

A developmental constraint on the fledging time of birds

DAVID R. CARRIER* AND JASON AURIEMMA

Department of Integrative Biology, University of California, Berkeley, CA 94720, U.S.A.

Received 7 August 1990, accepted for publication 16 January 1991

We examined the hypothesis that the rate of bone growth limits the minimum fledging time of birds. Previous observations in California gulls indicate that linear growth of wing bones may be the rate limiting factor in wing development. If bone growth is rate limiting, then birds with relatively long bones for their size could be expected to have longer fledging periods than birds with relatively short bones. We tested this by comparing the length of wing bones, relative to body mass, to the relative length of fledging periods among 25 families. The results support the hypothesis. A strong correlation exists between relative fledging period and relative bone length. Species which have relatively long bones for their body size tend to take longer to fly. In contrast, parameters that influence flight style and performance, such as size of the pectoralis muscle and wing loading, show little or no correlation with fledging time. The analysis also indicates that, when altricial and precocial species are considered together, bone length is more highly correlated with fledging time than is body mass or rate of increase in body mass during growth. These observations suggest that linear growth of bones does limit the growth of avian wings and that it is one of the factors that influences the fledging time of birds.

KEY WORDS:—Fledging – constraint – bone – growth.

CONTENTS

Introduction	61
Materials and methods	63
Specimen and measurements	63
Data analysis	63
Results	64
Morphometrics	64
Bone length and fledging time	65
Discussion	68
Is bone growth rate limiting?	70
Acknowledgements	71
References	71
Appendices	72

INTRODUCTION

What determines the amount of time required for a young bird to grow from a hatchling into a fledgling that can fly? One might expect that large species

*Author to whom correspondence should be addressed at: David Carrier, Division of Biology & Medicine, Box G, Brown University, Providence, Rhode Island 02912, U.S.A.

would take longer to begin flying than small species. Often, however, this is not the case. Variation in fledging time is largely independent of body size (Lack, 1968). Compare, for example, the 236-day fledging period of the royal albatross (Tickell, 1968) to the 14-day fledging period of a similar sized galliform, the American turkey (Hewitt, 1967). Such dramatic variation could result from a variety of factors as diverse as rate of growth or aerodynamic performance.

Several explanations for the broad differences in fledging time have been proposed. Lack (1968) suggests that the length of the fledging period is determined primarily by an interaction of factors influencing mortality of the chicks with those that influence the chick's food supply. He argues that species in which the young have a plentiful and rich diet grow faster and therefore fledge earlier than species with a poorer diet. Additionally, predation and other sources of chick mortality favour rapid growth and early fledging. Albatrosses provide a compelling example. They tend to nest on isolated islands that provide the young with protection from predators. However, the nesting sites are often so far from their feeding grounds that nestlings must endure prolonged periods without food. Thus, the extremely long fledging periods of albatrosses are consistent with Lack's hypothesis. Alternatively, Ricklefs (1973, 1979a, b) has shown that there is an inverse relationship between growth rate and relative maturity of locomotor function. Species that are precocial in their walking and flying abilities tend to grow 3-4 times more slowly than species that are altricial. Ricklefs attributes this to a conflict between cell proliferation and mature function. Tissues and organs that must function during ontogeny grow relatively slowly. Thus, there appears to be a compromise between selection for early fledging and selection for rapid growth.

An additional factor that may influence fledging period has emerged from recent observations on the ontogeny of the California gull, *Larus californicus*, (Carrier & Leon, 1990). In these gulls, components of the wing display two distinct patterns of growth. Aspects of the wing such as bone strength, muscle mass and feather surface area undergo very little growth throughout the major portion of the post-hatching growth period. Then, just before the time of fledging, rapid growth occurs. Delayed, or altricial, development of the wing is common among species of birds and has been suggested to facilitate rapid economical growth of the bird as a whole (O'Connor, 1977). In contrast, the bones of the wing increase in length at a rapid and relatively constant rate from the time of hatching to the attainment of adult size. If there is an advantage to be gained by postponing wing development (Ricklefs, 1973, 1979b; O'Connor, 1977, 1984; Carrier & Leon, 1990), why not delay bone growth as well? One possible explanation is that bones simply may require more time to grow than other tissues and so growth must be initiated earlier. If this were true, bone elongation would be the rate limiting factor in wing development.

If linear growth of bones does place minimum time requirements on wing development, birds with relatively long wings for their body size would take longer to fledge than birds with relatively short wings. Again, albatrosses provide a supporting example. They have the longest wings for their size and also have the longest fledging periods observed in birds. In this investigation, we address the hypothesis that bone growth is one of the factors that influences fledging time by comparing bone length and fledging period among 25 families of non-passerine birds and among species within six separate families.

MATERIALS AND METHODS

Specimens and measurements

Lengths of the humerus and ulna were measured from single individuals of 141 species from 25 families of non-passerine birds, and from single individuals of 11 species from the family Corvidae. Measurements were taken only from adult specimens, as indicated by complete ossification of articular surfaces. Estimates of the period from hatching to first flight and of adult body mass were gathered for each species from various compilations of these parameters in the ornithological literature (Appendix I). The species analysed were chosen on the basis of availability of skeletal material and references on fledging time. For most species, male specimens and estimates of male body mass were used. In a few cases, the lack of available specimens necessitated the use of female specimens and estimates of body mass.

Data analysis

To avoid taxonomic artifacts that could result from some families being represented by more species than other families, the primary analysis was done on mean values for each family. These were calculated by averaging body mass, fledging time and bone length values for species within each family.

The hypothesis predicts that birds with relatively long wing bones for their size will take longer to fledge than birds with shorter bones. This prediction was tested by removing the effect of body size and then comparing the relative length of the fledging period to the relative length of the wing bones (see Clutton-Brock & Harvey, 1984; Garland & Huey, 1987; Read & Harvey, 1989 for discussions of residual analysis). First, average values for body mass, bone length and fledging period were calculated for species within each family. The average values were log transformed and least-squares regressions were performed comparing fledging time against body mass and bone length against body mass. The vertical deviations (residuals) from the line of the regression were then calculated. A positive deviation from the line indicates that a particular family is characterized by species with long fledging periods or long bones for their body mass. The relative values (residuals) of fledging period were then regressed against those of bone length. If the hypothesis is false, relative fledging time will not be positively correlated with the relative bone length.

Data available from 16 families were analysed with multiple regression to provide an indication of the amount of variance in fledging time that can be accounted for by body size, by overall growth rate and by bone length. Average fledging time was the dependent variable, and average body mass, average rate of growth in body mass and average bone length were the independent variables. Values for rates of growth in body mass were taken from Ricklefs (1973). As in the previous analyses, regressions were run on log-transformed mean values for each family.

To examine the influence that different modes of flight have on the time to fledging, family means were again used to compare relative values of fledging time against relative values of three parameters of the wing that have a direct effect on flying ability (Greenewalt, 1975): mass of the pectoralis muscle, area of the wing and aspect ratio of the wing. Values for mass of the pectoralis muscle,

area of the wing and aspect ratio of the wing were taken from Hartman (1961), and are listed in Appendix II.

To assess whether or not a relationship exists within individual families, separate analyses were conducted on five families of non-passerines (Procellariidae, Phasianidae, Accipitridae, Laridae and Anatidae) and one family of Passeriformes (Corvidae, Appendix III). These families were chosen for analysis on the basis of availability of data. In these analyses, bone lengths and fledging periods of species within a particular family were regressed against body mass to obtain relative values (residuals). The relative values of fledging period were then regressed against those of bone length.

