MULTIVARIATE ANALYSIS OF AVIAN AND NON-AVIAN THEROPOD PEDAL PHALANGES

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Earth Science

MONTANA STATE UNIVERSITY
Bozeman, Montana

May 2008

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of a thesis submitted by

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citation, bibliographic style, and consistency, and is ready for submission to the Division of Graduate Education.

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May 2008

ACKNOWLEDGEMENTS

Firstly, I would like to thank my committee, David Varricchio, Robert Boik, and Jack Horner. I would also like to thank James Farlow, John Merck, Jay Rotella, Jack Fisher, Mike Habib, and other SVP members for helpful discussion regarding this project.

Thanks to James Dean at the Smithsonian for providing a missing measurement as well as other help during my NMNH visit.

This project could not have been completed without the help of the staff and use of the collections at the National Museum of Natural History, the American Museum of Natural History, the Museum of the Rockies, and Montana State University.

Thanks to the American Museum of Natural History for providing a Collections Study Grant which funded a portion of this research.

I would like to thank MSU graduate and undergraduate students both present and past for support, discussion, and encouragement throughout this research.

Finally, I would like to thank my family and friends for support throughout my academic career.

TABLE OF CONTENTS

LIST OF TABLES

Table Page

LIST OF FIGURES

Figure Page

ABSTRACT

`The relationship between morphology and behavior in theropods was examined using multivariate analyses performed on a set of linear measurements of pedal non-ungual phalanges in a sample of 132 extant and 13 extinct taxa. Principal component analysis reveals that modern birds with terrestrial lifestyles tend to cluster away from those with raptorial and non-predatory grasping lifestyles although the division is not clean. Most non-avian dinosaurs tend to cluster with terrestrial species although *Deinonychus* and some Tyrannosaurids cluster with raptorial taxa. Terrestrial taxa tend to have phalanges that are comparatively shorter distally, are relatively wide, and have shallow grooving of the distal trochleae, while grasping taxa show opposing trends. Predatory graspers have proportionately wider phalanges than non-predatory graspers.

Discriminant function analysis performs well in distinguishing among species with specialized behavior while taxa with less stereotyped behaviors are harder to classify. Predatory graspers are easily separated from non-predatory graspers. *Troodon* and *Elmisaurus* are grouped with terrestrial/cursorial taxa. *Tyrannosaurus*, *Allosaurus*, *Daspletosaurus*, and *Albertosaurus* are identified as terrestrial/cursorial with some possible predatory grasping ability. *Deinonychus* and *Bambiraptor* appear to have more grasping ability than *Troodon*.

INTRODUCTION

Theropod dinosaurs are a diverse group that includes the classic large-bodied predaors *Tyrannosaurus* and *Allosaurus*, the unusual Oviraptors and Therizinosaurs, the ancestors of modern birds, and modern birds themselves. Although recent strides have been made, many unanswered questions remain regarding the locomotor behavior of extinct members of the group. There are a variety of ways to approach locomotion in extinct taxa. Previous studies range from detailed analyses of footprints (e.g. Padian and Olsen, 1998; Breithaupt et al., 2001; Farlow, 2001; Day et al., 2002) to studies that use anatomical study of extant avian species to understand soft-tissue effects on locomotion (e.g. Vanden Berge, 1970; Cracraft, 1971; Patak and Baldwin, 1998; Hutchinson and Gatesy, 2000). Locomotor behavior is a contentious issue. Although large theropods led a terrestrial (Farlow et al., 2000) and possibly cursorial (Carrano, 1999) lifestyle, locomotor habits of smaller theropods are less clear. For instance, Manning et al. (2006) recently proposed that dromaeosaurs used their enlarged 2nd ungual to scale and hold onto prey, rather than the traditional hypothesis of using it to slash prey (Ostrom, 1969). There is also debate concerning the origins of avian flight and whether theropods closely related to birds were terrestrial and cursorial (Chiappe, 1997; Padian and Chiappe, 1998), arboreal, or scansorial (Xu et al., 2000; Zhang et al., 2002). One route to answering these questions lies in analysis of the hindlimb of modern birds and non-avian theropods. Morphological adaptations for grasping in non-avian theropods and early birds could be evidence for climbing behavior and lend support to the arboreal origin of flight while adaptations for cursorial behavior could be evidence for the terrestrial origin of flight.

Many anatomical studies of theropod locomotion have focused on the pelvis and the long bones of the hindlimb. For instance, Mattison (1998) collected data on both in order to differentiate among lifestyles in four categories: birds of prey, waterbirds, ground birds, and stalker-wader birds. She divided the initial four categories into subgroups based on behavioral differences and showed that some pelvic and hindlimb measurements separated both the subgroups and the original four lifestyle categories effectively.

Gatesy (1991) measured lengths and diameters of the femur, tibiotarsus, and tarsometatarsus of birds and non-avian theropods. He concluded that differences in hindlimb scaling between birds and non-avian theropods suggest that non-avian theropods held the femur in a more columnar position than modern birds. He also concluded that using limb ratios to compare locomotor styles in non-avian theropods to those in modern birds is tenuous due to this postural difference. Gatesy and Middleton (1997) found that non-avian theropods in comparison to birds show far less variation in hind limb proportions. They argued that functional constraints governed the variation that could evolve in the non-avian theropod hindlimb.

Studies of the osteology of the pes of both modern birds and non-avian theropods as related to locomotion are rare. One reason may be that the myology of the digits in non-avian theropods is difficult to reconstruct (Carrano and Hutchinson, 2002). McGowan (1979) found that only ¼ of muscle insertions and origins in the hindlimb were identifiable on the bones of *Apteryx* and that size of the muscle scar had almost no correlation with muscle size. Raikow (1985) provided a comprehensive classification of

the foot types of modern birds and he related this classification scheme to behavior. However, these classifications were based primarily on tendon arrangement and orientation of the digits. Digit orientation does not vary in non-avian theropods in the same patterns as Raikow (1985) described and tendon arrangements cannot currently be reconstructed. Thus, this classification scheme does not aid in inferring non-avian theropod behavior. Digit orientation techniques could be applied to fossil birds, but tendon arrangements would require soft-tissue preservation.

Fisher (1946) was one of the earliest authors to remark upon the correlation between digital lengths and behavior. He measured average phalangeal lengths of digits I-IV in a variety of vultures as well as the domestic chicken, osprey, and an eagle. He noted three important trends. One is that "Variation in the length of the digits is due for the most part to variation in the distal phalanges, but not always including the ungual phalanx or claw." The second trend he noted was grooving of the trochleae of the tarsometatarsus is associated with raptorial and perching birds. The final trend he noted is that "Relative lengths of the phalanges composing any single digit are reliable indices of the modification of that digit. For example, perching birds as a rule have reduced basal phalanges and lengthened distal phalanges." Fisher (1946) noted that the reverse was also true; more cursorial taxa showed distal shortening of the phalanges.

Sternberg (1932) also noted that trochlear grooving is associated with grasping ability when he interpreted *Troodon* as having strong grasping power due to relatively deep grooving in the distal trochlea of the final non-ungual phalanx. Neither Sternberg (1932) nor Fisher (1946) quantified this trend.

Jollie (1977) followed the work of Stresemann (1927-1934) who examined digit proportions in relation to feeding behavior in the genus *Falco*. Jollie (1977) examined Falconiformes and divided his discussion of this group roughly equally between osteology, myology, and visceral anatomy. Although he discussed foot osteology he did not take measurements, restricting his analysis to qualitative observation of differences. He noted that, in contrast to vultures and secretary birds, the basal phalanges of digits II and IV of eagles and falcons are relatively shorter than the distal phalanges. Like Fisher (1946), he noted the shortening of certain segments of the digits in grasping species.

Zhou and Farlow (2001) measured the lengths of phalanges in the pes in digits II – IV for their study of *Confuciusornis* behavior. They classified living birds into 3 categories based on behavior: arboreal species, ground species, and mainly arboreal species which spend some time on the ground. Principal components analysis was employed to find the factors most responsible for variation within the data. The authors found that the length of the distal phalanges tends to correlate with behavior; arboreal species tend to have relatively longer distal phalanges compared to ground species. They also found that birds of intermediate behavior and small size did not separate as well as specialists or larger birds on their plots.

Clark et al. (1998) briefly discussed relative phalangeal proportions in digit III of modern birds. They plotted the relative lengths (in percentage of the digit) of the phalanges and found that arboreal and terrestrial birds grouped separately. Hopson (2001) furthered this line of inquiry by examining the lengths of phalanges of digits I, II, and III in fossil and modern birds and non-avian theropods as a part of his study on the origin of

flight. Hopson (2001) was looking for a functional signal to distinguish grasping species from terrestrial species. He found that relative lengths of phalanges in all digits separated modern birds on the basis of behavior. Arboreal and raptorial species clustered together in morphospace separately from terrestrial species. He concluded that the information contained in measurements of digit II is redundant with that contained in measurements of digit III.

Previous studies which examined pedal morphology quantitatively (e.g. Fisher, 1946; Jollie, 1977; Hopson, 2001; Zhou and Farlow, 2001) mostly restricted their analyses to phalangeal lengths. Farlow et al. (in review) added a width measurement in addition to a length measurement in their study of non-avian theropod track-maker identification. They found that genera of modern birds did not necessarily cluster with their closest relatives in morphospace when plotted according to principal component scores or when grouped using cluster analysis.

This review of the literature reveals two trends: relative lengths of phalanges and extent of trochlear grooving correlate with behavior. These trends can be noted by contrasting a raptorial and cursorial taxon (Figure 1). The former trend has been investigated quantitatively (Fisher, 1946; Jollie, 1977; Hopson, 2001; Zhou and Farlow, 2001) while the latter trend has been discussed qualitatively (Sternberg, 1932; Fisher, 1946; Rassmussen et al., 2001). Questions that remain are whether measurements besides lengths of the digits are useful in inferring behavior and whether quantification of trochlear grooving is valuable.

Figure 1. Owl Contrasted with an Ostrich

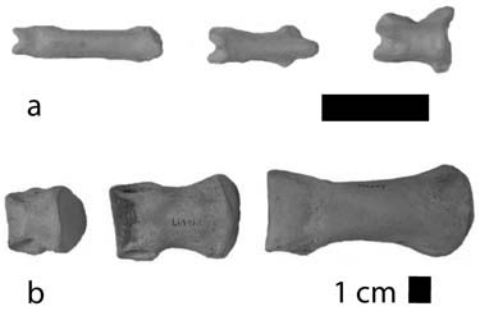

Fig. 1. (**a**) Digit III of the Short-eared Owl (*Asio flammeus flammeus*) contrasted with (**b**) Digit III of the Ostrich (*Struthio camelus*)

This study attempted to address some of these unresolved issues. It had three main purposes. The first was to identify additional metrics that were useful in inferring behavior from osteology in modern birds. Width and height measurements of the pedal phalanges were added to length data to determine whether these reflect behavior and whether their addition sharpened behavioral distinctions. The second purpose was to quantify trends that have previously been qualitatively described. Depth of trochlear grooving was measured in an attempt to quantify how much grooving is needed to infer a specimen has an arboreal or raptorial lifestyle. Both of these goals were independent of the third purpose, which was to use these measurements to infer the locomotor behavior of non-avian theropods and determine whether they showed a consistent trend in locomotor habits. Even without this application, the results of analysis of modern avian taxa should provide useful information about the relationship between morphology and behavior in modern birds as well as reveal morphological variation among the groups sampled. Finally, the results of the study are applicable to fossil birds as well as fossil non-avian dinosaurs.

To achieve these goals, a series of linear measurements were taken on the pedal phalanges of extant birds. These measurements were analyzed using statistical techniques to determine whether this information alone was sufficient to categorize the birds according to locomotor behavior, i.e. whether raptorial and arboreal taxa could be separated from terrestrial and cursorial taxa on the basis of pedal morphology.

MATERIALS AND METHODS

A sample of extant birds was examined from a variety of osteological collections as the starting data for this project. Three primary objectives drove the selection of sample taxa. First, specimens were chosen to include a diverse set of avian orders. Trends in morphology that span groups at a high taxonomic level can be inferred to represent important convergences. The second objective was to include groups of closely related taxa with disparate behaviors. This was intended to guard against phylogenetic signal rather than functional signal being observed when examining trends in morphology. The third objective was to include taxa that were comparable in size to at least small non-avian theropods in order to reduce the dangers associated with extrapolation.

Only specimens with complete digits were included because standard multivariate analyses remove observations with missing values. There was a lower practical size limit in species that could be measured; birds smaller than sparrow-sized were not measured.

The final dataset includes 132 extant birds. Groups present include the ratites, Cuculiformes, Tinamiformes, Galliformes, Gruiformes, Falconiformes, and Strigiformes. As non-avian theropods have not been interpreted as primarily aquatic, aquatic birds were excluded from this study. The collections used were those of the American Museum of Natural History (AMNH), National Museum of Natural History (NMNH), Smithsonian Institution (USNM), Museum of the Rockies (MOR), and Montana State University (MSU).

Measurements were taken on the non-ungual phalanges of digit III. Hopson (2001) used only digit III for part of his analyses. Zhou (1999) argued for the importance

of digit II as well as digit III in perching forms but found that plots based on measurements from digit I, II, and III worked equally well for separating groups.

The measurements for this study included four length measures, three widths, and three heights per phalanx. These measurements are diagrammed in Figure 2. The length labeled L2 was not used in the data analyses. It was replaced by the difference between it and L1 to provide the depth of the groove in the distal trochlea (labeled DTD). The length labeled L3 corresponds to the length measured by Hopson (2001) and Farlow et al. (2007). Due to the nature of the measurements, disarticulated phalanges were used that were manually reassembled into digits. An attempt was made to identify the assembled digit as belonging to the left or right foot but it is probable that this was not perfectly accurate, especially on smaller species. However, L3 is the only measurement that this identification could affect. These measurements are referred to in the text with a prefix indicating which phalanx they were derived from so P1L1 is L1 measured on phalanx 1, P2L1 is L1 measured on phalanx 2, etc.

An additional measurement of femur diameter at the smallest point of the shaft was taken as a proxy for body weight following similar methods from Maloiy et al. (1979). All measurements except one were taken by the author with a pair of Avenger digital calipers accurate to .02 mm. James Dean of the Smithsonian kindly provided one missing value.

