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Why do cavity nesters have a longer nestling period than open nesters?

A comparative study of alternative hypotheses

by

Corinne Tastayre B. Sc.

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Department of Biology

University of Ottawa

Ottawa, Canada

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Abstract

To reduce predation on their progeny, passerines evolved two basic nesting patterns:

1) concealing nests or constructing them in inaccessible places, or 2) breeding inside cavities where offspring are relatively protected. These two nesting patterns seem to lead to different length of nesting cycle. Nice (1957) was the first to report that cavity-nesting species have a longer nestling period than open-nesting species. However, because sample sizes of her and later published studies were generally small, there is a need for a new, large scale study that would confirm Nice's (1957) observation. If confirmed, then we should address the question: why does such a difference in nestling period exist? Two hypotheses have been proposed. Both are based on an assumption that cavity nesters suffer from lower predation than open nesters. The first hypothesis, proposed by Lack (1968), states that later fledging by young of cavity nesters as compared to open nesters is a result of a slower growth of young cavity nesters. The second hypothesis proposed by this study suggests that differences in nestling periods between open nesters and cavity nesters reflect different predation rates on nests of the two groups of passerines. Thus young open nesters should fledge

early due to higher nest predation, whereas young cavity nesters should stay longer in their safer nests.

The goals of my study were: 1) to verify the earlier observation that cavity nesters have a longer nestling period than open nesters; 2) to test the assumption that predation is more intense on nest contents of open nesters than cavity nesters, thereby presenting an important selective force favoring different lengths of the nestling periods of the two groups; and 3) to test two hypotheses on the occurrence of different length of nestling periods between the two groups of passerines.

My results demonstrated that 1) the nestling period is, on average, 5.4 days longer for cavity nesters than for open nesters of the same size; 2) daily mortality rates of open nesters are about twice as high as those of cavity nesters; 3) growth rates are somewhat slower for nestlings of cavity nesters than for those of open nesters; 4) the differences in growth rates of young explain only about 20% of the entire difference in nestling periods of cavity nesters and open nesters; and 5) young of open nesters leave their nest when their weight is at 79% of that of adults and their wing length is at 59% of that of adults, whereas young of cavity nesters are more fully developed when leaving their nest (weight at 94% and wing length at 77% of the

adult size).

My results support the view that predation is the major selective force that has presumably favored 1) somewhat faster nestling growth, and 2) earlier departure of young from nests of open nesters relative to those of cavity nesters.

Résumé

Dans le but de réduire la prédation sur leur progéniture, les passereaux ont développé deux stratégies de nidification: 1) ils camouflent leur nid ou le construisent dans un endroit inaccessible, ou 2) ils construisent leur nid dans une cavité qui est plus protégée. Ces deux stratégies de nidification mènent à des comportements différents. Nice (1957) a été la première à noter que les oiseaux nichant en cavité ont une période nidicole plus longue que les oiseaux nichant en nid ouvert. Par contre, à cause d'un faible échantillonnage de ses données et des données des études subséquentes, le besoin pour une nouvelle étude à plus grande échelle s'est fait sentir pour vérifier l'observation de Nice (1957). Si cette observation est confirmée, on peut se demander pourquoi une telle différence dans la durée des périodes nidicoles des deux groupes d'oiseaux existe. Deux hypothèses basées sur la supposition que la predation est plus élevée dans les nids ouverts que dans les cavités ont été proposées. La première hypothèse proposée par Lack 1968 énonce que le départ tardif des espèces d'oiseaux nichant en cavité est dû à la croissance plus lente de leurs oisillons comparé à la croissance des oisillons nichant en nid ouvert. La seconde hypothèse, proposée par cette étude, suggère

que la différence dans les périodes nidicoles entre les deux groupes d'oiseaux est le reflet de taux de prédation différents. Les oisillons des espèces nichant en nid ouvert devraient quitter le nid plus tôt à cause de la forte prédation alors que les oisillons en cavités devraient rester plus longtemps dans leur nid sécuritaire.

Les buts de cette étude sont: 1) vérifier l'observation d'une période nidicole plus longue pour les oiseaux nichant en cavité; 2) vérifier la supposition que la prédation plus intense sur les nids ouverts est la principale force de sélection favorisant une période nidicole plus courte; et 3) vérifier les deux hypothèses les plus plausibles expliquant différentes périodes nidicoles pour les deux groupes d'oiseaux.

Mes résultats démontrent que 1) la période nidicole est en moyenne de 5,4 jours plus longue pour les oiseaux nichant en cavité comparé aux espèces nichant en nid ouvert de même poids; la prédation quotidienne chez les oiseaux nichant en nid ouvert est près de deux fois plus grande que chez les oiseaux nichant en cavité; 3) la croissance est quelque peu plus lente chez les espèces nichant en cavité; 4) la différence dans les taux de croissance n'explique que 20% de la différence des périodes nidicoles entre nids ouverts et cavité; et 5) les oisillons des

espèces nichant à découvert quittent le nid quand leur poid correspond à 79% du poids adulte et que leur aile est à 59% de la longueur adulte, les oisillons des espèces nichant en cavité sont plus développés au moment du départ di nid (poids à 94% et aile à 77% de la taille adulte).

Mes résultats appuient la proposition que la prédation est la principale force de sélection qui favorise 1) une croissance plus rapide des oisillons et 2) un départ plus hâtif des jeunes des espèces nichant en nid ouvert comparé à ceux nichant en cavité.

General introduction

There are three main patterns of development in birds: precocial, semi-precocial and altricial. At hatching, precocial birds are covered with down, their eyes are open, and they can walk and feed by themselves a few hours after hatching (e.g.: waterfowl). Young of semi-precocial birds are also covered with down and their eyes are opened, but they stay in the nest and rely on their parents for feeding (e.g.: gulls). In contrast, newly hatched altricial birds are almost naked with a relatively small amount of down feathers, their eyes are closed, they cannot walk, and they totally depend on their parents until they fledge (e.g.: passerines)(Pettingill 1985).

During the nestling period, young of altricial species are extremely vulnerable to adverse weather conditions such as rain and cold and to predators because they cannot protect themselves. Because of that vulnerability, such birds have developed different nesting patterns to protect their offspring. Among passerines, all species build a nest. Most species construct a nest that has a cup or plate shape. The nest may be located on the ground, in a shrub or a tree, or on a cliff. Such nests are

generally referred to as open nests (they are not covered from above). To reduce vulnerability of their open nests to predators, birds generally construct them in well concealed or inaccessible locations. However, some other species exhibit another nesting pattern. They build their nest inside a cavity such as hollow tree, crevice, bank, bird house, or burrow. In addition, some species may create their own cavity by constructing a ball-shaped nest with a small lateral entrance that completely hides the content. All these species have been referred to as in the group of cavity nesters (von Haartman 1957). In passerines (Passeriformes), the open-nesting and cavity-nesting patterns are generally species-specific. Only a few species are opportunistic but these always exhibit a preferred nesting pattern (e.g.: House Finch, *Carpodacus mexicanus*) (Harrison 1975).

The two nesting patterns are generally associated with differences in breeding behavior that have interested biologists for many years. von Haartman (1957) described some differences such as territories, courtship behavior, egg color, clutch size and nesting period. All these differences seemed to be related to lower predation on nest contents in cavity-nesting species. Physical differences have also been noticed by Clark (1969) who

found that oral flange of nestlings is larger for cavity-nesting species because they need to be more visible for their parents that must feed them inside in their dark cavity nest.

Nice (1957) studies nesting success in altricial birds and found that cavity-nesting species suffered from lower predation than open-nesting ones. Three studies compared the development of pairs of cavity-nesting and open nesting closely related species and failed to detect any differences in growth and development: von Haartman (1957) compared *Ficedula hypoleuca* (cavity nester) and *Muscicapa striata* (open nester); Maher (1964) compared *Plectrophenax nivalis* (cavity nester) and *Calcarius lapponicus* (open nesters); while Pinkowsky (1975) compared *Sialia sialis* and *Turdus migratorius*. On the other hand, Lack (1968) proposed that a longer nestling period in cavity-nesting species is mostly caused by their a slower growth rates presumably due to food limitation and lower nest predation pressure.

More recent studies tend to re-evaluated the previous ones since they provided mostly observations with very few statistical information. Martin and Li (1992) divided cavity nesters into excavators and non-excavators. Their study of clutch size indicated that non-excavators lay larger clutches than

open-nesting species while excavators lay smaller clutches than non-excavator and open-nesting species. Martin (1993) proposed that this difference in clutch size between excavators and non-excavators could reflect relatively smaller breeding sites of non-excavators. Finally, Redfern (1994) examined nestling growth rates and found that growth of feathers was delayed in cavity-nesting species compared to open-nesting species.

All the above studies failed to consider a problem than when a given trait is present in two or more species, its presence could be explaines by two alternative evolutionary processes: convergent or parallel evolution (Pagel and Harvey 1988). In convergent evolution, species share a trait because they inherited it from a common ancestor. In parallel evolution, a trait appeared independently at different places in the phylogenetic tree presumably as a result of similar selective forces acting on different taxonomic group (Pagel and Harvey 1988). A comparison of pairs of species conducted by as von Haartman (1957), Maher (1964) or Pinkowski (1975) will provide information for their particular case but such approach cannot be used to predict a general evolutionary change. In contrast, a comparative study involving a large group of species represents a

more powerful approach in studying the evolution of a given trait. However, special care must be taken concerning a possible phylogenetic bias is related to convergent evolution (i.e.: due to common ancestry, species from a monophyletic group are expected to be more similar than species from different groups).

An example of this problem is evident from Martin and Li's (1992) study. These authors divided cavity-nesting species into excavators and non-excavators and all but one excavator species are woodpeckers (order Piciformes). Because the entire order of Piciformes consists of excavators, we should expect small variation in clutch sizes and nestling periods among species of this order due to their common ancestor rather than on a recent evolutionary force. Furthermore, all non-excavator and open nesters were passerines (order: Passeriformes).Therefore, we should also expect to find less variation between the non-excavators and open nesters in their nestling periods and clutch sizes since they share a common ancestor. Consequently, the significant results of Martin and Li (1992) study may mostly reflect phylogenetic biases.

Therefore, when comparing groups of species with respect to a given trait to find a general evolutionary force, a special

care should be made to select a trait that evolved independently in separate groups of species and where the evolution of that trait is of recent origin. The closer we are to the trait studied, the better our chances should be to find the right cause of selection for that trait (Pagel and Harvey 1988).

While in woodpeckers (Piciformes) and parrots (Psittaciformes) the cavity-nesting behavior is old and presumably evolved at the level of the order, in passerines (Passeriformes), there are many cases where cavity-nesting behavior appeared independently. This parallel evolution of the cavity-nesting habit at the species, genera and family levels make this trait a good candidate to a comparative study of different nesting habit in Passeriformes.

The goals of my study are: 1) to verify observations on open versus cavity nesters concerning their nestling period; 2) assuming that the nestling periods of cavity nesters and open nesters differ, I will test the assumption that predation is an important factor favoring this difference i.e.: open-nesting species should suffer from higher predation rates than cavity-nesting species. Finally, the third goal of my study is to test two hypotheses on the occurence of different length of

nestling periods in the two groups of passerines. The first hypothesis (Lack 1968) suggest that the different length of nestling periods between the two groups of birds is caused by their different growth rates i.e.: cavity nesters should have a slower growth rates than open nesters.

The second hypothesis that I propose is that different length of nestling periods of cavity nesters and open nesters is a result of different predation rates on nests of the two groups of passerines (i.e. higher predation on nests of open nesters should favor earlier fledging of their young, despite of their lower degree of development).

Chapter 1

Do cavity nesters have a longer nestling period than open nesters?

Introduction

In this chapter, I will focus on differences in the length of nestling period of cavity and open nesters. The nestling period is the period from hatching to nest departure. Before trying to explain the difference in the length of nestling periods, it is necessary to verify Nice's (1957) observation that the two groups of birds differ statistically. All earlier studies that addressed this problem provided only a limited support because of their small sample sizes (Nice 1957, Ricklefs 1968a) or because of their failure to deal with potential phylogenetic biases (Alerstam and Hogsted 1981, Martin and Li 1992). The most recent study conducted by Martin and Li (1992) evaluated the role of nesting patterns in the length of the nestling period of three groups of birds: cavity-nesting excavators and non-excavators, and open nesters. According to

that study, there is a difference between the three groups; the nestling period is apparently longer for excavators, followed by non-excavators and finally open nesters. As explained in the general introduction, the choice of groups of species created a phylogenetic bias that was addressed by using anecdotal examples. However, the study of Matin and Li (1992) also suffered from small sample sizes since species included in one monophyletic group should be represented as a single data point rather that several points since these points are not independent. For this reason, the degree of freedom was artificially inflated, thereby increasing risks of commiting a type I error (Felsenstein 1988). The grouping of data points in Martin and Li's study (1992) thus does not allow a valid comparison.

The phenomenon of different length of nestling periods in cavity versus open nesters remains unresolved because of problems such as the failure to correct for biases due to phylogeny and small sample sizes. Therefore, there is the need for a large-scale study that would first confirm the difference between the two groups of birds and then attempt to explain them.

Methods

To verify the observation that the nestling period is longer for cavity-nesting species than for open-nesting species among passerines, I censused as many species as possible from the northern hemisphere, recording the nestling period and the adult body weight for each. I obtained data on nestling periods from a literature review which was conducted for passerines of North America (Terres 1987, Erlich et al 1988) and Western Palearctic (Cramp 1988, 1992, 1993, 1994a, 1994b) (for details, see Appendix 2). From my analysis, I excluded tropical birds because their growth rates are lower than those of temperate zone passerines (Ricklefs 1968a).

I divided all birds into two category: cavity nesters and open nesters. Since there is a great amount of variation in nest types among species, I used a broad definition of cavity-nesting species. I considered a cavity-nesting species to be any species that usually nests in natural or artificial cavities (hollow trees, caves, burrows, inside buildings, nest boxes), on a vertical structure with an overhang (cliffs, crevices, bridges), in a ball- or gourd-shaped nest with a side entrance, and underground inside a burrow or under rocks with a tunnel for

entering. In contrast, open-nesting species are those that breed in cup-shaped nests (open nests) on the ground, in bushes, in trees, or in other unprotected locations. Nests on ground covered with surrounding grass or few rocks, nests in trees concealed with leaves or branches, and nests with overhang but not on a vertical structure were also placed in the category of open nests.

To compare the nestling period, I used two different statistical approaches. The first one is the most powerful when correcting for a possible phylogenetic bias is required. It has been suggested by Felsenstein (1985) who referred to it as the contrast approach, while others simply call it the Felsenstein method. The major point of this method is to match closely related pairs of taxa of open nesters and cavity nesters with no two pairs sharing a taxon or a branch of the phylogenetic tree. This way, within a pair, species are dependent while all pairs are independent. This method has been effectively used by Oakes (1992) who compared sexual dimorphism in lekking and non-lekking birds. Members of a pair must be of recent origin to allow effective detection of the actual cause of that evolutionary event; it has been recomended that members of a pair should be from the same family (Oakes 1992). To use this method, knowledge

of the phylogenetic tree of passerines is essential. I used the tree of to Dittman (personnal communication) that was constructed in 1994 the most recent literature sources. Based on this tree, I found twenty suitable pairs of taxa in passerines (Fig 1, Appendix 1). To compare the nestling periods of cavity nesters and open nesters I had to statistically correct for differences in thier body size. This was achieved by regressing nestling period on body weight of the suitable taxa founded. The difference between members of each pair was evaluated by calculating from the regression line. Finally, the difference between members within pairs was statistically evaluated using the Wilcoxon paired sample test (Zar 1984), since the distribution of data points was not normal.

This method of pairing taxa has the advantage of correcting for phylogeny but result in discarding a large amount of the data: only on those taxa where both patterns were found in a monophyletic group could be included(Felsenstein 1985). Because not enough pairs were found for the later described analyses of this study, I also used an analysis of covariance (Zar 1994) for one covariate (adult body size) and two groups (cavity and open nesters). This analysis does correct for the effect of weight on nestling period. Assumptions of linearity and homoscedasticity

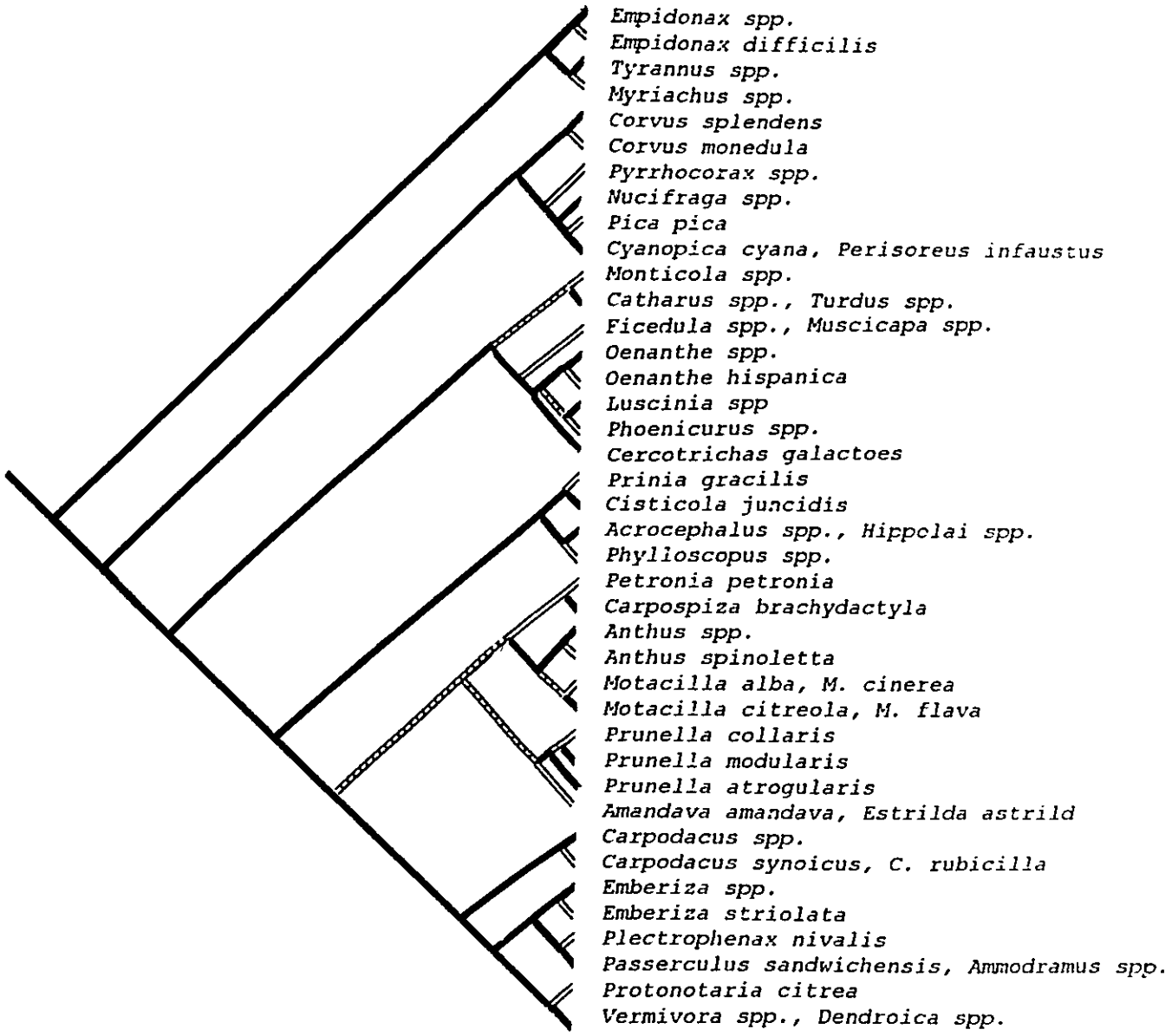

Fig 1.- Phylogeny of cavity-nesting passerines and their open-nesting relatives. Black indicates open nesters; white indicates cavity nesters; stripes branches indicates equivocal states.

were verify using d'Agostino and Levene test (Zar 1984). In order to meet these assumptions, a log-transformation of the adult body weight was required. In order to control for potential phylogenetic biases, I run the analysis at several taxonomic levels, pooling the data from a lower level to the next higher one. Pooling is done by using the mean of body weight and nestling period of the previous taxa for open and cavity nesters separately. I used taxonomic classification suggested by Deviller et al (1993). Pooling data reduces the impact of the dependence of variables within a monophyletic group which tends to overestimate degrees of freedom of the analysis (Pagel and Harvey 1991).

Results

A- The Felsenstein method.

Twenty pairs of closely related species which allow comparison as suggested by (Felsenstein 1985) were identified(See Appendix 1). The regression equation for these species was as follows:

Nestling period= 3.10 + .13 * log (adult weight).

Coefficient of determination is 0.60 suggesting that body weigth is a strong predictor of nesting period. A log transformation of the adult weight was required to meet the assumption of normality (d'Agostino test). The regression was used only as a reference to correct for adult body weight. The mean difference of nestling periods between cavity and open nesters is 3.11 days with a variance of 5.5 days. The distribution of the pairs was not normally distributed, so the Wilcoxon paired sample test was used to compare the nestling period. This test showed that the difference was highly significant ($P < 0.0005$).