RESULTS

Morphometrics

Allometric equations for fledging period and wing size and shape are given in Table 1. Fledging period was poorly correlated with body mass, but did tend to increase with size, scaling to the 0.14 power of body mass. The length of the bones of the wing was strongly correlated with body mass. If birds were geometrically similar the lengths of their bones would scale to the 0.33 power of body mass, and the mass of their pectoralis muscle would scale to the 1.0 power of body mass. Hence, allometric coefficients of 0.52 for humerus and 0.51 for ulna length indicate that families composed of larger birds have relatively long wing bones. In contrast, the mass of the pectoralis muscle showed negative allometry, scaling to the 0.89 power of body mass. Similar results from other studies are summarized by Calder (1984).

The performance characteristics of a wing can be inferred from wing surface area and aspect ratio (length/width). Large wing area increases manoeuvrability and allows for slow flight. Wing shape affects drag and hence the power required for flight. Long narrow wings produce less drag than short broad ones. If birds were geometrically similar, wing area would scale to the 0.66 power of body mass and aspect ratio would be independent of size. The allometric coefficients (Table 1) show that wing area is relatively greater, on average, in families

TABLE 1. Least-squares regressions of the form $Y = aX^b$, where X represents the family means for body mass in grams (A) or bone length in centimetres (B), and Y represents the family means for fledging period and various aspects of the wings of non passerine birds. Standard errors are given for b

Y	N	a	b	r^2	P
A					
Fledging period (days)	25	21.264	0.144 ± 0.060	0.201	0.0245
Humerus length (cm)	25	0.266	0.523 ± 0.030	0.927	0.0001
Ulna length (cm)	25	0.322	0.509 ± 0.034	0.908	0.0001
Aspect ratio	25	1.941	0.051 ± 0.030	0.116	0.1000
Wing area (cm ²)	25	4.572	0.868 ± 0.049	0.933	0.0001
Pectoralis mass (g)	25	0.322	0.892 ± 0.034	0.968	0.0001
B					
Fledging period against humerus length	25	25.229	0.358 ± 0.099	0.364	0.001
Fledging period against ulna length	25	23.571	0.374 ± 0.009	0.383	0.001

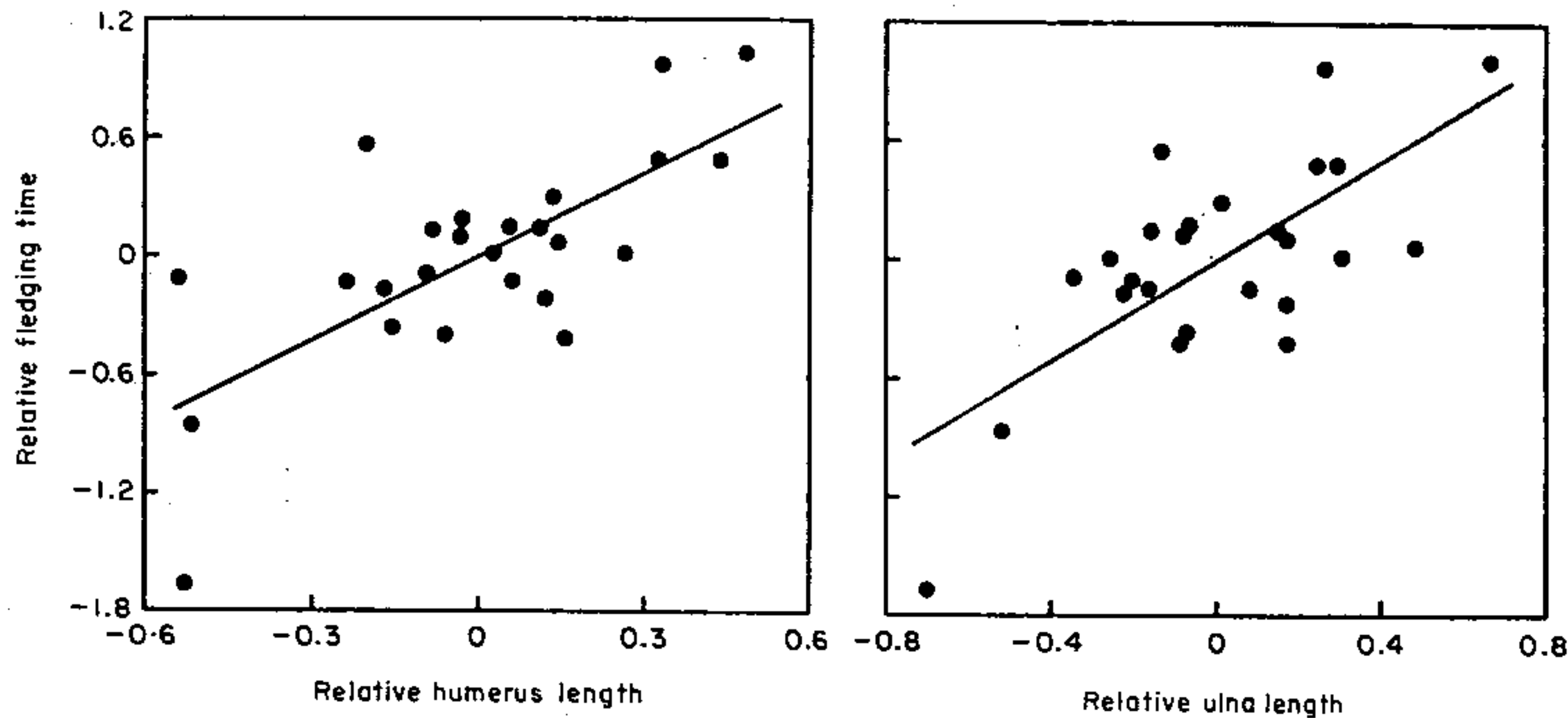


Figure 1. Body mass residuals of fledging period plotted against the body mass residuals of bone length for mean values of 25 families of non-passerine birds. In each graph, the outlier in the lower left hand corner represents Phasianidae. Equations of the plotted lines are listed in Table 2.

composed of larger birds, and that aspect ratio is independent of size. Similar scaling relationships have been reported by Greenewalt (1975).

Bone length and fledging time

Fledging period was positively related to the length of the wing bones (Table 1). However, the relationship actually improved once the effect of body size was removed (Table 2, Fig. 1). Thus, birds of families that have relatively long wing bones for their size tend to have relatively long fledging periods.

Species of the family Phasianidae are relatively precocial (Ricklefs, 1973) compared with those of the other families analysed in this investigation. They begin to fly long before their wing bones have reached adult lengths. Consequently, it may be inappropriate to include them in this analysis. However, when they were excluded the relationship did not change dramatically; relative fledging period was still positively correlated with relative bone length (Table 2).