Figure 2. Diagram of Measurements

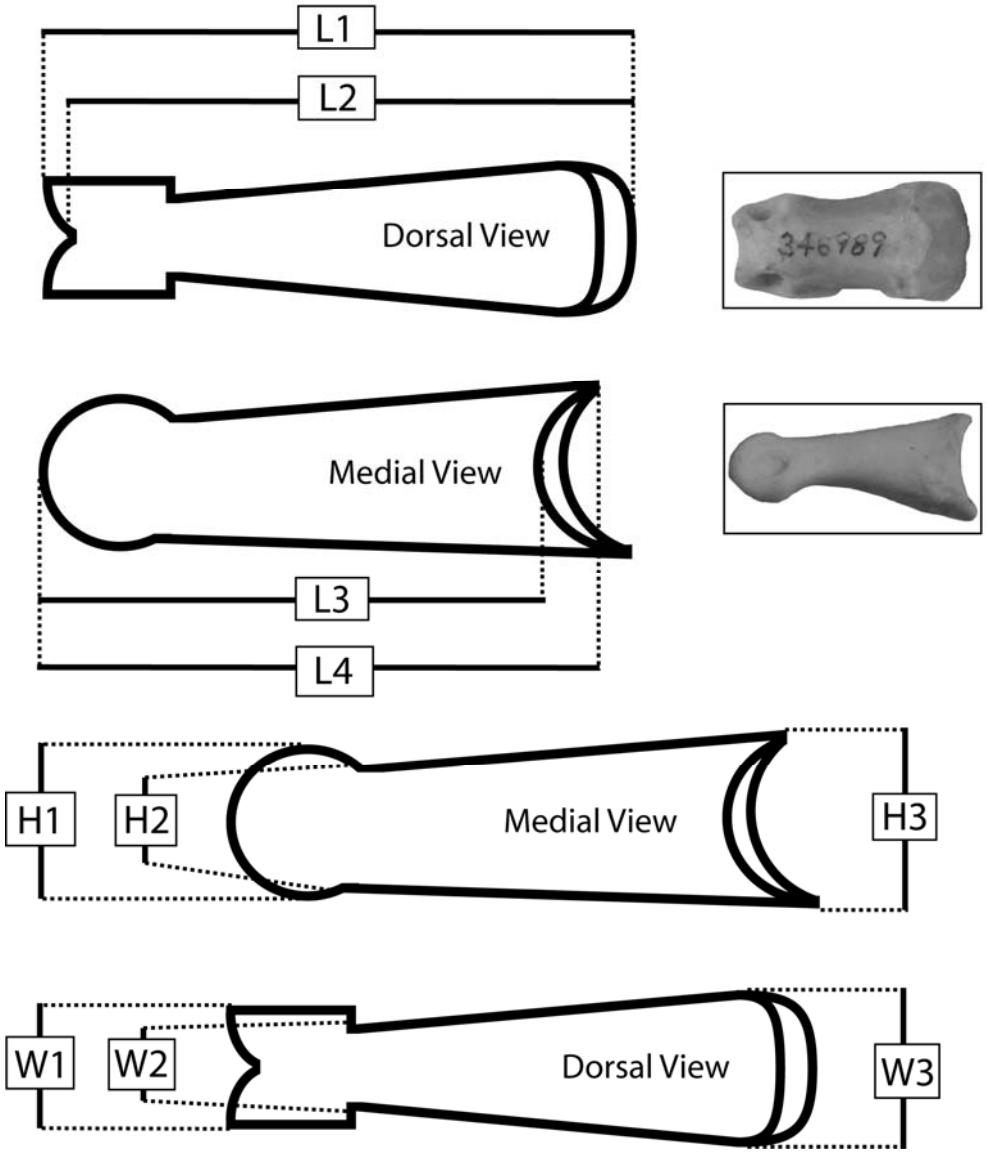

Fig. 2. Linear measurements taken on each phalanx are diagrammed. L1: Maximum extent of the ventral surface of the proximal articular surface to the outermost point of the distal trochlea. L2: Maximum extent of the ventral surface of the proximal articular surface to the base of the groove in the distal trochlea. Subtracted from L1 to provide a depth of the groove in the distal trochlea named DTD; not present in the final dataset. L3: Deepest extent of the proximal articular surface to the maximum extent of the distal trochlea. L4: Maximum extent of the dorsal surface of the proximal articular surface to the outermost point of the distal trochlea. H1: Maximum height of the distal trochlea. H2: Minimum height of the shaft of the phalanx. H3: Maximum height of the proximal articular surface. W1: Maximum width of the distal trochlea. W2: Maximum width of the proximal articular surface. W3: Minimum width of the shaft of the phalanx. The photos to the right represent the same view as the illustrated phalanges. These measurements were repeated for each of the three non-ungual phalanges of digit III.

Taxa were assigned to one of five behavioral categories: strongly arboreal/grasping (A1), weakly arboreal/grasping (A2), a mix of grasping and terrestrial (M), weakly terrestrial/cursorial (C2), or strongly terrestrial/cursorial (C1). A review of the literature using descriptions of foraging and roosting behavior was used to assign taxa to these categories. The primary source used was the del Hoyo et al. (1992-2006) series on the birds of the world, but the following additional sources were also used: Sick (1981), Short (1982), Hilty and Brown (1986), Wyllie (1993), Clement (2000), and Madge and McGowan (2002). Taxa classified as A1 were described as never being seen on the ground, while those in A2 were described as being seldom, rarely, or sometimes seen on the ground. Similarly, those classified as C1 were described as never being seen in trees or bushes while those classified as C2 were described as being sometimes seen in trees or bushes. Often species classified as C1 and C2 were described as initially running from intruders unlike those in A1 and A2 which were often described as initially flying to higher or farther branches when startled. Taxa in M usually had descriptions that described them as equally at home in the trees and on the ground as well as descriptions of foraging that indicated time evenly split between trees and ground. In the final dataset, 30 species were classified as A1, 19 as A2, 12 as M, 42 as C1, and 29 as C2.

Species coded as A1 include perchers and predatory graspers such as the Resplendent Quetzal, Vasa Parrot, falcons, and owls. Species coded as A2 include the White-crested Guan and Alagoas Curassow; while generally arboreal both occasionally forage on the ground. Some of the tragopans were coded M for foraging both in the trees and on the ground. Examples of taxa coded C2 include the Lesser Ground Cuckoo,

Crested Guineafowl, and Scaled Quail for their tendency to spend time on the ground. Finally, strongly terrestrial species coded as C1 include the Clapper Rail, Red Junglefowl, tinamous, and ratites.

Zhou (1999) hypothesized that extreme lengthening of the distal phalanx of digit II might be a raptorial adaptation, with arboreal species showing lengthening to a lesser extent. To test whether this might be true in digit III as well, and to determine whether birds with raptorial habits could be separated from those with only arboreal habits using these data, a second set of categories was created. This set (referred to as the "Feeding" set) divides the sample taxa into five categories depending on feeding and foraging behavior. The first category, arboreal non-raptor: ANR, consists of species that grasp substrates such as tree branches but do not grasp prey whereas the second category, arboreal raptor: AR, consists of the arboreal birds of prey which use their feet to grasp substrates and prey. The third category, terrestrial non-raptor: TNR, is comprised of species that stand on flat substrates and do not use the feet in prey acquisition in contrast to the fourth category, terrestrial raptor: TR, which is for species which stand on flat substrates but use the feet in prey acquisition or manipulation. Members of the final category, mixed non-raptor: MNR, forage on the ground and in trees equally, showing no preference for grasping or not grasping substrates. Members of MNR do not use the feet to predate.

Taxa coded as ANR include the parrots, perching cuckoos, jays, kingfishers, and cracids. Falcons, eagles, and owls comprise category AR. Tinamous, ratites, Galliformes, cranes, bustards, and vultures are the primary members of TNR. The TR category

includes only the seriemas and the Secretary Bird. Category M is a mix of taxa such as the Striped Cuckoo, Song Thrush, and some tragopans.

The non-avian dinosaurs measured for this study were from the collections of MOR and MSU. Specimens included original fossil material as well as casts obtained from other institutions. Measurements taken were the same as those taken on modern birds. Among the non-avian dinosaurs used in this study were *Troodon*, *Bambiraptor feinbergi* (a cast of Florida Institute of Paleontology (FIP) #001), *Saurornitholestes*, and *Deinonychus antirrhopus.* All are small- to medium-sized deinonychosaurian theropods closely related to birds and the last three are dromaeosaurids, the sister-group to troodontids (Sereno, 1999). An oviraptor, *Elmisaurus*, was measured. Oviraptors are nested within the Maniraptora, a group which also includes the Deinonychosauria and Avialae (Holtz and Osmólska, 1994). Large theropods more distantly related to birds include *Allosaurus* and three tyrannosaurids: *Albertosaurus*, *Daspletosaurus*, and *Tyrannosaurus rex*. Finally, there is a selection of ornithopods such as *Oryctodromeus cubicularis*, a small ornithopod recently interpreted as having forelimbs adapted for digging (Varricchio et al., 2007), and two larger hadrosaurs: an unidentified lambeosaur and *Brachylophosaurus*.

Extant birds are most closely related to the group comprised of the troodontids and dromaeosaurids. Taken together, this group can be labeled the Paraves (Sereno, 1999). The closest relatives to the Paraves used in this study are the oviraptors. The group that includes both of these clades is the Maniraptora (Sereno, 1999). The tyrannosaurids are the next most closely related group to the Maniraptora used in this study. The group

that includes these two is the Tyrannoraptora (Sereno, 1999). *Allosaurus* is the most basal theropod sampled for this study. The Neotetanurae unites the clade that includes *Allosaurus* with the Tyrannoraptora (Sereno, 1999). The ornithopods sampled are within the second major group of dinosaurs. Theropods are Saurischians while ornithopods are Ornithischians. Groups that are nested higher within the phylogeny can be described as "derived" while those that split off earlier, near the root, can be described as "basal".

Two multivariate statistical techniques were applied to the final dataset: principal components analysis (PCA) using the R 2.3.1 software package (R Development Core Team, 2006) and discriminant function analysis (DFA) using the SAS 9.1 software (SAS Institute Inc., 2007). These techniques were applied to the dataset comprised of the raw measurements exclusive of femur diameter as well as a scaled dataset where each measurement was divided by the femur diameter. This scaling was intended to account for body-size differences. Appendix A provides the raw dataset and category information for the modern birds while Appendix B provides the measurements for the non-avian dinosaurs. In the case of MOR 747, *Deinonychus,* there is no associated femur. To scale the measurements for this specimen, the femur of a different *Deinonychus* (Museum of Comparative Zoology, Harvard University (MCZ) #4371) was used as described in Ostrom (1976).

PCA is a multivariate exploratory tool (Manly, 2005). Previous authors examining pedal morphology and behavior found this analysis useful (e.g. Zhou, 1999; Hopson, 2001; Zhou and Farlow, 2001; Janis et al., 2002; Weisbecker and Warton, 2006). PCA produces a set of uncorrelated linear combinations of the variables that explain the total

variance of the sample (Manly, 2005). These combinations are referred to as principal components (PCs) and the coefficients of the variables in the linear combination are sometimes referred to as loadings of the variables. Analyses using both the covariance matrix and correlation matrix were performed.

Analysis of the covariance matrix does not standardize variances while analysis of the correlation matrix standardizes the variances of the original variables so that each contributes an equal amount to the total sample variance (Manly, 2005). Thus runs using the covariance matrix tend to load variables with larger variances while runs using the correlation matrix standardize the variables so that variables with large and small variances have equal weight. How the PCs load in the correlation matrix analysis depends solely upon the correlations among the variables. Finally, the PCs were plotted against the behavior categories to ascertain whether behavioral groups clustered.

DFA classifies observations into one of several known groups based on a sample of multivariate data (Manly, 2005). While principal components analysis is an exploratory technique that attempts to explain the variation present in the sample without regard to group information, DFA is a technique used to generate rules that classify observations into one of several predefined groups and to estimate error rates for classifying new data (Huberty, 1994; Manly, 2005). In order to determine which measurements were most useful in separating groups the STEPDISC procedure within SAS was used using the linear discriminant function. This procedure selects variables that are statistically significant for discrimination among the groups (Rencher, 1997). Thus a subset of variables that are most useful to the discrimination of the groups is

selected and used for the DFA rather than every variable measured for this study. The prior probabilities used for group membership were proportional to the sample. Linear discriminant, quadratic discriminant, and k-nearest neighbors functions were applied to the datasets. The first two procedures use linear and quadratic functions of the variables to categorize an observation (Rencher, 1997). In contrast, k-nearest neighbors classifies according to the group membership of the closest k neighbors in the training set (Huberty, 1994). The analyses were run multiple times using different numbers of neighbors to determine which provided the lowest estimated error rates. Cross-validation was employed to estimate the error rate for each of the previous functions (Manly, 2005).

RESULTS

Principal Components Analysis

When PCA of the raw data was performed, PC loadings primarily related to size differences rather than morphological differences among taxa. Consequently, these results are not discussed further and the results of the PCA of the femur diameter scaled data are presented. The component loadings and eigenvalues are presented in Appendix C.

When PCA on the covariance matrix was applied to the avian femur scaled dataset, PC1 accounted for 72.3% of the variation in the data (eigenvalue: 3.14) whereas PC2 accounted for 20% of the variation (eigenvalue: .87) and PC3 accounted for 3.3% of the variation (eigenvalue: .14). Even with the adjustment for body size, PC1 is a weighted average of all of the variables and can be interpreted as reflecting the size of the individual so it is excluded from Figure 3 which plots PC2 versus PC3 values for birds and non-avian dinosaurs. PC2 contrasts a weighted average of the measurements of length for phalanx 1 and a weighted average of the measurements of length for phalanx 3. Thus PC2 can be interpreted as contrasting taxa that have a long phalanx 1 and short phalanx 3 with taxa that have a short phalanx 1 and longer phalanx 3. PC3 contrasts a weighted average of lengths of phalanx 1 and 3 with a weighted average of lengths of phalanx 2. Taxa scoring highly on this component would have relatively long second phalanges compared to phalanges 1 and 3.

Figure 3. PC3 vs. PC3 for the Covariance Matrix

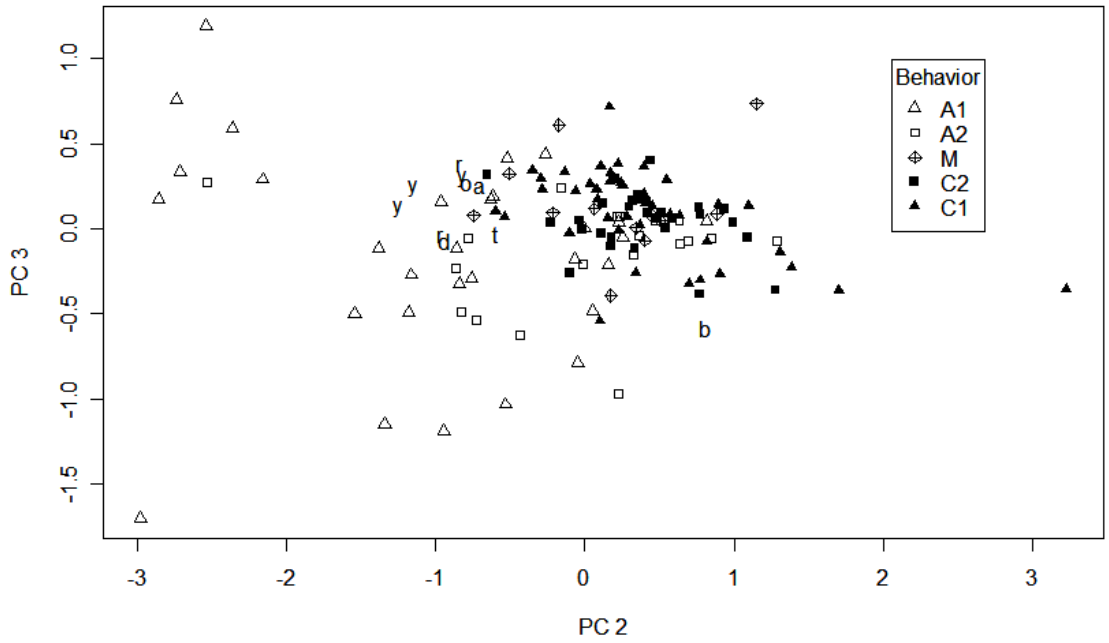

Fig. 3. Plot of PC2 versus PC3 using the covariance matrix on the scaled data. Taxa that score highly on PC2 have a relatively long phalanx 1 compared to phalanx 3. Taxa that score highly on PC3 have a relatively long phalanx 2 compared to phalanges 1 and 3. t, *Troodon*; b, *Bambiraptor* ; d, *Deinonychus*; a, *Allosaurus*; y, *Albertosaurus*, *Daspletosaurus*, *Tyrannosaurus*; o, *Oryctodromeus*; r, Lambeosaur, *Brachylophosaurus*

Given previous findings that perchers and graspers have elongate distal phalanges compared to proximal phalanges (Fisher, 1946; Jollie, 1977; Zhou and Farlow, 2001; Hopson, 2001) PC2 can be expected to separate taxa according to behavior, and Figure 3 provides some support for this. Arboreal/grasping species tend to occupy the lower left side of the plot while strongly terrestrial species tend to occupy the upper right side. This division is not simply a left/right side of the plot division, but runs diagonally due to the additional separation created by PC3. This trend is not strong in taxa with weaker affinities and the middle of the plot contains taxa from every behavioral category. PC3 alone weakly separates taxa by behavior but works better when plotted with PC2. Strongly arboreal/grasping taxa seem to show more variability on this component than

terrestrial species. Thus there may be more variability in the size of phalanx 2 compared to phalanges 1 and 3 in grasping/arboreal species than in terrestrial/cursorial species.

The strongly terrestrial species that scores unusually highly on PC2 in the middle right of the plot is the Clapper Rail. Its marsh habits are unlike the other terrestrial taxa in the sample and may account for its unusual score. The seven taxa that cluster on the upper left of the plot consist of the five Strigiformes and the two woodpecker species measured in this study.

Most of the non-avian dinosaurs cluster close to the middle of the plot in the area populated by morphologically unspecialized taxa. Some of the large theropods plot slightly closer to the cluster of raptors and woodpeckers on the upper left. The one exception to the clustering of the non-avian dinosaurs is *Bambiraptor* which scores comparatively lower on PC3 and higher on PC2. Although it is distant from the other non-avian dinosaur taxa it still occupies the same intermediate morphospace, not clearly terrestrial/cursorial or grasping/arboreal in morphology.

