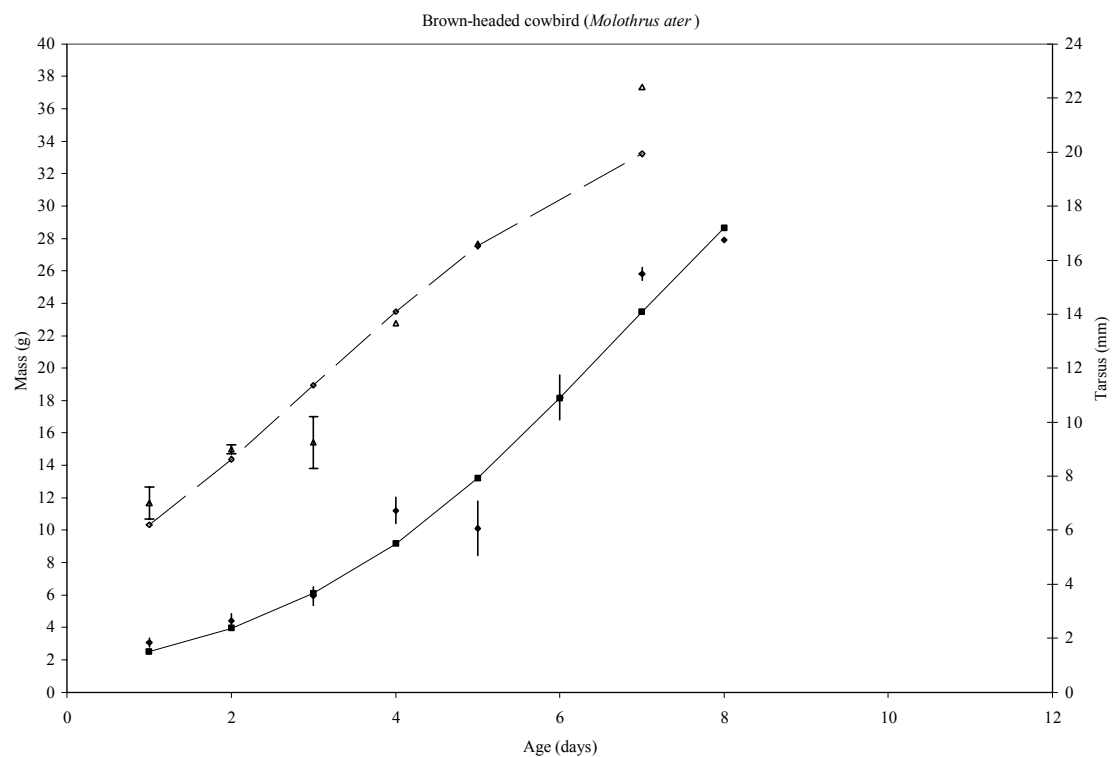


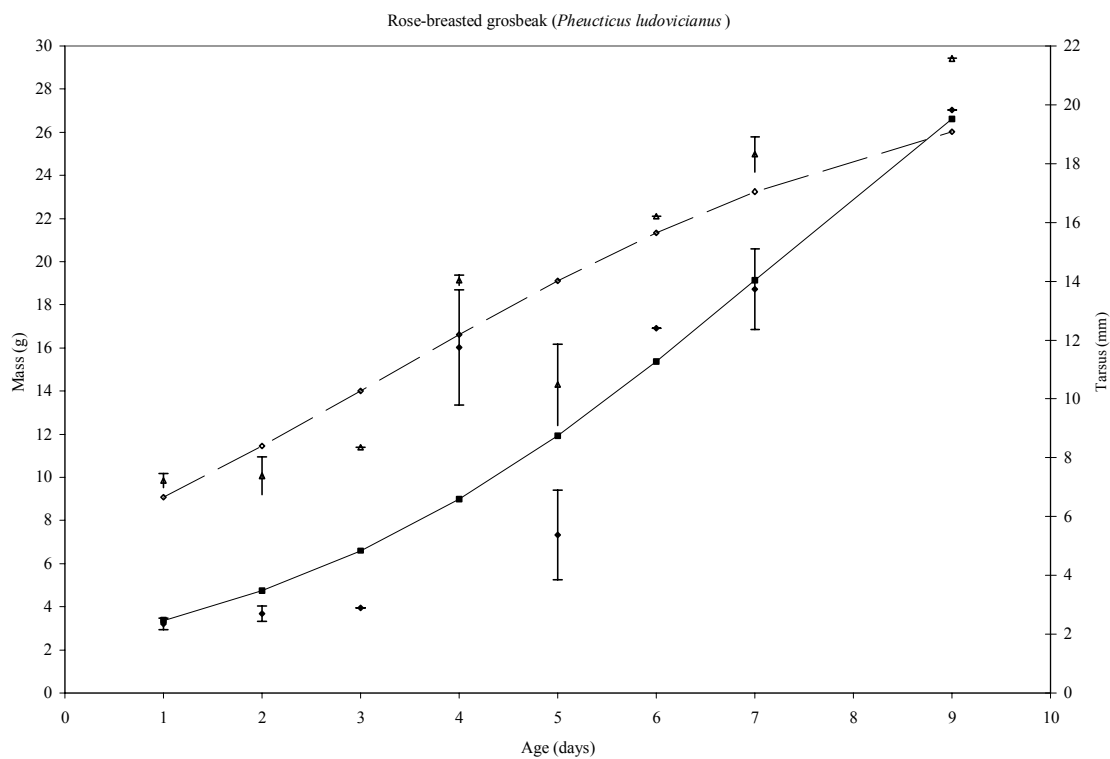
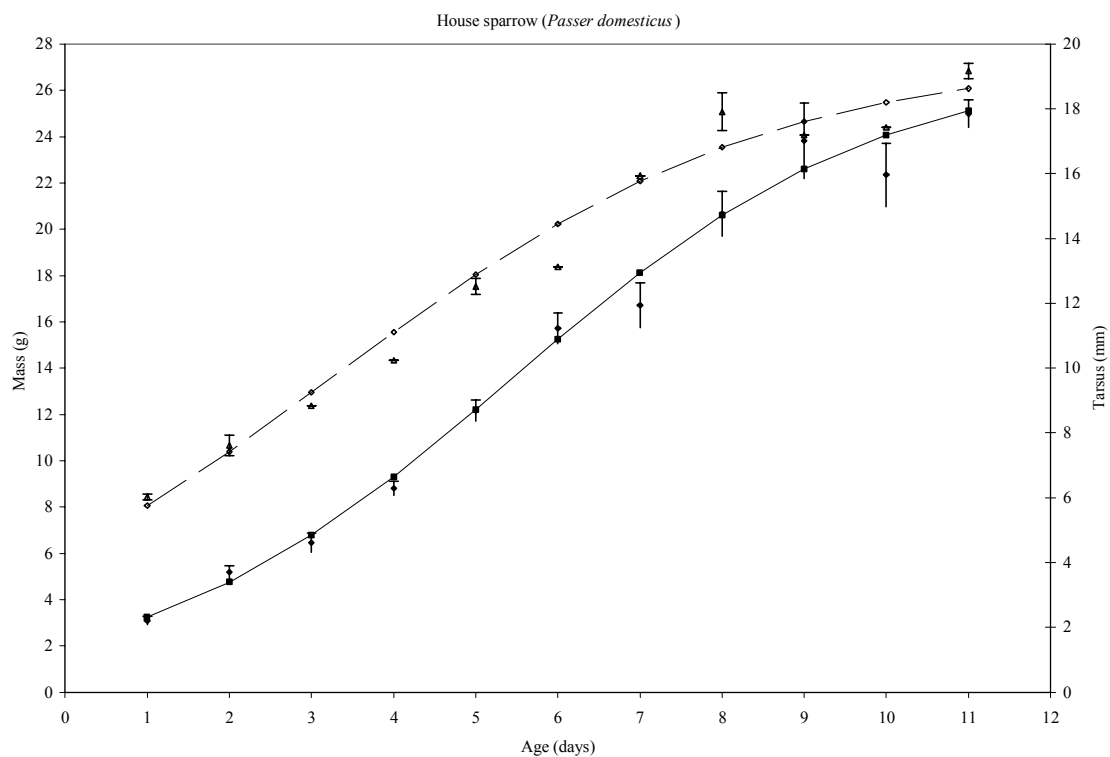