Not only was fledging period positively correlated with bone length, but it showed a higher correlation with fledging time than did either body mass or rate

TABLE 2. Least-squares regressions of the relative values of fledging period vs the relative values of various aspects of the wing for families of non-passerine birds. Equations are of the form $Y = bX$, where Y is the relative value of fledging period. Standard errors are given for b

X	N	b	r^2	P
Humerus length	25	1.416 ± 0.288	0.511	0.0001
Ulna length	25	1.267 ± 0.262	0.504	0.0001
Humerus length without Phasianidae	24	1.078 ± 0.267	0.425	0.0006
Ulna length without Phasianidae	24	0.930 ± 0.265	0.359	0.0020
Aspect ratio	25	0.870 ± 0.325	0.238	0.013
Wing area	25	0.045 ± 0.226	0.002	0.842
Pectoralis mass	25	-0.153 ± 0.323	0.010	0.640

TABLE 3. Variance in fledging period among families of birds explained by multiple regressions of the form: (Fledging period) = $C + a$ (body mass) + b (growth rate) + c (humerus length). Values of the dependent and independent variables were log transformed family means. Values for overall rate of growth are from Ricklefs, 1973). Results are presented for the full data set ($N = 16$) which includes families having both altricial and precocial wing development and for those families having altricial wing development ($N = 15$)

	Altricial and precocial families		Altricial families	
	Variance	P	Variance	P
Model	0.864	< 0.0001	0.915	< 0.0001
Body mass	0.360	< 0.0001	0.198	0.0068
Growth rate	0.030	0.0497	0.512	0.0002
Humerus length	0.473	< 0.0001	0.204	0.0061

of growth of body mass (Table 3). Multiple regression of body mass, bone length and overall growth rate, for the 16 families from which we were able to amass data, provided a statistical explanation for 86% of the variance in fledging time. Of the 86%, bone length explained more of the variance than did body mass (47% vs 36%), and growth rate explained only a small fraction. Although this relationship appears to be robust, exclusion of the family Phasianidae had a dramatic effect. When the analysis was run without the Phasianidae ($N = 15$) the model changed such that overall growth rate explained more of the variance than did bone length (Table 3). However, even in this case, humerus length explained a significant 20% of the variance in fledging time. This reversal in relative importance of bone length and growth rate was not observed when families other than Phasianidae were excluded from the analysis.

In a separate analysis, of the 25 families for which we have data on bone length and fledging period, multiple regression of body mass and humerus length were found to account for 64% ($P < 0.001$) of the variance in fledging period. In this analysis, as well, bone length explained more of the variance in fledging time than did body mass (44% vs 20%, $P < 0.001$).

The correlation between length of wing bones and fledging period was also present within individual families (Table 4). Figure 2 plots relative fledging period against relative bone length for species of Phasianidae, Procellariidae, Laridae, Anatidae, Accipitridae and Corvidae. In four of the six families (i.e. Procellariidae, Phasianidae, Accipitridae and Corvidae) there was a significant

TABLE 4. Least-squares regressions of the relative values of fledging period relative values of bone length for individual species of six families of birds. Standard errors are given for b

X	N	b	r^2	P
Procellariidae. Humerus length	18	1.301 ± 0.384	0.419	0.004
Phasianidae. Humerus length	8	1.070 ± 0.235	0.774	0.004
Accipitridae. Ulna length	22	0.613 ± 0.170	0.394	0.002
Laridae. Humerus length	8	0.848 ± 0.429	0.394	0.096
Anatidae. Humerus length	40	-0.261 ± 0.260	0.026	0.322
Corvidae. Ulna length	11	1.022 ± 0.224	0.697	0.001

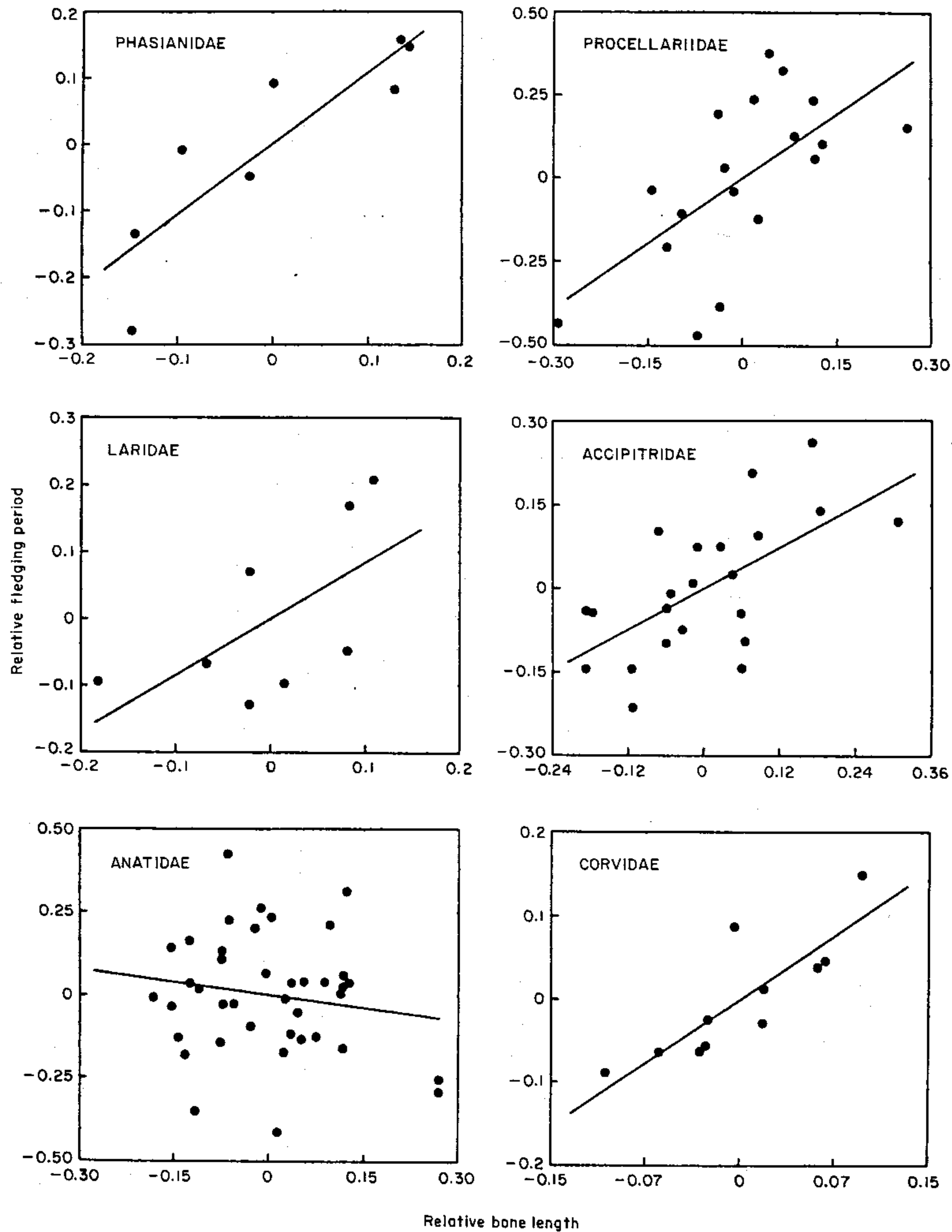


Figure 2. Body mass residuals of fledging period plotted against the body mass residuals of humerus length for species of Phasianidae, Procellariidae, Laridae and Anatidae, and against the body mass residuals of ulna length for species of Accipitridae and Corvidae. Equations of the plotted lines are listed in Table 4.