The question of whether phylogeny constrains morphology can be examined if the same PCs are plotted with points identified by avian orders rather than locomotor categories (Fig. 4). The upper left cluster of Strigiformes and woodpeckers is again apparent in this plot. The two Piciformes that plot towards the center with other taxa are both toucans rather than woodpeckers. The Gruiformes show a large amount of variation even though all are classified as strongly terrestrial/cursorial taxa. Similarly, the generally grasping/arboreal Coraciiformes seem to show a medium to large amount of variation,

and there is some separation between the kingfishers which score above zero on PC3 and the hornbills which score below zero. The Galliformes and Cuculiformes seem to be

Figure 4. Avian Orders and Non-Avian Dinosaurs Plotted by Covariance PCs

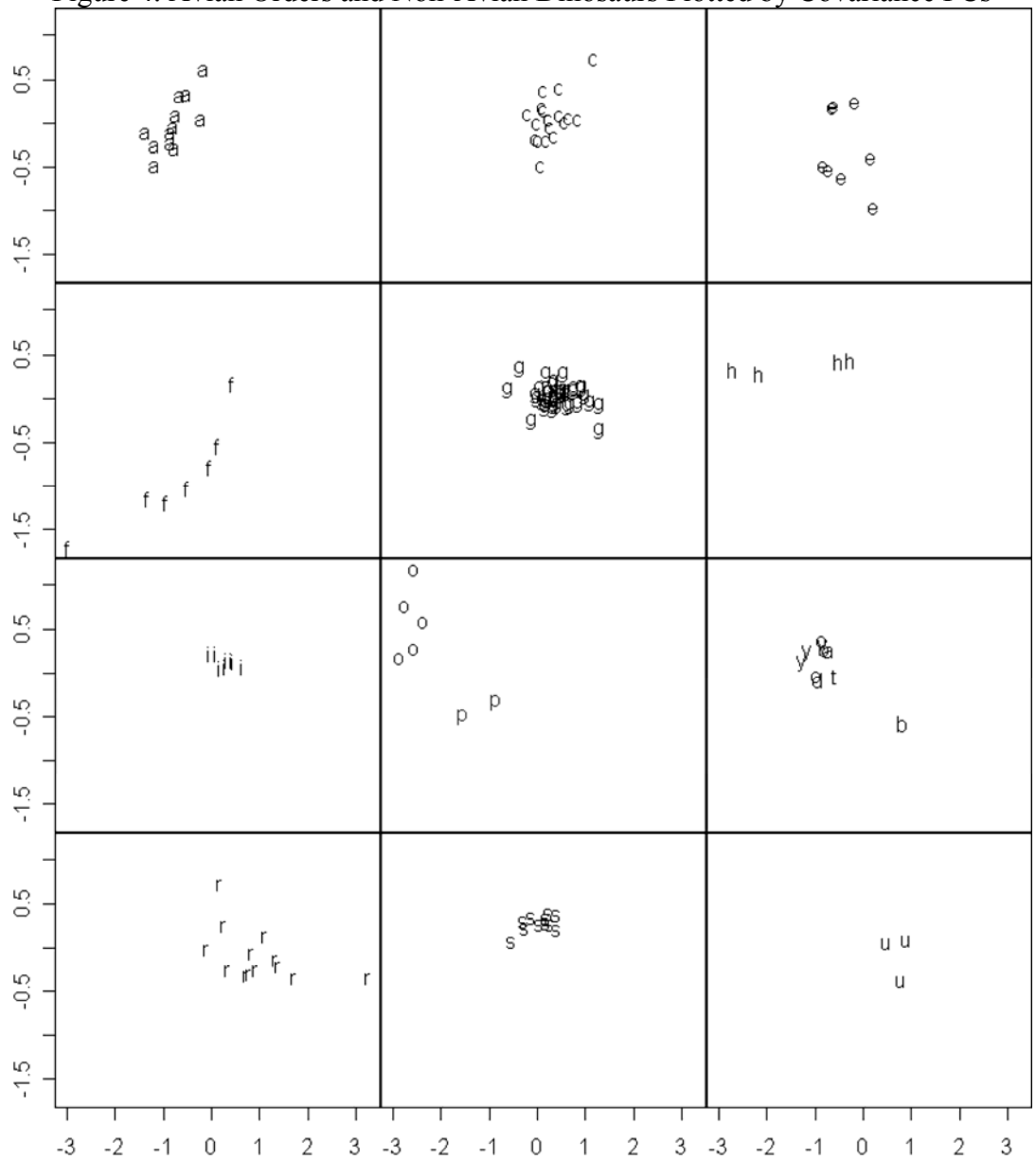

Fig. 4. Plot of PC2 versus PC3 using the covariance matrix on the scaled data for modern avian orders and non-avian dinosaurs: a, Passeriformes; c, Cuculiformes; e, Coraciiformes; f, Falconiformes; g, Galliformes; h, Piciformes; i, Tinamiformes; o, Strigiformes (appears with Psittaciformes); p, Psittaciformes; r, Gruiformes; s, Struthioniformes; u, Columbiformes; t, *Troodon*; b, *Bambiraptor* ; d, *Deinonychus*; a, *Allosaurus*; y, *Albertosaurus*, *Daspletosaurus*, *Tyrannosaurus*; o, *Oryctodromeus* (appears with non-avian dinosaurs); r, Lambeosaur, *Brachylophosaurus*

more restricted in area on the plot even though these orders include members of every behavioral category. The Falconiform with the very low PC3 score on the lower left represents the Osprey which Jollie (1977) noted as "aberrant" compared to accipitrids. The Falconiform that scores higher than the others on PC3 is the Turkey Vulture while the Secretary Bird scores second highest. These scores place the vulture into the area of the plot where terrestrial/cursorial taxa dominate and the Secretary Bird closer to this region than the remaining Falconiformes. The Cuculiform that sits apart from the rest towards the terrestrial/cursorial region is the Striped Cuckoo which was categorized as M. The three cuckoos that score highest on PC3 besides the Striped Cuckoo are the Greater and Lesser Roadrunners and the Lesser Ground Cuckoo. When plotted together there is no clean clustering of avian orders although some phylogenetic trends are present.

Figure 5 illustrates some of the morphological trends that the PCA highlights. Depicted are representative examples of phalanges of Digit III of modern birds from each of the five behavior categories as well as a raptorial taxon.

Figure 5. Digit III From 6 Birds

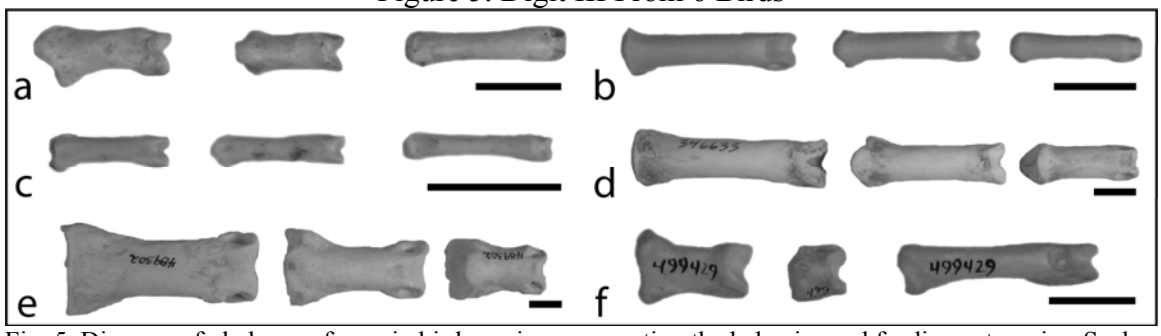

Fig. 5. Diagram of phalanges from six bird species representing the behavior and feeding categories. Scale bar = 1 cm. Species with classification according to behavior and feeding schemes: (**a**) Macaw (*Ara chloroptera*) A1, ANR (**b**) Guan (*Chamaepetes unicolor*) A2, ANR (**c**) Bowerbird (*Ptilorhynchus violaceus***)** M, MNR (**d**) Condor (*Vultur gryphus*) C2, TNR (**e**) Cassowary (*Casuarius unappendiculatus*) C1, TNR (**f**) Osprey (*Pandion haliaetus*) A1, AR

Distal phalanges tend to become relatively shorter compared to proximal phalanges from a-e (Fig. 5) as taxa go from grasping/arboreal behavior to terrestrial/cursorial behavior. Phalanges 2 and 3 of the Cassowary are proportionately broader than those of more generalized or grasping taxa (Fig. 5e). Grooving of the trochleae is readily apparent in the Macaw and Osprey while the Condor and Cassowary have shallower grooves (Fig. 5a,f,d-e). Finally, the extremely shortened middle phalanx of the Osprey is notable compared to the other taxa (Fig. 5f).

When the correlation matrix was used for PCA rather than the covariance matrix PC1 remains a measure of body size which accounts for 46.3% of the variation in the data (eigenvalue: 13.9). Thus PC2 and PC3 are plotted to show morphological trends that are independent of body size (Fig. 6). PC2 accounts for 23.5% of the variation (eigenvalue: 7.0). This component contrasts lengths of phalanges 1, 2, and 3 with widths of phalanges 1, 2, and 3. Taxa that score high on this component have relatively wider phalanges than those that score lower. PC3 accounts for 8.0% of the variation (eigenvalue: 2.4) present in the data. PC3 is more complex, positively loading the depth of the grooves in the distal trochleae of phalanages 1, 2, and 3 as well as a height of phalanges 2 and 3 and the lengths of phalanx 3. PC3 negatively loads lengths, widths, and heights of phalanx 1 and the widths of phalanx 2 and 3. This component contrasts taxa that have deeply grooved trochleae and a tall, elongate phalanx 3 with taxa that have a larger phalanx 1 and broad phalanges 2 and 3.

Similar to the covariance matrix analysis, there is some separation of behavioral groups when plotted by PC scores. Terrestrial species tend to score higher on PC2 and

lower on PC3 whereas the opposite is true for arboreal/grasping species. Compare the relatively tall, long, and grooved phalanges of the Macaw or Osprey (Fig. 5a,f) with the relatively short, wide, and shallowly grooved phalanges of the Cassowary (Fig. 5e) to see these trends. Similar to the previous plot, species with weaker affinities cluster in the

Figure 6. PC2 vs. PC3 for the Correlation Matrix

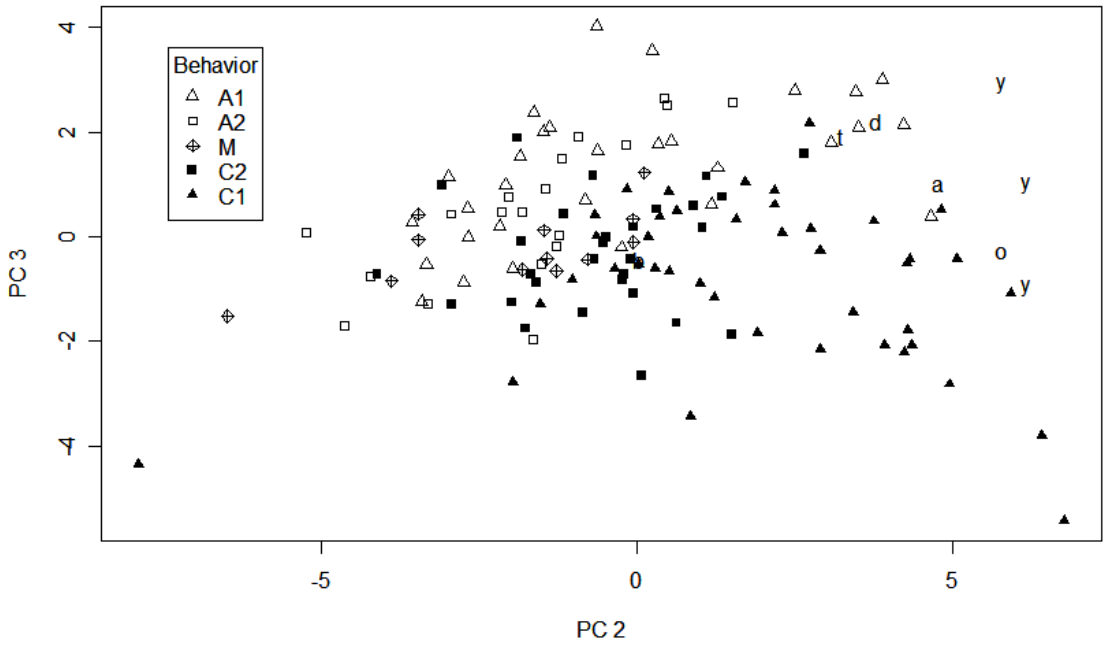

Fig. 6. Plot of PC2 versus PC3 using the correlation matrix on the scaled data. Taxa that score highly on PC2 have relatively wide phalanges. Taxa that score highly on PC3 have deep trochlear grooving and a tall, long phalanx 3. The lambeosaur and Brachylophosaurus score too high on PC2 to be plotted here. t, *Troodon*; b, *Bambiraptor*; d, *Deinonychus*; a, *Allosaurus*; y, *Albertosaurus*, *Daspletosaurus*, *Tyrannosaurus*; o, *Oryctodromeus*

middle of the plot with intermediate values on both components. The unusual terrestrial data point in the lower left once again represents the Clapper Rail.

Non-avian dinosaurs show more variation within morphospace in this plot than in the plot from the covariance matrix analysis. Most of the large theropods now trend towards the terrestrial/cursorial end of the plot. *Deinonychus*, *Troodon*, and *Bambiraptor* remain towards the center of the plot . Of the ornithopods, only *Oryctodromeus* is shown

because the lambeosaur and *Brachylophosaurus* score so highly on PC2 that they cannot be plotted without distorting the figure. The two hadrosaurs have phalanges that are wider than they are long, unlike any extant bird. Even the Cassowary (Fig. 5e) and the Ostrich both have phalanges that are more than twice as long as they are wide. The two points that are in the lower-right of both Fig. 6 and Fig. 7 are both ostriches.

Figure 7 plots the same data as Figure 6 according to avian orders. There are some differences in this plot when compared to Figure 4. First, in general, the avian orders appear to occupy larger areas of the plot, reflecting greater morphological diversity when the variables are standardized. Secondly, the Strigiformes and grasping Falconiformes are not as distinct from the other graspers compared to the covariance plot. The single Struthioniform that scores higher on PC3 than any of the others is the Kiwi. The two Piciformes that score the highest of any taxa on PC3 are the same two woodpeckers that grouped with the owls in Figures 3 and 4, the Red-necked Woodpecker and Greater Flameback. The Turkey Vulture now plots apart from the other Falconiformes to the left, scoring lower than the others on PC2 indicating that this taxon has relatively narrow phalanges compared to the other species. The Secretary Bird plots to the lower right of the other Falconiformes, clustering it with terrestrial/cursorial taxa. The Greater and Lesser Roadrunners cluster with three other taxa, the Coral-billed Ground Cuckoo, the Goliath Coucal, and the Red-capped Coua, to the right of the other Cuculiformes. Their scores on PC2 indicate they have relatively wider phalanges than other Cuckoos.