B- The analysis of covariance.

The analysis of covariance (the adult body weight entered as

a covariate) showed that the slopes of two regressions of nestling periods as a function of adult body weight did not statistically differ between cavity nesters and open nesters ($P > 0.5$). However, the intercepts (elevations) of the regressions for the two groups differed statistically ($P < 0.001$); at the species level, the young of cavity nesters spend, on average, 5.42 more days in their nest as compared to the young of open nesters of the same weight (Fig 2).

To correct for possible phylogenetic biases, I ran the analysis at higher taxonomic levels, using the mean of each lower level for analyses at the next higher level. With this correction, the differences between intercepts remained statistically significant at all taxonomic levels of analyses (Table 1). Therefore, the difference between the two groups in the length of nestling period is real rather than being an artefact of taxonomic bias.

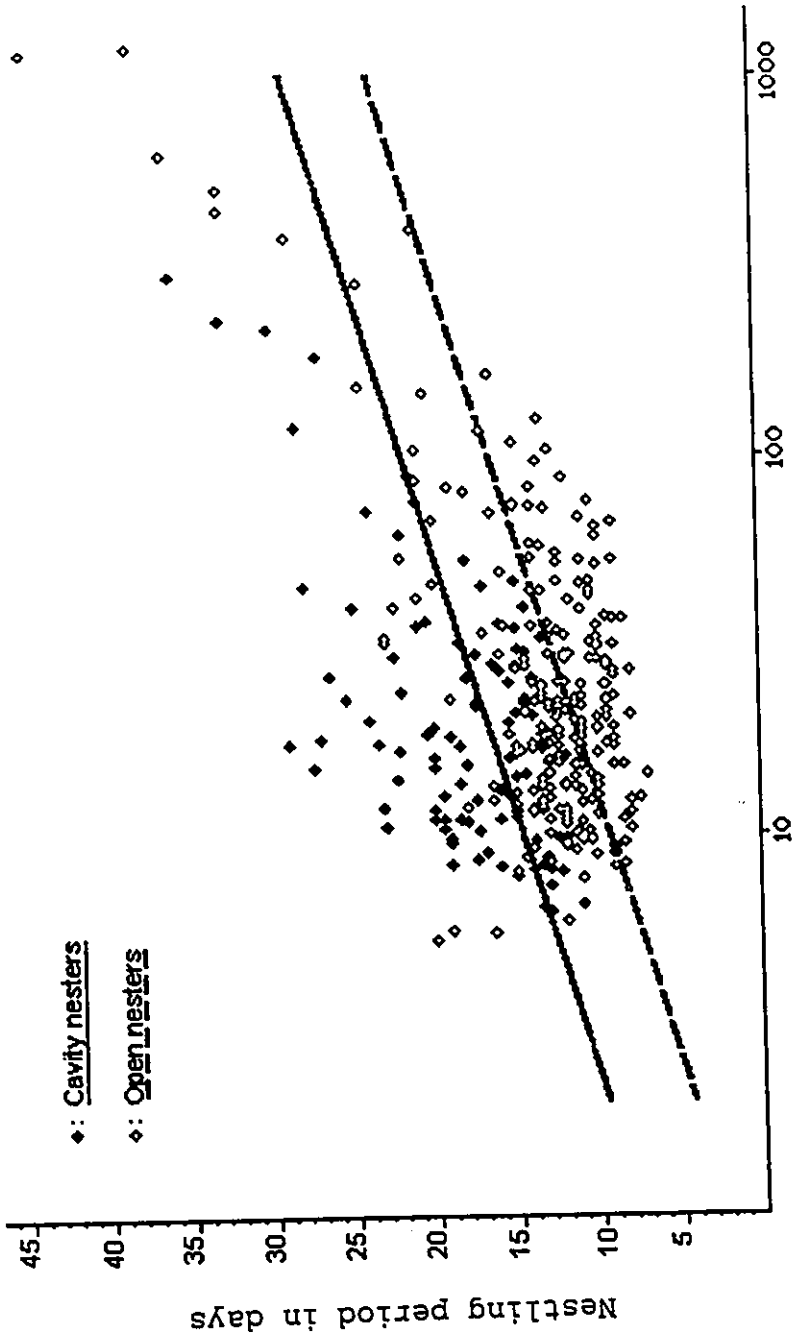

Fig. 2: Nestling period of cavity-nesting and open-nesting species of passerines related to adult weight (log scale)

Table 1: Results of the analysis of covariance comparing nestling periods of cavity-nesting and open-nesting species of passerines at different taxonomic levels. The values of slopes for the regression means are in day/g while the value for the elevations are in days.

Taxa	Test	Regression mean			F	d.f.	P
		Model	Open nesters(n)	Cavity nesters(n)			
Species	Slopes	3.114	3.458 (241)	3.615 (105)	0.0764	342	>0.25
	Elevations	4.939	2.070 (241)	7.492 (105)	164.92	343	<0.0001
Genera	Slopes	2.689	0.154 (98)	7.49 (48)	0.634	138	>0.25
	Elevations	5.769	4.124 (98)	5.764 (48)	114.91	139	<0.0001
Sub-family	Slopes	0.0574	0.0463 (26)	0.0679 (22)	0.6601	44	>0.25
	Elevations	13.721	11.877 (26)	16.032 (22)	24.139	45	<0.0001
Family	Slopes	0.0635	0.0485 (19)	0.0721 (16)	0.9911	31	>0.25
	Elevations	13.485	12.212 (19)	15.353 (16)	16.018	32	<0.0001

Discussion

My analysis established that cavity-nesting passerines have a longer nestling period than the open-nesting species. The difference between the two groups was 5.42 days at the species level when using the analysis of covariance and 3.11 days with the paired method. With both analyses this difference remained statistically different with the correction for phylogenetic bias. With both methods, my results thus verified the observation of Nice (1957) suggested that cavity nesters have a longer nestling period than open nesters. She reported a difference of four days for European species and eight for North American birds. Results of my method based on the analysis of covariance fall into the range of Nice's observation. However the use of the paired sample method yielded a smaller difference.

Martin and Li (1992) attempted to verify the same hypothesis but used several orders of birds without correcting for possible phylogenetic biases. However, relatively small sample sizes and lack of correction for phylogenetic biases presented the main problems and complicated interpretation of results of that study. In contrast the results of my study provide the more unbiased evidence that the difference between the nestling periods of

cavity nesters and open nesters is real.

Since the length of the nestling period increases with the size of birds, I would expect that the difference in the length of nestling periods of cavity nesters compared to open nesters should also increase. The identical slopes of the regressions for cavity nesters and open nesters, however, demonstrate that the difference of 5.4 days remains constant for passerine species of different size. The analysis based on pairs also demonstrated that there is lack of correlation with body size. I suggested that this could be a result of physiological constraints, increasing time limits with body size due to the limited breeding season, or some other unknown factors.

Now that the early observation of different nestling periods of cavity nesters and open nesters has been verified, I will try to explain in the following chapters why such a difference occurs. More specifically, I will test two plausible hypotheses on the occurrence of this difference: 1) that this difference is a result of different rates of development (Lack 1968), or 2) that the difference results from different timing of departure by young from their nest, which is rather independent of their stage of development at fledging. However, because both hypotheses assume that the driving force behind the different duration of

the nestling periods is predation, in the following chapter, I will first present a test of this key assumption.

Chapter 2

Do open nesters suffer from higher predation than cavity nesters? Test of the key assumption

Introduction

In the previous chapter, I established that young of cavity-nesting species have a longer nestling period than young of open-nesting species. So far, one hypothesis has been proposed to explain this difference in nestling periods. Lack (1968) proposed that cavity nesters fledge later because their growth rates are slower than those of open nesters. These slower growth rates, in turn, presumably reflect lower predation rates on offspring of cavity-nesting species because of lower accessibility of contents of their nests. In contrast, the open nesters experience high predation rates, that favor fast rates of development of young and consequently earlier fledging (Lack 1968). However, another plausible explanation for this difference is that the difference in the duration of nestling periods between the two groups of birds has been caused by different

timing of departure of young from their nest rather than by different growth rates. Some observation made by Maher (1964) when conparing *Plectrophenax nivalis* (cavity nesters) and *Calcarius lapponicus* (open nesters) seemed to support this hypothesis. Thus, according to this alternative hypothesis, cavity nesters stay in the nest longer because their safer nesting sites allow the young to stay longer and, consequently, leave their nest more fully developed. In contrast, because of strong nest predation pressures, young of open nesters should leave their nest as early as possible, regardless of the fact that they are relatively underdeveloped. However, the two hypotheses on different length of nestling periods could potentially provide a plausible explanation only if their key assumption of differential predation rates can be verified. This assumption states that due to the relative safety of cavities, predation pressures on nests of cavity nesters are reduced as compared to predation rates on nests of open nesters. Nice (1957) and Ricklefs (1969) reported that such a difference may exist between the two groups of birds but,in their analyses, these authors did not correct for potential phylogenetic biases.

In this chapter, I will establish if predation pressure is higher on unprotected (i.e. open) nests as opposed to more

protected nests (i.e. those inside cavities). In this comparative study of predation rates, I will examine two indices of nest predation. First I will compare the general nestling success (i.e. the number of young fledged / number of eggs hatched) of cavity-nesting and open-nesting species to determine if cavity-nesting species suffer from lower nestling losses (mostly due to predation) during their nestling period.

However, since young of cavity-nesting species stay longer in their nest than young of open-nesting species (see chapter 1), I will also compare daily mortality rates of the two groups of passerines. If, for each day spent in nest, the risks of death due to predation are lower for young of cavity nesters, young of cavity nesters could have evolved to stay longer in their nest and still realize a similar or possibly even higher nesting success than young of open nesters.

Methods

To establish if nest predation is lower for cavity nesters than for open nesters, I conducted a literature survey of birds of the northern hemisphere. In this analysis, I studied nesting success during the nestling period only. I used percentage of young that fledged as an index of predation rate. The reason for this choice is that most studies provide reliable data on nesting success (% of eggs hatched, % of young fledged), but the actual causes of nestling losses are difficult to directly measure. However, several studies, including a large-scale study of Ricklefs (1969), established that nest predation is the major cause of nestling failures in both passerines and non-passerines. Therefore, assuming that nest predation is the major cause of nestling losses, it is reasonable to use nesting success as an index of predation.

For my analyses, I chose only those studies that provided the number of eggs hatched, the number of fledglings, or when that information could be calculated from the information provided by the authors (see Appendix 2 for raw data and references to literature. Also, I excluded studies with less than 100 eggs per species because of high risks of bias due to a small

sample size. For species represented by more than one study, I added the number of hatchlings and nestlings. I used two measures of nest predation, nestling success and daily mortality rates. Nestling success is defined as the proportion of nestlings that fledged from all eggs hatched. This measure ignores different length of nestling periods of the two groups. Daily mortality rate is expressed as the number of young lost per day in the nest.

I used a Student's T-test to compare nestling success and daily mortality rates for the two groups of birds. Since residuals were normally distributed (D'Agostino test; Zar 1984) no transformation was needed. Since only three pairs on closely related species were available to control for phylogeny, I could not use the Felsenstein method. I had to use the Student T test at higher taxonomic levels control for possible phylogenetic bias. I took the mean survival rates and daily mortality rates of a lower taxonomic level to go to the next higher one.

Results

Nestling success;

Based on available data, at the species level, cavity nesters have a survival rate of 79% from hatching to fledgling while the corresponding survival rate of open nesters is 69%. This difference of 10% was significant at the specific level ($P > 0.025$) but not at higher taxonomic levels (Table 2) presumably as a result of smaller sample size. Therefore, results of the comparative analysis of cavity nesters and open nesters indicated that nesting success is affected by nest type.

Daily mortality rates;

The difference between cavity nesters and open nesters in daily mortality rates was significant at the species and genus levels of analyses (Table 2). At the species level, for open-nesting species, the risk of death per day was twice as high as that for cavity nesters (Fig. 3; Table 2). The difference between the two groups remained statistically significant up to the genera level but not for higher taxonomic levels (Table 2).

Table 2: Statistical results of the comparisons of nestling success and daily mortality rates in nests of open-nesting and cavity-nesting species of passerines conducted at different taxonomic levels. Nestling success is expressed as % of young fledged of all young hatched. Daily mortality rate is expressed as % young dead per day in nest.

Taxa	Test	Mean		T	d.f.	P
		Open nesters(n)	Cavity nesters(n)			
Species	Nestling success	68.65 (33)	79.09 (21)	2.200	52	<0.025
	Daily mortality	2.67 (33)	1.27 (21)	3.510	52	<0.0005
Genera	Nestling success	69.90 (28)	77.28 (16)	0.137	42	>0.05
	Daily mortality	2.63 (28)	1.39 (16)	2.705	42	<0.005
Sub-family	Nestling success	71.62 (10)	77.20 (11)	0.998	20	>0.25
	Daily mortality	2.18 (10)	1.44 (11)	1.675	20	>0.05
Family	Nestling success	70.02 (8)	77.32 (10)	1.226	16	>0.1
	Daily mortality	2.10 (8)	1.41 (10)	1.639	16	>0.05

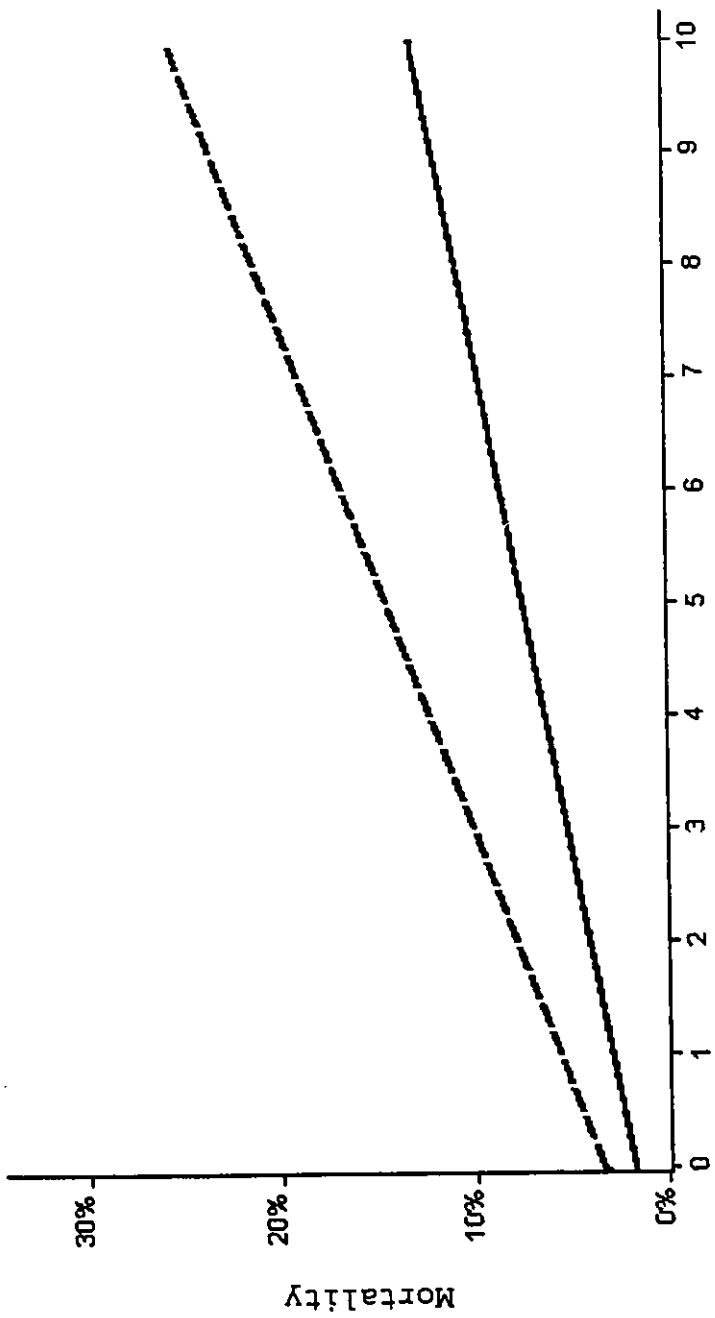

Fig. 3: Cumulative mortality rates of the nestlings of open-nesting (dashed line) and cavity-nesting (full line) species of passerines in relation to the amount of time spent in nest.

Discussion

The objective of this chapter was to verify the major assumption of the two hypotheses that nest predation rates should be lower for cavity nesters than for open nesters. Results of my comparative study support this assumption because: 1) despite their longer nestling period, survival of nestlings of cavity nesters until fledging was, on average, 10% higher than that of open nesters, and 2) the daily mortality rates were twice as high for open nesters as those for cavity nesters. Unfortunately, Felsenstein's method for controling for phylogeny could not be applied to this data set (small sample size) and the test at different taxonomic levels did not yield significant differences at higher taxonomic levels. The weaknesses of the grouping method is that sample size is reduced and we cannot establish if this lack of statistical difference is due to phylogenetic effect or reduction of sample size. However, I would argue that predation rates are likely to be affected by accessibility of the nest more than by the phylogeny.

The differential predation rates between cavity nesters and open nesters is consistent with the view that more intense predation on open nests than on nests in cavities presents a

strong selective force favoring various anti-predation adaptations especially in open nesters. These adaptations could include a faster developement of young in open-nesting species as suggested by Lack (1968), or earlier fledging by less well developed young of open nesters compared to cavity nesters as proposed by my alternative hypothesis.

Nice (1957) found similar differences in nesting success between cavity-nesting and open-nesting species of birds but did not provide statistical evaluation of their data. On the other hand, Martin and Li (1992) found no difference in nesting success between non-excavator cavity nesters and open nesters, while excavators had a higher nesting success. Problems associated with phylogenetic biases, definition of nesting success and lack of statistical evaluation may be the cause of such disagreements between the authors. In Nice's study (1957) nesting success was divided into egg period and nestling period, as in the present study. In Martin and Li's study (1992) nesting success was examined between the initiation of nest building and fledging. These authors also mentioned that most of the nest failures in cavity-nesting species occurred during nest building and egg period due to competition for nest site. Therefore, I conclude that overall nesting success including nest building, incubation

period and nestling period cannot be used as a reliable index of the nestling success.

Moller (1989) pointed out potential problems in studies of nesting success in cavity-nesting species. When using artificial nest boxes, in most experiments the breeding density and nesting productivity was higher than in natural cavities, presumably because boxes are safer than natural cavities and old nests are commonly removed from them to reduce parasites. All these factors are likely to increase nesting success above that in natural cavities. Several studies tried to obtain evidence for such a bias, and some did find that nestboxes affected nesting success (East and Perrins 1988, Nilsson 1984), while others failed to show that such an effect (Robertson et al 1990, Johnson and Kermott 1994, Brawn 1988). Again, problems due to different definitions of nesting success used by these authors may have affected the results of the earlier studies, thereby making the direct comparison between their results impossible.

None of the earlier studies that compared mortality patterns of cavity nesters and open nesters examined daily mortality rates. However, a comparative study of the open nesters and cavity nesters demonstrated that the daily mortality rates are the most appropriate indicator of predation pressure since the

length of the nestling periods differ between the two groups of birds.

To conclude, both indices of nest predation that I examined for a large sample of cavity nesters and open nesters confirmed that nest predation rates are higher for open nesters than for cavity nesters. This finding can only be explained by different levels of accessibility of nests (usually high above ground for tree cavities versus low in bushes or on the ground for open nests) and their contents (exposed in open nests versus concealed and out of reach in cavities). In any case, the observed differences in nest-predation rates in a predicted direction provide a strong support for the key assumption on which the two hypotheses on the occurrence of different length of nestling periods of cavity nesters and open nesters are based. Hence, nest predation presumably presents an important driving force that has been shaping different nesting patterns of the two groups of passerines. This result allows me to proceed with testing the key predictions of the two hypotheses.

Chapter 3

Do young of open nesters grow faster than young of cavity nesters ? Test of the differential development hypothesis

Introduction

Since the difference in the duration of the nestling period between cavity and open nesters was confirmed, it is necessary to attempt to explain why such a difference occurs. The first hypothesis was proposed by Lack (1968). According to Lack (1968), nestling growth rates depend especially on food availability and nestling mortality. Species that suffer from high predation should be under strong selection pressure for rapid nestling growth and for early departure from the nest. Therefore, according to Lack (1968), young of cavity nesters should exhibit slower growth than young of open nesters. The Lack's (1968) hypothesis thus assumes that differences in the nestling periods of cavity and open nesters are caused by their different growth rates. However, Pinkowski (1975), who compared the growth rates

of nestlings of Eastern Bluebird (*Sialia sialis*) and American Robin (*Turdus migratorius*), failed to support Lack's view. In addition studies conducted prior to the Lack's publication also failed to support this view (von Haartman 1957; Maher 1964).