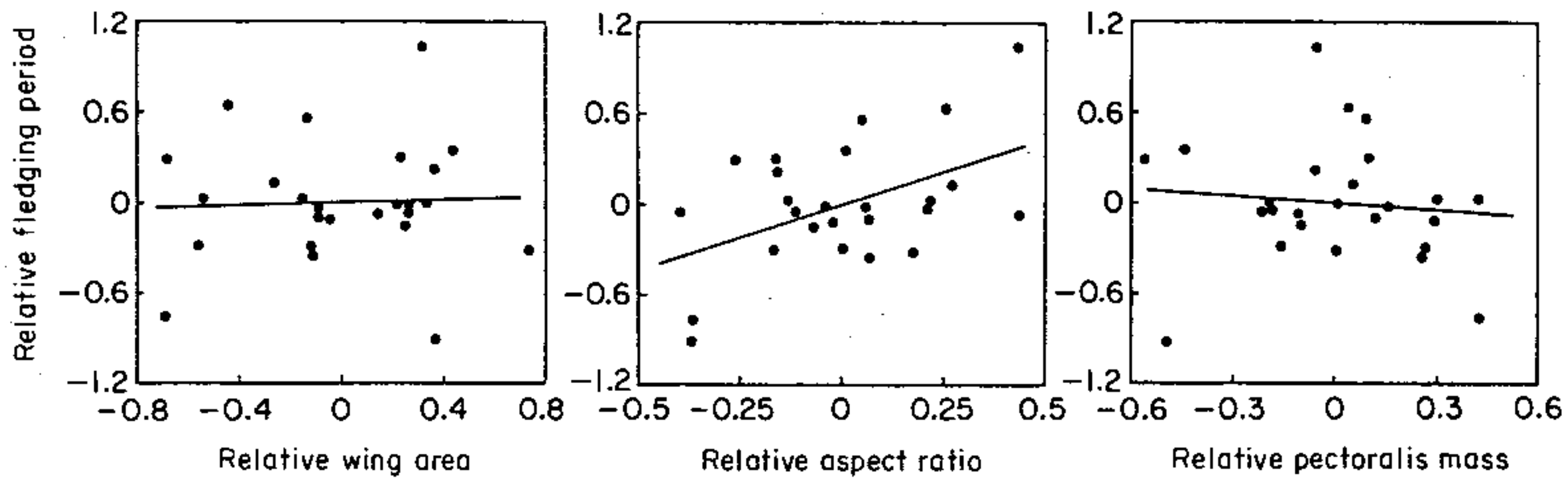


Figure 3. Body mass residuals of fledging period plotted against the body mass residuals of area of the wings, aspect ratio of the wings, and mass of the pectoralis muscle for mean values of 25 families of non-passerine birds. Equations of the plotted lines are listed in Table 2.

positive relationship between relative fledging period and relative bone length. A positive relationship was also found for Laridae, but it was not significant at the 0.05 level. The pattern displayed by species of the family Anatidae was not consistent with the hypothesis. The family as a group was not unusual, having fairly average residual values for humerus length (-0.083) and fledging time (-0.090). However, within the family, there was no correlation between relative bone length and relative fledging time.

Features of the wing other than bone length were not correlated or were weakly correlated with fledging period (Table 2, Fig. 3). The relative values of pectoralis mass and wing area varied independently of the relative values of fledging period. Those of aspect ratio showed a weak positive correlation with the relative values of fledging period.

DISCUSSION

Results of this analysis are consistent with the hypothesis that the rate of linear growth of wing bones limits the minimum fledging time of birds. Species with relatively long wing bones tend to have longer fledging periods than species with shorter bones. This pattern holds for comparisons of mean values from families, and for comparisons of species within individual families (with the exception of Anatidae). The hypothesis is further supported by the observation that when the full data set is considered bone length explains more of the variance in fledging period than does either body mass or rate of growth in body mass. Thus, we are left with the non-intuitive result that the time it takes young birds to fly appears to be influenced by the length of their wing bones.

A criticism of this analysis is that it assumes that the length of the fledging period is consistently related to the period required for bone growth. This assumption is not always valid. One has only to compare the Phasianidae with the Diomedidae to appreciate this (Ricklefs, 1973). Turkeys are capable of flight at two weeks, long before their wing bones have reached adult length. A similar sized albatross begins to fly at 37 weeks of age, after completion of wing bone growth. Thus, fledging period is not always related to the period required for bone growth. However, in most cases it is. Phasianidae are rather exceptional in their precocial flight (Fig. 1). Species of most families reach or closely approach adult size before they fly. This is true of all the other families analysed

here. To provide a comparison of families with more uniform modes of wing development, Phasianidae were excluded from the analysis. When this was done the relationship remained essentially unchanged (Table 2). Furthermore, the relationship holds for species within individual families. We expect the level of bone development at fledging to be relatively uniform within individual families. Consequently, a relationship between fledging period and bone length exists in spite of variation in the level of bone development at the time of fledging.

Analyses that rely heavily on correlation, as does this one, are never entirely satisfying. There is always the danger of attributing causation to the wrong variable. In this case, the most obvious factor that would make the observed correlation spurious is a relationship between mode of flight and the length of the fledging period. For instance, some modes of flight are likely to be more demanding of the locomotor system than others (e.g. soaring vs burst flapping) and could therefore require a longer period of developmental preparation. If fledging period was largely determined by the way a species flew, a spurious correlation with bone length might exist because the mode of flight is dependent on the shape and relative size of the wing. However, this analysis indicates that characters of the wing that influence flight performance, such as relative wing area and relative pectoralis mass, are not correlated with fledging time. Residuals of aspect ratio do exhibit a relatively weak correlation with residuals of fledging time. However, aspect ratio is largely determined by the length of the wing bones, so some level of correlation could be expected. The lack of correlation with pectoralis mass and wing area suggests that the way a species flies has little effect on its fledging time.

A second factor that might possibly lead to a spurious correlation between bone length and fledging time is overall rate of growth. The observed relationship might simply be a result of bone length being tightly correlated with overall rate of growth of the body. This analysis indicates the effect of overall growth rate is fairly complex. When the full data set is considered, overall growth rate explains only a very small proportion of the variance in fledging time. However, when the family Phasianidae is excluded from the analysis overall growth rate explains more of the variance than does either body mass or humerus length. (This result is consistent with the observations of Lack (1968) and O'Connor (1984), which show that—among altricial species, those that grow more rapidly tend to fledge sooner.) As mentioned above, Phasianidae is unique among the families analysed here because its members fledge while their wing bones are still experiencing significant growth (Ricklefs, 1973). Thus, the relationship appears to be sensitive to whether or not species with altricial and precocial wing development are considered together or separately. However, the important point is that even when only those families with altricial wing development are analysed bone length explains a significant 20% of the variance in fledging time. In other words, when the effect of overall growth rate is removed bone length still appears to play an important role in determining fledging period.

The family Anatidae is an exception to the general pattern. Within this family, fledging period is not correlated with bone length. Those species with relatively long wing bones do not have longer fledging periods. Why this is the case is not clear. However, there may be less selection for early fledging in Anatidae than in other groups. Young of Anatidae abandon their nest at an

early age and adopt an amphibious life style while they grow and mature. The relative high mobility of the young and their aquatic habitat may provide protection against predators.

Is bone growth rate limiting?

Clearly the rate of bone growth is not the only factor which influences the length of fledging periods. This analysis shows that there is substantial variation in fledging period that is not correlated with relative bone length. Other factors, such as those which influence overall growth rate (Lack, 1968; Ricklefs, 1979b; O'Connor, 1984), may ultimately be more important. Indeed, this analysis suggests that among families which experience altricial wing development overall growth rate does influence fledging time to a greater extent than does bone length. However, when the effect of overall growth rate is removed, bone length still is correlated with an important part of the variation in fledging time. This finding, combined with the observation that linear growth of the wing bones of gulls is initiated long before other aspects of wing growth, suggests that the rate at which bones increase in length does exert a strong influence on the minimum fledging time of birds.