Figure 7. Avian Orders and Non-Avian Dinosaurs Plotted by Correlation PCs

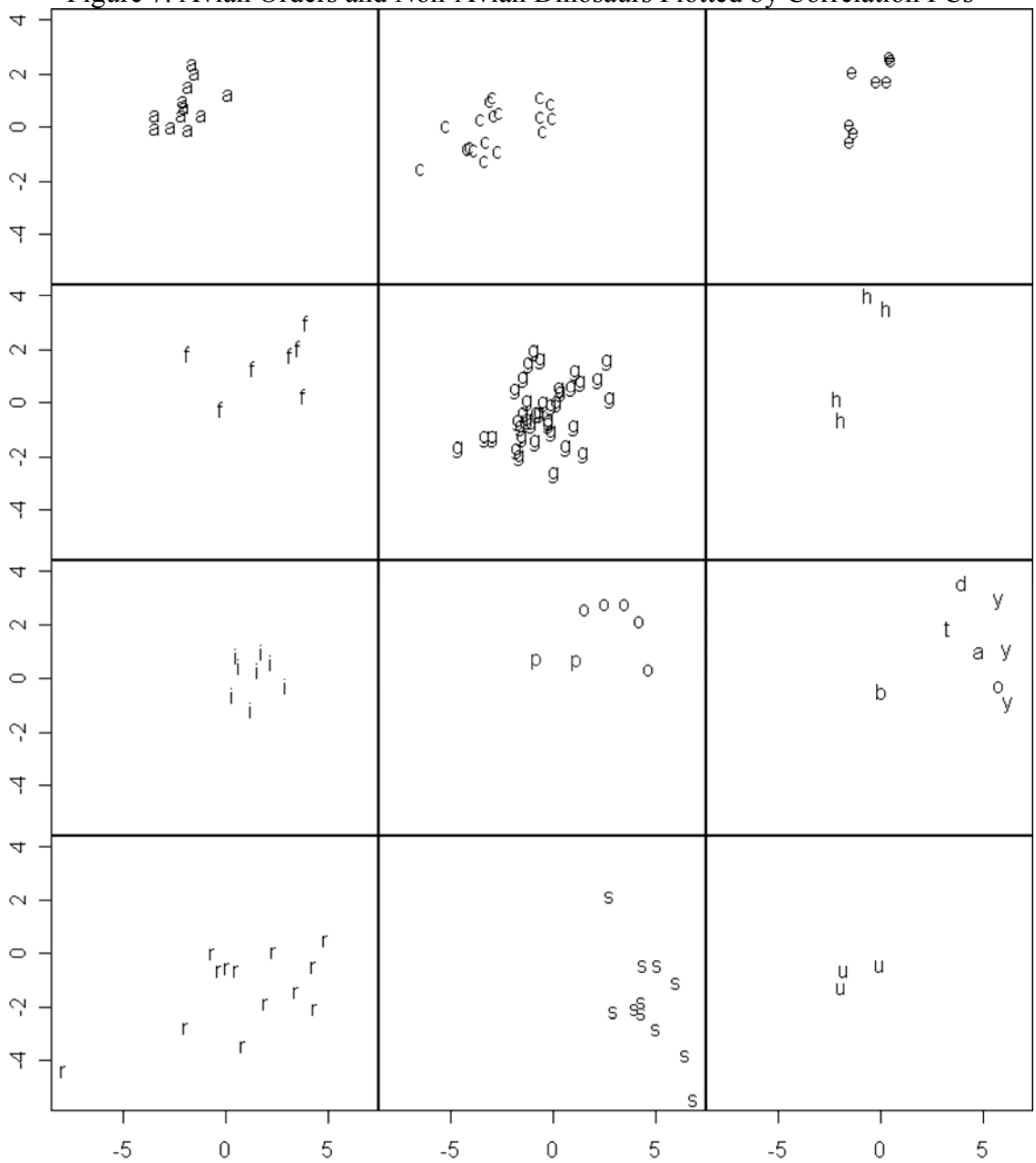

Fig. 7. Plot of PC2 versus PC3 using the correlation matrix on the scaled data for modern avian orders and non-avian dinosaurs: a, Passeriformes; c, Cuculiformes; e, Coraciiformes; f, Falconiformes; g, Galliformes; h, Piciformes; i, Tinamiformes; o, Strigiformes (appears with Psittaciformes); p, Psittaciformes; r, Gruiformes; s, Struthioniformes; t, Trogoniformes; t, *Troodon*; b, *Bambiraptor* ; d, *Deinonychus*; a, *Allosaurus*; y, *Albertosaurus*, *Daspletosaurus*, *Tyrannosaurus*; o, *Oryctodromeus* (appears with non-avian dinosaurs)

Discriminant Function Analysis

After PCA, DFA was applied to the dataset. As noted in the methods, a stepwise procedure was used to select fewer variables for use in the discriminant functions. This can decrease misclassification rates.

Table 1 presents the results from stepwise DFA run on the raw and femur diameter scaled datasets. It presents estimated error rates for each category as well as an overall estimated error rate for each discriminant procedure. The estimated error rates are the rates of misclassifying the holdout observation when implementing the jackknife procedure. The total error rate is a weighted average of the estimated error rates for each category. For this method one observation is selected and the discriminant functions are computed without this observation. Then this observation is categorized by the resulting rules. This procedure is repeated for each observation in the data set and the rate of miscategorization of the excluded observation is the estimated error rate (Johnson and Wichern, 1998). The STEPDISC procedure on the raw data chose variables P1L1, P1H2, P2L3, P2H1, P2H2, P3L3, P3W2, P3H1, and P3H3 for discrimination. The linear and k-nearest neighbors procedures produce comparable results with overall estimated error rates close to 36%. Taxa with stronger affinities towards arboreal/grasping or terrestrial behavior are easier to categorize. Estimated error rates increase as taxa move from strongly preferring one mode of locomotion to mixing terrestrial and arboreal behaviors with the highest error rates for taxa that show no clear preference.

The STEPDISC procedure chose the variables P1DTD, P1W1, P2L1, P2L4, P2W1, P2H1, P2H2, P3DTD, P3L4, P3H1, and P3H3 for the analysis of the femur

diameter scaled data. The total estimated error rates for the scaled data are reduced compared to those for the raw data. Table 1 shows that the same pattern of error rates holds for the scaled data as for the raw data. Taxa that show strong preferences for arboreal/grasping or terrestrial behavior are much easier to categorize than those with weaker preference. The quadratic and k-nearest neighbors results show this very well, with estimated error rates at 20% or less for categories A1 and C1 and high rates of not less than 40% for A2, M, and C2. Taxa with strong behavioral preferences can be accurately categorized by these procedures. Taxa without strong preferences do not show the specialized morphology needed to accurately categorize them.

Table 1. DFA Results for 5 Locomotor Categories

Dataset	Function	Estimated Error Rates					Total
n		30	19	12	29	42	Error
		A1	A2	M	C2	C1	Rate
Raw	Linear	0.300	0.421	0.917	0.333	0.262	0.368
	Quadratic	0.367	0.579	0.833	0.433	0.333	0.444
	K-nearest Neighbors†	0.233	0.474	0.750	0.467	0.214	0.361
Scaled	Linear	0.367	0.368	0.833	0.276	0.048	0.288
	Quadratic	0.200	0.684	1.000	0.483	0.167	0.394
	K-nearest Neighbors‡	0.200	0.526	0.750	0.414	0.095	0.312

†,‡ 3 nearest neighbors

Other researchers (Zhou, 1999; Hopson, 2001; Zhou and Farlow, 2001) investigating behavioral inference from pedal morphology have used three categories of behavior in their studies. Hopson (2001) categorized birds as “arboreal”, “terrestrial”, or “uncertain”. Zhou (1999) used “arboreal”, “terrestrial”, and “mainly arboreal” while Zhou and Farlow (2001) used “arboreal”, “ground”, and “mainly arboreal” as categories.

While the categories in this study cannot be neatly matched to these alternate categories, three categories can be created to make this study more comparable to this earlier work.

Table 2 presents the results of this attempt. The new categories result from lumping taxa of weak and strong affinities into one new category. Thus, A1 and A2 are combined into the "A_{new}" category and C1 and C2 are combined into the "C_{new}" category. The mixed category, M, remains the same as in previous analyses.

The stepwise function chose the variables P1L1, P3L3, P3W2, P3H1, and P3H3 for the raw data and P1DTD, P2L1, P2L4, P3L4, P3H1, and P3H3 for the femur diameter scaled data. There is substantial overlap between the variables chosen for use in the three

Table 2. DFA Results for 3 Locomotor Categories

Dataset	Function	Estimated Error Rates			Total Error
n		49	12	71	Rate
		A_{new}	M	C_{new}	
Raw	Linear	0.061	1.000	0.125	0.181
	Quadratic	0.388	0.583	0.250	0.331
	K-nearest Neighbors†	0.286	0.833	0.111	0.241
Scaled	Linear	0.082	0.833	0.056	0.136
	Quadratic	0.122	0.917	0.085	0.174
	K-nearest Neighbors‡	0.061	0.583	0.070	0.114

†,‡ 3 nearest neighbors

category analysis and those chosen for the five category analysis. The estimated total error rates are over 10% lower for the three category DFA compared to the five category DFA for every classification rule. The estimated error rates for the new categories also are much lower than those for the five categories excluding category M which retains its high estimated error rates. It is easier to classify the sample taxa into these three new categories than into the original five categories given these data.

The final DFA performed on the avian dataset was performed using the "Feeding" categories previously described (Table 3).

Table 3. DFA Results for Feeding Categories

Dataset *n*	Function	Estimated Error Rates					Total Error Rate
		40 ANR	66 TNR	12 MNR	10 AR	4 TR	
Raw	Linear	0.125	0.179	1.000	0.200	0.750	0.256
	Quadratic	0.125	0.149	1.000	1.000	1.000	0.308
	K-nearest neighbors†	0.075	0.119	0.667	0.300	0.750	0.188
Scaled	Linear	0.200	0.106	0.750	0.000	0.500	0.197
	Quadratic	0.175	0.091	1.000	1.000	1.000	0.296
	K-nearest neighbors‡	0.200	0.076	0.917	0.000	0.750	0.205

†,‡ 3 nearest neighbors

The STEPDISC procedure chose P1L3, P1W1, P1W3, P1H1, P2L1, P2L3, P2L4, P2W3, P2H1, P3L1, P3DTD, P3W1, P3H2, and P3H3 for the raw data while it selected P1DTD, P1L3, P1L4, P1W1, P1H1, P1H2, P2L3, P2W2, P2H1, P3DTD, P3L4, P3W1, P3W2, P3H1, P3H2, and P3H3 for analysis of the scaled data. The linear and nearest neighbor procedure results support Zhou's (1999) observations that arboreal non-raptors and arboreal raptors may be separable by morphology. The estimated error rates for arboreal raptors are low when using linear or k-nearest neighbors procedures, especially for the scaled data where no errors in categorization were made. Terrestrial predators are not easily separated from the other groups based on these data although only four specimens were categorized as such. Estimated error rates for the remaining non-predatory taxa are relatively low although again species showing no preference for grasping or terrestrial behavior are difficult to categorize as such.

When these algorithms were applied to non-avian dinosaurs, the k-nearest neighbors using three neighbors and linear discriminant procedures often resulted in very

similar estimated error rates as seen by comparing Tables 4 and 5. Each specimen is assigned to the category with the highest posterior probability; this probability follows the category that the taxon was assigned to. The coefficients and constants necessary to compute these linear discriminant functions on a new observation are listed in Appendix D.

Troodon is categorized as a strongly terrestrial/cursorial taxon by the discriminant rules except in the feeding category k-nearest neighbors analysis. Note that in this case an assignment was made using two of three neighbors, rather than all three. It may not be surprising, then, that the resulting assignment is unlikely to be correct. The majority of these data indicate that *Troodon*'s pes resembles those of birds that are well-adapted for terrestrial locomotion.

Bambiraptor is not consistently categorized by the discriminant rules and is sometimes grouped into the categories indicating intermediate rather than specialized behavior. *Bambiraptor* is never grouped with three neighbors of the same behavioral category using k-nearest neighbors and the posterior probabilities of group membership in the linear discriminant analyses are generally low. The measurements taken for this study do not allow it to be categorized with confidence into one of the 5 categories. This indicates that *Bambiraptor*'s pedal morphology is unlike birds with strong behavioral affinities, and instead is more similar to avian generalists.

The results for *Deinonychus* are similar to those of *Bambiraptor*. The raw and scaled datasets tend to classify *Deinonychus* differently and mutually exclusively. While the raw dataset classifies *Deinonychus* generally as terrestrial/cursorial the scaled dataset

Table 4. K-Nearest Neighbors Results for Non-Avian Dinosaurs

Taxa	K-Nearest Neighbors Analyses					
	Raw			Scaled		
	5 Categories	3 Categories	Feeding	5 Categories	3 Categories	Feeding
Troodon formosus MOR563	C1 (1.00)	C_{new} (1.00)	ANR (0.67)	N/A	C_{new} (1.00)	TNR (0.67)
Troodon MOR 748	C1 (1.00)	C_{new} (1.00)	-	-	-	TNR (1.00)
Bambiraptor feinbergi FIP 001 (cast)	C1 (0.67)	A_{new} (0.67)	N/A	M (0.67)	A_{new} (0.67)	ANR (0.67)
Deinonychus antirrhopus MOR 747	C1 (1.00)	C_{new} (0.67)	AR (1.00)			
With MCZ 4371 femur				A2 (1.00)	A_{new} (0.67)	ANR (0.67)
Saurornitholestes (cast)	-	C_{new} (1.00)	-	-	-	-
Elmisaurus elegans MOR 752	C2 (0.67)	C_{new} (1.00)	TR (0.67)	-	-	-
Albertosaurus MOR 657 (cast)	C1 (0.67)	C_{new} (0.67)	AR (1.00)	C1 (1.00)	C_{new} (1.00)	TNR (1.00)
Daspletosaurus MOR 590	C1 (0.67)	C_{new} (0.67)	AR (1.00)	C1 (1.00)	C_{new} (0.67)	TNR (0.67)
Tyrannosaurus rex MOR 555	C1 (0.67)	C_{new} (0.67)	AR (0.67)	C1 (1.00)	C_{new} (1.00)	TNR (1.00)
Allosaurus MOR 693	C1 (0.67)	C_{new} (1.00)	AR (0.67)	C1 (0.67)	C_{new} (1.00)	TNR (1.00)
Oryctodromeus cubicularis MOR 1642	N/A	C_{new} (1.00)	TNR (1.00)	C1 (1.00)	C_{new} (1.00)	TNR (1.00)
Lambeosaur MOR 471	N/A	C_{new} (0.67)	AR (0.67)	C1 (1.00)	C_{new} (1.00)	TNR (1.00)
Brachylophosaurus MOR 794	C1 (0.67)	A_{new} (0.67)	AR (0.67)	C1 (1.00)	C_{new} (1.00)	TNR (1.00)

Table 4: Results of 3-nearest neighbor analysis on non-avian dinosaur taxa. The assigned category is given followed by the posterior probability of membership. Dashes indicate missing data that prevented the procedure from being run on the taxon while N/A indicates that there was no consensus of nearest neighbors.

Table 5. Linear Discriminant Results for Non-Avian Dinosaurs

Taxa	Linear Discriminant Analyses					
	Raw			Scaled		
	5 Categories	3 Categories	Feeding	5 Categories	3 Categories	Feeding
Troodon formosus MOR563	C1 (1.00)	C_{new} (1.00)	TNR (0.98)	C1 (0.95)	C_{new} (0.82)	TNR (0.90)
Troodon MOR 748	C1 (1.00)	C_{new} (1.00)	-	-	-	TNR (1.00)
Bambiraptor feinbergi FIP 001 (cast)	A2 (0.55)	C_{new} (0.73)	TR (0.98)	A2 (0.76)	A_{new} (0.88)	AR (0.84)
Deinonychus antirrhopus MOR 747	C1 (0.89)	C_{new} (0.87)	AR (1.00)			
With MCZ 4371 femur				A2 (0.49)	A_{new} (0.69)	ANR (0.50)
Saurornitholestes (cast)	-	C_{new} (1.00)	-	-	-	-
Elmisaurus elegans MOR 752	C1 (0.70)	C_{new} (1.00)	TR (0.70)	-	-	-
Albertosaurus MOR 657 (cast)	A1 (1.00)	A_{new} (1.00)	AR (1.00)	C1 (1.00)	C_{new} (0.92)	TNR (0.93)
Daspletosaurus MOR 590	C1 (1.00)	A_{new} (1.00)	AR (1.00)	C1 (1.00)	C_{new} (0.82)	ANR (0.58)
Tyrannosaurus rex MOR 555	C1 (1.00)	C_{new} (1.00)	AR (1.00)	C1 (1.00)	C_{new} (1.00)	TNR (1.00)
Allosaurus MOR 693	C1 (1.00)	C_{new} (1.00)	AR (1.00)	C1 (0.99)	C_{new} (0.97)	ANR (0.58)
Oryctodromeus cubicularis MOR 1642	C1 (0.34)	C_{new} (0.94)	TNR (0.95)	C1 (0.98)	C_{new} (1.00)	TNR (0.99)
Lambeosaur MOR 471	A2 (1.00)	A_{new} (1.00)	AR (1.00)	C1 (0.99)	C_{new} (1.00)	TNR (0.98)
Brachylophosaurus MOR 794	A1 (1.00)	A_{new} (1.00)	AR (1.00)	C1 (1.00)	C_{new} (1.00)	TNR (1.00)

Table 5: Results of linear discriminant analysis on non-avian dinosaur taxa. The assigned category is given followed by the posterior probability of membership. Dashes indicate missing data that prevented the procedure from being run on the taxon.

generally classifies it as grasping/arboreal. These categorizations generally have low posterior probabilities. Like *Bambiraptor*, these data seem to indicate that the pedal morphology of *Deinonychus* is similar to avian taxa that do not have specialized behavior but instead have some capacity for both terrestrial and grasping behavior.

The *Saurornitholestes* specimen only has sufficient material for the three category discriminant function to be run. Like *Troodon* it is categorized as terrestrial/cursorial. However without the results of the other rules it is difficult to determine how much confidence can be placed in this result.