The earlier studies that examined or have implications for the Lack's (1968) hypothesis concentrated on body weight as an indicator of body size (von Haartamn 1957, Maher 1964, Ricklefs 1968a, Pinkowski 1975). Most of these studies found little evidence for such a difference but their sample sizes were generally small. In addition, authors of those studies have not attempted to correct for phylogeny biases. Furthermore, the earlier studies examined differences in body weight growth rates as an index of the degree of development of birds. However, there could be other differences that are not reflected by body weight. For example, Redfern (1994) found that the initiation of feather growth was delayed in cavity nesters. This suggested that early departure could be associated with faster development of mobility, resulting in a faster growth of wing and tarsus. Therefore, in addition to body weight, I will also examine wing and tarsus growth rates to gain a better understanding of development of locomotory skills.

Methods

In this analysis I used data from two different sources: 1) my own data that I collected in the Hull-Ottawa region in summers of 1993 and 1994, and 2) data obtained from earlier published studies. With respect to data that I collected, I measured nestlings of several cavity-nesting and open-nesting species on a daily basis. Cavity nesters were attracted to nest boxes and included Tree Swallow (*Tachycineta bicolor*), House Wren (*Troglodytes aedon*), European Starling (*Sturnus vulgaris*) and House Sparrow (*Passer domesticus*). Nests of open nesters were found in the same area on ground, in shrubs or trees and included Yellow Warbler (*Dendroica petechia*), Red-winged Blackbird (*Agelaius phoeniceus*), Catbird (*Dumetella carolinensis*), House Finch (*Carpodacus mexicanus*), Cedar Waxwing (*Bombycilla cedrorum*), Alder Flycatcher (*Empidonax alnorum*), American Robin (*Turdus migratorius*), and Song Sparrow (*Melospiza melodia*).

Measurements of nestlings were taken daily from hatching to fledging. Weight was measured using Pesola balances with range of 5g (accuracy of 0.1g), 50g (accuracy of 0.5g), or 100g (accuracy of 1g), according to nestling weight. The wing length was measured as the length of the unflattened wing from carpal joint

to the longest primary feather (if any). Measurements were taken with a ruler (to the nearest 1mm) or caliper (to the nearest 0.1mm) when too small. Tarsus measurements (to the nearest 0.1mm) were made with caliper from the inter tarsal joint to the last leg scale before the toes emerge.

To increase the sample size, I also included published data on 50 additional species. I only chose those studies that reported daily measurements since some authors described hatching day as day 0, 0.5, or 1 this could lead to erroneous evaluation of age at inflection point. In my study, I used day 0 as hatching day.

A typical growth curve has a sigmoïd shape (Fig. 4). Mathematical, sigmoïd curves are described by their asymptote and by their inflection point. Comparing sigmoïd curves statistically is difficult. In contrast, comparison of regression lines is relatively easy. Ricklefs (1967a) proposed a method for choosing the best transformation of growth curves to allow their comparison. His method proposes three models of sigmoïd curves that differ by the position of the asymptote. The first step of his method is to tranform the measurements of one species with each model and to plot them on a graph of transformed data as a function of age with a roughly estimated asymptote. Then, the

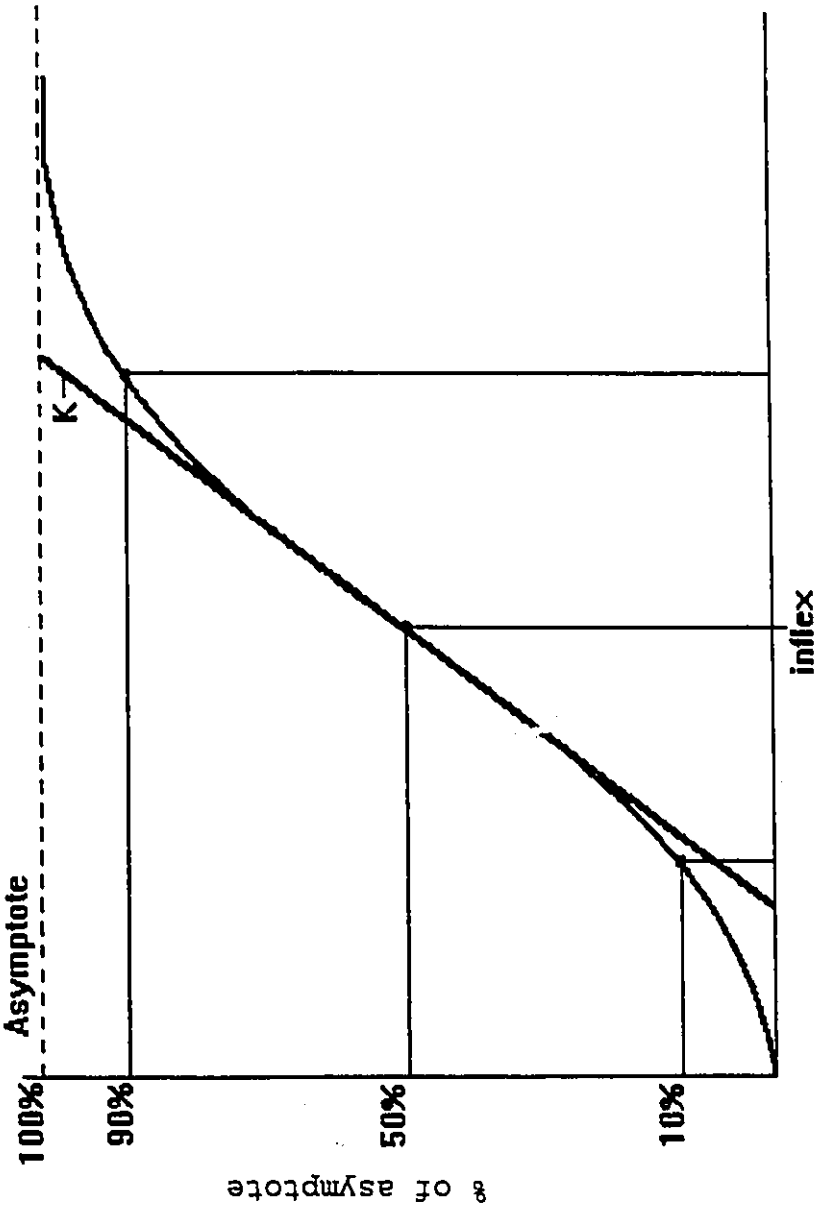

Fig. 4 : Logistic growth curve showing an asymptote, K, inflection point (inflex) and 10%-90% growth interval.

second step consists of choosing the appropriate transformation that gives the straightest line. This could be evaluated visually or statistically with simple linear regression. I used the statistical method (i.e. selected the regression with the highest r^2) to choose the best model. When a model is choosen for one type of measurement, it is important to use the same transformation for all species to allow comparison. The best model for weight and tarsus was logistic equation (Conversion factor = 0.25 ln (A / (1-A))) and for wing length the Gompert equation (Conversion factor = 1 / e * ln (-1 / ln A)) where A is the estimated asyptote.

The third step of this method consists of finding the asymptote for measurements of each species. The asymptote is the highest measurement that the bird will reach when fully grown. To estimate the asymptote, I examined the growth curve and estimated the value of its asymptote. Then, I transformed the data points with the chosen mathematical model and tried several values for the asymptote. With each new asymptote, I calculated the simple linear regression using all points between 10% and 90% of the estimated asymptote, as suggessted by Ricklefs (1967a). To find the best asymptote for each species, I tried several asymptotes around my first estimate until the correlation of the

the regression slope could not be increased (i.e. until the higest r^2 was reached). The interval between each trial was 0.1 (see Ricklefs 1967a). This step of finding an asymptote and slope was made for each species and each measured body trait. With this information, I evaluated the growth rates (K) and the position of the inflexion point.

Since larger birds take longer to grow, I compared growth rates of cavity-nesting species and open-nesting species with an analysis of covariance (Zar 1984), with the asymptote as the covariate. Two characteristics of the curve remain and can be used to examine differences in growth. The first factor is K that indicates the growth rates. If K was smaller for cavity nesters, then this would imply that they take longer to grow to the same size as open nesters (Fig 5). Another factor is the position of the curve, similar curves can be laterally moved (Fig 6). Therefore, one of the growth curves exhibits a delay in the initiation of growth. To compare the lateral position of two curves, the inflexion point is used as a reference point. If the age at inflexion was higher for cavity nesters, then this would suggest that their growth is delayed and this could explain why they stay longer in their nest.

To establish if cavity and open nesters differ in their

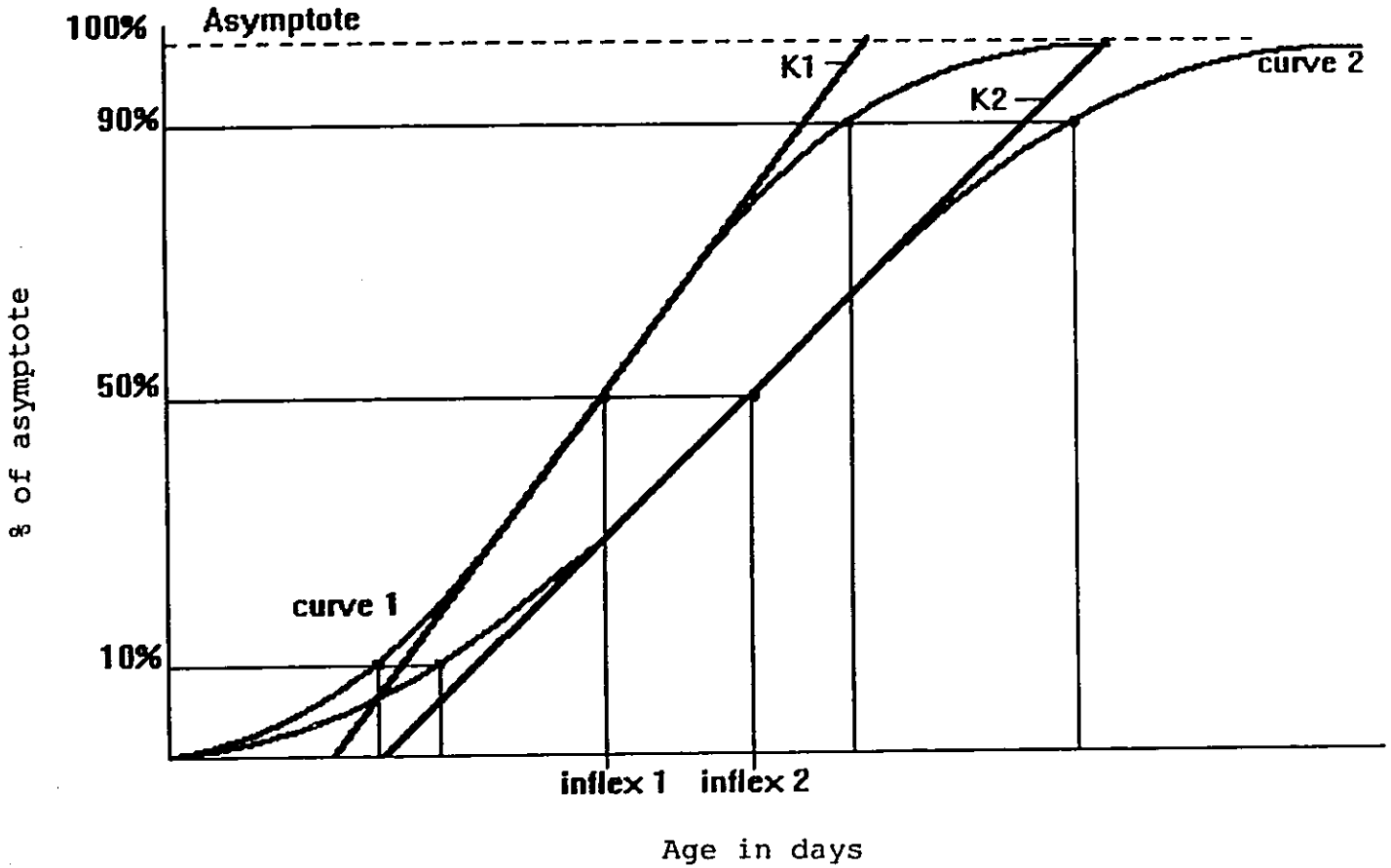

Fig. 5: Two logistic growth curves with the same asymptote but with different growth rates (K1, K2), curve 2 being slower.

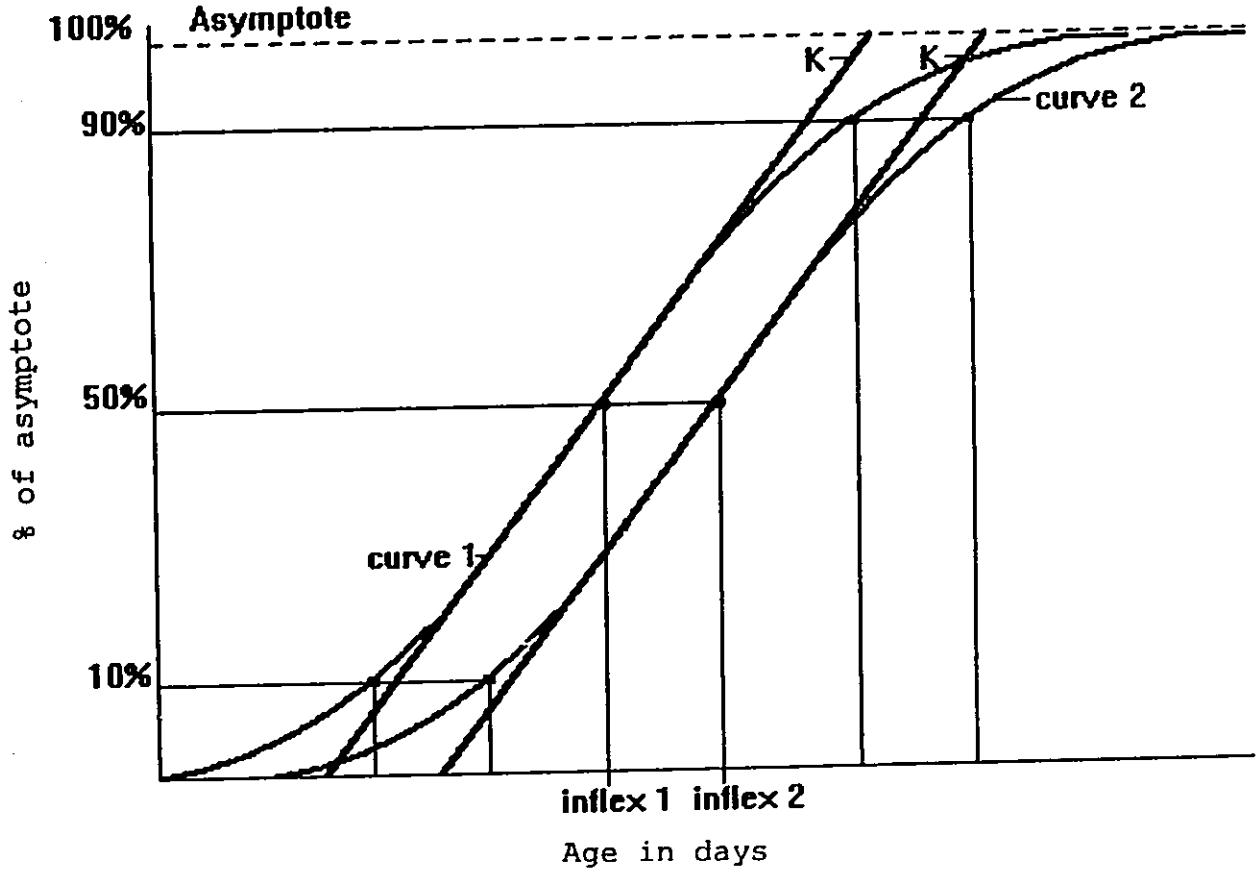

Fig. 6 : Two logistic growth curves with the same asymptote, same K value but curve 2 has a delay in the start of growth which results in a later age at inflection.

growth rates (K) and age at inflexion, I compared their calculated values using an analysis of covariance (the asymptote entered as a covariate; Zar 1984). I compared weight growth rates (Appendix 4), wing growth rates (Appendix 5) and tarsus growth rates (Appendix 6). Because too few pairs of closely related species were available, I corrected for a possible phylogenetic bias by running the analysis for each of these characteristics at different taxonomic levels (see methods in chapter 1 for a detailed explanation).

Results

Weight growth curves;

The comparison of weight growth curves by analysis of covariance (i.e. the regressions obtained for the two groups of birds) yielded two pieces of information: 1) homogeneity of slopes of the regressions, and 2) differences in interceps. My results revealed that for the open nesters and cavity nesters: 1) the slopes were similar (-.00174 K/gr; $P > 0.25$), but 2) the interceps were different ($P < 0.0005$); the K value for cavity nesters was smaller by 0.1046 than the K value for open nesters (Fig. 7). When grouping taxa, the difference remained significant until the sub-family level. This is problably because for analysis at the family level the sample size became too small to detect any differences. Because with the grouping of taxa the effect of asymptote disappeared, I used a Student's T-test for comparisons at sub-family and family levels (Table 3).

The difference in age at inflection was 1.14 extra days for cavity nesters ($P < 0.01$), that is consistent with the difference in growth rates (Fig 8). Again, the analysis at the inflection showed that the slopes were similar ($P < 0.25$) but the intercepts

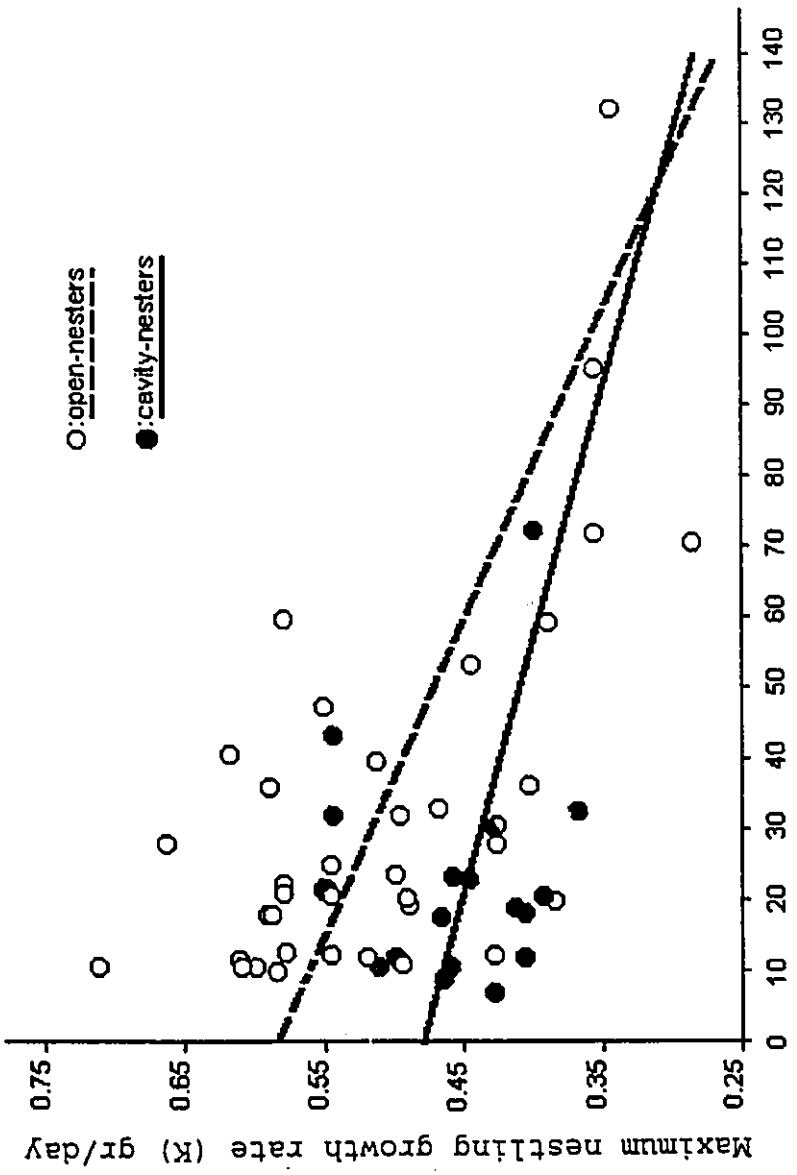

Fig. 7: Maximum growth rate of nestlings (K) in relation with asymptote (in grams) for cavity-nesting and open-nesting passerines.

Table 3: Results of the analysis of covariance comparing weight growth rates for cavity-nesting and open-nesting species of passerines at different taxonomic levels. The means of the regression models are in g/day for slope and days for elevations. For sub-family and family levels, a Student's T-test was used since no significant relationship between K and asymptote was detected..