Why bones should grow more slowly than other tissues is not immediately obvious. The growth of endochondral bones is a complicated process which involves multiplication, growth and degeneration of cartilage cells in the growth plate, vascularization of the degenerated cartilage, formation of a network of bone trabeculae on the cartilage framework by the ingrowing connective tissue cells, and finally, the remodelling and structural modification of this bony tissue (Sissons, 1971). Which processes limit the maximum rate of linear growth of endochondral bones is not known. Consequently, we are not yet able to identify the causal basis of the pattern observed in this analysis.

One aspect of avian biology which might explain why bone growth limits wing development is simply the amount of growth that does occur. When birds are compared with mammals, birds are found to have much longer humeri and ulnae (Table 5). This difference increases as body size increases, so that the larger species of birds (10–12 kg) have wing bones that are on average three times longer than those of equivalent sized mammals. No other group of extant vertebrates has limb bones that even begin to approach this relative length. Viewed from this perspective, it is not unreasonable to envision the exceptionally long fledging periods of species of albatross as time spent waiting for their bones to grow.

TABLE 5. Allometric equations of the length of the bones of the forelimb of mammals and the wing of birds. Units of length are cm and those of mass are g

<i>Mammals</i>		
Humerus	Length = $0.42 (\text{mass})^{0.36}$	Alexander <i>et al.</i> , 1979
	Length = $0.57 (\text{mass})^{0.31}$	Biewener, 1983
Ulna	Length = $0.52 (\text{mass})^{0.36}$	Alexander <i>et al.</i> , 1979
Radius	Length = $0.52 (\text{mass})^{0.32}$	Biewener, 1983
<i>Birds</i>		
Humerus	Length = $0.27 (\text{mass})^{0.52}$	This study
	Length = $0.42 (\text{mass})^{0.48}$	Prange <i>et al.</i> , 1979
Ulna	Length = $0.32 (\text{mass})^{0.51}$	This study

In summary, although other factors must also influence the length of fledging periods, bone growth does appear to play an important role in this aspect of avian biology. This suggestion is supported by several observations. First, in California gulls, the bones of the wing grow rapidly and continuously throughout the post-hatching growth period, while other aspects of wing do not undergo significant growth until shortly before fledging. Second, families and species that have relatively long bones for their size tend to have longer fledging periods than families and species with relatively short bones. Third, the relationship between bone length and fledging time remains strong when potentially confounding variables such as overall rate of growth or factors which influence style and performance of flight are considered. Thus, linear growth of bones does appear to limit the rate of wing growth, and does appear to play a significant role in determining fledging time. What it is about endochondral growth that is rate limiting for birds remains unclear.

ACKNOWLEDGEMENTS

We thank Enrique Lessa for guidance in the statistical analysis of the data and for critical discussions on this topic. We are also grateful to Clifford Baron, Sharon Emerson, Colleen Farmer, Carl Gans, Lisa Leon, Raymond O'Connor, John Olson, Robert Ricklefs and Marvilee Wake for discussions on this topic and/or helpful comments on the manuscript. Robert Storer and Ned Johnson provided access to skeletal material in the collections of the Museum of Natural History, University of Michigan and the Museum of Vertebrate Zoology, University of California, respectively.

REFERENCES

- ALEXANDER, R. McN., JAYES, A. S. MALOIJ, G. M. O. & WATHUTA, E. M., 1979. Allometry of the limb bones of mammals from shrews (*Sorex*) to elephants (*Loxodonta*). *Journal of Zoology (London)*, 189: 305-314.
- BIEWENER, A. A., 1983. Allometry of quadrupedal locomotion: the scaling of duty factor, bone curvature and limb orientation to body size. *Journal of Experimental Biology*, 105: 147-171.
- BROWN, L. & AMADON, D., 1968. *Eagles, Hawks and Falcons of the World*. Feltham: Hamlyn Publishing Group.
- BROWN, L. H., URBAN, E. K. & NEWMAN, K., 1982. *The Birds of Africa. Vol. I*. London: Academic Press.
- CLADER, W. A., 1984. *Size, Function and Life History*. Cambridge: Harvard University Press.
- CARRIER, D. R. & LEON, L. R., 1990. Skeletal growth and function in the California gull. *Journal of Zoology (London)*, 222: 375-389.
- CLUTTON-BROCK, T. H. & HARVEY, P. H., 1984. Comparative approaches to investigating adaptation. In J. R. Krebs & N. B. Davies (Eds), *Behavioral Ecology: an Evolutionary Approach*, 2nd edition: 7-29. Oxford: Blackwell.
- CRAMP, S., 1980. *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palaearctic*. London: Oxford University Press.
- EHRlich, P. R. & DOBKIN, D. S., 1988. *The Birder's Handbook*. New York: Simon and Schuster Inc.
- GARLAND, T., JR. & HUEY, R. B., 1987. Testing symmorphosis: does structure match functional requirements? *Evolution*, 41: 1404-1409.
- GREENEWALT, C. H., 1975. The flight of birds. *Transactions of the American Philosophical Society*, 65: 1-67.
- GROSS, W. A. O., 1935. The life history cycle of Leach's Petrel (*Oceanodroma leucorhoa leucorhoa*) on the outer sea islands of the Bay of Fundy. *Auk*, 52: 382-399.
- HARRISON, C., 1978. *A Field Guide to the Nestlings of North American Birds*. New York: Collins.
- HARTMAN, F. A., 1961. Locomotor mechanisms of birds. *Smithsonian Miscellaneous Collection*, 143: 1-91.
- HEWITT, O. R., 1967. *The Wild Turkey and Its Management*. Washington: The Wildlife Society.
- HOFFMEISTER, D. F. & SELTZER, H. W., 1947. The postnatal development of two broods of Great Horned Owls (*Bubo virginianus*). *University of Kansas Publications, Museum of Natural History*, 1: 157-173.
- JOHNSGARD, P. A., 1975. *Waterfowl of North America*. Bloomington, Indiana University Press.