Elmisaurus is consistently classified as terrestrial/cursorial even though posterior probabilities are not always high. The DFA for feeding behavior also consistently categorizes this taxon as a terrestrial predator although again the posterior probabilities could be higher. Although the posterior probabilities vary, the categorization of *Elmisaurus* as a terrestrial predator is consistent and matches current interpretations of this taxon.

The large theropods, *Allosaurus*, *Albertosaurus*, *Daspletosaurus*, and *Tyrannosaurus* are classified consistently when using k-nearest neighbors. *Allosaurus* and *Tyrannosaurus* are also consistently classified by the linear discriminant functions. In these cases, the taxa are repeatedly classified as strongly terrestrial. There is inconsistency in the results for feeding behavior. The functions using the raw data classify these taxa with the arboreal birds of prey while the functions using the scaled data classify them with terrestrial species. Additionally, the linear discriminant functions on the raw data for *Albertosaurus* and *Daspletosaurus* classify these taxa with

arboreal/grasping species. It is almost certain that these taxa were terrestrial predators in terms of behavior. However, the role of the pes in feeding behavior is less clear as the raw and scaled data give differing results.

Oryctodromeus is classified as terrestrial by both linear discriminant and k-nearest neighbor rules. The categorization is consistent and the posterior probabilities are generally high. The functions for feeding behavior consistently classify *Oryctodromeus* as being a terrestrial non-predator. The classification of the lambeosaur and *Brachylophosaurus* are inconsistent. These taxa are generally classified with terrestrial/cursorial non-predators using the scaled data but classified as arboreal/grasping predators using the raw data. This inconsistency may relate to the distinctive pedal phalangeal morphology of these taxa.

DISCUSSION

Morphometric study of pes in theropods was performed by applying PCA and DFA in order to infer the behavior of extinct members of the group. Although an attempt was made to control for body size, this method did not completely eliminate size differences from the results. Methods that are robust against scaling of the variables performed better at separating specialist groups from each other. In contrast it was more difficult to discriminate among generalists.

The observations in the dataset were scaled by dividing each measure by the femur diameter of the individual in order to try to adjust for size differences. Nonetheless PC1 still can be interpreted as reflecting size. Size is a concern because in living birds those that are heaviest (the large ratites) are strictly terrestrial while few small birds are strictly terrestrial. Further, there is likely a maximum theoretical size beyond which arboreal behavior is impractical such as for the largest non-avian theropods. This size bias leads to the conclusion that PC1 cannot be used to accurately separate behaviors. There would be a trend for more terrestrial taxa to score highly on PC1 as a byproduct of large birds tending to have more terrestrial habits.

PCA performed on the correlation matrix appears to be less subject to this size bias than PCA performed on the covariance matrix. PC1 still reflects size, but it accounts for 26% less of the variation present in the data than PC1 in the covariance matrix PCA. PC2 contrasts taxa having long and thin phalanges versus those with short, wide phalanges while PC3 is interpreted similarly to PC2 for the covariance matrix. PC3 contrasts lengths of phalanx 3 and depth of the distal grooves of the trochleae against

lengths, widths, and height of phalanx 1 and widths of phalanges 2 and 3. The depth of the groove in the distal trochlea has been noted previously as indicative of behavior (Sternberg, 1932; Fisher, 1946) and these results support this finding. Most specialized terrestrial taxa, especially large graviportal ones (Storer, 1971), have relatively short, wide phalanges. Additionally, these taxa have a short phalanx 3 compared to phalanx 1 and a shallow groove in the distal trochleae of all the phalanges in digit III. These results suggest that using the correlation matrix is more useful in examining the relationship between morphology and behavior than using the covariance matrix.

While PCA is subject to the problem of scaling, DFA is not affected by differences in scaling among variables (Manly, 2005). Discrimination of species with more specialized behavior is easier than discriminating among generalists. This is the case for both the raw and scaled data. In general, error rates are lower for the scaled data than for the raw data. Taxa in categories A1 and C1 are much more consistently correctly assigned than taxa in categories A2 and C2. Taxa showing mixed behavior (the M category) are very difficult to correctly discriminate from those in A2 and C2.

When the original five behavioral groups are consolidated into three categories, results greatly improve. Estimated error rates remain high for mixed taxa but these make up a small proportion (9%) of the sample. These results compare favorably to the separation of categories observed in previous studies with 3 categories (Zhou, 1999; Hopson, 2001; Zhou and Farlow, 2001). With the data taken for this study, it is easier to discriminate among groups when weakly and strongly inclined species are grouped into the same category than when they are split. Alternatively, it may be possible that

discrimination among a larger number of groups that better represent the continuum of behavior that organisms show is possible with these measurements. However with an increasing number of groups a much larger sample size would also be required.

The analysis of the feeding categories indicates that arboreal predators are distinguishable from arboreal non-predators. When linear discriminant or k-nearest neighbors analyses are applied, the estimated error rates for AR are comparable to the best rates observed for A1 and C1. Avian terrestrial predators do not use the foot in a similar way to raptorial species. This likely explains why terrestrial predators are not easily separated from terrestrial non-predators. For instance, the Secretary bird stamps on prey items to kill them (Storer, 1971) rather than using the foot and talons to crush or suffocate like a raptor (Csermely et al., 1998). Additionally the sample size of terrestrial predators was small due to the low number of extant birds which feed in this way.

Both PCA and DFA computed on these data support previous workers' findings on the importance of relative phalangeal lengths. They also support the importance of features such as trochlear grooving and shape of the phalanx (low and wide versus high and thin). The analyses also highlight differences in the taxa sampled such as varying approaches to grasping and varying approaches to terrestrial locomotion. Finally, the analyses highlight variability within the avian orders sampled.

PCA conducted on the covariance matrix supports previous research into the relationship between morphology and behavior. Fisher (1946), Zhou (1999), Hopson (2001), and Zhou and Farlow (2001) found that terrestrial species tend to have shortened distal phalanges and lengthened proximal phalanges while the reverse is true for

arboreal/grasping species. In this study, PC2 recovered this variation, contrasting the lengths of phalanges 1 and 3 which separated grasping/arboreal species from terrestrial/cursorial species.

Taxa with a relatively short phalanx 2 compared to phalanges 1 and 3 score low on PC3 in the covariance matrix PCA. Of the 6 taxa that score the lowest on PC3, 5 are birds of prey. The Harpy Eagle, Golden Eagle, Gyrfalcon, Common Kestrel, and Osprey all show this trend with the addition of the Black-casqued Hornbill. This is in contrast to the cluster of taxa already noted that score relatively high on this component and low on PC2, five of which are owls and two of which are woodpeckers. Given that terrestrial species show less variation on this component than arboreal/grasping species, these two extremes may represent different morphological strategies for acquiring a strong grip. Owls represent a relatively longer middle phalanx while eagles and falcons represent a relatively short middle phalanx.

The Clapper Rail scores highly on PC2 and is separated from the rest of the C1 taxa. As noted, this may be a result of its marsh habitat. Raikow (1985) noted that terrestrial taxa that walk on soft substrates, such as Rails, tend to have elongated toes in contrast to those that walk on solid ground where the usual pattern is to reduce digit length. This difference in morphology is reflected in the PC plot.

Plotting avian orders according to the correlation matrix PCs (Fig. 7) shows a wide range of morphologies in the taxa sampled. Passeriformes show little variation in both PC2 and PC3. Almost all score negative on PC2, indicating that their phalanges are relatively long and thin. They score positive on PC3 indicating that they possess

arboreal/grasping features such as relatively deep trochlear grooves and an elongate phalanx 3. Cuculiformes show medium amounts of variation in PC2 but less variation in PC3 indicating more variation in lengths and widths of all phalanges than in amount of trochlear grooving and relative length of phalanx 3. Falconiformes display a similar pattern with more variation in PC2 than in PC 3. However, while Cuculiformes all score negative on PC2, most Falconiformes score positive indicating that Falconiformes have relatively wide phalanges compared to their lengths even though they score high on PC3. Strigiformes all score positive on PC 2 and PC3, clustering them in the upper right of the graph. Like Falconiformes this indicates they have relatively wide phalanges but retain the grasping/arboreal trochlear grooving and elongate phalanx 3. Predatory graspers may have mechanical or phylogenetic constraints that cause them to develop broad phalanges like terrestrial/cursorial taxa that nonetheless retain the grooving and phalanx 3 length proportions of grasping/arboreal taxa.

Galliformes have the most variation of the orders sampled. Members occupy every quadrant of the PC plot. Gruiformes show a large amount of variation in PC2 with less in PC3 even though every member of this order is classified as strongly terrestrial/cursorial. Coraciiformes and Tinamiformes have little variation in PC2 and PC3 so they cluster together closely. These groups have low diversity in locomotor behavior.

Struthioniformes and Piciformes are unlike the other orders in having noticeably more variation in PC3 than in PC2. Both groups have low locomotor diversity; the Piciformes sampled were all classified as strongly grasping/arboreal while the

Struthioniformes sampled were all classified as strongly terrestrial/cursorial. The Kiwi is the only ratite to score positive on PC3 while the ostrich scores lower than any other Struthioniformes member.

There is some clustering of orders on this plot (Fig. 7) but it tends to be in groups with less locomotor diversity. Groups such as Cuculiformes with members of every locomotor category show large variation in morphospace. This suggests that function has a larger role in phalangeal morphology than phylogeny.

DFA reinforces the importance of certain variables found to be useful in PCA. Stepwise selection of variables for the raw dataset often results in the selection of lengths, widths, and heights with a greater proportion of these belonging to the proximal phalanges. The proximal phalanges being larger, much of the variation among species is contained in these variables. In contrast, stepwise selection of the scaled dataset results in more lengths, widths, and heights of the distal phalanges as well as the depth of the grooves in the distal trochleae.

The non-avian dinosaurs sampled for this study produce a variety of results when plotted according to PCs and classified according to DFA. Certain taxa, such as *Troodon*, *Allosaurus*, *Tyrannosaurus*, and *Elmisaurus* are classified consistently. A consideration of the limits of sampling makes interpretation of taxa such as *Daspletosaurus*, *Albertosaurus*, *Brachylophosaurus*, and the lambeosaur possible.

A few patterns emerge when non-avian dinosaurs are plotted according to correlation matrix PCs (Fig. 6). Most taxa score high on PC2, reflecting relatively wide phalanges. The only exception is *Bambiraptor* which scores close to zero. *Troodon* and

Deinonychus plot close to the predatory graspers. *Albertosaurus*, *Daspletosaurus*, and *Allosaurus* score similarly to the Falconiformes and Strigiformes on PC3 but have even wider phalanges comparatively, pushing them to the right on the plot. *Oryctodromeus* and *Tyrannosaurus* plot closer to the ratites.

The most basal theropod sampled was *Allosaurus*. When DFA is applied to *Allosaurus* it is consistently categorized as a strongly terrestrial/cursorial taxon in the locomotor categories. The feeding category discriminant functions group *Allosaurus* with arboreal predators and non-predators. This discrepancy in the feeding categories may be explained by the PC plot. According to the PCs *Allosaurus* resembles arboreal taxa in relative lengths of digits and trochlear grooving while also having wide and short phalanges that are more characteristic of both predatory birds and terrestrial taxa.

More derived than *Allosaurus* are the three tyrannosaurids sampled. *Tyrannosaurus* is categorized similarly to *Allosaurus*. Locomotor category is always terrestrial/cursorial while the raw dataset feeding category runs group this taxon with the arboreal predators. *Albertosaurus* and *Daspletosaurus* are generally grouped with terrestrial/cursorial taxa but are sometimes classified as arboreal/grasping taxa. The raw dataset analyses categorize *Allosaurus* and the tyrannosaurids with the arboreal raptors. While it is impossible that these taxa were arboreal, the possibility that they may have had some prey-handling capacity in the foot is intriguing given that some large theropods such as *Tyrannosaurus* had greatly reduced forelimbs. This may explain the errors in classifying the locomotor behavior of *Albertosaurus* and *Daspletosaurus* using the linear discriminant rules. Since the behavior categories do not discriminate between predatory

graspers and non-predatory graspers this potential predatory grasping ability may result in grouping these two terrestrial non-avian theropods with avian arboreal/grasping taxa. This may also explain why *Albertosaurus*, *Daspletosaurus*, and *Allosaurus* plotted close to the predatory birds on the PC plot.

The oviraptor *Elmisaurus* is always classified as terrestrial/cursorial by DFA. These data indicate that the pedal morphology of *Elmisaurus* was well-adapted for terrestrial locomotion. *Elmisaurus* is classified as a terrestrial predator in the feeding category analyses which may indicate that the foot was used for prey handling. This would match Varricchio's (2001) interpretation of the elongate distal phalanges of this taxon being used for climbing or prey capture.

Although they are in sister-groups to each other, the results of *Troodon* do not closely match those for *Bambiraptor* and *Deinonychus*. While *Troodon* was originally described as having a foot that had "considerable grasping power" (Sternberg, 1932) these data indicate that *Troodon* was well-adapted for terrestrial (and probably cursorial) locomotion. The locomotor functions always classify *Troodon* as terrestrial/cursorial and, with one exception, the feeding behavior rules classify *Troodon* as terrestrial/cursorial. In contrast, *Bambiraptor* and *Deinonychus* have morphologies that appear to be less specialized, with deeper grooves in the distal trochleae and less distal reduction of phalangeal length. The analyses support this observation in having difficulty categorizing these taxa according to both locomotor and feeding behaviors. Although both had arms well-adapted for grasping (Senter, 2006) it is not unreasonable for these taxa to also have

used their legs in prey acquisition or handling. This behavior would select for a generalized morphology of the type seen here.

Although all of these taxa are usually interpreted as predators, the discriminant procedures seldom classify them as such and when they do they ally the multi-ton theropods with the arboreal rather than terrestrial predators. As noted, a significant hindrance to correct classification may be the low number of extant avian terrestrial predators and their lack of grasping with the feet in predation.

Turning from the saurischians to the ornithischians, the results for the ornithopods are mixed. *Oryctodromeus* matches current interpretations as a terrestrial/cursorial non-predator. The classifications for the lambeosaur and *Brachylophosaurus* are contradictory. These taxa were not predatory and were much too large to be arboreal and yet the raw dataset analysis clusters them with the arboreal predators. These results are interpreted as an artifact of the highly derived morphology of the distal phalanges in these taxa. Grooving of the articular surfaces in these ornithopods appears to involve the entire bone, unlike the theropod condition where grooving is limited to the trochlea while the overall shape of the phalanx remains the same. The extreme amount of proximodistal compression may also make some measurements that depend on finding the narrow part of the shaft between articulation surfaces not homologous for these taxa and theropods. These results should not be interpreted as providing evidence for grasping ability or intermediate morphology for these taxa, but instead be interpreted as demonstrating the limits of these techniques.

Although both may be informative, it may be that the raw data results are more meaningful when applied to the non-avian dinosaurs. Femur diameter was used a proxy for body weight, however it is likely that non-avian dinosaurs held the femur more vertically than modern birds (Gatesy, 1991; Hutchinson and Gatesy, 2000; Carrano and Hutchinson, 2002) which would increase torsional forces on the femur and result in differing femur shape (Carrano, 1998). However, the measure may be more defensible in troodontids and dromaeosaurs as the femur already shows signs of moving to a more avian orientation (Carrano, 1998). The raw data are not scaled according to femur diameter so these results are independent of this consideration.

CONCLUSION

Taxa with specialized behaviors are categorized by the functions developed in this study with low error rates. This indicates that taxa with specialized behaviors have distinct morphologies. The measurements used in this study are useful in capturing this morphological variation. Using subsets of the measurements improves the ability to discriminate, reduces the noise, and increases behavioral signal. Lengths alone can be used to discriminate among behaviors, but there are real improvements to estimated error rates when widths, heights, and the depth of the groove of the distal trochlea are added. Phylogeny does not appear to greatly constrain the morphological changes necessary to discriminate among behavioral groups.

It is also possible to separate raptorial from arboreal species using the same set of measurements with confidence. This indicates that there are morphological differences in digit III between predatory graspers and taxa that grasp branches and non-prey substrates such as those found throughout the foot noted by previous researchers (Fisher, 1946; Zhou, 1999). Additionally, predatory graspers appear to have stouter phalanges than non-predatory taxa. There are also differences within predatory taxa with owls differing from falcons and eagles in relative length of phalanx 2. Terrestrial predators may be separable from terrestrial non-predatory taxa, however this sample is insufficient to determine the viability of this approach.