Taxa	Test	Regression mean			F	d.f.	P
		Model	Open nesters(n)	Cavity nesters(n)			
Species	Slopes	-0.00174	-0.00225 (37)	-0.00139 (16)	0.4622	50	>0.25
	Elevations	0.548	0.583 (37)	0.478 (16)	15.66	51	<0.0005
Genera	Slopes	-0.00182	-0.00223 (29)	-0.00108 (13)	0.7189	38	>0.25
	Elevations	0.543	0.578 (29)	0.475 (13)	8.554	39	<0.01
Sub-family	K (g/day)	0.476	0.502(13)	0.446 (11)	1.9686	22	<0.05
Family	K (g/day)	0.470	0.485 (13)	0.450 (10)	1.204	18	>0.10

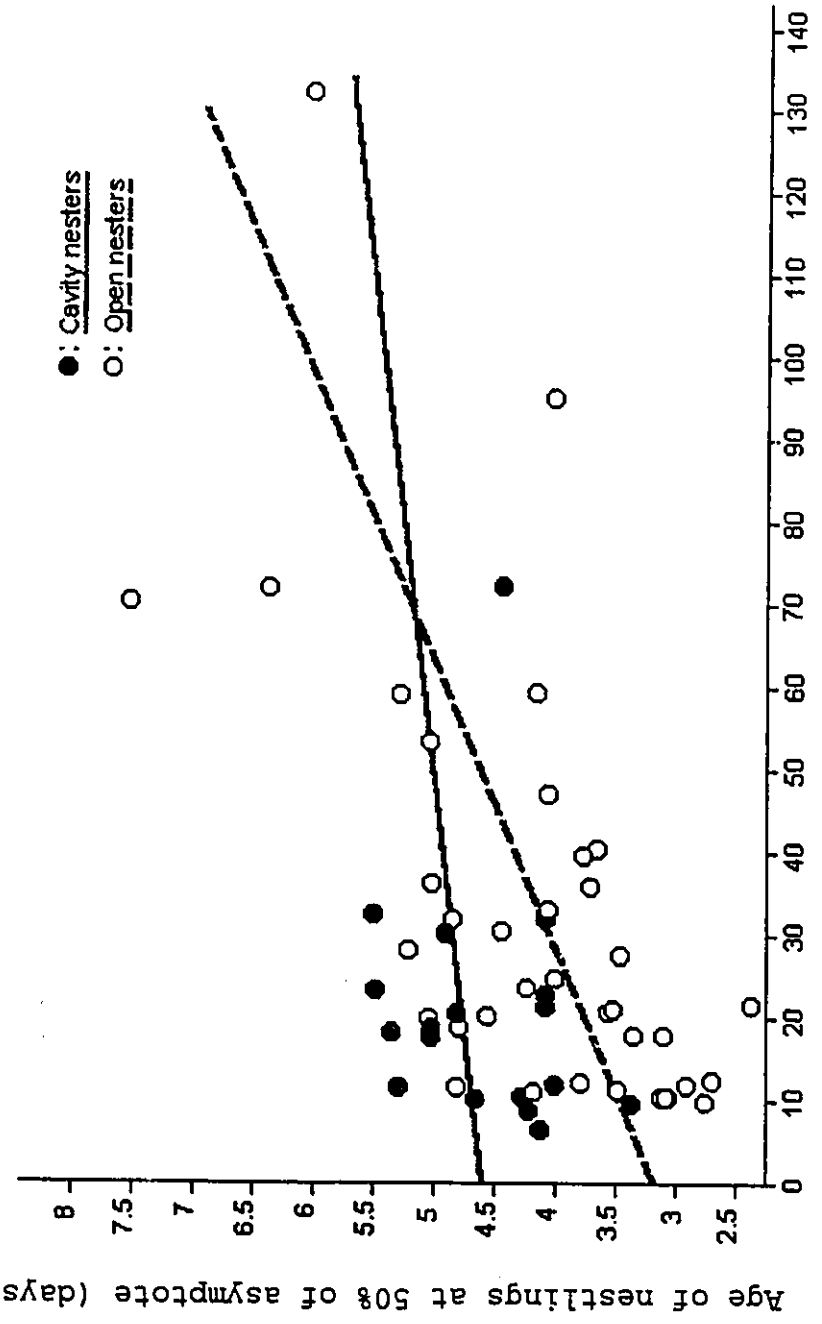

Fig. 8 : Age of nestlings when reaching the inflection point of their growth curve for weight, inflection point being 50% of asymptote.

Table 4: Results of the analysis of covariance comparing age at inflexion of the weight growth curve for cavity-nesting and open-nesting species at different taxonomic levels. The means of the regression models are in days/g for slope and in g for elevations. For Sub-family and Family levels, a Student's T-test was used since no significant relashionship between age at inflexion and asymptote was detected.

Taxa	Test	Regression mean			F	d.f.	P
		Model	Open nesters(n)	Cavity nesters(n)			
Species	Slopes	0.0205	0.0264 (37)	0.00672 (16)	1.1882	51	>0.1
	Elevations	3.783	3.370 (37)	4.525 (16)	8.3123	52	<0.01
Genera	Slopes	0.0216	0.0264 (29)	0.00708 (13)	1.3725	38	0.25
	Elevations	3.719	3.361 (29)	4.499 (13)	4.5919	39	>0.05
Sub-family	Age at inflexion	4.465	4.307 (13)	4.651 (11)	0.9212	22	>0.01
Family	Age at inflexion	4.624	4.627 (10)	4.620 (10)	0.0192	18	>0.25

were significantly different ($P < 0.0005$). Grouping the species into higher taxa to control for biases due to phylogeny, and re-analysing the data indicated that no significant differences persisted above the species level (Table 4). A phylogenetic bias or the large decrease in sample size may have caused this lack of significant differences.

Wing growth curves;

Growth of wing presents a different situation than weight. When comparing K values for cavity-nesting and open-nesting species, neither slopes nor intercepts were statistically significantly different ($P > 0.25$ and $P > 0.1$, respectively; Fig 9), regardless of the taxonomic level of the analyses (Table 5).

When comparing the age at inflection, I found that the slopes were similar ($P > 0.5$) for cavity and open nesters but that the intercepts were different (Fig 10). Cavity nesters reach the inflexion point of their growth curve at an older age (1.42 days older) than open nesters. The lack of difference in slopes indicates that the difference between the same size open and cavity nesters remains similar for birds of different sizes. When I combined data into higher taxonomic groups, the difference remained significant up to the sub-family level, but not at the family level (Table 6), presumably due to a small sample size. The lack of difference in growth rates along with a difference in age at inflexion indicate that there is a delay in the initiation of growth of wing in cavity-nesting, compared to open-nesting passerines.

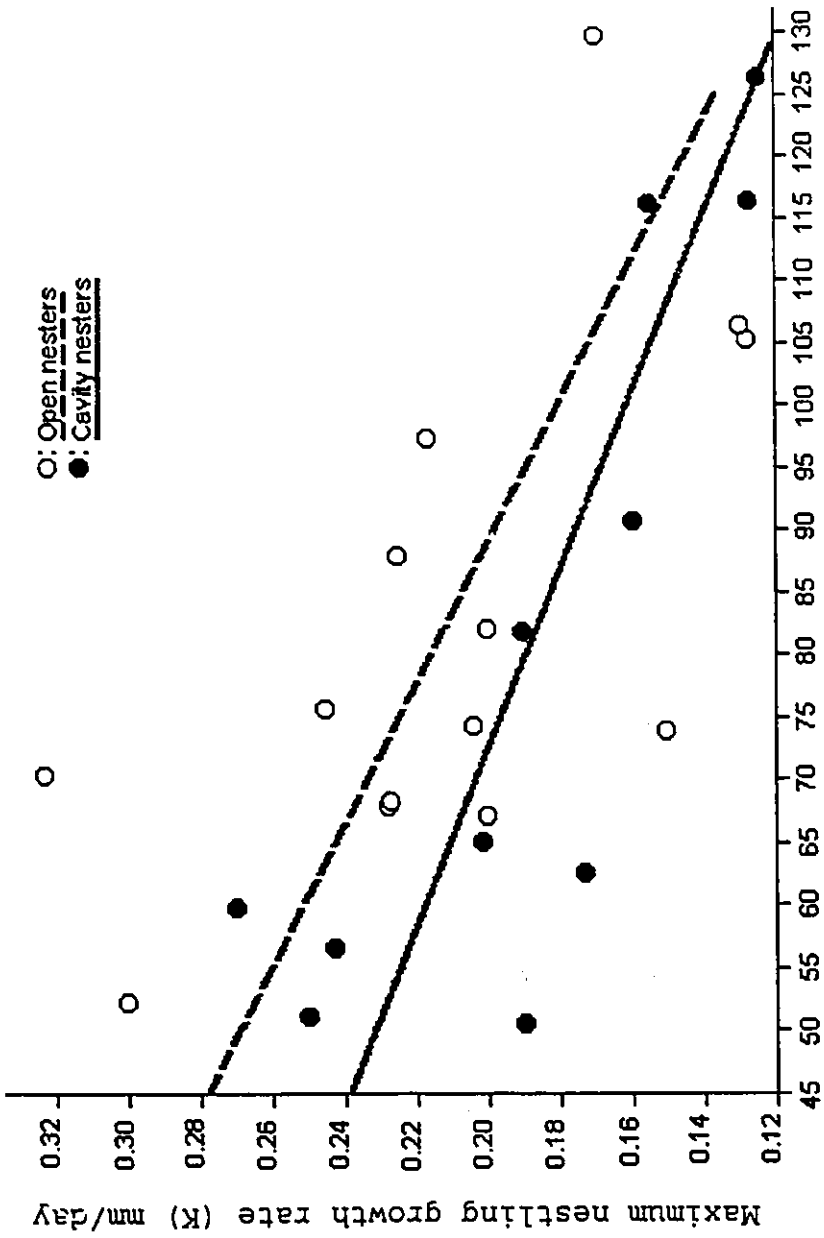

Fig. 9 : Maximum growth rates of nestling wing chord (K) in relation to the asymptote (in mm) of wing chord for cavity-nesting and open-nesting passerines.

Table 5: Statistical results of the comparison of the wing growth rates for cavity-nesting and open-nesting species of passerines at different taxonomic levels. The value for the means of slopes are in mm / day while the values for the means of elevations are in days.

Taxa	Test	Regression mean			F	d.f.	P
		Model	Open nesters(n)	Cavity nesters(n)			
Species	Slopes	-0.00141	-0.00164 (14)	-0.00131	0.2742	21	>0.25
	Elevations	0.312	0.3423 (14)	0.2903 (11)	2.7743	22	>0.10
Genera	Slopes	-0.00139	-0.00164 (14)	-0.00105 (7)	0.6428	17	>0.25
	Elevations	0.312	0.342 (14)	0.264 (7)	2.6164	18	>0.10
Sub-family	Slopes	-0.00115	-0.00312 (8)	-0.00105 (7)	0.5504	11	>0.25
	Elevations	0.302	0.312 (8)	0.264 (7)	1.0849	12	>0.25
Family	Slopes	-0.00112	-0.00144 (6)	-0.00105 (7)	0.1393	9	>0.25
	Elevations	0.275	0.307 (6)	0.264 (7)	0.1391	10	>0.25

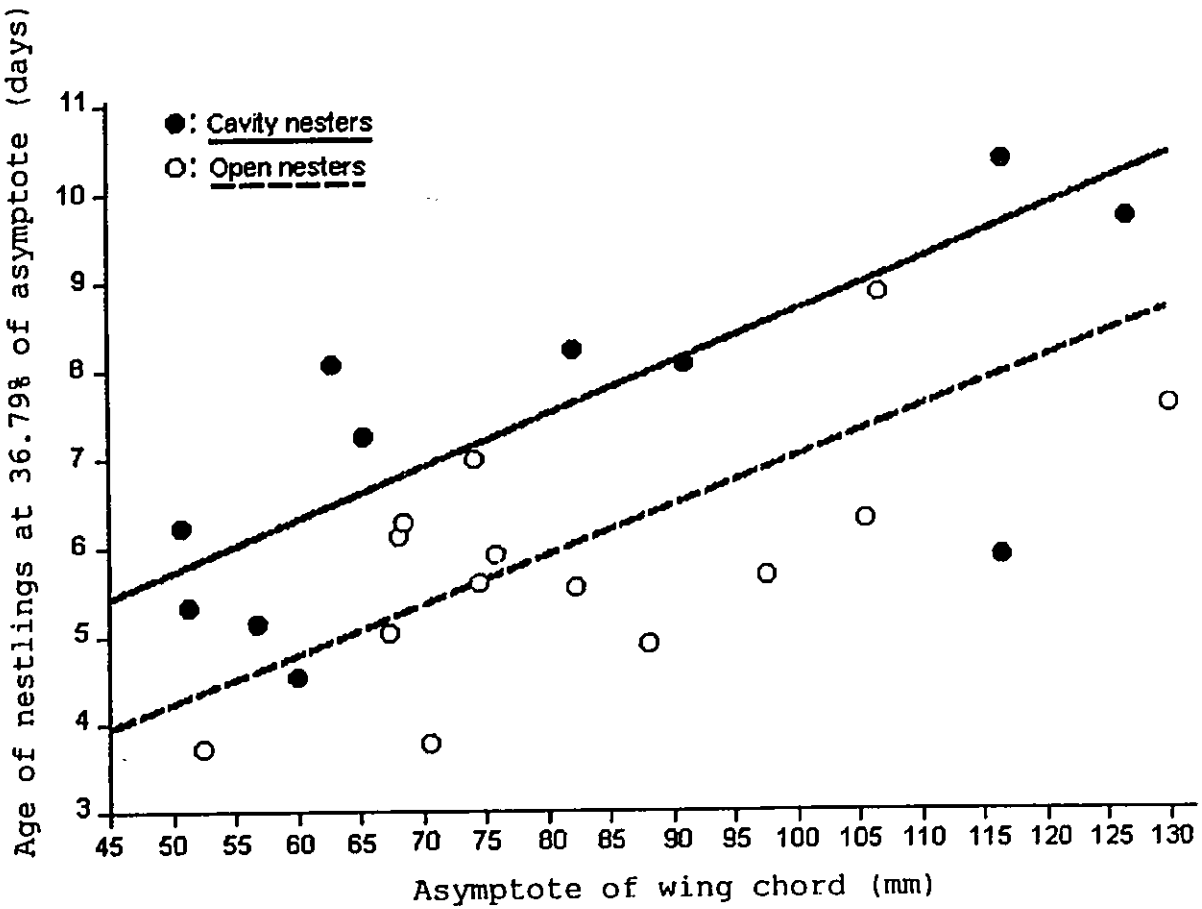

Fig.10: Age of nestlings of cavity-nesting and open nesting species of passerines when reaching the inflection point of their growth curve for wing chord, inflection point being 36.79% of the asymptote.

Table 6: Statistical results of the comparison of the age at inflexion of wing growth curve for cavity-nesting and open-nesting species of passerines at different taxonomic levels. The value for the means of slopes are in day / mm while for the values for the means of intercepts are in m.

Taxa	Test	Regression mean			F	d.f.	P
		Model	Open nesters (n)	Cavity nesters (n)			
Species	Slopes	0.0544	0.0557 (14)	0.0571 (11)	0.0048	21	>0.25
	Elevations	2.227	1.454 (14)	2.871 (11)	12.018	22	<0.0025
Genera	Slopes	0.0546	0.557 (14)	0.049 (11)	0.1025	17	>0.25
	Elevations	2.063	1.454 (14)	3.583 (7)	9.9460	18	<0.01
Sub-family	Slopes	0.05332	0.0594 (8)	0.0490 (7)	0.1021	11	>0.25
	Elevations	2.550	1.343 (8)	3.583 (7)	6.2992	12	<0.05
Family	Slopes	0.0493	0.0525 (6)	0.0490 (7)	0.0012	9	>0.25
	Elevations	3.0494	2.384 (6)	3.583 (7)	3.7751	10	>0.1

Tarsus growth curves;

When comparing tarsus growth, I found that the slopes of regressions obtained for cavity-nesting and open-nesting passerines did not significantly differ from zero ($F = 3.96$, $d.f. = 21$, $P > 0.05$). Therefore, a Students' T-test was more appropriate for comparing mean growth rates and age at inflection of cavity and open nesters. The analysis revealed no significant differences for either growth rate ($T = 0.718$, $d.f. = 20$, and $P > 0.25$), or age at inflexion ($T = 0.784$, $d.f. = 20$, and $P > 0.25$). At the species level, the mean growth rate for both groups was 0.4156 mm / day, while the mean age at inflection was 2.57 days (Table 7).

Grouping the species into higher taxa to control for biases due to phylogeny did not reveal new significant differences (Table 7) for either growth rates or age at inflection. These results suggest that the cavity nesters and open nesters exhibit similar tarsus growth rates.

Table 7: Statistical results of the comparison of growth rate (K) and age at inflexion (Xo) of tarsus length for cavity-nesting and open-nesting passerines at different taxonomic levels. Values for K are in mm, while values for Xo are in days.

Taxa	Test	Mean		T	d.f.	P
		Open nesters (n)	Cavity nesters (n)			
Species	K	0.4318 (19)	0.3995 (5)	0.7180	20	>0.25
	Xo	2.5547 (19)	2.5848 (5)	0.784	20	>0.25
Genera	K	0.4297 (16)	0.3995 (5)	0.6589	19	>0.25
	Xo	2.5794 (16)	2.5840 (5)	0.0121	19	>0.25
Sub-family	K	0.4195 (9)	0.3995 (5)	0.5201	12	>0.25
	Xo	2.7028 (9)	2.5840 (5)	0.2989	12	>0.25
Family	K	0.4210 (6)	0.3995 (5)	0.5569	9	>0.25
	Xo	2.8725 (6)	2.5840 (5)	0.6580	9	>0.25

Discussion

In general, growth of nestling cavity nesters is slower especially when weight (an indicator of general body size) is considered. Although, both groups exhibited similar growth rates of wing length, the cavity nesters exhibited a delay in the initial growth.

The observation of slower growth for cavity nesters compared to open nesters supports the Lack's (1968) hypothesis that cavity nesters may have a longer nestling period due to their slower growth. The different growth rates (as indicated by weight) between the two groups of passerines may be a result of food limitation due to brood size. Cavity nesters lay larger clutches than open nesters (Martin 1993). Because parents have more young to feed, food may be limited. However, in unmanipulated clutches, it seems that growth rates are not affected by clutch size (Nur 1984, Hochachka and Smith 1991) suggesting that birds raise as many young as they can adequately feed.

The difference in weight growth rates does not mean that the Ricklefs' proposition (1979) that the nestling growth may be at its maximum due to a physiological constraint, has to be rejected. When considering tarsus growth (this represents growth

of a single bone), no significant differences were found between the two groups. The physiological constraint in growth is possible in tarsus, but not in the general size of the bird (indicated by its weight). Tarsus growth may be limited because of cell proliferation, therefore resulting in similar tarsus growth rates for the two groups of passerines. However, the small sample size for cavity-nesting species may provide an explaination why no statistical difference in tarsus growth rates was found.

The delay in the growth of wing length has also been observed by Redfern (1994) who examined the growth of the flight feathers in cavity-nesting birds. A plausible explanation for this phenomenon is that the open-nesting species have been under stronger selection to develop their wings more rapidly (i.e. earlier) to escape predators.

However, not all the variation in nestling periods can be explained by the difference in growth rates (only 1.14 days at 50% of weight). Therefore, the remaining 4 days of difference in the length of nestling periods between the two groups of birds have to be explained by other factors. Reduced predation on nests of cavity nesters (see Chapter 2) offers a plausible explanation for this difference, because it should allow young of cavity

nesters to stay longer in their nest. The longer stay in the nest should, in turn, lead to further growth and consequently more fully developed young at fledgling. In the following chapter, I will test this explanation by comparing the degree of development at fledging of young of cavity nesters to that of open nesters.

Chapter 4

Do young of cavity nesters leave their nests more fully developed than young of open nesters ? Test of the differential departure hypothesis

Introduction

In the previous chapter, I established that Lack's (1968) hypothesis of slower growth rates in cavity-nesting passerines cannot completely explain the difference in nestling period. Maher (1964) found that nestlings of *Plectrophenax nivalis* (cavity nester) are bigger when leaving their nest than those of a closely related species, *Calcarius lapponicus* (open nester). Ideally, young birds should leave their nest only when completely developed and capable of moving around and escaping effectively from predators. However, their timing of departure (i.e. fledging) with respect to their state of development may be altered by selective pressures such as predation. High nest predation should favor early (i.e., relatively premature) fledging if the departure from the nest will may reduce chances of young being killed by predators. In such a case, young should

leave their nest at a less advanced stage of development. In contrast, lower predation should allow longer stay in the nest and hence reaching a more advanced stage of development at fledging.

The goal of this chapter is to test the alternative hypothesis that, as a result of different nest predation pressure (as found in Chapter 2), the young of open nesters should fledge relatively prematurely (i.e. at a less advanced developmental stage) than the young of cavity nesters. The final body size that a young bird will reach is the adult body size. According to the alternative hypothesis, the nestlings of cavity-nesting species should take extra time in nest and presumably grow to a larger size that is closer to the adult size as compared to nestlings of open-nesting species that leave their nest earlier, when they are presumably much smaller than the adults of their species. Consequently, the skills such as flying and walking should be more fully developed in cavity nesters at fledging and this should theoretically result in higher chances of survival. In my study, I will examine weight, wing and tarsus in the two groups of passerines as indicators of their general size, flight and walking skills.