- JOHNSGARD, P. A., 1978. *Ducks, Geese and Swans of the World*. Lincoln: University of Nebraska Press.
- LACK, D., 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen and Co. Ltd.
- LINDSEY, J. R., 1986. *The Seabirds of Australia*. London, Angus and Robertson Publishers.
- MILBY, T. T. & HENDERSON, E. W., 1937. The comparative growth rates of turkey, ducks, geese and pheasants. *Poultry Science*, 16: 166-165.
- NELSON, J. B., 1964. Factors influencing clutch-size and chick growth in the North Atlantic Gannet *Sula bassana*. *Ibis*, 106: 63-77.
- O'CONNOR, R. J., 1977. Differential growth and body composition in altricial passerines. *Ibis*, 119: 147-166.
- O'CONNOR, R. J., 1984. *The Growth and Development of Birds*. Chichester: John Wiley & Sons.
- PALMER, R. S., 1962. *Handbook of North American Birds*. New Haven: Yale University Press.
- PRANGE, H. D., ANDERSON, J. F. & RAHN, H., 1979. Scaling of skeletal mass to body mass in birds and mammals. *American Naturalist*, 113: 103-122.
- RAHN, H., ACKERMAN, R. A. & PAGANELLI, C. V., 1984. Eggs, yolk and embryonic growth rate. In G. Causey Whittow & H. Rahn (Eds), *Seabird Energetics*. New York: Plenum Press.
- READ, A. F. & HARVEY, P. H., 1989. Life history differences among the eutherian radiations. *Journal of Zoology (London)*, 219: 329-353.
- RICE, D. W. & KENYON, K. W., 1962. Breeding cycles and behavior of Laysan and Black-footed Albatrosses. *Auk*, 79: 517-567.
- RICKLEFS, R. E., 1973. Patterns of growth in birds. II. Growth rate and mode of development. *Ibis*, 115: 177-201.
- RICKLEFS, R. E., 1979a. Patterns of growth in birds V: A comparative study of development in the Starling, Common Tern and Japanese Quail. *Auk*, 96: 10-30.
- RICKLEFS, R. E., 1979b. Adaptation, constraint, and compromise in avian postnatal development. *Biological Review*, 54: 269-290.
- RITTER, L. V., 1983. Growth, development and behavior of nestling Turkey Vultures in central California. In S. R. Wilbur & J. A. Jackson (Eds), *Vulture Biology and Management*. Berkeley: University of California Press.
- ROEST, A. I., 1957. Notes on the American Sparrow Hawk. *Auk*, 74: 1-19.
- RUTGERS, A. & NORRIS, K. A., 1970. *Encyclopedia of Aviculture. Vol. 1*. London: Blandford Press.
- RUTTER, R. J., 1969. A contribution to the biology of the Grey Jay (*Perisoreus canadensis*). *Canadian Field Naturalist*, 83: 300-316.
- SISSIONS, H. A., 1971. The growth of bone. In G. H. Bourne (Ed.), *The Biochemistry and Physiology of Bone*. New York: Academic Press.
- SMITH, J. E. & DIEM, K. L., 1972. Growth and development of young California Gulls (*Larus californicus*). *Condor*, 74: 462-470.
- TERRES, J. K., 1980. *The Audubon Society Encyclopedia of North American Birds*. New York: Alfred A. Knopf.
- TICKELL, W. L. N., 1968. The biology of the great albatrosses, *Diomedea exulans* and *Diomedea epomophora*. In O. L. Austin (Ed.), *Antarctic Research Series No. 12*. American Geographical Union.
- WATSON, A., 1957. The behavior, breeding, and food-ecology of the Snowy Owl *Nyctea scandiaca*. *Ibis*, 99: 419-462.

APPENDIX I

	Body mass (g)	Humerus length (cm)	Ulna length (cm)	Fledging period (days)	Reference
Family Picipedidae					
<i>Podiceps auritus</i>	458	7.8	6.9	58	Cramp, 1980
<i>Podiceps grisegena</i>	1113	10.6	9.6	72	Cramp, 1980
Family Diomedidae					
<i>Diomedea nigripes</i>	3200	27.5	28.4	140	Rice & Kenyon, 1962
<i>Diomedea epomophora</i>	8290	42.0	42.2	236	Tickell, 1968
<i>Diomedea exulans</i>	8700	40.6	41.2	278	Tickell, 1968
<i>Diomedea immutabilis</i>	2450	26.1	25.3	165	Rice & Kenyon, 1962
<i>Phoebastria palpebrata</i>	3000	25.3	25.6	140	Rahn <i>et al.</i> , 1984
Family Procellariidae					
<i>Pterodroma brevirostris</i>	330	8.3	8.6	60	Rahn <i>et al.</i> , 1984
<i>Pterodroma lessonii</i>	590	10.8	10.9	105	Rahn <i>et al.</i> , 1984
<i>Pterodroma inexpectata</i>	316	8.3	8.4	98	Rahn <i>et al.</i> , 1984
<i>Halobaena caerulea</i>	180	6.3	6.1	58	Rahn <i>et al.</i> , 1984
<i>Pachyptila vittata</i>	196	6.0	5.9	55	Rahn <i>et al.</i> , 1984

APPENDIX I—continued

	Body mass (g)	Humerus length (cm)	Ulna length (cm)	Fledging period (days)	Reference
<i>Pachyptila desolata</i>	200	5.9	5.6	50	Rahn <i>et al.</i> , 1984
<i>Bulweria bulwerii</i>	92	6.4	6.3	62	Rahn <i>et al.</i> , 1984
<i>Procellaria aequinoctialis</i>	1130	14.8	14.5	95	Rahn <i>et al.</i> , 1984
<i>Calonectris diomedea</i>	890	12.9	13.0	93	Rahn <i>et al.</i> , 1984
<i>Puffinus gravis</i>	880	11.5	11.1	84	Terres, 1980
<i>Puffinus tenuirostris</i>	530	9.9	9.4	94	Palmer, 1962
<i>Puffinus puffinus</i>	478	8.1	7.6	70	Rahn <i>et al.</i> , 1984
<i>Puffinus lherminieri</i>	130	6.3	6.0	72	Rahn <i>et al.</i> , 1984
<i>Puffinus griseus</i>	787	10.9		97	Palmer, 1962
<i>Macronectes giganteus</i>	4600	25.2	24.3	119	Rahn <i>et al.</i> , 1984
<i>Fulmarus glacialis</i>	780	10.5	10.0	50	Rahn <i>et al.</i> , 1984
<i>Daption capense</i>	450	8.8	8.5	49	Rahn <i>et al.</i> , 1984
<i>Pagodroma nivea</i>	425	6.6	6.1	46	Rahn <i>et al.</i> , 1984
Family Hydrobatidae					
<i>Oceanodroma leucorhoe</i>	44	3.4	3.4	67	Gross, 1935
<i>Oceanites oceanicus</i>	34	2.3	2.2	52	Lindsey, 1986
Family Sulidae					
<i>Morus bassanus</i>	3000	22.5	19.4	90	Nelson, 1964
<i>Sula leucogaster</i>	1310	15.7	17.2	98	Ricklefs, 1973
<i>Sula dactylatra</i>	1900	18.3	19.6	122	Ricklefs, 1973
<i>Sula sula</i>	715	16.2	17.4	100	Palmer, 1962
Family Phalacrocoracidae					
<i>Phalacrocorax auritus</i>	1900	14.3	15.2	42	Palmer, 1962
<i>Phalacrocorax pelagicus</i>	2041	12.3	12.9	45	Terres, 1980
Family Pelecanidae					
<i>Pelecanus occidentalis</i>	4200	24.2	36.5	76	Ricklefs, 1973
Family Fregatidae					
<i>Fregata magnificens</i>	1340	18.7	24.7	154	Cramp, 1980
<i>Fregata minor</i>	1300	18.4	24.0	180	Ricklefs, 1973
Family Anatidae					
<i>Aythya collaris</i>	725	7.8	6.5	52	Johnsgard, 1975
<i>Aythya valisineria</i>	1268	9.4	7.8	62	Johnsgard, 1975
<i>Aythya affinis</i>	861	7.9	6.6	49	Johnsgard, 1975
<i>Aythya americana</i>	1133	9.4	7.9	65	Johnsgard, 1975
<i>Aythya marila</i>	997	8.8	7.3	47	Johnsgard, 1978
<i>Branta canadensis</i>	1268	13.3	12.3	42	Johnsgard, 1975
<i>Branta bernicla</i>	1825	12.3	11.1	49	Johnsgard, 1978
<i>Anser caerulescens</i>	2744	14.6	13.8	42	Johnsgard, 1975
<i>Anser rossi</i>	1315	13.5	12.8	41	Johnsgard, 1975
<i>Anser canagicus</i>	2766	13.4	12.5	55	Johnsgard, 1978
<i>Anser indicus</i>	2500	15.6	14.5	53	Johnsgard, 1978
<i>Cygnus columbianus</i>	7100	25.0	24.5	78	Johnsgard, 1975
<i>Cygnus cygnus</i>	11900	27.8	26.7	110	Johnsgard, 1978
<i>Cygnus buccinator</i>	9400	28.6	27.1	110	Johnsgard, 1975
<i>Aix sponsa</i>	680	7.2	5.6	60	Johnsgard, 1975
<i>Anas acuta</i>	997	9.4	8.1	46	Johnsgard, 1975
<i>Anas americana</i>	770	8.4	6.8	51	Johnsgard, 1975
<i>Anas clypeata</i>	634	7.7	6.3	45	Johnsgard, 1975
<i>Anas discors</i>	408	6.2	5.2	43	Johnsgard, 1975
<i>Anas platyrhynchos</i>	1361	9.4	7.6	56	Johnsgard, 1975
<i>Anas rubripes</i>	1244	8.9	7.1	56	Johnsgard, 1975
<i>Anas strepera</i>	730	8.8	7.2	49	Johnsgard, 1975
<i>Anas crecca</i>	356	6.2	5.2	44	Harrison, 1978
<i>Anas flavirostris</i>	450	7.2	6.2	46	Johnsgard, 1978
<i>Anas gibberifrons</i>	507	7.4	6.1	56	Johnsgard, 1978
<i>Anas querquedula</i>	391	6.4	5.2	38	Johnsgard, 1978