Applying the discriminant procedures derived from modern birds to closely related and sized non-avian dinosaur taxa produces interpretable and reasonable results. *Troodon* is consistently found to be well-adapted for terrestrial/cursorial locomotor

behavior. *Bambiraptor* and *Deinonychus* appear to have more intermediate morphology indicative of some ability to grasp with the foot, possibly related to predation. It should be noted that *Bambiraptor* may be a juvenile dromaeosaur rather than a separate genus unto itself. If this is the case, variation between *Bambiraptor* and other dromaeosaurs may be ontogenetic rather than phylogenetic.

The non-avian Neotetanurae examined for this study appear to have had different grasping ability in the feet. The results for the tyrannosaurids, *Allosaurus*, and *Elmisaurus* indicate that these taxa may have had some grasping ability related to predation in the foot. If this is true, then it seems more likely that this predatory grasping ability was present in the ancestors of birds while *Troodon* lost this ability. In this scenario, grasping ability for prey handling may have been an exaptation for arboreal behavior in birds.

The categorizations resulting from applying the discriminant rules to distantly related dinosaur taxa must be examined skeptically. The feet of small ornithopods are similar to those of theropods. Therefore, applying the discriminant rules to these taxa is probably valid. The feet of large ornithopods are highly derived and using modern birds as analogues for these is not appropriate in this case. It should be noted that ornithopods are distantly related to theropods and could have different evolutionary constraints and pressures acting on them so parallels drawn should be made with caution.

Overall, the measurements examined in this study contribute useful additional morphological information for investigating theropod behavior. Discrimination among taxa with intermediate behaviors is not possible with these data. This likely reflects the

real continuum of morphologies and behaviors present in the natural world. That species without strong preferences for certain behaviors have generalist morphologies would not be surprising. Thus it may not be possible to discriminate among species with weak tendencies towards grasping or terrestrial locomotion by pedal morphology alone.

Future research directions include culling the most useful measures from the stepwise analysis and taking them on digits II and IV and possibly I if modern birds are the focus of study. Fossil birds also would be an interesting addition to the test dataset. Given the availability of cheap digital photography, methods using image analysis rather than linear measures may also be fruitful. Additionally these methods have the advantage of scaling to much smaller and larger taxa more easily.

Given work on hindlimb scaling (Gatesy, 1991) and pelvic morphology (Mattison, 1998) it may be fruitful to combine the most useful measures in distinguishing locomotor categories into a single combined study. The major disadvantage of such work when applied to fossil taxa is the availability of sufficient non-deformed material with which to work.

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APPENDICES

APPENDIX A

MEASUREMENTS OF BIRDS

Species	Femur d	P1L1	P1LDTD	P1L3A	P1L4
Megapodius freycinet duperrigi AMNH1389	7.28	18.7	0.61	18.26	18.86
Alectura lathami AMNH522bis	10.37	22.13	0.37	21.96	22.14
Crax rubra AMNH6272	9.21	27.48	0.82	27.16	27.6
Crax/Mitu mitu AMNH3815	8.95	27.49	0.64	26.75	28.22
Penelope pileata AMNH3798	8.46	23.03	1.13	21.51	22.56
Nothocrax urumutum AMNH6043	7.04	20.34	0.51	20.01	20.64
Ortalis canicollis AMNH25628	4.43	17.59	0.4	17.09	17.9
Coracopsis vasa AMNH2307	4.54	12.51	0.51	12.03	13.3
Carpococcyx renauldi AMNH12164	5.66	15.16	0.49	14.98	15.08
Geococcyx velox AMNH2167	3.7	10.12	0.3	9.7	10.61
Crotophaga ani AMNH5343	2.59	9.15	0.4	8.91	9.36
Piaya cayana AMNH5174	2.9	9.15	0.35	8.6	9.17
Cuculus sparveroides AMNH23219	2.63	8.16	0.28	7.76	8.33
Coccyzus melacoryphus AMNH23920	1.82	6.53	0.06	6.4	6.85
Pharomacrus mocinno AMNH5890	2.87	6.42	0.33	6.03	6.47
Grus antigone AMNH11428	14.51	45.22	1.15	44.15	44.93
Grus/Bugeranus carunculatus AMNH10218	13.56	44.01	0.99	43.15	44.71
Anthropoides virgo AMNH9177	8.98	28.68	0.77	27.5	28.92
Anthropoides paradisea AMNH1716	10.99	33.94	1.2	31.9	32.71
Cariama cristata AMNH1392	8.54	22.09	0.42	21.32	21.33
Chunga burmeisteri AMNH4250	6.96	24.2	0.5	22.66	23.2
Tinamus major robustus AMNH5283	5.28	12.86	0.23	12.41	12.82
Crypturellus tataupa AMNH6903	3.42	8.85	0.28	8.43	8.89
Nothoprocta ornata AMNH6503	5.36	13.07	0.51	12	12.43
Nothura maculosa AMNH3540	3.57	9.63	0.16	9.2	9.59
Nothura boraquira AMNH25427	3.64	10.58	0.37	10.22	10.7
Eudromia elegans AMNH26842	4.71	10.98	0.52	10.4	10.54
Apteryx australis AMNH4437	11.85	23.3	1.04	21.58	21.98
Casuarius unappendiculatus AMNH2729	18.43	43.07	0.19	41.43	41.62
Casuarius casuarius AMNH3870	26.13	51.93	1.45	50.47	51.05
Pterocnemia pennata AMNH12892	24.78	47.46	0.05	44.55	44.84
Callipepla squamata AMNH21530	3.3	9.71	0.2	9.36	9.69
Tragopan satyra AMNH614	7.81	22.48	0.57	21.56	22.59
Tragopan caboti AMNH16364	5.6	17.16	0.61	16.74	17.27
Coturnix japonica AMNH26503	2.98	9.84	0.27	9.57	9.83
Alectoris graeca chukar AMNH2769	4.3	13.01	0.42	12.78	13.26
Tetraogallus himalayensis AMNH25536	9.57	21.04	0.9	19.74	19.86
Arborophila torqueola AMNH2554	4.13	13.08	0.38	12.45	12.77
Gallus gallus AMNH4031	10.4	21.59	0.63	21.11	21.58
Numida meleagris AMNH23327	7.23	20.74	0.5	19.64	20.49
Guttera edouardi schoutedeni AMNH6045	7.03	20.97	0.33	20.28	20.89
Harpia harpyja AMNH2041	14.5	32.76	1.11	31.74	32.15
Aquila chrysaetos AMNH2038	14.36	29.12	1.5	28.07	28.81
Falco rusticolus AMNH2003	8.96	23.46	0.68	22.7	23.2
Rallus longirostris AMNH24509	3.91	20.58	0.21	20.39	20.65
Athene noctua AMNH25249	3.18	5.33	0.5	4.91	5.33

Species	Femur d	P1L1	P1LDTD	P1L3A	P1L4
Tyto alba AMNH16544	5.24	8.01	1.04	7.67	8.05
Morococcyx erythropygus AMNH4578	2.57	7.9	0.23	7.66	8.14
Clamator levaillantii AMNH16891	2.65	8.3	0.22	8	8.48
Corvus brachyrhynchos AMNH17603	4.58	10.81	0.34	10.51	11.29
Tinamus solitarius AMNH21983	6.47	15.45	0.22	14.16	14.79
Rhea americana USNM19915	20.51	40.04	0.24	37.3	36.79
Casuarius casuarius (juv) USNM18217	21.74	51.05	0.69	49.05	48.86
Centropus goliath USNM557168	5.36	14.5	0.64	13.84	14.82
Geococcyx californianus USNM430251	4.54	11.92	0.39	11.26	12.15
Megapodius freycinet USNM557000	6.67	17.73	0.79	17.63	18.24
Sagittarius serpentarius USNM322093	12.53	29.5	0.33	29.11	29.44
Tinamus tao tao USNM345738	5.84	15.33	0.49	14.6	15.36
Strix varia USNM502622	5.64	8.96	1.37	8.54	8.97
Meleagris gallopavo USNM556351	11.59	32.61	0.76	32.01	32.51
Cariama cristata USNM555731	7.89	23.97	0.57	23.45	23.03
Grus grus USNM610381	9.3	36.32	0.57	35.48	35.93
Tetrao urogallus USNM500264	8.98	25.82	0.87	24.42	26.38
Cathartes aura USNM621368	8.68	26.37	0.56	25.02	25.48
Dromaius novaehollandiae teaching collections	26.39	63.11	1.19	58.21	59.13
Coua ruficeps ruficeps USNM432195	3.28	10.05	0.86	9.44	9.99
Guira guira USNM428557	2.72	10.07	0.55	9.65	10.22
Eudynamis scolopacea chinensis USNM292053	3.23	11.07	0.36	10.61	11.51
Rhamphococcyx curvirostris harringtoni USNM562043	2.8	9.82	0.54	9.37	9.95
Aburria pipile USNM345799	7.43	19.33	0.55	18.53	18.94
Dendrortyx leucophrys USNM343477	4.34	15.59	0.27	15.56	15.97
Tympanuchus cupido USNM576678	5.56	18.74	0.73	17.88	18.65
Lagopus lagopus USNM622649	4.74	12.36	0.48	11.39	12.16
Ara chloroptera USNM623234	5.75	14.25	1.13	12.91	15.51
Vultur gryphus USNM346633	17.48	47.71	0.67	45.01	45.55
Gymnogyps californianus USNM489359	13.95	39.76	1.01	37.49	39.57
Cyanocorax cyanomelas USNM227413	3.01	8.89	0.38	8.8	9.05
Talegalla jobiensis USNM146774	.	20.36	0.56	20.09	20.34
Macrocephalon maleo USNM225130	6.93	24.34	0.51	23.39	24.07
Chamaepetes unicolor USNM613282	7.17	20.77	0.42	20.34	21.07
Ithaginis cruentus geoffrayi USNM319178	5.61	17.48	0.28	16.81	17.51
Tragopan temminckii USNM553832	5.12	17.46	0.5	16.76	17.69
Lophophorus impeyanus USNM347359	7.2	21.24	0.75	19.97	21.03
Rollulus rouloul USNM344458	3.58	11.87	0.41	11.29	11.82
Francolinus coqui USNM347708	3.31	10.07	0.23	9.76	10.15
Crossoptilon auritum USNM430712	7.47	19.74	0.69	18.13	19.93
Cyanocitta stelleri USNM555365	2.57	7.07	0.19	7.04	7.2
Zenaida aurita zenaida USNM292525	2.74	8.85	0.14	8.56	9.16
Leucosarcia melanoleuca USNM345193	3.55	12.74	0.66	12.23	12.98
Phaps chalcoptera USNM322219	3.12	9.12	0.25	8.71	9.59
Philemon argenticeps USNM227839	2.22	6.79	0.2	6.55	6.82
Ptilonorhynchus violaceus USNM559121	2.94	9.11	0.63	9.03	9.08

Species	Femur d	P1L1	P1LDTD	P1L3A	P1L4
Gymnorhina tibicen USNM612723	3.8	9.99	0.78	9.85	10.11
Paradisea raggiana salvadorii USNM489056	3.03	8.34	0.57	8.13	8.47
Pteroglossus aracari USNM347341	3.19	9.23	0.48	9.02	9.89
Rupicola peruviana sanguinolenta USNM428736	3.19	8.55	0.4	8.39	8.65
Asio flammeus flammeus USNM18960	3.78	8.76	1.79	7.39	7.58
Lepidogrammus/Phaenicophaeus cumingi USNM6130	3	10.11	0.35	9.76	10.22
Dasylophus/Phaenicophaeus superciliosus cagayensis	2.33	8.49	0.34	8.13	8.8
Tapera naevia USNM623126	1.88	7.52	0.15	7.31	7.76
Casuarius bennetti USNM346989	21.17	56.49	0.66	53.38	54.19
Casuarius unappendiculatus USNM489302	23.5	58.78	1.4	56.11	53.95
Struthio camelus molybdophanes USNM346697	37.99	86.96	0.93	82.9	87.91
Falco tinnunculus USNM610371	3.66	11.29	0.12	11.2	11.17
Pandion haliaetus USNM499429	6.78	13.42	1	13.26	13.26
Penelope superciliaris jacupemba USNM345795	7.2	22.39	0.3	22.04	22.91
Penelope marail USNM621703	6.28	17.26	0.56	16.9	17.63
Crax fasciolata USNM428612	7.72	26.77	0.68	25.8	27.82
Ceryle/Megaceryle maxima USNM560529	3.09	7.35	0.2	6.92	8.06
Chloroceryle amazona USNM559478	2.16	5.36	0.18	5.14	5.83
Turdus philomelos clarki USNM498650	2.11	6.41	0.26	6.35	6.47
Cephalopterus ornatus USNM346051	4.26	10.78	0.45	10.55	11.24
Gymnoderus foetidus USNM612074	2.91	7.3	0.33	7.21	7.61
Campephilus rubricollis USNM562222	3.41	6.73	0.61	5.92	6.24
Chrysocolaptes lucidus guttacristatus USNM343518	3.02	5.16	0.48	4.8	5.24
Ramphastos sulfuratus USNM612338	3.83	11.36	0.4	11.05	12.06
Saurothera vetula longirostris USNM225866	2.66	9.46	0.2	9.11	9.66
Centrocercus urophasianus USNM17991	7.32	19.77	0.88	18.45	19.84
Pavo muticus USNM343982	10.12	28.48	0.82	27.09	27.82
Polyplectron bicalcaratum USNM561448	4.85	17.38	0.46	16.58	17.23
Ceratogymna atrata USNM291326	5.81	19.31	0.52	18.77	19.44
Buceros bicornis USNM19336	11.61	26.01	0.83	25.26	26.4
Aceros/Rhyticeros plicatus USNM558296	8.51	19.09	0.47	18.37	19.11
Tockus deckeni USNM431796	3.28	9.89	0.22	9.74	10.07
Penelopides panini manillae USNM613075	5.06	13.07	0.4	12.84	13.05
Momotus momotus aequatorialis USNM428784	2.49	7.45	0.25	6.95	7.44
Choriotis/Ardeotis kori USNM491382	19.01	35.25	1.05	34.35	34.51
Neotis cafra/denhami USNM322694	13.48	26.35	0.73	24.61	26.4
Chlamydotis undulata macqueenii USNM430485	6.99	16.67	0.29	15.34	16.03
Eupodotis senegalensis USNM500301	5.73	15.55	0.62	14.92	15.25
Bubo bubo USNM610383	8.25	13.88	2.26	13.56	13.25
Struthio camelus (juv) teaching collections	23.72	58.85	0.95	55.6	58.55
Pica hudsonia teaching collections	2.72	7.93	0.1	7.58	7.88

Species	P1W1	P1W2	P1W3	P1H1	P1H2
Megapodius freycinet duperrigi AMNH1389	4.2	3.61	6.78	4.55	5.99
Alectura lathami AMNH522bis	5.4	4.05	7.34	4.65	7.32
Crax rubra AMNH6272	6.66	4.56	9.36	5.94	8.64
Crax/Mitu mitu AMNH3815	5.59	4.28	7.64	5.4	7.6
Penelope pileata AMNH3798	4.78	3.53	6.13	4.63	6.32
Nothocrax urumutum AMNH6043	4.7	3.36	5.77	4.07	6.22
Ortalis canicollis AMNH25628	3.06	2.28	4.26	3.06	4.33
Coracopsis vasa AMNH2307	3.73	2.84	5.17	2.98	4.01
Carpococcyx renauldi AMNH12164	3.31	2.77	4.63	3.65	4.21
Geococcyx velox AMNH2167	2.92	2.13	3.01	2.67	2.93
Crotophaga ani AMNH5343	1.82	1.53	2.35	1.71	2.15
Piaya cayana AMNH5174	1.96	1.36	2.28	1.63	2.35
Cuculus sparveroides AMNH23219	1.68	1.38	2.22	1.63	2.13
Coccyzus melacoryphus AMNH23920	1.27	0.88	1.72	1.23	1.43
Pharomacrus mocinno AMNH5890	2.19	1.62	2.82	1.77	2.28
Grus antigone AMNH11428	8.69	6.79	12.27	8.59	13.8
Grus/Bugeranus carunculatus AMNH10218	7.82	6.24	11.23	8.56	13
Anthropoides virgo AMNH9177	5.46	4.16	7.6	5.83	9.01
Anthropoides paradisea AMNH1716	7.3	5.21	10.28	7.08	12.04
Cariama cristata AMNH1392	5.03	4.02	6.91	4.24	7.15
Chunga burmeisteri AMNH4250	5.8	3.92	7.89	4.87	8.03
Tinamus major robustus AMNH5283	3.41	2.43	4.21	3.32	4.7
Crypturellus tataupa AMNH6903	2.2	1.46	2.83	1.94	3.02
Nothoprocta ornata AMNH6503	3.67	2.5	4.84	3.51	5.26
Nothura maculosa AMNH3540	2.42	1.58	3.2	2.37	3.48
Nothura boraquira AMNH25427	2.65	1.77	3.21	2.24	3.52
Eudromia elegans AMNH26842	3.59	2.16	4.01	2.93	4.51
Apteryx australis AMNH4437	6.86	4.4	8	6.58	9.77
Casuarius unappendiculatus AMNH2729	16.22	10.71	20.6	12.29	17.16
Casuarius casuarius AMNH3870	19.11	14.24	24.65	14.18	22.55
Pterocnemia pennata AMNH12892	18.61	11.91	19.74	12.45	20.28
Callipepla squamata AMNH21530	2.38	1.66	2.98	2.07	3.01
Tragopan satyra AMNH614	5.32	3.95	7.53	4.5	7.28
Tragopan caboti AMNH16364	4.04	2.68	4.93	3.31	4.67
Coturnix japonica AMNH26503	2.02	1.55	2.8	1.88	2.86
Alectoris graeca chukar AMNH2769	3.12	2.22	4.1	2.91	4.19
Tetraogallus himalayensis AMNH25536	6.23	4.41	8.25	5.48	8.05
Arborophila torqueola AMNH2554	3.39	2.17	4.62	2.8	3.96
Gallus gallus AMNH4031	6.97	5.6	10.18	5.71	9.09
Numida meleagris AMNH23327	4.88	3.62	6.6	4.57	6.98
Guttera edouardi schoutedeni AMNH6045	4.59	3.52	6.5	4.46	6.78
Harpia harpyja AMNH2041	9.33	6.94	12.34	8.17	9.01
Aquila chrysaetos AMNH2038	9.1	6.29	11.6	8.11	9.97
Falco rusticolus AMNH2003	5.18	4.32	8.97	5.03	6.13
Rallus longirostris AMNH24509	2.53	2.11	3.35	2.48	3.81
Athene noctua AMNH25249	3.48	3.07	4.11	3.03	3.87