Methods

To evaluate the degree of development at fledging, I measured weight, wing chord and tarsus length of nestlings on the day of fledging for a given species. Data were obtained in the same way as described earlier (see Chapter 3). When considering development, I assumed that the adult size is the final size that would eventually be reached by nestlings. Therefore, I used an index of development calculated as % of adult size (weight of young / mean weight of adult * 100). When a nest was found empty because of departure of fledglings, measurements from the previous day were used in calculation of this index. To increase sample size, I also included published data. I included only those studies that provided measurements at fledging or % of adult size at fledging. The measurements considered in the analysis are: weight (Appendix 7) as an indicator of general size of nestlings, wing length (Appendix 8) as an indicator of flight abilities, and tarsus length (Appendix 9) as an indicator of walking abilities.

The comparison of the two groups was made by Student's t-test for each of the measurements. Because data were normally distributed and homoscedastic, they were not transformed. To

control for possible phylogenetic biases, I conduct this analysis at different taxonomic levels (see chapter 1 for details).

Results

The comparison of weight at fledging revealed that the young of cavity nesters are 93.3% of adult weight while the young of open nesters leave their nest at only 79.8% of their parents' size. This difference of 13.5 % is highly significant ($P < 0.0005$; Table 8) and remained significant through all groupings (except at the family level) for control of phylogenetic biases (Table 8).

The analises of wing length shows even greater differences between the two groups of birds in the degree of development when young leave their nest. Cavity nesters have wings that are 77.1% of the adult wing length when leaving nest, while wings of open nesters are of only 59.2% of the adult size. This difference of 17.9% was highly significant and remained significant through all taxonomic levels (Table 8). This statistical difference in wing length reflects a real biological difference for the birds that I observed while gathering data. When leaving their nest, young birds from open nests cannot effectively fly, they can jump from twig to twig or run to hide in grass, sometimes they will fly for few feet downward but they cannot sustain flight. In contrast, the young of cavity nesters on their first departure can fly long distances, can fly upward for over 50 meters and

Table 8: Statistical results of the comparison of % adult weight, % adult wing length, and % adult tarsus length of open-nesting and cavity-nesting species of passerines for different taxonomic levels.

Taxa	Test	Mean		T	d.f.	P
		Open nesters(n)	Cavity nesters(n)			
Species	Weight	79.80 (42)	93.34 (29)	5.3836	69	<0.0005
	Wing	59.17 (17)	77.05 (14)	7.3183	29	<0.0005
	Tarsus	99.64 (20)	97.32 (7)	0.9949	25	>0.5
Genera	Weight	79.91 (32)	93.66 (20)	4.8391	50	<0.0005
	Wing	58.82 (26)	79.18 (11)	8.2577	24	<0.0005
	Tarsus	99.68 (19)	97.32 (7)	0.9834	24	>0.5
Sub-family	Weight	83.34 (14)	92.40 (14)	2.2946	26	<0.005
	Wing	58.87 (8)	76.52 (7)	6.5779	13	<0.0005
	Tarsus	101.7 (9)	97.45 (5)	1.5764	12	<0.05
Family	Weight	84.51 (11)	91.2 (12)	1.6350	21	>0.05
	Wing	59.25 (6)	76.52 (7)	5.059	11	<0.0005
	Tarsus	102.6 (6)	97.45 (5)	2.5722	9	>0.05

most of them will fly until they disappear from sight. Their flight appears to be almost as effective as that of the adults with the major difference of fine maneuverability.

When leaving nest, young of cavity and open nesters have a tarsus almost fully developed (97.2% vs. 99.6% of the adult length, respectively). Consequently, no significant differences were detected between the two groups at any taxonomic levels ($P > 0.5$; Table 8). Complete development (i.e. adult size) was reached at around 8 days of age for smaller species (< 20 g).

Discussion

My data demonstrated that, in general, the young of cavity-nesting passerines are more fully developed (with the exception of tarsus length) at fledging than those of open-nesting species. Higher predation pressure on young of open nesters thus evidently presents a strong selective force favoring earlier departure of young from their nests. The development of individual body parts evidently corresponds to the actual needs of nestlings as opposed to their preparation for future needs (O'Connor 1977). My data suggest that, of the body parts measured, tarsus is the first one to attain the adult size. Tarsus length should be a reliable indicator of walking abilities. A well developed tarsus should allow a nestling to move inside the nest. This should allow the young to orient itself toward its parents when begging to obtain food (O'Connor 1977), and compete more effectively with its siblings for parental attention and care (Ricklefs 1982). Also, walking abilities allow a nestling to escape from a predator by moving to well concealed locations (Werschkul 1979). Another factor that should promote an early development of legs in all species is thermoregulation. Leg muscles are used for thermoregulation in very young birds (Ricklefs 1979) and, therefore, should be

under selection for early development.

The cavity-nesting birds are relatively heavier than the open-nesting species when leaving the nest. The extra time spent in the nest by cavity nesters evidently allows them to grow bigger. Several studies demonstrated that bigger nestlings have better chances of surviving during the period from the post-fledging to the time when young become fully independent (e.g.: Krementz et al 1989, Garnett 1981, Tinbergen and Boerlijst 1990, Magrath 1991). On the other hand, risks of predation decrease when nestlings of open nesters leave their nest. Since nestling predation is high for open nesters, the risks of staying in their nest longer probably exceed those of early departure. This should explain why young of open nesters leave their nest before reaching the adult size.

An alternative explanation for the greater body weight of cavity-nesting species is that the weight of nestlings exceeds the adult body weight during the nestling period. Before fledging their weight decreases and continues decreasing during the first post fledging days (see Ricklefs 1968b). This weight recession is due to loss of water when nestlings' tissues mature (Ricklefs 1968b). Since weight continues to decrease after fledging in cavity-nesting species, it is possible that their

fledging weight presents an overestimate. This would also result in an overestimate of the difference in fledging weight between cavity nesters and open nesters.

Considering the wing length, the most interesting difference between the two groups is that young of the cavity-nesting passerines leave their nests with more fully developed wings than young of the open-nesting species. This difference should have important consequences for their survival rates. The open-nesting birds leave their nest before being capable of extended flight. Birds with such limited flight skills should evidently suffer from higher predation (Sullivan 1989). Therefore, in general, it should benefit a young bird to stay in its nest as long as necessary to fly effectively. For open nesters, nestlings face a choice between: 1) staying in the nest longer, while constantly facing relatively high risks of predation; and 2) leaving the nest early, thereby reducing risks of nest predation by moving away from the nest and other siblings and hiding in dense vegetation or by escaping from approaching predators to inaccessible (protected) places. Evidently we need data on survival rates of young cavity and open nesters from the post fledging period to establish whether, as a result of their more complete development, the young of

cavity nesters benefit from higher chances of survival than the young of open nesters.

General discussion

The main objective of this study was to explain why the nestling periods of cavity nesters are longer than those of open nesters. The observations of longer nestling periods of cavity nesters made by several authors for small samples of birds have been confirmed by a large-scale comparative study; I found that for birds of the same size, young of cavity-nesting species stay in their nest approximately 5.4 days longer than young of open-nesting species. The nest period is the most dangerous period during a bird's life. During the nest stage, young altricial birds can't escape from dangers such as rain or predators. When a nest is affected by such an element, usually the complete clutch or brood is destroyed. Many studies have found that predation is the major cause of nestling losses in birds (e.g. Ricklefs 1969, Martin 1992). The high predation pressure is thus an effective driving force that presumably favors selection for rapid growth rates and relatively early departure from nests.

My results also indicate that the cavity nesters exhibit significantly slower growth rates. However, in addition to

physiological constraints, other factors can affect growth rates. Perhaps the most important factor of these is food limitation. Limited food resources have been reported to slow down development of nestlings (e.g.: Bryant 1975, Blancher and Robertson 1987). In addition, cavity nesters lay larger clutches than the open-nesting species (e.g. Martin 1993). Therefore, parents have to feed more young and this could also lead to reduced rates of food delivery to each nestling if food is limited. However, studies comparing growth rates of nestlings in relation to brood size did not support this view when clutches were not artificially manipulated (e.g. Paytner 1954, Dyrcz 1974, Nur 1984).

The lack of differences in growth rates of tarsus may reflect a physiological constraint of cell proliferation (Ricklefs 1979). While growth of every body part is unlikely to be limited by such a constraint, the growth of bones has been found to be consistent with this hypothesis (Carrier and Auriemma 1992). Tarsus length is the measure of growth of bones, so there should be less variation in growth rate of this trait than of the wing (this measure includes feathers and bones) and weight (this includes the entire bird). Another factor that may induce a maximum growth rate for tarsus is sibling competition. All

passerines lay clutches consisting of several eggs. Therefore, a nestling must compete with its nest mates to attract its parents' attention. Being able to move around in the nest to get closer to a parent is essential for nestlings and should lead to a maximum growth of body parts important for locomotion, thereby improving mobility of young while in the nest (Werschkul and Jackson 1979).

However, the difference in growth rates of cavity-nesting and open-nesting species cannot adequately explain the entire difference in nestling periods between the two groups of birds. This difference in nestling periods must also be due to a relatively premature departure of nestlings from open nests. I found that nestlings of open nesters leave their nest at an earlier stage of development than those of cavity nesters. The tarsus is of the same size for both groups, but weight is lower and wings are shorter for open-nesting species.

The difference in the length of the nestling period between the two groups of passerines can be interpreted in terms of 1) the parent-offspring conflict (Trivers 1974) and 2) "food-predation" conflict experienced by the young. The parent-offspring conflict in this case refers to a situation when the offspring demand parental care for as long as possible, while parents should encourage their young to leave the nest and

become independent as early as possible to reduce costs associated with parental care and possibly be free to start a new breeding attempt (Trivers 1974). The parent-offspring conflict is present in all birds, regardless of their nesting habits. If this was the only force affecting the nestling period, then this type of conflict should have similar effects on timing of fledging of the two groups (i.e. cavity nesters and open nesters). However, the outcome of this conflict should ultimately be decided by the success of one group (parent or offspring) in manipulating the other.

In the second type of situation, the "food-predation conflict", nestlings are the only ones involved in making the decision when to depart from their nest. The two most important factors affecting the timing of departure by nestlings are presumably food and predation. Considering food, staying in the nest longer should increase the efficacy of parental feeding because parents do not have to search for their young (they always deliver food to the same central place - the nest) and the young do not have to expend energy by searching for food or by following their parents. Therefore, leaving the nest earlier should reduce the food delivery efficiency by parents.

The food argument suggests that staying in the nest is going to always increase the rate of food delivery by parents to their young. The parent-offspring conflict related to the parental care (feeding young) cannot explain different timing of fledging by young of open nesters and cavity nesters. The timing of fledging with respect to the age of young is thus presumably controlled by predation pressures on young in and outside their nest. The predation argument can be summarized as follows: I've established that predation on nestlings of open nesters is higher than that on young of cavity nesters. Predation on fledglings (i.e. outside their nest) should, however, be similar for both groups of birds, and should generally decrease as the ability of fledglings to escape from predators, (this is represented by a single curve on Fig. 11). With respect to predation, fledging should, theoretically, occur when the risks of predation inside the nest exceed those outside the nest. Because the risks of predation inside the nest are generally higher for open nesters, their young should be selected to fledge earlier than the young of cavity-nesting species (see Fig. 10).

When leaving their nest, the young of open-nesting species can be considered premature since they cannot accomplish normal activities such as flight (Sullivan 1989). When working with

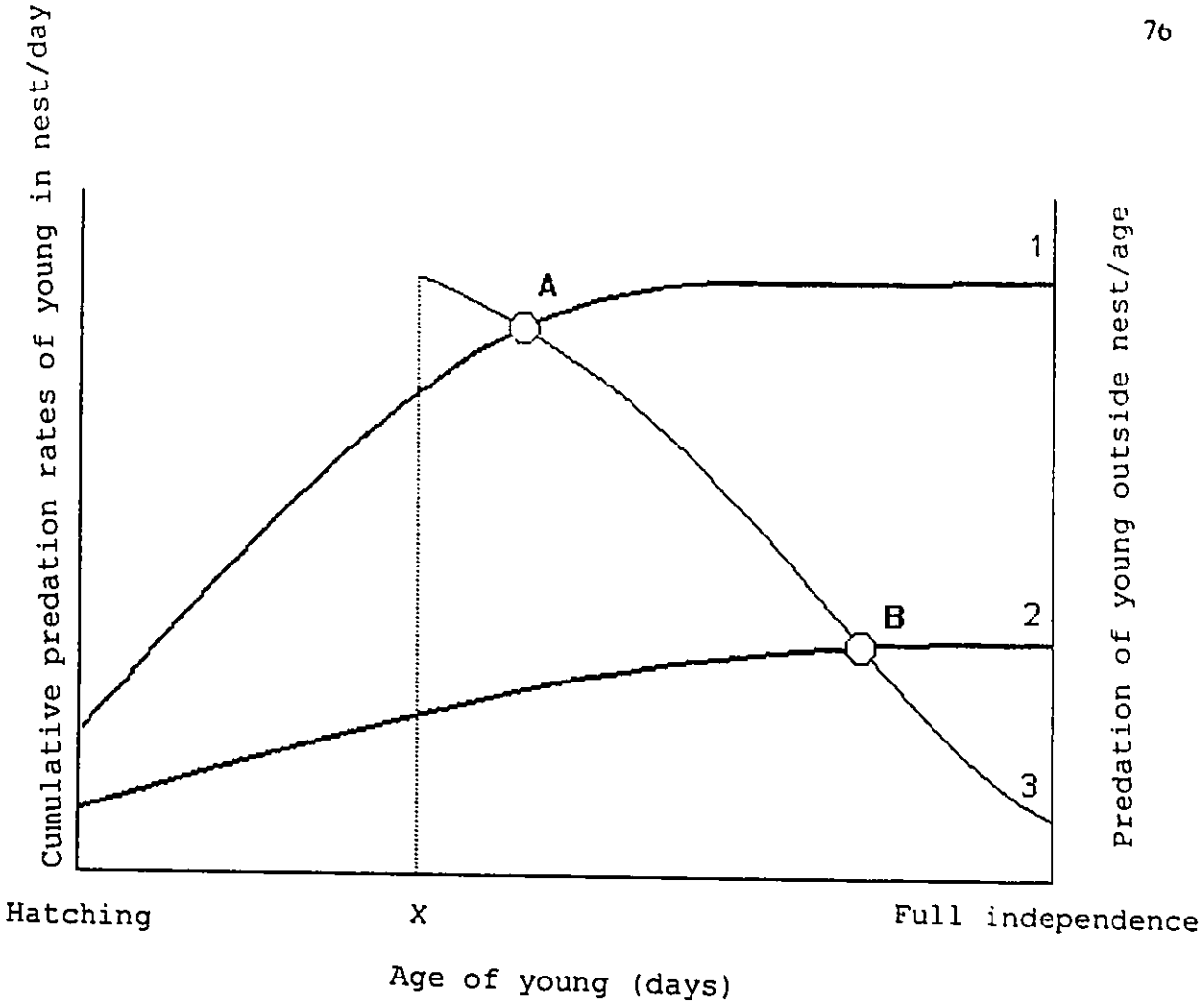

Fig. 11: Graphical representation of the food-predation model. The nest predation rates are higher for open nesters (curve 1) than for cavity nesters (curve 2). The predation pressure on young outside the nest (curve 3) reflects the mobility of young (i.e. as the ability of young to escape from predators improves, predation rates on fledglings should decrease). The curve 3 is started at age X because fledging is physically impossible at an earlier age. Fledging should occur when risks of predation inside the nest exceed those outside the nest. Since predation on young inside the nest is higher in open nesters as compared to cavity nesters, the point of departure is earlier for open nesters (A) than for cavity nesters (B).

Junco hyemalis Sullivan (1989) found that nestlings that left the nest too early suffered from higher predation than those who left the nest when more fully developped. Since the predation pressure is relatively high during the nestling period and lower during the post fledging period, the timing of departure of young of open nesters will be mostly determined by their ability to walk around and move away from their nest, thereby at least partly reducing high predation on nests. This is also facilitated by the habitat of open-nesting species that allows nestlings to escape. Open-nesting species generally prefer well concealed situations for their nests such as dense grass, shrubs and trees (Li and Martin 1991). These habitats provide numerous perches, running routes, and hiding places for nestlings that are not capable of active flight.

In cavity-nesting species, the habitat around the cavity nest tends to be more open in general (Li and Martin 1991). Presumably greater vulnerability of fledglings to predators in such exposed habitats should generally make early fledging highly risky for nestlings. The cavity-nesting species select nest sites that are not concealed and that are higher above ground to reduce predation pressure (Li and Martin 1991). Their choice of cavities seems more influenced by their availability and by accessibility

of nest contents from outside. Since the nest contents of cavity nesters are out of sight and easy reach, they are better protected from predators. The location of the cavity entrance away from branches should further reduce accessibility of nest contents to predators. The early walking abilities cannot help a nestling to leave a nest located inside a frequently deep cavity (i.e. the high location of an entrance relative to the nest cup presents a physical barrier). This factor plus the reduced predation should consequently favor departure of young at a time when their flight abilities are well developed.

The relative safety of young of cavity nesters suggests a question of how would their departure from the nest be controlled? Lemel (1989) found that when some young fledged while others remained inside, the fledglings received more food from their parents. Therefore, when one nestling leaves the nest, the others soon should follow to maximize feeding by their parents. This suggests that parents manipulate their offspring through feeding rates, thereby forcing them to fledge more or less simultaneously. In the brood there is usually a dominant nestling (generally the oldest one) that monopolizes food and parental care. Therefore, nestlings in a poorer condition should attempt to leave the nest first in order to attract more

attention from its parents. The others should soon follow if they are to also benefit from a similar amount of parental care.

Since non-related cavity-nesting species exhibit the same shift in the length of nestling period, it is possible that some factors other than predation may contribute to these differences. For example, proximal factors such as darkness, reduced stimulation from outside, and physical barrier due to "domed" nature of a nest are common factors in all cavities, but their role in duration of nestling period is yet to be tested. Although, since slower growth rates and later departure from the nest evolved independently in several groups of species with the appearance of cavity-nesting habit, this parallel evolution suggest a common evolutionary force such as lower predation.

If predation pressure on nest contents in cavities is lower, why then do all bird species not breed in cavities? Martin and Li (1992) found that the breeding adults of cavity-nesting species suffer from higher adult mortality (presumably due to predation) than those of open nesters. In addition, cavities are limited, and competition for them is intense among birds, usually limiting the number of breeding pairs (Nilsson 1984, Finch 1990). Furthermore, competitors for cavities also include other animals such as insects and small mammals. Several studies demonstrated

that increasing the number of cavities usually resulted in a corresponding increase in density of breeding pairs (e.g. Brush 1983).

Several authors considered the problem of competition for limited cavities. Alerstam and Högstedt (1981), for example, suggested that resident species should have an advantage over migrants since they can find their cavity and settle in it before migrants arrive. Also, aggressive species such as starlings and wrens should be more effective in acquisition and defense of nesting cavities. Furthermore, some species may actively evict previous cavity owners by destroying their clutch (e.g. Finch 1990).

In an experimental study of nest predation, Martin (1988) found that having different nesting habits for different species of birds breeding in the same area is an advantage since this should reduce the chances of predators finding all nests. This is probably the main reason for the existence of such a great variety of nesting habits among birds.

Conclusion

In general, this comparative study decisively demonstrated that cavity-nesting passerines have a longer nestling period than the open-nesting species. My analysis of published data on nest predation suggests that predation pressure is an important factor that may have led to 1) faster growth of young of open-nesting species, and 2) their relatively premature fledging. This is presumably because the open-nesting species suffer from higher nest predation rates than the cavity nesters. In contrast, the cavity-nesting species are better protected from predators and consequently fledge at a later age. Furthermore, as a result of delayed fledging, the young of cavity nesters leave their nest more fully developed than the young of open nesters. These findings support the two hypotheses on the occurrence of different nestling periods of cavity nesters and open nesters.

The hypothesis on the role of predation in the evolution of longer nestling periods in cavity nesters as opposed to open nesters is based on several assumptions, some of which remain to be verified. Among these, the greater survival of young of cavity nesters between fledging and full independence must be tested.

There is also a need to compare survival rates of young inside and oustside the nest to verify the major assumption of the "food-predation" model. Also, the relative importance of darkness inside the cavity nests and deep cavities presenting a physical barrier for the young will have to be critically examined because they too could contribute to the longer nestling periods of cavity-nesting passerines.

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Appendix 1

Matched pairs for comparison of open nesters and cavity nesters nestling period.