***Oscine: Passeroidea***

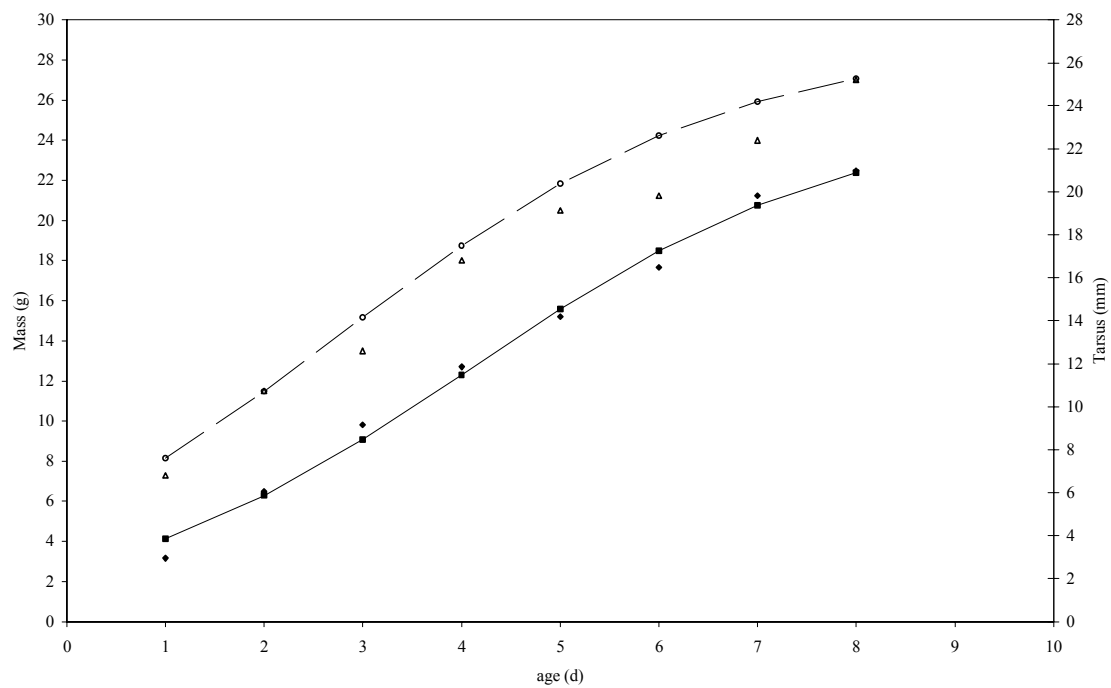
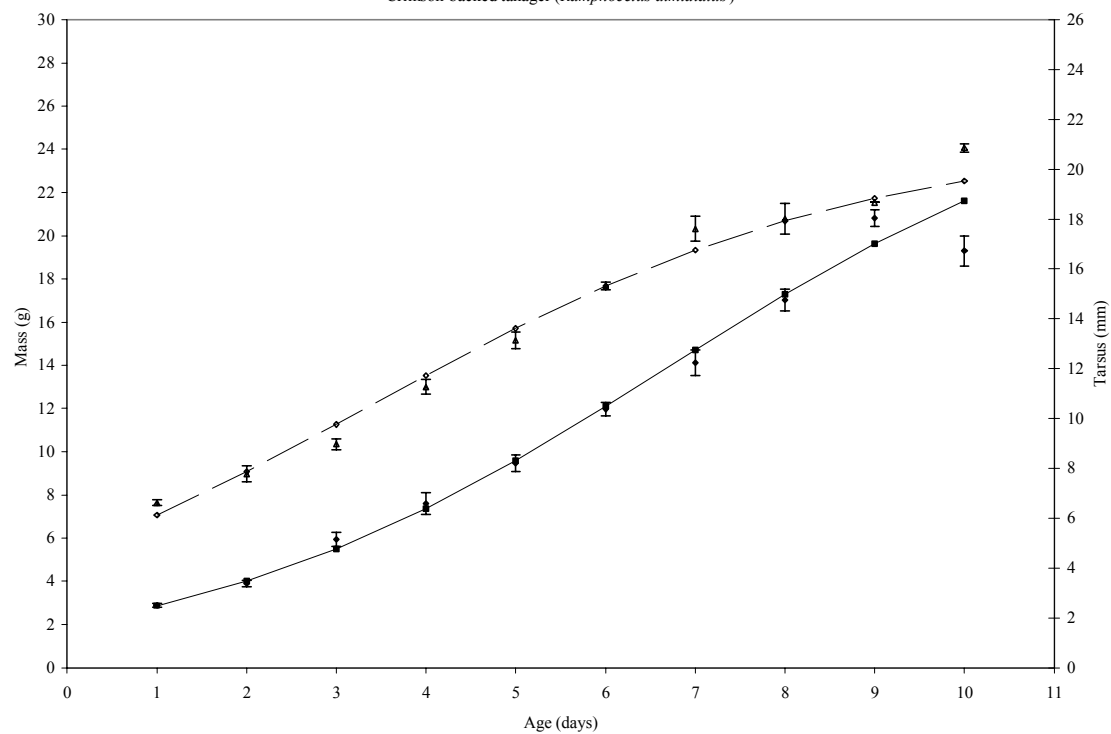




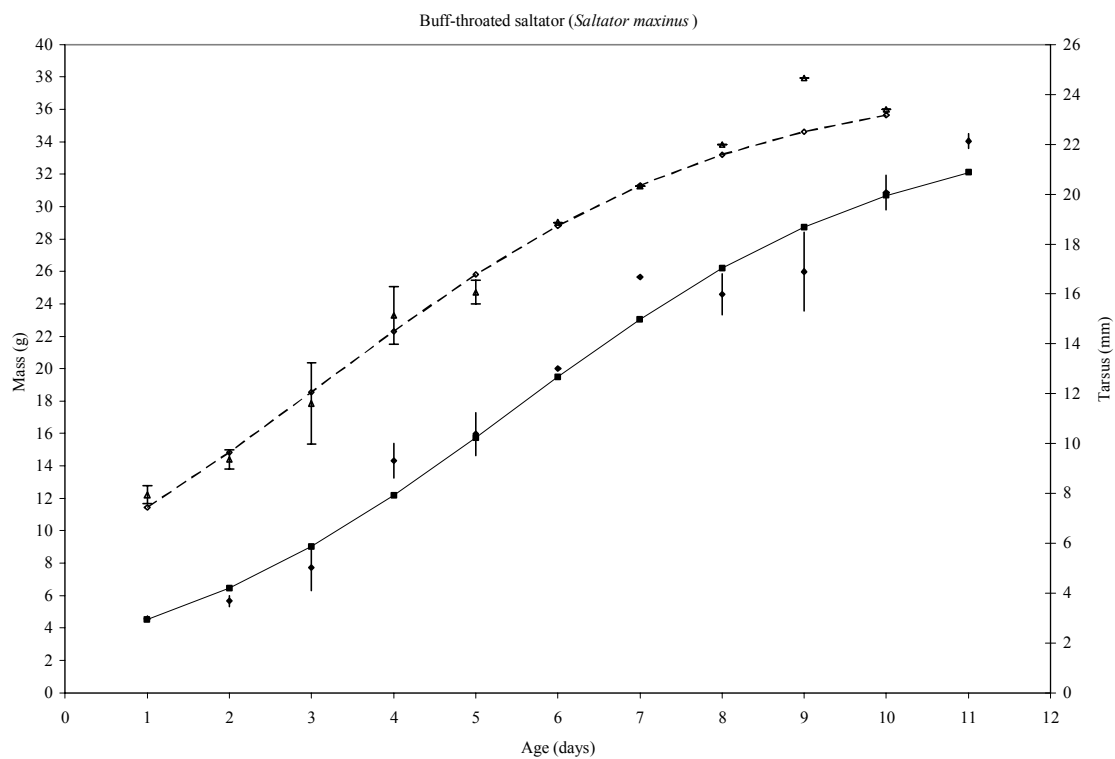