Species	P1W1	P1W2	P1W3	P1H1	P1H2
Tyto alba AMNH16544	5.31	4.59	8.27	4.27	6.35
Morococcyx erythropygus AMNH4578	1.51	1.31	1.96	1.54	1.12
Clamator levaillantii AMNH16891	1.7	1.31	2.22	1.67	1.83
Corvus brachyrhynchos AMNH17603	3	2.21	4.33	2.89	3.73
Tinamus solitarius AMNH21983	3.99	2.91	5.48	3.61	5.71
Rhea americana USNM19915	16.97	12.57	20.04	12.33	20.82
Casuarius casuarius (juv) USNM18217	18.94	12.98	22.72	13.14	20.6
Centropus goliath USNM557168	3.66	3.03	4.78	3.58	4.65
Geococcyx californianus USNM430251	3.11	2.3	3.39	2.53	3.35
Megapodius freycinet USNM557000	4.23	3.43	6.64	4.18	5.59
Sagittarius serpentarius USNM322093	7.12	5.51	10.19	6.69	8.41
Tinamus tao tao USNM345738	3.63	2.68	4.78	3.86	6.08
Strix varia USNM502622	6.22	5.43	8.24	5.86	7.23
Meleagris gallopavo USNM556351	8.93	6.03	13.01	7.56	11.72
Cariama cristata USNM555731	5.74	4.33	7.92	4.94	8.44
Grus grus USNM610381	6.96	5.05	9.72	7.2	10.75
Tetrao urogallus USNM500264	6.24	4.24	8.07	5.88	8.36
Cathartes aura USNM621368	5.24	4.07	6.75	5.7	7.37
Dromaius novaehollandiae teaching collections	23.69	16.77	30.05	15.66	24.36
Coua ruficeps ruficeps USNM432195	2.58	2.08	3.47	2.65	3.38
Guira guira USNM428557	2.07	1.65	2.51	2.12	2.37
Eudynamis scolopacea chinensis USNM292053	2.54	1.84	3.09	2.08	2.5
Rhamphococcyx curvirostris harringtoni USNM562043	2.19	1.61	2.67	1.86	2.23
Aburria pipile USNM345799	4.35	2.99	5.19	3.48	5
Dendrortyx leucophrys USNM343477	2.99	2.44	4.29	3.17	4.51
Tympanuchus cupido USNM576678	3.83	2.59	4.92	3.55	5.6
Lagopus lagopus USNM622649	2.55	1.98	3.98	2.9	4.44
Ara chloroptera USNM623234	5.56	4.36	6.93	4.06	5.59
Vultur gryphus USNM346633	11.93	9.28	13.89	11.46	14.44
Gymnogyps californianus USNM489359	9.76	7.46	11.7	9.82	12
Cyanocorax cyanomelas USNM227413	2.33	1.68	3.16	2.16	2.76
Talegalla jobiensis USNM146774	4.58	3.5	6.16	4.39	6.39
Macrocephalon maleo USNM225130	5.15	3.76	7.16	4.76	6.77
Chamaepetes unicolor USNM613282	4.46	3.23	5.6	4.11	5.45
Ithaginis cruentus geoffrayi USNM319178	3.99	2.68	5.11	3.56	5.53
Tragopan temminckii USNM553832	4.57	3.01	5.65	3.57	5.19
Lophophorus impeyanus USNM347359	5.38	4.34	6.87	5.08	7.35
Rollulus rouloul USNM344458	2.6	1.89	3.28	2.53	3.55
Francolinus coqui USNM347708	2.52	1.65	3.6	2.55	3.93
Crossoptilon auritum USNM430712	5.05	3.75	6.84	4.29	6.62
Cyanocitta stelleri USNM555365	1.79	1.36	2.36	1.76	2.18
Zenaida aurita zenaida USNM292525	1.76	1.32	2.19	1.77	2.53
Leucosarcia melanoleuca USNM345193	2.71	1.86	3.45	2.46	3.89
Phaps chalcoptera USNM322219	2.15	1.72	2.66	2.28	3.19
Philemon argenticeps USNM227839	1.58	1.15	2.24	1.69	2.21
Ptilonorhynchus violaceus USNM559121	2.3	1.71	2.85	2.34	2.91

Species	P1W1	P1W2	P1W3	P1H1	P1H2
Gymnorhina tibicen USNM612723	2.92	2.35	3.87	2.92	3.64
Paradisea raggiana salvadorii USNM489056	2.33	1.63	2.88	2.43	3.1
Pteroglossus aracari USNM347341	2.83	1.93	2.99	2.38	3.27
Rupicola peruviana sanguinolenta USNM428736	2.08	1.56	2.69	2.18	2.96
Asio flammeus flammeus USNM18960	4.76	3.4	6.06	3.88	4.89
Lepidogrammus/Phaenicophaeus cumingi USNM6130	2.4	1.94	3.15	2.13	2.42
Dasylophus/Phaenicophaeus superciliosus cagayensis	1.83	1.37	2.3	1.62	1.92
Tapera naevia USNM623126	1.46	1.08	1.76	1.35	1.69
Casuarius bennetti USNM346989	17.67	11.92	23.83	14.41	23.06
Casuarius unappendiculatus USNM489302	21.44	15.88	27.11	14.54	23.2
Struthio camelus molybdophanes USNM346697	38.55	25.83	41.72	28.09	41.67
Falco tinnunculus USNM610371	2.52	1.72	3.85	2.62	2.89
Pandion haliaetus USNM499429	5.71	5.17	8.34	6.14	8.93
Penelope superciliaris jacupemba USNM345795	4.86	3.46	5.86	4.26	2.98
Penelope marail USNM621703	3.81	2.74	4.7	3.4	4.71
Crax fasciolata USNM428612	5.8	4.26	7.55	5.29	7.42
Ceryle/Megaceryle maxima USNM560529	2.2	1.47	2.43	2.41	1.65
Chloroceryle amazona USNM559478	1.39	1	1.5	1.58	1.99
Turdus philomelos clarki USNM498650	1.61	1.07	1.92	1.46	1.76
Cephalopterus ornatus USNM346051	2.69	1.9	2.84	2.59	3.61
Gymnoderus foetidus USNM612074	1.93	1.42	2.48	1.83	2.43
Campephilus rubricollis USNM562222	2.53	1.82	2.39	2.19	3.97
Chrysocolaptes lucidus guttacristatus USNM343518	2.52	2.01	2.23	2.13	4
Ramphastos sulfuratus USNM612338	3.57	2.45	3.61	2.89	4.05
Saurothera vetula longirostris USNM225866	1.98	1.37	2.44	1.69	2.25
Centrocercus urophasianus USNM17991	4.56	3.37	6.21	4.39	6.82
Pavo muticus USNM343982	7.1	4.9	8.77	5.97	9.14
Polyplectron bicalcaratum USNM561448	3.76	2.39	4.54	3.47	4.79
Ceratogymna atrata USNM291326	4.21	3.01	4.82	3.41	3.81
Buceros bicornis USNM19336	6.48	4.88	8.11	5.64	5.73
Aceros/Rhyticeros plicatus USNM558296	4.72	4.33	5.77	4.23	4.82
Tockus deckeni USNM431796	2.12	1.53	2.4	1.93	2.4
Penelopides panini manillae USNM613075	2.97	2.25	3.08	2.76	3.03
Momotus momotus aequatorialis USNM428784	1.77	1.29	1.85	1.88	2.69
Choriotis/Ardeotis kori USNM491382	11.57	7.24	14.61	8.56	16.52
Neotis cafra/denhami USNM322694	8.75	5.49	10.26	6.44	11.36
Chlamydotis undulata macqueenii USNM430485	5.68	3.38	6.09	4.04	6.99
Eupodotis senegalensis USNM500301	3.88	2.91	4.98	3.38	5.9
Bubo bubo USNM610383	8.92	7.64	11.85	8.69	9.98
Struthio camelus (juv) teaching collections	27.57	15.71	30.42	19.77	32.46
Pica hudsonia teaching collections	1.97	1.53	2.51	1.77	2.32

Species	P1H3	P2L1	P2DTD	P2L3A	P2L4
Megapodius freycinet duperrigi AMNH1389	3.09	14.08	0.72	12.28	14.34
Alectura lathami AMNH522bis	3.78	14.22	0.47	12.65	13.94
Crax rubra AMNH6272	4.47	21.01	0.32	20.23	21.43
Crax/Mitu mitu AMNH3815	3.65	20.26	0.61	20.42	22.21
Penelope pileata AMNH3798	3.35	18.85	0.73	17.85	19.59
Nothocrax urumutum AMNH6043	2.8	16.45	0.84	15.21	16.98
Ortalis canicollis AMNH25628	2.25	14.43	0.36	13.93	14.91
Coracopsis vasa AMNH2307	2.22	11.1	0.59	10.29	11.55
Carpococcyx renauldi AMNH12164	2.77	13.23	0.42	12.49	13.52
Geococcyx velox AMNH2167	1.74	9.6	0.72	9.1	9.32
Crotophaga ani AMNH5343	1.12	8.61	0.22	8.1	8.74
Piaya cayana AMNH5174	1.11	7.93	0.26	7.64	8.04
Cuculus sparveroides AMNH23219	1.26	7.25	0.25	6.82	7.39
Coccyzus melacoryphus AMNH23920	0.78	6.3	0.26	5.86	6.25
Pharomacrus mocinno AMNH5890	1.22	6.39	0.25	5.77	6.43
Grus antigone AMNH11428	5.63	30.43	0.76	28.53	30.74
Grus/Bugeranus carunculatus AMNH10218	6.4	28.25	1.16	26.48	28.52
Anthropoides virgo AMNH9177	3.75	18.49	0.74	16.99	18.68
Anthropoides paradisea AMNH1716	4.93	21.37	0.91	18.93	21.09
Cariama cristata AMNH1392	3.27	13.8	0.82	12.01	13.6
Chunga burmeisteri AMNH4250	3.48	17.87	0.4	15.39	17.28
Tinamus major robustus AMNH5283	2.33	9.41	0.28	8.83	9.66
Crypturellus tataupa AMNH6903	1.37	6.74	0.18	6.23	6.92
Nothoprocta ornata AMNH6503	2.2	10.15	0.59	9.17	10.37
Nothura maculosa AMNH3540	1.46	7.2	0.08	6.54	7.23
Nothura boraquira AMNH25427	1.42	7.87	0.21	7.37	8.19
Eudromia elegans AMNH26842	1.96	8.01	0.36	7.05	8.15
Apteryx australis AMNH4437	4.52	17.68	0.59	15.37	17.68
Casuarius unappendiculatus AMNH2729	9.02	29.93	0.41	28.56	31.96
Casuarius casuarius AMNH3870	12.25	38.57	1.46	34.98	38.98
Pterocnemia pennata AMNH12892	8.35	33.45	0.45	29.49	33.4
Callipepla squamata AMNH21530	1.34	8.35	0.24	7.79	8.34
Tragopan satyra AMNH614	3.24	19.92	0.59	18.81	20.07
Tragopan caboti AMNH16364	2.43	14.48	0.52	13.75	14.98
Coturnix japonica AMNH26503	1.27	8.12	0.24	7.67	8.1
Alectoris graeca chukar AMNH2769	1.91	11.65	0.3	10.58	11.29
Tetraogallus himalayensis AMNH25536	3.55	19.27	0.75	16.42	17.95
Arborophila torqueola AMNH2554	1.74	11.2	0.28	10.48	11.27
Gallus gallus AMNH4031	4.25	18.44	0.44	16.97	17.72
Numida meleagris AMNH23327	3.35	15.3	0.43	13.92	15.37
Guttera edouardi schoutedeni AMNH6045	3.41	16.11	0.34	15.15	16.5
Harpia harpyja AMNH2041	5.7	14.21	1.53	11.86	16.5
Aquila chrysaetos AMNH2038	5.83	12.04	1.15	11.15	15.87
Falco rusticolus AMNH2003	3.72	12.82	0.6	11.95	13.84
Rallus longirostris AMNH24509	1.9	15.31	0.28	14.74	15.47
Athene noctua AMNH25249	2.73	6.49	0.64	5.5	7.44

Species	P1H3	P2L1	P2DTD	P2L3A	P2L4
Tyto alba AMNH16544	4.16	13.63	0.92	12.4	15.15
Morococcyx erythropygus AMNH4578	2.16	7.9	0.19	7.46	7.91
Clamator levaillantii AMNH16891	1.13	7.43	0.15	7.03	7.59
Corvus brachyrhynchos AMNH17603	1.93	10.66	0.5	9.79	10.56
Tinamus solitarius AMNH21983	2.52	11.03	0.5	9.76	10.44
Rhea americana USNM19915	9.65	25.28	0.34	23.26	26.09
Casuarius casuarius (juv) USNM18217	9.75	35.46	1.28	32.67	36.03
Centropus goliath USNM557168	2.12	12.95	0.52	12.02	13.17
Geococcyx californianus USNM430251	1.84	10.48	0.45	9.63	10.56
Megapodius freycinet USNM557000	3.03	13.56	0.6	12.02	13.93
Sagittarius serpentarius USNM322093	4.42	15.09	0.55	12.65	15.13
Tinamus tao tao USNM345738	2.51	11.58	0.33	10.59	11.78
Strix varia USNM502622	4.59	12.61	1.75	10.73	15.25
Meleagris gallopavo USNM556351	5.25	24.13	0.71	22.74	24.76
Cariama cristata USNM555731	3.89	14.49	0.37	12.98	14.55
Grus grus USNM610381	4.43	23.54	0.72	22.2	24.24
Tetrao urogallus USNM500264	3.58	19.28	0.76	18.38	19.89
Cathartes aura USNM621368	3.99	22.3	2.56	21.04	22.97
Dromaius novaehollandiae teaching collections	12.56	40.5	0.59	37.69	41.62
Coua ruficeps ruficeps USNM432195	1.99	8.4	0.4	7.7	8.46
Guira guira USNM428557	1.46	9.03	0.3	8.55	9.31
Eudynamis scolopacea chinensis USNM292053	1.42	9.9	0.22	9.23	10.07
Rhamphococcyx curvirostris harringtoni USNM562043	1.15	8.22	0.31	7.75	8.39
Aburria pipile USNM345799	2.69	16.17	0.56	15.4	16.9
Dendrortyx leucophrys USNM343477	1.92	13.09	0.31	12.52	13.42
Tympanuchus cupido USNM576678	2.4	13.78	0.46	13.1	14.06
Lagopus lagopus USNM622649	1.88	8.92	0.44	7.95	8.95
Ara chloroptera USNM623234	3.07	12.35	1.03	10.38	13.02
Vultur gryphus USNM346633	8.73	35.77	1.24	32.63	37.3
Gymnogyps californianus USNM489359	6.45	31.25	1.3	29.7	33.46
Cyanocorax cyanomelas USNM227413	1.38	8.78	0.28	8.2	8.77
Talegalla jobiensis USNM146774	3.7	15.15	0.25	13.84	15.39
Macrocephalon maleo USNM225130	3.55	14.97	0.5	14.24	15.2
Chamaepetes unicolor USNM613282	2.98	16.98	0.53	16.31	17.59
Ithaginis cruentus geoffrayi USNM319178	2.27	14.44	0.45	13.54	14.43
Tragopan temminckii USNM553832	2.58	14.92	0.53	14.14	15.02
Lophophorus impeyanus USNM347359	3.4	18.68	0.59	16.8	18.79
Rollulus rouloul USNM344458	1.49	9.77	0.31	8.9	9.55
Francolinus coqui USNM347708	1.5	7.43	0.36	6.9	7.46
Crossoptilon auritum USNM430712	3.42	15.98	0.51	15.72	15.95
Cyanocitta stelleri USNM555365	1.13	7.18	0.19	6.78	7.19
Zenaida aurita zenaida USNM292525	1.32	7.24	0.18	6.77	7.37
Leucosarcia melanoleuca USNM345193	1.93	9.35	0.48	8.69	9.57
Phaps chalcoptera USNM322219	1.66	7.12	0.17	6.54	7.43
Philemon argenticeps USNM227839	1.09	6.44	0.19	6.04	6.47
Ptilonorhynchus violaceus USNM559121	1.47	9.97	0.4	9.27	10.08