Paired taxa	Mean nestling period	Mean adult weigth
Tyrannidae		
1. Open: *Empidonax flaviventris* *E. virescens, E. alnorum* *E. minimus, E. fulvifrons* *E. oberholseri*	14.5	11.20
Cavity: *Empidonax difficilis*	16	11.05
2. Open: *Tyrannus forficatus, T. tyrannus*	13.75	27.75
Cavity: *Myriachus cinerascens, M. crinitus*	15.75	31.88
Corvidae		
1. Open: *C. splendens*	24.5	285
Cavity: *Corvus monedula*	33	23
2. Open: *Nucifraga cloumbiana, N. caryocatactes*	22.5	149.5
Cavity: *Pyrrhocorax pyrrhocorax* *P. graculus*	33	261.75
3. Open: *Cyanopica cyana* *Perisoreus infaustus*	18	79.85
Cavity: *Pica pica*	27	184.5

Appendix 1

Muscicapidae				
1. Open:	*Catharus guttatus, C. Fuscescens*			
	C. minimus, C. mustelinus			
	C. ustulatus, Turdus migratorius			
	T. torquatus, T. merula, T. ruficollis			
	T. pilaris, T. iliacus, T. philomelos			
	T. viscivorus	12.55	62.85	
Cavity:	*Monticola saxatilis, M. solitarius*		16.5	49.9
2. Open:	*Cercothrichas galactoes*	12.5	21.8	
Cavity:	*Ficedula hypoleuca, F. albicollis*		13.87	14.05
	F. semitorquata, F. parva			
	Muscicapa striata			
3. Open:	*Luscinia luscinia, L. megarhynchos*			
	L. svecia	11.2	21.47	
Cavity:	*Phoenicurus ochruros,*	16	18.93	
	P. Phoenicurus, P. erythrogaster			
4. Open:	*Oenanthe hispanica*	11.5	18	
Cavity:	*Oenanthe leucopyga, E. leucura*	14.63	26.63	
	O. oenanthe, O. lugens, O. finschii			
	O. pleschanka, O. deserti			
	O. isabellina			
Sylvidae				
1 . Open:	*Cisticola juncidis*	14.5	8.9	
Cavity:	*Prinia gracilis*	13.5	6.5	

2.	Open:	*Acrocephalus melanopognon*		
		A. paludicola, A. Schoeneobaenus		
		A. scirpaeus, A. dumetorum		
		A. palustris, A. arundinaceus		
		A. stentoreus, Hippolai icterina		
		H. polyglotta, H. caligata	12.51	13.17
	Cavity:	*Phylloscopus collybita, P. bonelli*		13.22 8.2
Passeridae				
1.	Open:	*Carpospiza brachydactyla*	11	23.1
	Cavity:	*Petronia petronia*	18.5	32.1
2.	Open:	*Anthus campestris, A. trivialis*		
		A. hodgsoni, A. gustavi		
		A. pratensis, A. cervinus		
		A. rubescens	12.94	21.63
	Cavity:	*Anthus spinoletta*	14.5	22.8
3.	Open:	*Motacilla citreola, M. flava*	11.3	17.95
	Cavity:	*Motacilla alba, M. cinerea*	14	19.85
4.	Open:	*Prunella modularis*	11.5	20.1
	Cavity:	*Prunella collaris*	16	35.9
5.	Open:	*Prunella atrogularis*	12.5	18.3
	Cavity:	*Amandava amandava*	19	9.15
		Estrilda astrild		
6.	Open:	*Carpodacus erythrinus*		
		C. purpureus, C. mexicanus	13.33	23.11
	Cavity:	*Carpodacus synoicus, C. rubicilla*		16 33.2

Appendix 1

7.	Open: *Emberiza leucocephalos, E. cirlus E. cia, E. hortulana, E. caesia E. pusilla, E. rustica, E. aureola E. rutila, E. melanocephala E. pallasi, E. schoeniclus*	11.23	22.41
	Cavity: *Emberiza striolata*	18	15.3
8.	Open: *Passerculus sandwichensis Ammodramus bairdii A. savannarum*	10.25	17.61
	Cavity: *Plectrophenax nivalis*	13.5	33
9.	Open *Vermivora pinus, V. celata V. ruficapilla, Dendroica petechia D. pensylvanica, D. magnolia D. caerulescens, D. coronata D. virens, D. pinus, D. kirtlandii D. discolor, D. palmarum D. castanea, D. striata*	10.46	10.3
	Cavity: *Protonotaria citrea*	11	16.1

*as cited in Appendix 2

Appendix 2

Nestling periods of passerines of the northern hemisphere

Family Sub-family *Genus species*	Nest type	Nestling period (days)	Adult size (grams)
Tyrannidae			
Fluvicolinae			
Contopus borealis	Open [c]	23 [c]	33.2 [c]
Contopus virens	Open [c]	16.5 [c]	13.4 [c]
Empidonax flaviventris	Open [c]	13 [c]	10.95 [c]
Empidonax virescens	Open [c]	13.5 [c]	13.7 [c]
Empidonax alnorum	Open [c]	13.5 [c]	13.4 [c]
Empidonax minimus	Open [c]	14 [a]	9.24 [c]
Empidonax difficilis	Cavity [c]	16 [c]	11.05 [c]
Empidonax fulvifrons	Open [c]	15 [c]	8.1 [c]
Empidonax oberholseri	Open [c]	18 [c]	11.8 [c]
Sayornis phoebe	Open [c]	15.5 [c]	18.35 [c]
Tyranninae			
Myiarchus cinerascens	Cavity [c]	16.5[c]	28.5[c]
Myiarchus crinitus	Cavity [c]	15 [c]	35.25 [c]
Tyrannus forficatus	Open [c]	14 [c]	11.5 [d]
Tyrannus tyrannus	Open [c]	13.5 [c]	44 [c]
Laniidae			
Lanius collurio	Open [b]	14.5 [b]	29.2 [b]
Lanius minor	Open [b]	17 [b]	49.7 [b]
Lanius ludovicianus	Open [c]	20 [c]	45.9 [c]
Lanius excubitor	Open [c]	20 [c]	67.5 [c]
Lanius senator	Open [b]	17 [b]	34 [b]
Lanius nubicus	Open [b]	19 [b]	22.8 [b]
Vireonidae			
Vireo bellii	Open [c]	11.25 [c]	10.2 [c]
Vireo solitarius	Open [c]	14[a]	16.85 [c]
Vireo flavifrons	Open [c]	15 [c]	17.25 [c]
Vireo philadelphicus	Open [c]	13[a]	13.22 [c]
Vireo olivaceus	Open [c]	11 [c]	19 [c]
Vireo gilvus	Open [c]	13 [c]	15.5 [c]

Corvidae			
Gymnorhinus cyanocephalus	Open [c]	21 [c]	103.3 [c]
Cyanocitta cristata	Open [c]	19 [c]	82.48 [c]
Aphelocoma coerulescens	Open [c]	18 [c]	80.2 [c]
Garrulus glandarius	Open [b]	16.5 [b]	164.8 [b]
Perisoreus infaustus	Open [b]	21 [b]	85.8 [b]
Cyanopica cyana	Open [b]	15 [b]	73.9 [b]
Pica pica	Cavity [c]	27[a]	184.5 [c]
Nucifraga columbiana	Open [c]	20.5[a]	146 [c]
Nucifraga caryocatactes	Open [b]	24.5 [b]	153 [b]
Pyrrhocorax pyrrhocorax	Cavity [b]	36 [b]	304.6 [b]
Pyrrhocorax graculus	Cavity [c]	30 [b]	218.9 [b]
Corvus monedula	Cavity [b]	33 [b]	232 [b]
Corvus splendens	Open [b]	24.5 [b]	285 [b]
Corvus frugilegus	Open [b]	33 [b]	454.4 [b]
Corvus caurinus	Open [c]	28.8 [f]	380 [f]
Corvus ossifragus	Open [c]	21 [c]	400 [c]
Corvus corone	Open [b]	33 [b]	515.6 [b]
Corvus cryptoleucus	Open [c]	38.5 [c]	1234 [c]
Corvus ruficollis	Open [b]	36.5 [b]	635.4 [b]
Corvus corax	Open [b]	45 [b]	1198.3 [b]
Oriolidae			
Oriolus oriolus	Open [b]	16.5 [b]	70.4 [b]
Bombycillidae			
Bombycillinae			
Bombycilla garrulus	Open [c]	14 [c]	58.7 [b]
Bombycilla cedrorum	Open [c]	16 [c]	30.05 [c]
Cinclidae			
Cinclus cinclus	Cavity [b]	22 [b]	62 [b]
Muscicapidae			
Turdinae			
Monticola saxatilis	Cavity [b]	15 [b]	46.7 [b]
Monticola solitarius	Cavity [b]	18 [b]	53.1 [b]
Sialia sialis	Cavity [c]	17.5 [c]	30.13 [c]
Sialia currucoides	Cavity [c]	22.5[a]	29.6 [g]

Catharus fuscescens	Open c	10 c	31.5 c
Catharus minimus	Open c	12 c	29.6 c
Catharus ustulatus	Open c	12 c	30.1 c
Catharus guttatus	Open c	12 c	29.55 c
Catharus mustelinus	Open c	12.5 c	52.33 c
Turdus torquatus	Open b	15 b	108.8 b
Turdus merula	Open b	13.6 b	96.8 b
Turdus ruficollis	Open b	12.9 b	104 b
Turdus pilaris	Open c	14 c	83 c
Turdus iliacus	Open b	10 b	64.4 b
Turdus philomelos	Open b	13.2 b	72.6 b
Turdus viscivorus	Open b	13.5 b	124.5 b
Turdus migratorius	Open c	15 c	74.5 c
Muscicapinae			
Muscicapa striata	Cavity b	13 b	15.6 b
Ficedula hypoleuca	Cavity b	15.5 b	12.8 b
Ficedula albicollis	Cavity b	15.9 b	13.2 b
Ficedula semitorquata	Cavity b	15 b	14.2 b
Ficedula parva	Cavity b	12.5 b	9.8 b
Saxicolinae			
Erithacus rubecula	Cavity b	13.4 b	17.3 b
Luscinia luscinia	Open b	9.6 b	25 b
Luscinia megarhynchos	Open b	11 b	22 b
Luscinia svecica	Open b	13 b	17.4 b
Cercotrichas galactotes	Open b	12.5 b	21.8 b
Phoenicurus ochruros	Cavity b	15.5 b	15.9 b
Phoenicurus phoenicurus	Cavity b	14.5 b	14.8 b
Phoenicurus erythrogaster	Cavity b	18 b	26.1 b
Saxicola rubetra	Open b	12.5 b	17.1 b
Saxicola torquata	Open b	13.5 b	14 b
Oenanthe leucopyga	Cavity b	14 b	26 b
Oenanthe leucura	Cavity b	14.5 b	39.8 b
Oenanthe oenanthe	Cavity c	15 c	30.83 c
Oenanthe lugens	Cavity b	14.5 b	22.5 b
Oenanthe finschii	Cavity b	15.5 b	25.3 b
Oenanthe pleschanka	Cavity b	13.5 b	18.5 b
Oenanthe hispanica	Open b	11.5 b	18 b
Oenanthe deserti	Cavity b	15.5 b	19.7 b
Oenanthe isabellina	Cavity b	14.5 b	30.4 b

Sturnidae			
Sturnus roseus	Cavity b	24 b	72 b
Sturnus vulgaris	Cavity c	21 c	76.15 c
Sturnus unicolor	Cavity b	21.5 b	88.8 b
Acridotheres tristis	Cavity b	28.5 b	119.5 b
Mimidae			
Dumetella carolinensis	Open c	12.5 c	34.68 c
Mimus polyglottos	Open c	11 c	53 c
Toxostoma rufum	Open c	11 c	68.68 c
Sittidae			
Sittinae			
Sitta europaea	Cavity b	23 b	11.8 b
Sitta whiteheadi	Cavity b	23 b	11.8 b
Sitta ledanti	Cavity b	23.5 b	17.3 b
Sitta krueperi	Cavity b	17.5 b	12.3 b
Sitta pusilla	Cavity c	18 c	10.8 c
Sitta canadensis	Cavity c	19.5 c	10.35 c
Sitta carolinensis	Cavity c	14 c	20.7 c
Sitta neumayer	Cavity b	26.5 b	26.5 b
Sitta tephronota	Cavity b	25 b	40 b
Tichodrominae			
Tichodroma muraria	Cavity b	29 b	17.4 b
Certhiidae			
Certhia familiaris	Cavity b	16.8 b	9 b
Certhia americana	Cavity c	13.5 c	8.38 c
Certhia brachydactyla	Cavity b	17.5 b	87 b
Troglodytidae			
Campylorhynchus brunneicapillus	Cavity c	21 c	35.5 h
Cistothorus platensis	Cavity c	13 c	8.15 c
Cistothorus palustris	Cavity c	13.5 c	11.67 c
Thryothorus ludovicianus	Cavity c	13.5 c	16.95 c
Troglodytes troglodytes	Cavity c	17.3 b	10.3 b
Troglodytes aedon	Cavity c	15 c	11.68 c

Polioptilidae			
Polioptila melanura	Open [c]	11 [c]	6.55 [c]
Paridae			
Remizinae			
Remiz pendulinus	Cavity [b]	23 [b]	9.1 [b]
Parinae			
Parus palustris	Cavity [b]	18.5 [b]	11.1 [b]
Parus lugubris	Cavity [b]	22.2 [b]	16.7 [b]
Parus montanus	Cavity [b]	18.5 [b]	17.1 [b]
Parus carolinensis	Cavity [c]	15[a]	11.25 [c]
Parus cinctus	Cavity [b]	19.5 [b]	12.7 [b]
Parus ater	Cavity [b]	19 [b]	9.5 [b]
Parus cristatus	Cavity [b]	20 [b]	11.6 [b]
Parus major	Cavity [b]	19 [b]	18.2 [b]
Parus caeruleus	Cavity [c]	19.5 [b]	11.1 [b]
Parus cyanus	Cavity [b]	16 [b]	13 [b]
Parus inornatus	Cavity [c]	18.5 [c]	13.7 [c]
Parus bicolor	Cavity [c]	17.5 [c]	22.18 [c]
Aegithalidae			
Aegithalos caudatus	Cavity [b]	16 [b]	8.3 [b]
Hirundinidae			
Tachycineta bicolor	Cavity [c]	20 [c]	19.3 [c]
Tachycineta thalassina	Cavity [c]	20[a]	16 [c]
Progne subis	Cavity [c]	28 [c]	45.1 [c]
Stelgidopteryx serripennis	Cavity [c]	20 [c]	15.1 [c]
Riparia riparia	Cavity [c]	22.3 [b]	14 [b]
Riparia paludicola	Cavity [b]	20 [b]	11 [b]
Hirundo rupestris	Cavity [b]	25.5 [b]	23 [b]
Hirundo fuligula	Cavity [b]	27.5 [b]	15 [b]
Hirundo rustica	Cavity [c]	20.5	18.4 [c]
Hirundo daurica	Cavity [b]	24 [b]	20 [b]
Hirundo fulva	Cavity [c]	22[a]	23.83 [i]
Delichon urbica	Cavity [b]	27 [b]	18 [b]

Regulidae			
Regulus calendula	Open c	12 c	6 c
Regulus regulus	Open b	19 b	5.6 b
Regulus ignicapillus	Open b	20 b	5.3 b
Regulus satrapa	Open c	16.5 c	5.55 c
Pycnonotidae			
Pycnonotus barbatus	Open b	13 b	33.7 b
Pycnonotus xanthopygos	Open b	14 b	44 b
Pycnonotus leucogenys	Open b	10 b	31.7 b
Sylviidae			
Cettia cetti	Open b	15 b	12.9 b
Locustella naevia	Open b	11 b	13 b
Locustella fluviatilis	Open b	15 b	16.4 b
Locustella luscinioides	Open b	13 b	15.8 b
Acrocephalus melanopogon	Open b	12 b	11.4 b
Acrocephalus paludicola	Open b	13.5 b	12.2 b
Acrocephalus schoenobaenus	Open b	13.5 b	11.8 b
Acrocephalus scirpaceus	Open b	11 b	10.9 b
Acrocephalus dumetorum	Open b	12 b	11.7 b
Acrocephalus palustris	Open b	10.5 b	12.3 b
Acrocephalus arundinaceus	Open b	13 b	30 b
Acrocephalus stentoreus	Open b	12 b	25.1 b
Hippolais caligata	Open b	13 b	8.5 b
Hippolais pallida	Open b	13 b	10.1 b
Hippolais polyglotta	Open b	12 b	11 b
Hippolais icterina	Open b	13.5 b	12.4 b
Cisticola juncidis	Open b	14.5 b	8.9 b
Scotocerca inquieta	Cavity b	14 b	8.2 b
Prinia gracilis	Cavity b	13.5 b	6.5 b
Phylloscopus trochilus	Cavity b	13 b	8.8 b
Phylloscopus collybita	Cavity b	15 b	7.8 b
Phylloscopus bonelli	Cavity b	12.5 b	8.1 b
Phylloscopus sibilatrix	Cavity b	12 b	9.9 b
Phylloscopus subviridis	Cavity b	13 b	6.3 b
Phylloscopus borealis	Cavity	13.8 b	9.7 b
Phylloscopus nitidus	Cavity b	13 b	7.4 b

Sylvia atricapilla	Open [b]	11 [b]	18.3 [b]
Sylvia borin	Open [b]	10 [b]	19.1 [b]
Sylvia communis	Open [b]	11 [b]	15.3 [b]
Sylvia curruca	Open [b]	11 [b]	12.2 [b]
Sylvia nisoria	Open [b]	11 [b]	25 [b]
Sylvia leucomelaena	Open [b]	13.5 [b]	14.1 [b]
Sylvia melanocephala	Open [b]	12.5 [b]	11.6 [b]
Sylvia cantillans	Open [b]	11.5 [b]	10.1 [b]
Sylvia mystacea	Open [b]	10.5 [b]	9.8 [b]
Sylvia conspicillata	Open [b]	11.5 [b]	9.2 [b]
Sylvia undata	Open [b]	12 [b]	9.6 [b]
Sylvia sarda	Open [b]	12 [b]	9.4 [b]
Timaliidae			
Turdoides altirostris	Open [b]	10 [b]	33 [b]
Turdoides caudatus	Open [b]	11.7 [b]	41.9 [b]
Turdoides squamiceps	Open [b]	14 [b]	73.5 [b]
Panurus biarmicus	Open [b]	11.2 [b]	15.3 [b]
Alaudidae			
Melanocorypha calandra	Open [b]	10 [b]	61 [b]
Melanocorypha bimaculata	Open [b]	9 [b]	53.3 [b]
Calendrella brachydactyla	Open [b]	9.5 [b]	23 [b]
Calendrella rufescens	Open [b]	9 [b]	23.3 [b]
Galerida cristata	Open [b]	9 [b]	67 [b]
Galerida theklae	Open [b]	9 [b]	37 [b]
Lullula arborea	Open [b]	10.5 [b]	29 [b]
Alauda arvensis	Open [c]	9.5 [c]	37.5 [c]
Eremophila alpestris	Open [c]	10.5 [c]	32 [c]
Passeridae			
Passer domesticus	Cavity [c]	16 [c]	27.2 [c]
Passer hispaniolensis	Cavity [b]	15 [b]	28 [b]
Passer moabiticus	Cavity [b]	12 [b]	16.1 [b]
Passer montanus	Cavity [b]	17.5 [b]	22 [b]
Petronia petronia	Cavity [b]	18.5 [b]	32.1 [b]
Carpospiza brachydactyla	Open [b]	11 [b]	23.1 [b]
Montifringilla nivalis	Cavity [b]	20.5 [b]	36.4 [b]

Motacillidae			
Motacilla alba	Cavity c	14.5 c	22.2 b
Motacilla citreola	Open b	12.5 b	19.1 b
Motacilla flava	Open c	11.1 b	16.8 b
Motacilla cinerea	Cavity b	13.5 b	17.5 b
Anthus campestris	Open b	13.5 b	25 b
Anthus trivialis	Open b	13 b	22.2 b
Anthus hodgsoni	Open b	11.5 b	22.1 b
Anthus gustavi	Open b	13 b	21.7 b
Anthus pratensis	Open b	12.5 b	18.8 b
Anthus cervinus	Open b	12.6 b	20.4 b
Anthus spinoletta	Cavity b	14.5 b	22.8 b
Anthus rubescens	Open c	14.5 c	21.2 c
Prunellidae			
Prunella collaris	Cavity b	16 b	35.9 b
Prunella atrogularis	Open b	12.5 b	18.3 b
Prunella modularis	Open b	11.5 b	20.1 b
Estrildidae			
Estridinae			
Estrilda astrild	Cavity b	19 b	8.4 b
Amandava amandava	Cavity b	19 b	9.9 b
Fringillidae			
Fringilidae			
Fringilla coelebs	Open b	13.9 b	22.6 b
Fringilla teydea	Open b	17.5 b	30.1 b
Fringilla montifringilla	Open b	13.5 b	23.5 b
Carduelinae			
Serinus pusillus	Open b	15 b	11.6 b
Serinus serinus	Open b	14 b	11.7 b
Serinus syriacus	Open b	15 b	15.3 b
Serinus canaria	Open b	16.5 b	12.3 b
Serinus citrinella	Open b	16.5 b	12.3 b