APPENDIX I—continued

	Body mass (g)	Humerus length (cm)	Ulna length (cm)	Fledging period (days)	Reference
<i>Anas rhynchotis</i>	614	7.7	6.4	49	Johnsgard, 1978
<i>Bucephala clangula</i>	997	8.0	6.6	61	Johnsgard, 1975
<i>Clangula hyemalis</i>	815	7.4	6.2	35	Johnsgard, 1975
<i>Histrionicus histrionicus</i>	670	6.7	5.4	40	Johnsgard, 1975
<i>Melanitta nigra</i>	1087	10.0	8.6	46	Johnsgard, 1975
<i>Mergus merganser</i>	1522	9.5	7.6	65	Johnsgard, 1975
<i>Mergus serrator</i>	1133	9.0	7.0	59	Johnsgard, 1975
<i>Mergus cucullatus</i>	540	6.4	5.0	70	Johnsgard, 1978
<i>Oxyura jamaicensis</i>	589	7.2	5.8	59	Johnsgard, 1975
<i>Somateria fischeri</i>	1647	9.9	8.4	50	Johnsgard, 1975
<i>Somateria mollissima</i>	2500	11.9	10.0	60	Johnsgard, 1975
<i>Cereopsis novaehollandiae</i>	5290	18.4	17.4	70	Johnsgard, 1978
<i>Polysticta stelleri</i>	860	7.1	5.9	50	Johnsgard, 1978
<i>Tadorna tadorna</i>	1559	12.5	11.0	60	Johnsgard, 1978
Family Cathartidae					
<i>Gymnogyps californianus</i>	9500	26.7	31.2	165	Palmer, 1962
<i>Vultur gryphus</i>	12000	28.7	31.5	180	Brown & Amadon 1968
<i>Cathartes aura</i>	1600	15.1	18.3	60	Ritter, 1983
Family Accipitridae					
<i>Aegypius monachus</i>	12000	24.6	33.2	120	Cramp, 1980
<i>Aquila heliaca</i>	3900	19.6	23.1	70	Brown <i>et al.</i> , 1982
<i>Aquila chrysaetos</i>	400	19.3	22.5	75	Brown <i>et al.</i> , 1982
<i>Gypaetus barbatus</i>	6150	23.9	27.5	110	Cramp, 1980
<i>Gyps fulvus</i>	10500	26.2	32.7	115	Brown <i>et al.</i> , 1982
<i>Haliaeetus leucocephalus</i>	5350	21.8	24.9	75	Palmer, 1962
<i>Haliaeetus albicilla</i>	5572	22.8	26.4	75	Cramp, 1980
<i>Torgos tracheliotus</i>	6800	24.2	34.1	126	Cramp, 1980
<i>Buteo lagopus</i>	1100	11.8	13.3	41	Cramp, 1980
<i>Buteo buteo</i>	720	9.8	10.8	41	Brown & Amadon, 1968
<i>Buteo jamaicensis</i>	1028	10.7	12.1	45	Brown & Amadon, 1968
<i>Buteo lineatus</i>	550	8.7	9.5	39	Brown & Amadon, 1968
<i>Buteo platypterus</i>	420	7.4	8.4	41	Brown & Amadon, 1968
<i>Accipiter cooperii</i>	308	6.5	6.7	32	Brown & Amadon, 1967
<i>Accipiter gentilis</i>	860	9.5	9.9	45	Brown & Amadon, 1968
<i>Accipiter striatus</i>	102	4.2	4.9	23	Brown & Amadon, 1968
<i>Accipiter nisus</i>	140	5.1	5.8	26	Brown & Amadon, 1968
<i>Circus cyaneus</i>	357	7.8	8.9	36	Brown & Amadon, 1968
<i>Elanus leucurus</i>	274	8.2	9.7	37	Brown & Amadon, 1968
<i>Ictinia mississippiensis</i>	243	7.1	7.9	34	Brown & Amadon, 1968
<i>Milvus migrans</i>	429	11.0	12.4	42	Brown & Amadon, 1968
<i>Butastur indicus</i>	407	8.6	9.4	35	Brown & Amadon, 1968
Family Sagittariidae					
<i>Sagittarius serpentarius</i>	3809	19.3	20.1	84	Brown & Amadon, 1968
Family Falconidae					
<i>Falco peregrinus</i>	706	8.3	10.5	39	Terres, 1980
<i>Falco rusticolus</i>	1614	10.3	12.0	48	Terres, 1980
<i>Falco sparverius</i>	112	4.1	4.7	31	Roest, 1957
Family Phoenicopteridae					
<i>Phoeniconaias minor</i>	1900	15.4	17.5	73	Brown <i>et al.</i> , 1982
Family Ardeidae					
<i>Ardea herodias</i>	2948	19.6	24.0	60	Harrison, 1978
<i>Nycticorax nycticorax</i>	908	11.8	12.0	42	Terres, 1980
Family Ciconiidae					
<i>Mycteria americana</i>	4536	17.2	22.1	55	Harrison, 1978
<i>Leptoptilos crumeniferus</i>	5000	26.1	35.2	105	Brown <i>et al.</i> , 1982