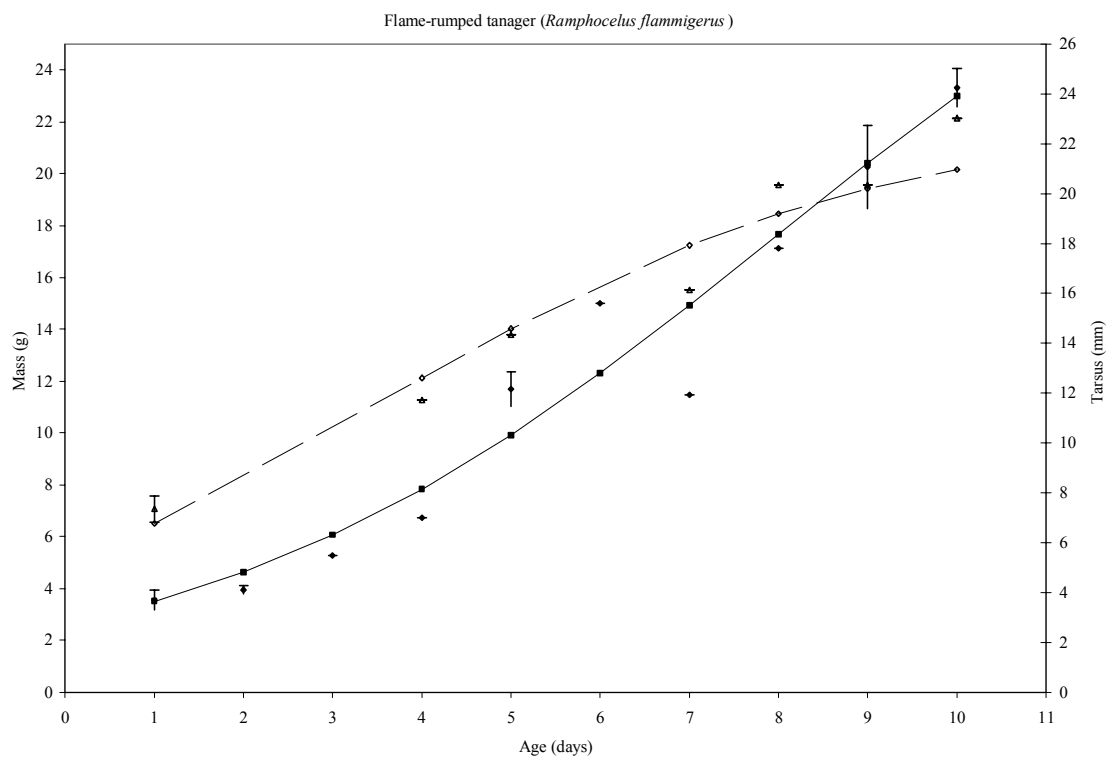


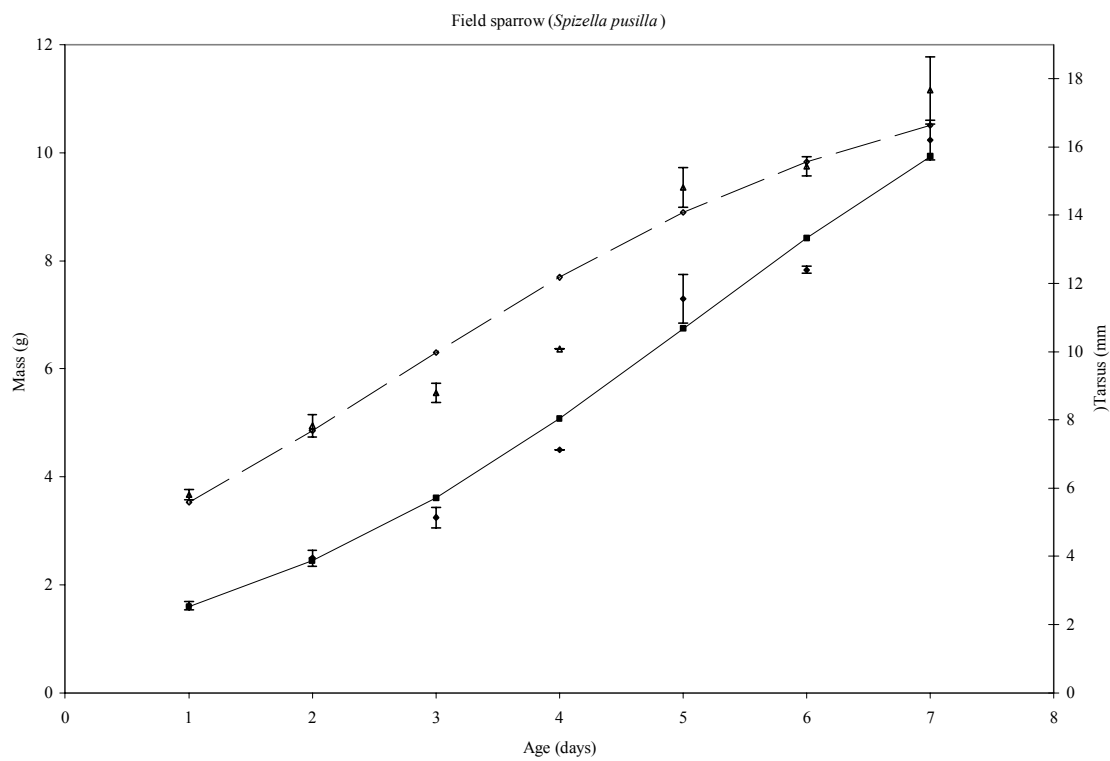
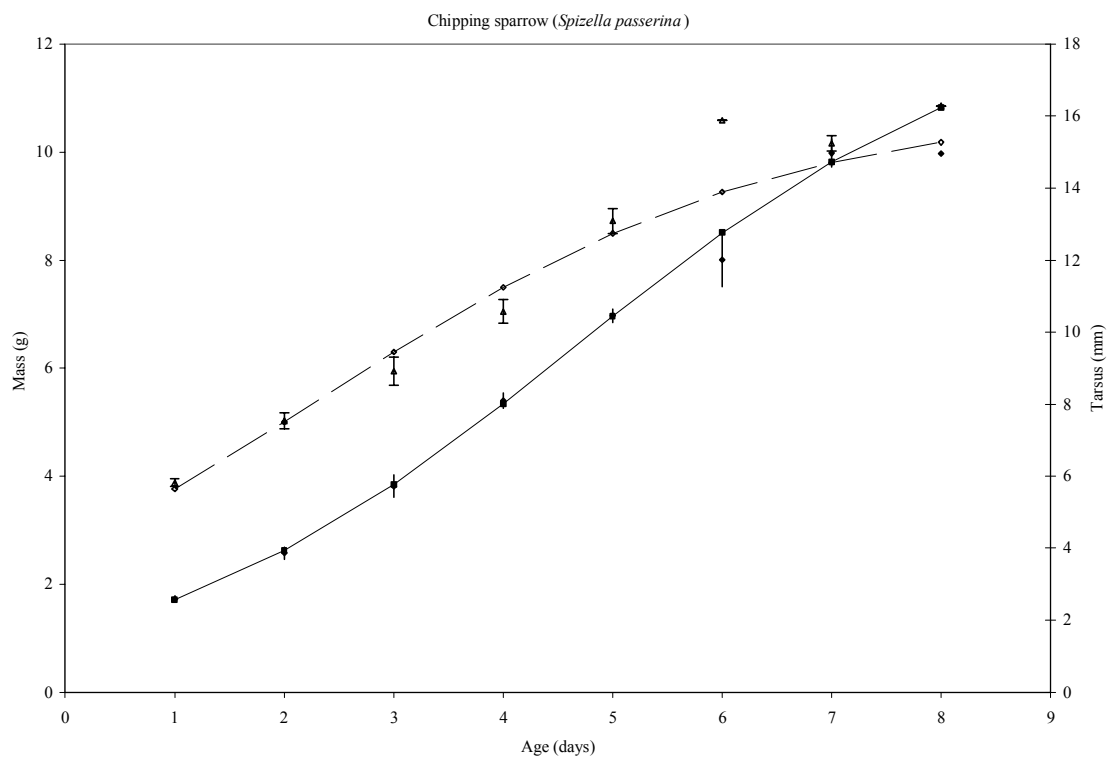