Carduelis chloris	Open b	14.4 b	27.9 b
Carduelis spinus	Open b	14 b	13 b
Carduelis pinus	Open c	15 c	12 c
Carduelis tristis	Open c	13 c	12.55 c
Carduelis carduelis	Open c	14.7 b	16.7 b
Carduelis hornemanni	Open c	13 c	18.5 c
Carduelis flammea	Open c	12 c	13.5 c
Carduelis flavirostris	Open b	11.5 b	15.3 b
Carduelis cannabina	Open b	13.5 b	18.2 b
Rhodopechys sanguinea	Open b	14 b	25.7 b
Rhodopechys githaginea	Open b	13.5 b	19.2 b
Rhodopechys obsoleta	Open b	13.5 b	24.7 b
Carpodacus erythrinus	Open b	11.5 b	22.9 b
Carpodacus purpureus	Open c	14 c	25.42 c
Carpodacus mexicanus	Open c	14.5 c	21 c
Carpodacus synoicus	Cavity b	15 b	20.9 b
Carpodacus rubicilla	Cavity b	17 b	45.5 b
Pinicola enucleator	Open c	14 b	53.5 b
Loxia pytyopsittacus	Open b	22 b	53.2 b
Loxia scotica	Open b	21 b	42.2 b
Loxia curvirostra	Open b	22.5 b	39.6 b
Loxia leucoptera	Open b	23 b	32 b
Pyrrhula pyrrhula	Open b	15 b	27.4 b
Coccothraustes coccothraustes	Open b	12.5 b	55.3 b
Hesrperiphona verpertina	Open c	13.5 c	57.75 c
Emberizidae			
Emberizinae			
Emberiza citrinella	Open b	12 b	29.1 b
Emberiza leucocephalos	Open b	9.5 b	27.8 b
Emberiza cirlus	Open b	12 b	25.3 b
Emberiza cia	Open b	11.5 b	23 b
Emberiza hortulana	Open b	12.5 b	22.6 b
Emberiza caesia	Open b	12.5 b	21.5 b
Emberiza striolata	Cavity b	18 b	15.3 b
Emberiza pusilla	Open b	7 b	14.5 b
Emberiza rustica	Open b	9 b	19.2 b
Emberiza aureola	Open b	12 b	21.3 b
Emberiza rutila	Open b	12.5 b	25.1 b
Emberiza melanocephala	Open b	14.5 b	28 b
Emberiza pallasi	Open b	10 b	14 b
Emberiza schoeniclus	Open b	11 b	19.9 b

Milaria calandra	Open [b]	11 [b]	46 [b]
Calcarius lapponicus	Open [c]	9 [c]	27 [c]
Calcarius ornatus	Open [c]	10 [c]	20
Plectrophenax nivalis	Cavity [c]	13.5 [c]	33 [c]
Calamospiza melanocorys	Open [c]	8.5[a]	37 [c]
Passerella iliaca	Open [c]	10[a]	35.46 [c]
Melospiza melodia	Open [c]	10 [c]	20.4 [c]
Melospiza lincolnii	Open [c]	9.5 [c]	17.5 [c]
Melospiza georgiana	Open [c]	12.5 [c]	16.3 [c]
Zonotrchia leucophrys	Open [c]	10 [c]	29.14 [c]
Zonotrichia atricapilla	Open [c]	9 [j]	31.8 [j]
Junco hyemalis	Open [c]	11[a]	17.1 [c]
Junco phaeonotus	Open [c]	9 [c]	27 [c]
Passerculus sandwichensis	Open [c]	14 [c]	17.35 [c]
Ammodramus maritimus	Open [c]	9.5 [c]	20.5 [c]
Ammodramus caudacutus	Open [c]	10 [c]	16.5 [c]
Ammodramus bairdii	Open [c]	9 [c]	17.1 [c]
Ammodramus savannarum	Open [c]	9	18
Spizella arborea	Open [c]	9.5 [c]	21.36 [c]
Spizella passerina	Open [c]	10 [c]	13.43 [c]
Spizella pallida	Open [c]	8 [c]	11.45 [c]
Spizella breweri	Open [c]	8.5[a]	11 [c]
Spizella pusilla	Open [c]	7.5 [c]	12.5 [c]
Pooecetes gramineus	Open [c]	9.5 [c]	24.75 [c]
Chondestes grammacus	Open [c]	9.5 [c]	27.1 [c]
Amphispiza belli	Open [c]	10[a]	19.3 [k]
Aimophila carpalis	Open [c]	8.5[a]	15.2 [l]
Pipilo erythrophthalmus	Open [c]	11 [c]	39.43 [c]
Pipilo aberti	Open [c]	12.5[a]	46.8 [m]
Parulinae			
Vermivora pinus	Open [c]	10.5 [c]	9.65 [c]
Vermivora celata	Open [c]	9[a]	9.3 [c]
Vermivora ruficapilla	Open [c]	11 [c]	7.7 [c]

Dendroica petechia	Open c	10.5 c	10.3 c
Dendroica pensylvanica	Open c	11 c	9.75 c
Dendroica magnolia	Open c	9 c	8.95 c
Dendroica caerulescens	Open c	10 c	11.87 c
Dendroica coronata	Open c	13 c	14.4 c
Dendroica virens	Open c	9 c	9 c
Dendroica pinus	Open c	10 c	14.1 c
Dedroica kirtlandii	Open c	12.5 c	15.6 c
Dendroica discolor	Open c	9 c	8.23 c
Dendroica palmarum	Open c	12 c	10.65 c
Dendroica castanea	Open c	11.5 c	13.4 c
Dendroica striata	Open c	11.5 c	14.28 c
Mniotilta varia	Open c	10 c	11.33 c
Setophaga ruticilla	Open c	8.5 c	8.4 c
Protonotaria citrea	Cavity c	11 c	16.1 c
Helmitheros vermivorus	Open c	10 c	12.7 c
Limnothlypis swainsonii	Open c	12 c	13.7 c
Seiurus aurocapillus	Open c	8 c	20.55 c
Seiurus noveboracensis	Open c	10a	18.85 c
Seiurus motacilla	Open c	9.5 c	22.4 c
Oporornis formosus	Open c	10 c	14 c
Oporornis philadelphia	Open c	8 c	12.13 c
Geothlypis trichas	Open c	8 c	10.45 c
Wilsonia citrina	Open c	8.5 c	9.6 c
Wilsonia pusilla	Open c	10.5 c	14.4 c
Myioborus pictus	Open c	11a	9.8 n
Icteria virens	Open c	9 c	26.4 c
Thraupinae			
Piranga olivacea	Open c	11.7 c	30.1 c
Cardinalinae			
Spiza americana	Open c	8 c	27.25 c
Pheuctitus ludovicianus	Open c	10.5 c	46.5 c
Cardinalis cardinalis	Open c	10.5 c	43.85 c
Guiraca caerulea	Open c	9.5a	28.4 c

Passerina cyanea	Open [c]	9 [c]	15.38 [c]
Passerina ciris	Open [c]	13 [c]	14.75 [c]
Icterinae			
Icterus galbula	Open [c]	13 [c]	36.1 [c]
Icterus spurius	Open [c]	12.5 [c]	20.9 [c]
Xanthocephalus xanthocephalus	Open [c]	10.5 [c]	76.63 [o]
Agelaius phoeniceus	Open [c]	10 [c]	51.75 [c]
Sturnella neglecta	Open [c]	12[a]	87.5 [c]
Quiscalus quiscula	Open [c]	17 [c]	116.7 [c]
Molothrus ater	Open [c]	10.5[a]	42.8 [c]
Dolichonyx oryzivorus	Open [c]	12 [c]	33.7 [c]

a: reference from Ehrlich et al 1988
b: reference from Cramp 1988, 1992, 1993, 1994a, 1994b.
c: reference from Terres 1987
d: reference fron Davis et al 1963
e: reference from Bateman and Balda 1973
f: reference from Butler et al 1984
g: reference from Herlugson 1983
h: reference from Ricklefs 1975
i: reference from Stoner 1945
j: reference from Knapton et al 1984
k: reference from Peterson et al 1986
l: reference from Austin and Ricklefs 1977
m: reference from Finch 1984
n: reference from Marshall and Balda 1974
o: reference from Ortega and Cruz 1992

Appendix 3
Nestling success of passerines

Family Sub-family *Genus species*	Nest type	No egg hatched	No egg fledge	Nestling period	% fledged	daily mortality	Source
Tyrannidae							
Fluvicolinae							
Sayornis phoebe	C	392	348	15.2	88.78	0.74	Faanes 1980
		302	229	15.2	80.96	1.25	Hills and Gates 1988
		129	104	15.5	95.41	0.30	Kendeigh 1942
		621	531	16	85.51	0.91	Weeks 1979
Sayornis saya	C	124	96	15	77.42	1.51	Ohlendorf 1976
Tyranninae							
Myriachus crinitus	C	193	138	14	71.50	2.04	Taylor and Kreshner 1991
Corvidae							
Corvus caurinus	O	553	245	28.8	44.30	1.93	Butler et al 1984
Corvus brachyrhynchos	O	325	115	31.5	35.60	2.04	Ignatuk and Clark 1991

Bombycillidae							
Bombycillinae							
Bombycilla cedrorum	O	189	171	14	90.48	0.68	Putnam 1949
Cinclidae							
Cinclus cinclus	C	1212	1020	22	84.16	0.70	Shaw 1978
Muscicapidae							
Turdinae							
Sialia sialis	C	279	189	18.8	67.74	1.72	Kendeigh 1942
		3943	2786	17.5	70.66	1.68	Laskey 1943
		213	172	17.5	80.75	1.10	Thomas 1946
		131	127	17.5	96.95	0.17	Walkinshaw 1941
Catharus mustelinus	O	142	92	12.5	64.79	2.82	Longcore and Jones 1979
Turdus philomelos	O	1034	808	13.2	78.14	1.66	Silva 1949
Turdus migratorius	O	157	131	12.5	83.44	1.32	Howell 1942
		563	465	15	82.59	1.16	Kendeigh 1942
		316	246	13	77.85	1.70	Young 1955
Sturnidae							
Sturnus vulgaris	C	731	615	21	85.30	0.70	Dunnet 1955
		551	321	21	58.26	1.99	Ricklefs and Peters 1979

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Mimidae							
Dumetella carolinensis	O	179	152	12.5	84.92	1.21	Keindegh 1942
Toxostoma curvirostre	O	138	85	16	61.59	2.40	Fischer 1980
Troglodytidae							
Cistothorus palustris	C	326	22	14	6.74	6.66	Kale 1965
Troglodytes aedon	C	425	390	16	91.76	0.52	Baldwin and Bowen 1928
		4823	4771	15.5	98.92	0.07	Kendeigh 1942
		199	161	16	80.90	1.19	Walkinshaw 1941
		135	118	16	87.41	0.79	Kuerzi 1941
Paridae							
Parinae							
Parus carolinensis	C	202	172	16.8	85.15	0.88	Albano 1992
Parus ater	C	153	131	19	85.62	0.76	Mackenzie 1950**
Parus major	C	1653	1416	19	85.66	0.75	Gibb 1950
		425	340	19	80.00	1.05	Mackenzie 1950**
		4579	3938	19	86.00	0.74	Wolda 1929**

Hirundinidae							
Tachycineta bicolor	C	1176	886	20	75.34	1.23	Chapman 1955
		310	303	20	97.74	0.10	Kuerzi 1941
		1424	857	20	60.18	1.99	Low 1934
		163	123	20	75.46	1.23	Shelley 1937
		248	196	20	79.03	1.05	Stuchbury and Robertson 1988
		358	340	20	94.97	0.25	Weydenmeyer 1935
Progne subis	C	1347	1015	28	75.35	0.88	Allen and Nice 1952
Stelgidopteryx serripennis	C	327	275	16	84.10	0.99	Lunk 1962*
Hirundo pyrrhonota	C	189	171	23.6	90.48	0.40	Grant and Quay 1977
Hirundo daurica	C	446	415	24	93.05	0.29	de Lope Rebollo 1980
Delichon urbica	C	378	356	30.6	94.18	0.19	Bryant 1975
Alaudidae							
Emerophila alpestris	O	79	46	10	58.23	4.18	Pickwell 1931*

Passeridae							
Passer domesticus	C	719	560	14.3	77.89	1.55	Anderson 1994
		422	390	16	92.42	0.47	Murphy 1978
		159	104	14.6	65.41	2.37	Pitts 1979
		758	584	16	77.04	1.44	Sappington 1977
Motacillidae							
Anthus rubescens	O	286	222	14.5	77.62	1.54	Verbeek 1970
Motacilla alba	C	3651	3017	14.5	82.63	1.20	Mason and Lyczynski 1980
Motacilla cinerea	C	526	419	13.5	79.66	1.51	Mason and Lyczynski 1980
Fringillidae							
Carduelinae							
Carduelis tristis	O	241	160	13	66.39	2.59	Holcomb 1969a
		149	99	12.5	66.44	2.68	Holcomb 1972
		463	396	13	85.53	1.11	Middleton 1979
		455	338	12.3	74.29	2.09	Stokes 1950
		77	33	13	42.86	4.40	Nolan 1963
		113	80	13	70.80	2.25	Walkinshaw 1939**
Carpodacus mexicanus	O	80	57	15.1	71.25	1.90	Evenden 1957

Emberizidae							
Emberizidae							
Calcarius mccownii	O	92	71	10	77.17	2.28	Mickey 1943
		145	82	10	56.55	4.35	With 1994
Melospiza melodia	O	173	116	10	67.05	3.30	Kendeigh 1942
		389	243	11	62.47	3.41	Nice 1957
Zonotrichia leucophrys	O	1646	839	10	50.97	4.90	Petrinovitch and Patterson 1983
Zonotrichia albicollis	O	171	110	9	64.33	3.96	Knapton et al 1984
Passerculus sandwichensis	O	569	390	9	68.54	3.50	Dixon 1978
		479	301	8	62.84	4.65	Lapointe and Bédard 1986
		42	22	8	52.38	5.95	Nolan 1963
		89	85	9.4	95.51	0.48	Welsh 1975
Spizella passerina	O	104	93	10	89.42	1.06	Walkinshaw 1944
Spizella pusilla	O	888	620	11	69.82	2.74	Walkinshaw 1952
Aimophila aestivalis	O	206	91	9	44.17	6.20	Haggerty 1988

Appendix 3

Parulinae							
Dendroica petechia	O	546	340	10.5	62.27	3.59	Goosen and Sealy 1982
		119	91	7	76.47	3.36	Schrantz 1943
Dendroica discolor	O	47	24	9	51.06	5.44	Nolan 1963
Protonotaria citrea	C	700	620	10.75	88.57	1.06	Petit 1989
		259	206	11	79.54	1.86	Walkinshaw 1941*
Seiurus aurocapillus	O	102	70	8	68.63	3.92	Hann 1937
Myioborus pictus	O	33	26	9	78.79	2.36	Marshall and Balda 1974
Icteria virens	O	43	30	9.5	69.77	3.18	Thompson and Nolan 1973
Cardinalinae							
Spiza americana	O	55	55	9	100.0	0.00	Hamerson 1974
Icterinae							
Icterus spurius	O	131	126	13	96.18	0.29	Dennis 1948
Xanthocephalus xanthocephalus	O	314	99	13	31.53	5.27	Fautin 1941
		167	111	13	66.47	2.58	Young 1963*

Agelaius phoeniceus	O	258	170	10.5	65.89	3.25	Beer and Tibbits 1950*
		319	195	10	61.13	3.89	Caccamise 1976
		760	471	10	61.97	3.80	Caccamise 1978
		823	675	10.5	82.02	1.71	Smith 1943
		330	201	10.5	60.91	3.72	Weins 1965
		156	105	10.5	67.31	3.11	Williams 1940
		795	367	10.5	46.16	5.13	Young 1963*
Sturnella magna	O	243	195	12	80.25	1.65	Roseberry and Klimstra 1970
Quiscalus quiscula	O	209	135	12	64.59	2.95	Petersen 1950*
		117	77	12	65.81	2.85	Weins 1965
Euphagus cyanocephalus	O	327	205	13	62.29	2.90	La Rivers 1944
Dolichonyx oryzivorus	O	378	345	12	91.27	0.73	Wittenberger 1978

* As cited in Ricklefs 1969
** As cited in Nice 1957

Appendix 4
Growth rates of weight among passerines

Family Sub-family *Genus species*	Nest type	Growth rate	Age at inflexion	Asymptote (grams)	Source
Tyrannidae					
Fluvicolinae					
Empidonax alnorum	O	0.5463	3.87	11.9	Present study
Sayornis phoebe	C	0.4132	5.14	18.5	Murphy 1981
Tyranninae					
Tyrannus verticalis	O	0.4948	4.27	10.8	Davis et al 1963
Tyrannus tyrannus	O	0.4272	4.54	30.4	Murphy 1981
Laniidae					
Lanius collurio	O	0.4271	5.35	27.6	Diehl and Myrcha 1973
Corvidae					
Gymnorhinus cyanocephalus	O	0.3564	6.56	71.6	Bateman and Balda 1973
Aphelocoma coerulescens	O	0.3055	7.82	65.8	Woolfenden 1978
	O	0.2677	7.72	74.2	Ritter 1984
Cyanocorax beecheii	O	0.3448	6.21	131.9	Winterstein and Raitt 1983
Bombycillidae					
Bombycillinae					
Bombycilla cedrorum	O	0.4369	5.74	34.5	Putnam 1949
	O	0.5564	4.20	29.0	Present study

Muscicapidae					
Turdinae					
Sialia currucoides	C	0.4208	5.34	29.7	Herlugson 1983
	C	0.4345	4.71	30.3	Shantz 1986
Turdus grayi	O	0.4427	5.17	53.0	Dyrcz 1983
Turdus migratorius	O	0.4894	4.81	61.6	Howell 1942
	O	0.6714	3.68	56.9	Present study
Saxicolinae					
Erithacus rubecula	C	0.3929	4.92	20.2	Lees 1949
Sturnidae					
Sturnus vulgaris	C	0.4005	4.54	72.0	Present study
Mimidae					
Dumetella carolinensis	O	0.4686	4.14	32.8	Present study
Mimus polyglottos	O	0.5133	3.85	39.3	Fischer 1983
Oreoscoptes montanus	O	0.4026	5.14	36.1	Killpack 1970
Toxostoma longirostre	O	0.6178	3.72	40.2	Fischer 1983
Toxostomacurvirostre	O	0.3898	5.42	58.9	Fischer 1983
Troglodytidae					
Campilorhynchus brunneicapillus	C	0.3676	5.64	32.4	Anderson & Anderson 1961
Troglodytes aedon	C	0.5457	3.42	9.5	Present study
Polioptilidae					
Auriparus flaviceps	C	0.4290	4.21	6.4	Taylor 1971

Paridae					
Parinae					
Parus atricapillus	C	0.4582	4.77	10.0	Kluyver 1961
Parus montanus	C	0.4067	5.42	11.5	Orell 1983
Parus major	C	0.4005	5.94	19.3	Schifferli 1973
	C	0.4141	5.04	16.6	Orell 1983
Hirundinidae					
Tachycineta bicolor	C	0.5518	4.16	21.2	Present study
Tachycineta thalassina	C	0.4668	4.54	17.3	Edson 1943
Hirundo rustica	C	0.4585	5.62	23.1	De Braey 1946
Sylviidae					
Acrocephalus scirpaceus	O	0.6100	3.55	11.0	Dyrcz 1974
Acrocephalus arundinaceus	O	0.5473	4.08	24.6	Dyrcz 1974
Phylloscopus trochilus	C	0.5123	4.37	10.3	Tiainen 1978
Phylloscopus collybita	C	0.4656	4.30	8.5	Tiainen 1978
Phylloscopus sibilatrix	C	0.4995	4.08	11.6	Tiainen 1978
Passeridae					
Passer domesticus	C	0.4944	4.34	21.5	Blem 1986
	C	0.4004	3.99	23.6	Weaver 1942
Motacillidae					
Anthus pratensis	O	0.4908	4.91	18.5	Pedroli and Graf-Jaccottet 1978
Anthus rubescens	O	0.5921	3.41	17.6	Verbeek 1970

Fringillidae					
Carduelinae					
Carduelis tristis	O	0.4263	4.93	11.5	Holcomb 1969
Carpodacus mexicanus	O	0.3851	5.16	19.6	Present study
Emberizidae					
Emberizinae					
Calcarius mccownii	O	0.4914	4.66	19.9	Mickey 1943
Calcarius lapponicus	O	0.5000	4.32	23.4	Maher 1964
Plectrophenax nivalis	C	0.5448	4.16	31.8	Maher 1964
Melospiza melodia	O	0.5749	2.94	17.6	Present study
	O	0.6006	3.36	17.7	Sodge et al 1991
Zonotrichia leucophrys	O	0.5462	3.87	20.0	Banks 1959
	O	0.6375	3.29	20.9	Morton et al 1972
	O	0.5559	3.59	21.6	King and Hubbard 1981
Zonotrichia albicollis	O	0.5473	3.63	20.5	Knapton et al 1984
Passerculus sandwichensis	O	0.5202	2.94	11.6	Dawson and Evans 1957
Spizella passerina	O	0.5731	2.73	10.1	Dawson and Evans 1957
	O	0.5984	3.48	10.6	Walkinshaw 1944
	O	0.6574	3.25	9.9	Weaver 1937
Spizella pusilla	O	0.5996	3.11	10.4	Best 1977
Aimophila carpalis	O	0.5790	2.72	12.2	Austin and Ricklefs 1977
Pipilo erythrophthalmus	O	0.5782	2.39	21.5	Barbour 1950