APPENDIX I—continued

	Body mass (g)	Humerus length (cm)	Ulna length (cm)	Fledging period (days)	Reference
Family Phasianidae					
<i>Dendragapus obscurus</i>	1194	6.6	7.0	10	Terres, 1980
<i>Centrocercus urophasianus</i>	1927	10.8	10.5	14	Terres, 1980
<i>Alectoris graeca</i>	600	4.9	4.7	8	Cramp, 1980
<i>Pavo cristatus</i>	3430	13.6	12.5	14	Rutgers & Norris, 1970
<i>Phasianus colchicus</i>	1295	7.7	6.2	11	Milby & Henderson, 1937
<i>Meleagris gallopavo</i>	7400	15.1	12.8	14	Hewitt, 1967
<i>Lagopus lagopus</i>	459	5.8	5.6	12	Harrison, 1978
<i>Lophortyx californica</i>	168	3.3	2.9	10	Harrison, 1978
Family Gruidae					
<i>Grus grus</i>	5500	22.1	24.9	68	Cramp, 1980
<i>Grus canadensis</i>	4376	23.2	21.0	70	Harrison, 1978
<i>Grus americana</i>	7300		27.0	115	Harrison, 1978
Family Otidae					
<i>Otis tarda</i>	12000	21.6	22.9	35	Cramp, 1980
Family Laridae					
<i>Larus glaucescens</i>	1800	12.9	14.5	42	Rahn <i>et al.</i> , 1984
<i>Larus hyperboreus</i>	1400	14.3	15.1	40	Rahn <i>et al.</i> , 1984
<i>Larus occidentalis</i>	900	13.4	14.6	50	Rahn <i>et al.</i> , 1984
<i>Larus argentatus</i>	1054	13.8	15.6	40	Ricklefs, 1973
<i>Larus californicus</i>	615	11.4	12.8	45	Smith & Diem, 1972
<i>Sterna albifrons</i>	40	3.8	4.3	25	Rahn <i>et al.</i> , 1984
<i>Hydroprogne caspia</i>	767	10.6	12.1	37	Rahn <i>et al.</i> , 1984
<i>Chlidonias nigra</i>	46	4.0	4.8	21	Rahn <i>et al.</i> , 1984
Family Gaviidae					
<i>Gavia arctica</i>	2050	15.1	12.3	60	Palmer, 1962
<i>Gavia immer</i>	3500	19.6	16.0	77	Palmer, 1962
Family Strigidae					
<i>Bubo virginianus</i>	1435	13.1	15.2	70	Hoffmeister & Selter, 1947
<i>Aegolius acadicus</i>	91	4.2	5.0	30	Terres, 1980
<i>Strix nebulosa</i>	985	13.2	14.1	65	Cramp, 1980
<i>Micrathene whitneyi</i>	45	3.0	3.8	30	Terres, 1980
<i>Nyctea scandiaca</i>	1650	14.3	15.9	50	Watson, 1957
Family Tytonidae					
<i>Tyto alba</i>	570	9.6	11.1	54	Terres, 1980
Family Apodidae					
<i>Chaetura pelagica</i>	23	0.8	1.3	30	Terres, 1980
Family Trochilidae					
<i>Calypte anna</i>	4	0.4	0.45	20	Terres, 1980
<i>Calypte costae</i>	3	0.4	0.46	22	Terres, 1980

APPENDIX II

	Body mass (g)	Fledging period (days)	Wing area (cm ²)	Aspect ratio (l/w)	Pectoral mass (g)
Pelecanidae					
<i>Pelecanus occidentalis</i>	3702	76	4405	3.89	518
Phalacrocoracidae					
<i>Phalacrocorax auritus</i>	1808	42	1754	2.86	221
Fregatidae					
<i>Fregata magnificens</i>	1667	154	3920	4.38	228

APPENDIX II—continued

	Body mass (g)	Fledging period (days)	Wing area (cm ²)	Aspect ratio (l/w)	Pectoral mass (g)
Ardeidae					
<i>Ardea herodias</i>	2576	60	5306	2.63	358
<i>Butorides virescens</i>	211	23	601	2.34	30
<i>Florida caerulea</i>	375	30	1106	2.60	53
<i>Bubulcus ibis</i>	295	40	900	2.69	48
<i>Casmerodius albus</i>	935	42	2637	2.60	127
<i>Nycticorax nycticorax</i>	725	42	1760	2.49	104
Ciconiidae					
<i>Mycteria americana</i>	2704	55	4161	2.85	497
Threskiornithidae					
<i>Eudocimus albus</i>	908	35	1498	2.33	183
Anatidae					
<i>Anas acuta</i>	675	45	763	3.37	164
Cathartidae					
<i>Coragyps atratus</i>	2065	70	3283	2.20	330
<i>Cathartes aura</i>	1426	80	4239	2.65	225
Accipitridae					
<i>Elanoides forficatus</i>	445	42	1210	3.37	62
<i>Accipiter striatus</i>	171	23	597	2.18	38
<i>Buteo lineatus</i>	475	42	1491	2.24	54
<i>Buteo platypterus</i>	360	41	969	2.28	50
Pandionidae					
<i>Pandion haliaetus</i>	1530	53	3305	3.00	225
Falconidae					
<i>Falco peregrinus</i>	825	42	1394	3.06	158
<i>Falco sparverius</i>	86	31	299	2.63	13
Phasianidae					
<i>Colinus floridanus</i>	150	14	178	1.74	43
Rallidae					
<i>Fulica americana</i>	562	56	562	2.07	52
Charadriidae					
<i>Charadrius vociferus</i>	81	25	270	3.00	19
Scolopacidae					
<i>Actitis macularia</i>	29	16	109	2.51	6
<i>Capella gallinago</i>	99	18	193	2.63	28
Laridae					
<i>Larus argentatus</i>	907	49	1914	3.53	144
<i>Sterna hirunda</i>	115	28	424	4.48	18
<i>Thalasseus maximus</i>	475	35	978	4.69	68
<i>Thalasseus sandvicensis</i>	330	35	980	3.72	42
Columbidae					
<i>Columba livia</i>	307	37	568	2.28	72
Psittacidae					
<i>Melopsitticus undulatus</i>	33	36	83	2.44	8
Cuculidae					
<i>Crotophaga sulcirostris</i>	73	10	273	1.67	9
Tytonidae					
<i>Tyto alba</i>	439	56	1392	2.68	47
Strigidae					
<i>Strix varia</i>	718	42	1788	1.83	92

APPENDIX II—continued

	Body mass (g)	Fledging period (days)	Wing area (cm ²)	Aspect ratio (l/w)	Pectoral mass (g)
Caprimulgidae					
<i>Chordeiles minor</i>	60	21	336	3.26	12
<i>Caprimulgus carolinensis</i>	110	17	564	2.56	22
Trochilidae					
<i>Archilochus colubris</i>	3.4	22	8.5	2.67	1
Alcedinidae					
<i>Megasceryle torquata</i>	317	35	624	2.33	49
<i>Chloroceryle americana</i>	37	26	123	2.19	6
Picidae					
<i>Melanerpes formicivorus</i>	79	32	291	2.07	15

APPENDIX III

	Body mass (g)	Humerus length (cm)	Ulna length (cm)	Fledging period (days)	Reference
Family Corvidae					
<i>Corvus bennetti</i>	539	6.3	7.2	31	Ehrlich, 1988
<i>Corvus cryptoleucus</i>	567	7.4	8.8	36	Ehrlich, 1988
<i>Corvus corax</i>	907	9.3	10.8	41	Ehrlich, 1988
<i>Aphelocoma coerulescens</i>	68	2.9	3.1	18	Ehrlich, 1988
<i>Aphelocoma ultramarina</i>	99	3.8	4.2	24	Ehrlich, 1988
<i>Cyanocitta cristata</i>	92	3.2	3.5	19	Ehrlich, 1988
<i>Cyanocorax morio</i>	272	4.9	5.6	26	Ehrlich, 1988
<i>Gymnorhinus cyanocephala</i>	101	3.4	3.9	21	Ehrlich, 1988
<i>Nucifraga columbiana</i>	150	3.8	4.4	22	Ehrlich, 1988
<i>Perisoreus canadensis</i>	68	3.0	3.2	18	Rutter, 1969
<i>Pica pica</i>	184	4.4	5.0	27	Ehrlich, 1988