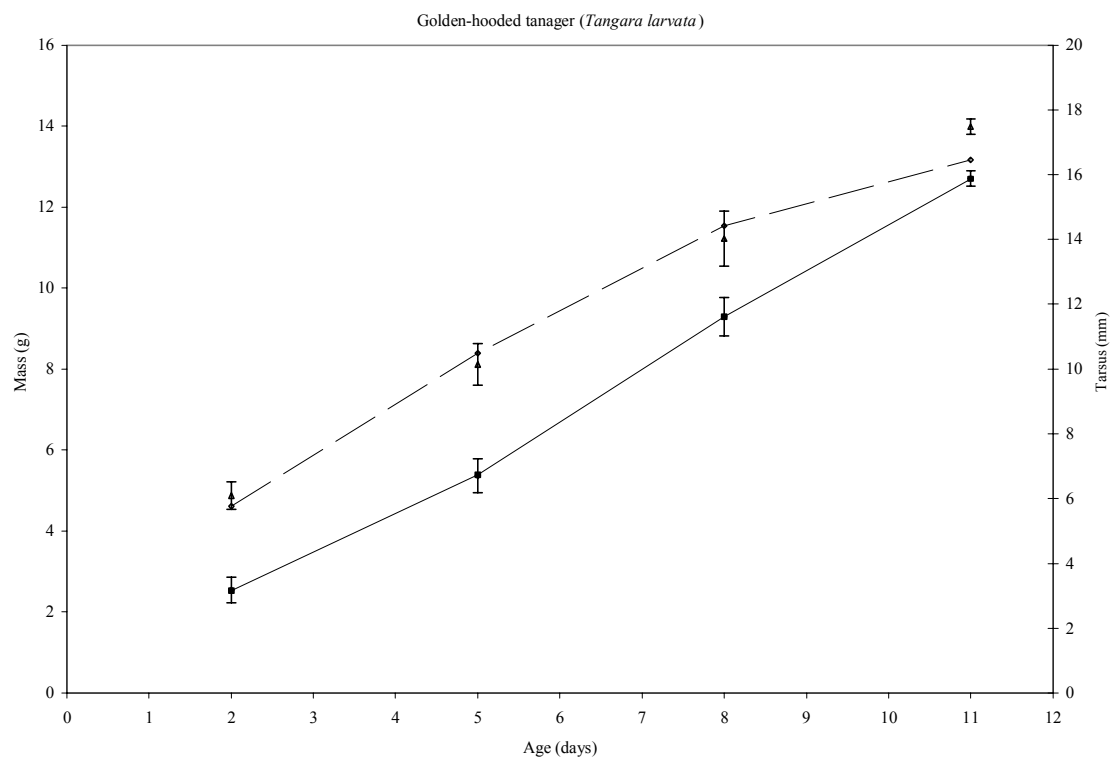
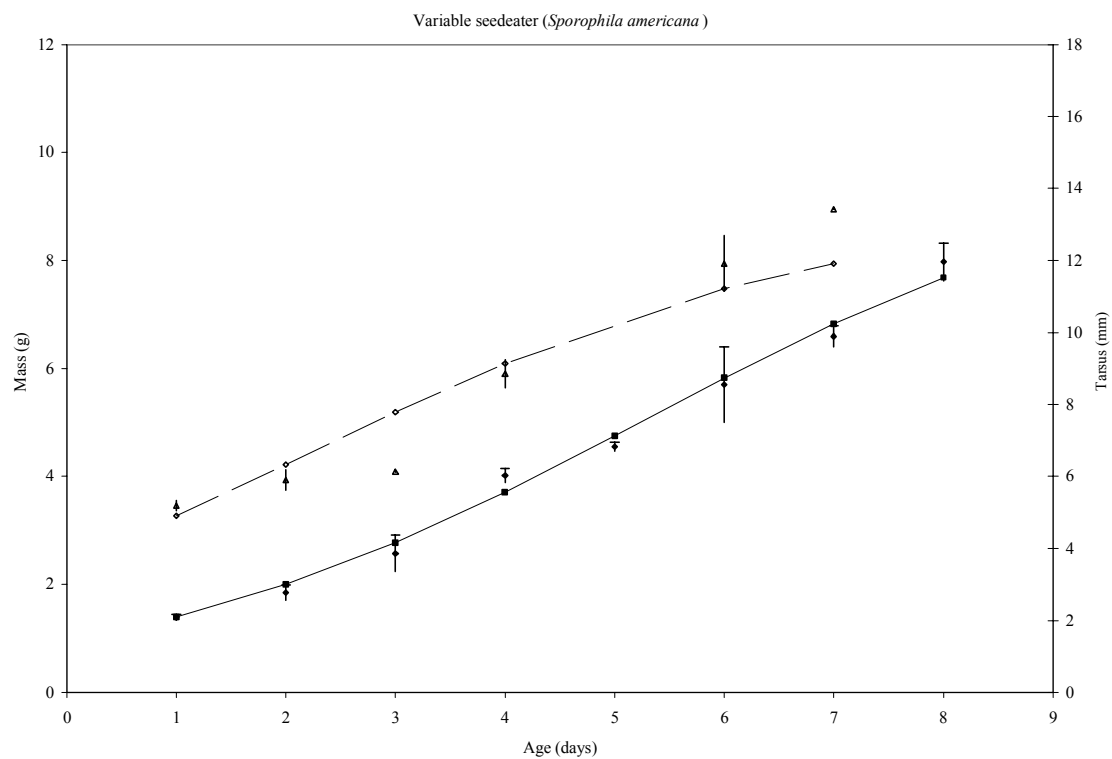


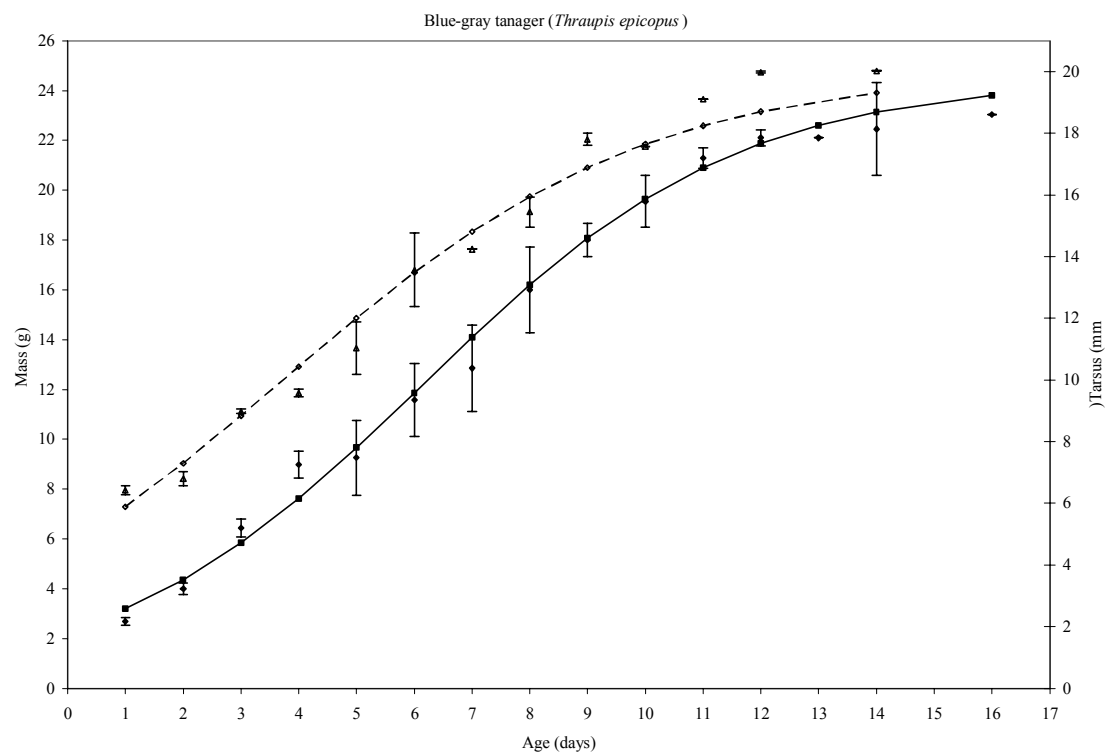
Eastern towhee (*Pipilo erythrophthalmus*)Crimson-backed tanager (*Ramphocelus dimidiatus*)











Appendix 7: Summary growth curves of paired temperate and tropical passerines. Values for temperate species are black while tropical species are gray. Mean mass (g) (solid diamond) and tarsus length (mm) (open triangle) and corresponding growth curves of mass (solid square and solid line) and tarsus length (open diamond and dashed line). Species are organized alphabetically by Sibley and Ahlquist's (1990) super family classification.