Parulinae					
Dendroica petechia	O	0.6261	3.35	9.7	Schrantz 1943
	O	0.5445	2.20	9.5	Present study
Geothlypis trichas	O	0.7122	3.13	10.2	Stewart 1953
Icterinae					
Xanthocephalus xanthocephalus	O	0.5209	4.36	49	Crawford 1977
	O	0.5826	3.93	44.7	Willson 1966
Agelaius phoeniceus	O	0.5141	4.19	37.1	Crawford 1977
	O	0.6650	3.39	34.5	Present study
Quiscalus mexicanus	O	0.3543	4.11	94.9	Gotie and Kroll 1973
Molothrus ater	O	0.6628	3.52	27.5	Scott 1979

Appendix 5
Growth rate of wing chord among passerines

Family Sub-family *Genus species*	Nest type	Growth (K)	Age at inflexion (days)	Asymptote (mm)	Source
Tyrannidae					
Fluvicolinae					
Empidonax alnorum	O	0.1503	7.00	73.9	Present study
Bombycillidae					
Bombycillinae					
Bombycilla cedrorum	O	0.1310	8.90	106.3	Present study
Muscicapidae					
Turdinae					
Sialia sialis	C	0.1874	8.24	81.8	Pinkowski 1975
Sialia currucoides	C	0.1285	10.39	116.3	Shantz 1986
Turdus migratorius	O	0.1770	6.42	103.0	Howell 1942
	O	0.2468	4.94	91.4	Present study
Sturnidae					
Sturnus vulgaris	C	0.1540	8.52	116.2	Present study
Mimidae					
Dumetella carolinensis	O	0.1959	5.54	82.0	Present study
Oreoscoptes montanus	O	0.1292	8.96	105.2	Killpack 1970

Troglodytidae					
Troglodytes aedon	C	0.1866	6.23	50.5	Present study
Paridae					
Parus montanus	C	0.1712	8.07	62.5	Orell 1983
Parus major	C	0.1972	7.27	65.0	Orell 1983
Hirundinidae					
Tachycineta bicolor	C	0.1259	9.75	126.3	Present study
Sylviidae					
Phylloscopus trochilus	C	0.2358	5.16	56.5	Tiainen 1978
Phylloscopus collybita	C	0.2423	5.34	51.0	Tiainen 1978
Phylloscopus sibilatrix	C	0.2611	4.54	59.7	Tiainen 1978
Passeridae					
Passer domesticus	C	0.2274	5.54	71.2	Present study
	C	0.0897	10.63	110.1	Weaver 1942
Fringillidae					
Carduelinae					
Carpodacus mexicanus	O	0.2216	6.28	68.3	Present study
Emberizidae					
Emberizinae					
Calcarius mccownii	O	0.2383	5.92	75.5	Mickey 1945
Melospiza melodia	O	0.2001	5.60	74.2	Present study
Spizella passerina	O	0.1706	6.50	77.7	Walkinshaw 1944
	O	0.2733	5.26	57.9	Weaver 1937

Aimophila carpalis	O	0.2890	3.74	52.1	Austin and Ricklefs 1977
Pipilo erythrophthalmus	O	0.1681	7.61	129.8	Barbour 1950
Parulinae					
Dendroica petechia	O	0.1962	5.04	67.0	Present study
Icterinae					
Agelaius phoeniceus	O	0.3353	3.51	70.9	Present study
	O	0.2858	4.05	69.8	Holcomb and Twiest 1971
Molothrus ater	O	0.2196	4.92	87.8	Scott 1979

Appendix 6
Growth rate of tarsus among passerines

Family Sub-family *Genus species*	Nest type	Growth rate(K)	Age at inflexion	Asymptote (mm)	Source
Tyrannidae					
Fluvicolinae					
Empidonax alnorum	O	0.2874	2.64	17.6	Present study
Sayornis phoebi	C	0.3203	3.55	18.5	Murphy 1981
Tyrannidae					
Tyrannus tyrannus	O	0.3509	2.49	18.9	Murphy 1981
Corvidae					
Aphelocoma coerulescens	O	0.2428	6.22	39.8	Woolfenden 1978
Bombycillidae					
Bombycillinae					
Bombycilla cedrorum	O	0.4543	2.19	17.4	Present study
Muscicapidae					
Turdinae					
Sialia currucoides	C	0.3496	2.88	28.1	Shantz 1986
Turdus migratorius	O	0.5572	3.05	33.6	Present study
	O	0.4034	3.83	35.4	Howell 1942

Sturnidae					
Sturnus vulgaris	C	0.4536	2.50	31.8	Present study
Mimidae					
Dumetella carolinensis	O	0.4967	3.03	28.8	Present study
Oreoscoptes montanus	O	0.2259	3.76	40.0	Killpack 1970
Troglodytidae					
Troglodytes aedon	C	0.4679	2.78	18.1	Present study
Hirundinidae					
Tachycineta bicolor	C	0.4061	1.21	12.6	Present study
Fringillidae					
Carduelinae					
Carpodacus mexicanus	O	0.4432	3.35	19.9	Present study
Emberizidae					
Emberizinae					
Melospiza melodia	O	0.4401	1.81	22.9	Present study
	O	0.3885	2.08	26.7	Sodge et al 1991
Spizella passerina	O	0.5091	2.06	18.1	Walkinshaw 1944
Spizella pusilla	O	0.4237	2.26	23.1	Best 1977
Aimophila carpalis	O	0.5604	1.62	19.3	Austin and Ricklefs 1977
Pipilo erythrophthalmus	O	0.4311	1.86	27.8	Barbour 1950
Parulinae					
Dendroica petechia	O	0.6171	1.22	17.7	Present study
Geothlypis thichas	O	0.4064	2.59	25.3	Stewart 1953

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Icterinae					
Xanthocephalus xanthocephalus	O	0.3549	3.25	45.6	Willson 1966
Agelaius phoeniceus	O	0.4510	2.41	30.5	Present study
	O	0.4796	2.88	28.5	Holcomb and Twiest 1971
Molothrus ater	O	0.4210	3.07	25.9	Scott 1979

Appendix 7
Weight at fledgling of passerines

Family Sub family *Genus species*	Nest type	Fledging weight (g)	Adult weight (g)	% of adult	Source
Tyrannidae					
Fluvicolinae					
Empidonax alnorum	O	11.5	13.4 [a]	85.82	Present study
Sayornis phoebi	C	17.47	19.7	88.68	Murphy 1981
Tyranninae					
Tyrannus forficatus	O	10	11.5	86.96	Davis et al 1963
Tyrannus tyrannus	O	27.79	31.9	93.39	Murphy 1981
Laniidae					
Lanius collurio	O	22.5	29.2 [b]	77.05	Diehl anr Myrcha 1973
Lanius excubitor	O	54.6	61.8	88.35	Degen et al 1992
Corvidae					
Gymnorhinus cyanocephalus	O	75.79	103.3	73.37	Bateman and Balda 1973
Aphelocoma coerulescens	O	59.75	79.2	75.44	Woolfenden 1978
	O	80	92.9	86.11	Ritter 1984
Cyanocorax beecheii	O	129.4	193.3	66.94	Winterstein and Raitt 1983

Corvus caurinus	O	300	380	78.95	Butler et al 1984
Corvus brachyrhynchos	O	380	454 a	83.70	Ignatuk and Clark 1991
Bombycillidae					
Bombycillinae					
Bombycilla cedrorum	O	26.5	30.5 a	86.89	Present study
	O	34.18	30.5 a	112.05	Putnam 1949
Muscicapidae					
Turdinae					
Sialia sialis	C	27.2	30.1 a	90.37	Hamilton 1945
Sialia currucoides	C	19.9	28 a	71.07	Power 1966
	C	29.61	29.6	100.03	Herlugson 1983
	C	27	28	96.43	Shantz 1986
Turdus migratorius	O	57.6	74.5 a	77.31	Present study
	O	56.5	80.8	69.93	Howell 1942
Muscicapinae					
Ficedula hypoleuca	C	14.1	12.8 b	110.2	Järvinen and Ylimaunu 1986
Saxicolinae					
Erithacus rubecula	C	18.2	17.3 b	105.2	Lack and Silva 1949
	C	18.6	20	93.00	Lees 1949
Phoenicurus phoenicurus	C	15.8	14.8 b	106.8	Järvinen 1989
Oenanthe oenanthe	C	22.51	25	90.04	Moreno 1987

Sturnidae					
Sturnus vulgaris	C	77.5	76.15 a	101.77	Present study
Mimidae					
Dumetella carolinensis	O	30.6	35.1 a	87.18	Present study
Mimus polyglottos	O	34.99	47.81	73.19	Fischer 1983
Troglodytidae					
Campylorhynchus brunneicapillus	C	32	35.5 a	90.14	Anderson and Anderson 1961
Troglodytes aedon	C	10.02	10.95 a	91.51	Present study
	C	9.82	10.44	94.06	Zach 1982
Paridae					
Parinae					
Parus montanus	C	11.52	17.1 b	67.37	Orell 1983
Parus atricapillus	C	11.3	12.2	92.62	Kluyver 1961
Parus major	C	17.9	18.2 b	98.35	Schifferli 1973
	C	16.5	18.2 b	90.66	Lemel 1989
	C	16.67	18.2 b	91.59	Orell 1983
Parus caeruleus	C	11	11.5	95.65	O'Connor 1977
Hirundinidae					
Tachycineta bicolor	C	21.12	19.3 a	109.43	Present study
	C	19.45	19.3 a	100.78	Paynter 1954
	C	19.77	22.63	87.36	Zach and Mayoh 1982
Tachycineta thalassina	C	16.5	16	103.13	Edson 1945

Riparia riparia	C	13.3	13.7	97.08	Turner and Bryant 1979
	C	15	14.4	104.17	Turner and Bryant 1979
Hirundo rustica	C	17.5	19.63	89.15	Stoner 1935
	C	19.6	19	103.16	Turner and Bryant 1979
	C	18.15	19	95.53	Allen et al 1952
	C	18.5	19	97.37	DeBraey 1946
Hirundo phyrronota	C	21.5	23.83	90.22	Stoner 1945
Delichon urbica	C	18.3	19.6	93.37	Turner and Bryant 1979
	C	17.7	19.4	91.24	O'Connor 1977
Regulidae					
Regulus regulus	O	6.5	6.5	100	Haftorn 1978
Sylviidae					
Acrocephalus scirpaceus	O	10.8	10.9 b	99.08	Dyrcz 1974
Acrocephalus arundinaceus	O	25.7	30 b	85.67	Dyrcz 1974
Phylloscopus trochilus	C	9.24	9.38	98.51	Tiainen 1978
Phylloscopus collybita	C	8.50	7.81	108.8	Tiainen 1978
Phylloscopus sibilatrix	C	9.27	10.05	92.24	Tiainen 1978
Alaudidae					
Eremophila alpestris	O	20	31.45	63.59	Verbeek 1967

Passeridae					
Passer domesticus	C	24.63	26.8 a	91.90	Present study
	C	26.5	30	88.33	Yom-Tov and Ar 1980
	C	24	28.3	84.81	Blem 1975
	C	24.5	28	87.50	O'Connor 1977
	C	22.5	26.8 a	83.96	Weaver 1942
	C	23.76	27.06	87.80	Seel 1970
Passer montanus	C	19.51	21.96	88.84	Seel 1970
Motacillidae					
Anthus pratensis	O	18.3	18.8 b	97.34	Pedroli and Graf-Jaccottet 1978
Anthus rubescens	O	18.5	21.2	87.26	Verbeek 1970
Fringillidae					
Carduelinae					
Carduelis tristis	O	11.56	12.55 a	92.11	Holcomb 1970
Carpodacus mexicanus	O	20	21 a	95.24	Present study
Emberizidae					
Emberizinae					
Calcarius pictus	O	18.8	27.2	69.12	Maher 1964
Plectrophenax nivalis	C	30.9	38.4	80.47	Maher 1964
Melospiza melodia	O	18.8	21.6	87.04	Sodge et al 1991
	O	16.5	20.4 a	80.88	Present study

Zonotrichia leucophrys	O	20.78	30.48 a	69.18	Morton et al 1972
	O	19	30.48 a	62.34	Banks 1959
	O	19.7	30.48 a	64.63	King and Hubbard 1981
Zonotrichia albicollis	O	20.3	26.35 a	77.03	Knapton et al 1984
Zonotrichia atricapilla	O	23.1	31.8	72.64	Hendricks 1987
Passerculus sandwichensis	O	14.98	19.26	77.78	Rogers 1985
Spizella pusilla	O	10.4	12.8	81.25	Dawson and Evans 1957
Spizella passerina	O	10.3	11.8 a	87.29	Walkinshaw 1944
	O	10.1	12.8	78.91	Weaver 1937
	O	10.9	11.6	93.97	Dawson and Evans 1957
Spizella pallida	O	10.1	11.57 a	87.29	Salt 1966
Pooecetes gramineus	O	18	25.7	70.04	Dawson and Evans 1960
	O	17.61	24.75 a	71.15	Adams et al 1994
Amphispiza belli	O	13.94	19.3	72.23	Petersen et al 1986
Aimophila carpalis	O	11.9	15.3	77.78	Austin and Ricklefs 1977
Pipilo erythrophthalmus	O	22.47	39.4 a	57.03	Barbour 1950
Pipilo aberti	O	32.8	46.8	70.09	Finch 1984
Parulinae					
Dendroica petechia	O	8.78	10.03 a	87.54	Present study
	O	8.78	10.03 a	87.54	Schrantz 1943
Protonotaria citrea	C	11.63	14.4 a	80.76	Petit 1989

Oporornis agilis	O	10	13.35	74.91	Walkinshaw and Dyer 1961
Geothlypis trichas	O	9.8	10.45 a	93.77	Stewart 1953
Myioborus pictus	O	8.8	9.8	89.80	Marshall and Balda 1974
Thrauphinae					
Euphonia hirundinacea	C	13.5	16.97	79.55	Sargent 1993
Icterinae					
Xanthocephalus xanthocephalus	O	41.4	76.63 d	54.03	Richter 1984
	O	45.2	76.63 d	58.98	Willson 1966
	O	45.9	76.63	59.90	Ortega and Cruz 1992
	O	46.63	76.63 d	60.85	Crawford 1977
Agelaius phoeniceus	O	34.99	51.75 a	67.61	Crawford 1977
	O	32.24	51.75 a	62.3	Ricklefs 1967b
	O	34.96	51.75 a	67.56	Present study
Molothrus ater	O	28	44.1 a	63.49	Scott 1979

a: as cited in Terres 1987.
b: as cited in Cramp 1969, 1992, 1993, 1994a, 1994b.
c: as cited in Ricklefs 1975.
d: as cited in Ortega and Cruz 1992.

Appendix 8
Wing chord at fledgling of passerines

Family Sub family *Genus species*	Nest type	Fledgling wing (mm)	Adult wing (mm)	% of adult	Source
Tyrannidae					
Fluvicolinae					
Empidonax alnorum	O	41.5	70.35 a	58.99	Present study
Bombycillidae					
Bombycillinae					
Bombycilla cedrorum	O	61.33	94.75 a	64.73	Present study
Muscicapidae					
Turdinae					
Sialia sialis	C	67.3	94.75 a	70.85	Pinkowski 1975
Sialia currucoides	C	80	113	70.80	Shantz 1986
Turdus migratorius	O	66.3	126.6	52.37	Howell 1942
	O	67	113.3 a	59.16	Present study
Sturnidae					
Sturnus vulgaris	C	95.05	130 a	73.12	Present study
Mimidae					
Dumetella carolinensis	O	52.8	91 a	58.02	Present study
Oreoscoptes montanus	O	48.8	98 a	49.80	Killpack 1970

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Troglodytidae					
Campylorhynchus brunneicapillus	C	73.9	84.5 a	87.5	Austin and Ricklefs 1977
Troglodytes aedon	C	37	50 a	74.00	Present study
Paridae					
Parus caeruleus	C	50.3	63	79.84	O'Connor 1977
Hirundinidae					
Tachycineta bicolor	C	92.25	112 a	82.37	Present study
Riparia riparia	C	96.6	107.2	90.11	Turner and Bryant 1979
Hirundo rustica	C	94.1	118.8 a	79.8	Ricklefs 1967b
	C	102	128.1	79.63	Turner and Bryant 1979
Delichon urbica	C	100.6	107	94.02	O'Connor 1977
	C	89.4	111.5	80.18	Turner and Bryant 1977
Sylviidae					
Phylloscopus trochilus	C	49.51	68.99	71.76	Tiainen 1978
Phylloscopus collybita	C	42.90	63.88	67.16	Tiainen 1978
Phylloscopus sibilatrix	C	51.67	77.32	66.83	Tiainen 1978
Passeridae					
Passer domesticus	C	55.25	77 a	71.75	Present study
	C	58.2	75	77.6	O'Connor 1977
	C	64	77 a	83.66	Weaver 1942

Fringillidae					
Carduelinae					
Carpodacus mexicanus	O	49.5	77 a	64.29	Present study
Emberizidae					
Emberizinae					
Calcarius mccownii	O	50.75	87 a	58.33	Mickey 1963
Melospiza melodia	O	38.3	67 a	57.16	Present study
	O	39.8	60.3	66.00	Sodge et al 1991
Spizella passerina	O	39.9	66	60.45	Weaver 1937
	O	46	68.75 a	66.91	Walkinshaw 1944
Aimophila aestivalis	O	41.8	59.5 a	70.00	Haggerty 1994
Aimophila carpalis	O	41.4	60.9	67.98	Austin and Ricklefs 1977
Pipilo erythrophthalmus	O	43	85.5 a	50.29	Barbour 1950
Pipilo aberti	O	52.8	89.5 a	59.00	Finch 1984

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Parulinae					
Dendroica petechia	O	32.9	62.5 [a]	52.64	Present study
Opornis agilis	O	36	68.5	52.55	Walkinshaw and Dyer 1961
Icterinae					
Agelaius phoeniceus	O	59.8	108 [a]	55.4	Ricklefs 1967b
	O	58.2	108 [a]	53.89	Holcomb and Twiest 1971
	O	61.25	108 [a]	56.71	Present study
Molothrus ater	O	64	101.8 [a]	62.90	Scott 1979

a: as cited in Pyle et al 1987.

Appendix 9

Tarsus at fledgling of passerines

Family Sub family *Genus species*	Nest type	Fledgling tarsus (mm)	Adult tarsus	% of adult (mm)	Source
Tyrannidae					
Fluvicolinae					
Sayornis phoebi	C	17.41	18.3	95.14	Murphy 1981
Tyranninae					
Tyrannus crinitus	C	18.26	19.4	94.12	Murphy 1981
Corvidae					
Aphelocoma coerulescens	O	36.38	38.7	94	Woolfenden 1978
Bombycillidae					
Bombycillinae					
Bombycilla cedrorum	O	17.17	15.9 a	107.9	Present study
Muscicapidae					
Turdinae					
Sialia currucoides	C	27	27	100	Shantz 1986
Turdus migratorius	O	33.2	34.1 a	97.36	Present study
	O	32.8	32.9	99.70	Howell 1942
Sturnidae					
Sturnus vulgaris	O	30.74	29.3 a	104.9	Present study

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Mimidae					
Dumetella carolinensis	O	27.4	27.4 a	100	Present study
Oreoscoptes montanus	O	33	30.4 a	108.6	Killpack 1970
Troglodytidae					
Troglodytes aedon	C	17.68	17.5 a	101	Present study
Hirundinidae					
Tachycineta bicolor	C	12	12.5 a	96	Present study
Hirundo rustica	C	10.73	11.3 a	95	Ricklefs 1967b
Hirundo pyrrhonota	C	11	11	100	Stoner 1945
Fringillidae					
Carduelinae					
Carpodacus mexicanus	O	18.5	17.2 a	107.6	Present study
Emberizidae					
Emberizinae					
Melospiza melodia	O	21.67	21.8 a	99.4	Present study
	O	39.8	41	97.07	Sodge et al 1991
Zonotrichia atricapilla	O	22	24.4 a	90.16	Hendricks 1987
Spizella passerina	O	17	16.7 a	101.8	Walkinshaw 1944
	O	16.7	16.7 a	100	Reynolds and Knapton 1984
Amphispiza belli	O	23.1	25.4	90.94	Petersen et al 1986
Aimophila aestivalis	O	19.1	19.3 a	99	Haggerty 1994
Aimophila carpalis	O	18.8	19	98.95	Austin and Ricklefs 1977

Pipilo erythrophthalmus	O	27	27.7 [a]	97.47	Barbour 1950
Parulinae					
Dendroica petechia	O	17.6	18.1 [a]	97.23	Present study
	O	21.7	18.1 [a]	119.9	Walkinshaw and Dyer 1961
Oporornis agilis	O	21.25	20.5	103.7	Stewart 1953
Icterinae					
Xanthocephalus xanthocephalus	O	31.5	34.3 [a]	91.84	Richter 1984
Agelaius phoeniceus	O	28.6	28.6 [a]	100	Ricklefs 1967b
	O	28.64	28.6 [a]	100.1	Present study
	O	27.6	28.6 [a]	96.5	Holcomb and Twiest 1971
Quiscalus major	O	51.1	51.1 [a]	100	Bancroft 1984
Molothrus ater	O	24	25.9 [a]	92.66	Scott 1979

a: As cited in Godfrey 1986.