Species	P1H3	P2L1	P2DTD	P2L3A	P2L4
Gymnorhina tibicen USNM612723	1.72	10.55	0.17	9.83	10.58
Paradisea raggiana salvadorii USNM489056	1.65	9.01	0.38	8.32	8.97
Pteroglossus aracari USNM347341	1.62	10.01	0.38	9.17	10.69
Rupicola peruviana sanguinolenta USNM428736	1.47	8.54	0.16	7.93	8.56
Asio flammeus flammeus USNM18960	2.88	9.31	0.67	8.03	10.89
Lepidogrammus/Phaenicophaeus cumingi USNM6130	1.44	9.09	0.26	8.73	9.52
Dasylophus/Phaenicophaeus superciliosus cagayensis	1.06	7.59	0.19	7.34	7.91
Tapera naevia USNM623126	0.83	7.94	0.18	7.73	8.06
Casuarius bennetti USNM346989	9.17	41.99	1.64	38.97	43.37
Casuarius unappendiculatus USNM489302	12.28	42.46	1.71	38.73	43.24
Struthio camelus molybdophanes USNM346697	18.93	54.55	1.75	50.77	57.42
Falco tinnunculus USNM610371	1.57	7.34	0.27	6.95	7.84
Pandion haliaetus USNM499429	3.52	6.84	1.11	5.37	6.41
Penelope superciliaris jacupemba USNM345795	5.69	18.04	0.71	16.88	18.63
Penelope marail USNM621703	2.38	14.68	0.42	14.11	15.44
Crax fasciolata USNM428612	3.99	21.16	0.8	19.92	22.15
Ceryle/Megaceryle maxima USNM560529	3.12	6.76	0.28	6.34	7.61
Chloroceryle amazona USNM559478	1.05	5.39	0.16	5.1	5.82
Turdus philomelos clarki USNM498650	0.88	7.37	0.17	6.99	7.27
Cephalopterus ornatus USNM346051	1.8	10.08	0.38	9.54	10.29
Gymnoderus foetidus USNM612074	1.36	7.19	0.2	6.8	7.4
Campephilus rubricollis USNM562222	1.25	8.38	0.41	7.57	9.02
Chrysocolaptes lucidus guttacristatus USNM343518	1.82	7.48	0.37	6.68	8.05
Ramphastos sulfuratus USNM612338	1.86	11.76	0.19	10.85	12.86
Saurothera vetula longirostris USNM225866	1.09	8.19	0.16	7.92	8.35
Centrocercus urophasianus USNM17991	2.96	15.04	0.49	13.98	15.47
Pavo muticus USNM343982	4.35	21.15	0.75	20.4	22.21
Polyplectron bicalcaratum USNM561448	2.35	14.55	0.34	13.8	14.93
Ceratogymna atrata USNM291326	2.38	12.71	0.3	12.15	12.9
Buceros bicornis USNM19336	4.88	19.58	0.25	18.4	19.76
Aceros/Rhyticeros plicatus USNM558296	3.17	14.82	0.46	14.32	15.02
Tockus deckeni USNM431796	1.33	7.76	0.22	7.32	7.92
Penelopides panini manillae USNM613075	2.12	9.62	0.19	9.14	9.66
Momotus momotus aequatorialis USNM428784	1.14	6.83	0.17	6.64	7.26
Choriotis/Ardeotis kori USNM491382	5.87	19.42	0.78	17.61	20.48
Neotis cafra/denhami USNM322694	4.01	25.13	1.05	13.24	25.8
Chlamydotis undulata macqueenii USNM430485	2.4	11.15	0.25	10.33	11.92
Eupodotis senegalensis USNM500301	2.37	8.76	0.53	8.05	9.18
Bubo bubo USNM610383	6.4	16.37	1.47	12.62	18.38
Struthio camelus (juv) teaching collections	13.29	31.35	0.21	30.45	32.64
Pica hudsonia teaching collections	1.08	7.39	0.12	6.99	7.53

Species	P2W1	P2W2	P2W3	P2H1	P2H2
Megapodius freycinet duperrigi AMNH1389	4.41	3.38	5.11	3.92	5.64
Alectura lathami AMNH522bis	5.02	3.78	5.98	3.82	5.83
Crax rubra AMNH6272	6.5	4.1	7.38	4.85	7.59
Crax/Mitu mitu AMNH3815	4.43	3.57	6.17	4.43	6.47
Penelope pileata AMNH3798	3.68	3.24	5	3.75	5.01
Nothocrax urumutum AMNH6043	3.97	3	5.21	3.41	5
Ortalis canicollis AMNH25628	2.54	2.21	3.44	2.38	3.51
Coracopsis vasa AMNH2307	2.99	2.35	3.74	2.91	3.43
Carpococcyx renauldi AMNH12164	2.89	2.38	3.65	2.89	3.61
Geococcyx velox AMNH2167	2.15	1.77	3.47	1.82	3.24
Crotophaga ani AMNH5343	1.64	1.43	2.07	1.38	1.91
Piaya cayana AMNH5174	1.53	1.15	2.09	1.29	1.96
Cuculus sparveroides AMNH23219	1.41	1.09	1.89	1.34	1.81
Coccyzus melacoryphus AMNH23920	1.01	0.73	1.26	1.01	1.23
Pharomacrus mocinno AMNH5890	1.75	1.4	2.25	1.62	1.9
Grus antigone AMNH11428	7.81	5.96	9.52	5.83	10.19
Grus/Bugeranus carunculatus AMNH10218	5.88	5.27	8.2	5.66	9.42
Anthropoides virgo AMNH9177	4.62	3.72	6.01	4.07	6.05
Anthropoides paradisea AMNH1716	5.58	4.72	8.46	4.85	8.07
Cariama cristata AMNH1392	5.05	3.82	5.49	3.46	5.65
Chunga burmeisteri AMNH4250	5.49	3.84	6.7	3.81	6.38
Tinamus major robustus AMNH5283	2.73	1.99	3.69	2.25	3.64
Crypturellus tataupa AMNH6903	1.73	1.22	2.3	1.69	2.17
Nothoprocta ornata AMNH6503	3.13	2.11	4.01	2.79	4.23
Nothura maculosa AMNH3540	1.95	1.4	2.96	1.72	2.7
Nothura boraquira AMNH25427	2.21	1.52	2.71	1.85	2.78
Eudromia elegans AMNH26842	3.04	1.83	3.72	2.26	3.41
Apteryx australis AMNH4437	5.8	4.53	7.18	5.74	8.61
Casuarius unappendiculatus AMNH2729	13.35	10.57	16.45	9.47	12.79
Casuarius casuarius AMNH3870	16.93	12.46	20.61	10.71	15.78
Pterocnemia pennata AMNH12892	16.66	11.81	16.96	10.81	13.98
Callipepla squamata AMNH21530	2.03	1.49	2.54	1.7	2.47
Tragopan satyra AMNH614	4.42	3.57	5.92	3.95	5.68
Tragopan caboti AMNH16364	3.52	2.5	4.2	2.55	3.76
Coturnix japonica AMNH26503	1.68	1.42	2.22	1.37	2.22
Alectoris graeca chukar AMNH2769	2.52	1.89	3.48	2.32	3.29
Tetraogallus himalayensis AMNH25536	5.86	4.09	6.79	4.4	6.7
Arborophila torqueola AMNH2554	2.68	2.12	3.45	2.47	3.28
Gallus gallus AMNH4031	6.12	4.81	8.41	4.6	7.04
Numida meleagris AMNH23327	4.27	3.34	5.46	3.57	5.49
Guttera edouardi schoutedeni AMNH6045	4.24	3.02	5.52	3.37	5.35
Harpia harpyja AMNH2041	7.88	7.26	9.24	6.84	9.29
Aquila chrysaetos AMNH2038	8.54	7.54	9.6	7.14	9.41
Falco rusticolus AMNH2003	4.74	3.93	5.93	4.22	5.82
Rallus longirostris AMNH24509	2.06	1.82	2.8	1.71	2.85
Athene noctua AMNH25249	2.81	2.54	3.27	2.51	3.63

Species	P2W1	P2W2	P2W3	P2H1	P2H2
Tyto alba AMNH16544	3.83	3.01	4.57	4.48	5.22
Morococcyx erythropygus AMNH4578	1.31	1.14	1.79	1.2	1.71
Clamator levaillantii AMNH16891	1.4	1.22	1.83	1.26	1.62
Corvus brachyrhynchos AMNH17603	2.77	2.16	3.22	2.55	3.23
Tinamus solitarius AMNH21983	3.29	2.44	4.42	2.66	4.1
Rhea americana USNM19915	14.64	12.07	15.67	10.48	14.87
Casuarius casuarius (juv) USNM18217	15.49	11.65	18.65	9.95	15.15
Centropus goliath USNM557168	3.29	2.89	4.04	3.02	3.99
Geococcyx californianus USNM430251	2.57	2.09	2.99	2.02	2.89
Megapodius freycinet USNM557000	3.86	3.29	4.68	3.55	2.91
Sagittarius serpentarius USNM322093	7.3	6.45	8.07	6.12	7.83
Tinamus tao tao USNM345738	2.91	2.18	4.14	2.81	4.62
Strix varia USNM502622	5.17	3.63	5.46	5.19	6.43
Meleagris gallopavo USNM556351	7.58	5.52	10.57	6.34	9.05
Cariama cristata USNM555731	5.04	4.16	6.18	4.12	6.03
Grus grus USNM610381	5.6	4.25	7.06	4.6	7.86
Tetrao urogallus USNM500264	5.09	3.63	6.6	4.3	6.52
Cathartes aura USNM621368	4.55	3.63	5.7	4.71	6.26
Dromaius novaehollandiae teaching collections	20.06	14.52	22.54	11.63	18.16
Coua ruficeps ruficeps USNM432195	2.2	1.91	2.84	2.02	2.68
Guira guira USNM428557	1.75	1.48	2.26	1.65	2.17
Eudynamis scolopacea chinensis USNM292053	2.15	1.66	2.47	1.81	2.48
Rhamphococcyx curvirostris harringtoni USNM562043	1.82	1.46	2.1	1.44	1.99
Aburria pipile USNM345799	3.65	2.91	4.48	2.87	3.97
Dendrortyx leucophrys USNM343477	2.47	2.14	3.2	2.58	3.6
Tympanuchus cupido USNM576678	2.97	2.24	3.81	2.64	4.22
Lagopus lagopus USNM622649	2.35	1.78	3.09	2.27	3.59
Ara chloroptera USNM623234	4.42	3.83	5.28	3.67	4.95
Vultur gryphus USNM346633	10.32	8.35	12.5	9.44	13.36
Gymnogyps californianus USNM489359	7.76	6.75	10.72	8.09	11.18
Cyanocorax cyanomelas USNM227413	2.23	1.6	2.34	1.79	2.42
Talegalla jobiensis USNM146774	4.25	3.3	5.01	3.57	5.26
Macrocephalon maleo USNM225130	4.4	3.56	6.07	3.79	5.16
Chamaepetes unicolor USNM613282	3.58	2.98	4.42	3.35	4.46
Ithaginis cruentus geoffrayi USNM319178	3.25	2.43	4.19	2.84	4.2
Tragopan temminckii USNM553832	3.42	2.59	4.71	3.02	4.16
Lophophorus impeyanus USNM347359	4.39	4.01	6.06	4.03	6.24
Rollulus rouloul USNM344458	2.09	1.61	2.63	2.08	2.76
Francolinus coqui USNM347708	2.12	1.54	2.86	1.96	2.74
Crossoptilon auritum USNM430712	4.08	3.35	5.14	3.62	4.99
Cyanocitta stelleri USNM555365	1.71	1.27	1.78	1.47	2.02
Zenaida aurita zenaida USNM292525	1.58	1.19	1.9	1.36	2.05
Leucosarcia melanoleuca USNM345193	2.34	1.79	2.93	2.06	2.81
Phaps chalcoptera USNM322219	1.86	1.47	2.25	1.69	2.65
Philemon argenticeps USNM227839	1.49	1.13	1.89	1.24	1.73
Ptilonorhynchus violaceus USNM559121	2.06	1.61	2.52	1.86	2.46

Species	P2W1	P2W2	P2W3	P2H1	P2H2
Gymnorhina tibicen USNM612723	2.57	1.85	2.96	2.15	3.12
Paradisea raggiana salvadorii USNM489056	2.19	1.6	2.69	1.95	2.67
Pteroglossus aracari USNM347341	2.28	1.92	2.72	2.27	2.94
Rupicola peruviana sanguinolenta USNM428736	1.93	1.34	2.42	1.72	2.3
Asio flammeus flammeus USNM18960	3.45	2.28	3.79	3.76	4.1
Lepidogrammus/Phaenicophaeus cumingi USNM6130	2.01	1.61	2.45	1.65	2.09
Dasylophus/Phaenicophaeus superciliosus cagayensis	1.43	1.17	1.88	1.41	1.78
Tapera naevia USNM623126	1.19	0.92	1.55	1.04	1.4
Casuarius bennetti USNM346989	15.2	11.09	18.52	11.27	16.25
Casuarius unappendiculatus USNM489302	17.71	12.27	23.13	11.2	16.15
Struthio camelus molybdophanes USNM346697	35.66	26.69	37.54	22	30.12
Falco tinnunculus USNM610371	2.24	1.58	2.86	2.17	2.62
Pandion haliaetus USNM499429	5.17	5.38	6.53	5.7	6.75
Penelope superciliaris jacupemba USNM345795	3.96	3.02	4.9	3.28	4.47
Penelope marail USNM621703	3.11	2.38	3.84	2.89	3.75
Crax fasciolata USNM428612	5.53	3.76	6.84	4.09	5.95
Ceryle/Megaceryle maxima USNM560529	2.07	1.56	2.48	1.77	2.82
Chloroceryle amazona USNM559478	1.26	0.85	1.49	1.26	1.56
Turdus philomelos clarki USNM498650	1.46	0.98	1.69	1.06	1.58
Cephalopterus ornatus USNM346051	2.4	1.73	2.82	2.02	2.91
Gymnoderus foetidus USNM612074	1.75	1.43	2.04	1.67	2.02
Campephilus rubricollis USNM562222	2.09	1.45	2.4	2.05	3.03
Chrysocolaptes lucidus guttacristatus USNM343518	2.08	1.41	2.5	1.84	2.77
Ramphastos sulfuratus USNM612338	2.74	2.3	3.2	2.47	3.23
Saurothera vetula longirostris USNM225866	1.52	1.19	2.11	1.31	1.96
Centrocercus urophasianus USNM17991	3.71	3.02	4.98	3.12	5.06
Pavo muticus USNM343982	5.52	4.35	7.48	4.76	7.11
Polyplectron bicalcaratum USNM561448	3.04	2.24	3.71	2.7	3.65
Ceratogymna atrata USNM291326	3.69	2.76	4.15	2.69	3.16
Buceros bicornis USNM19336	6.03	4.11	6.79	4.87	5.03
Aceros/Rhyticeros plicatus USNM558296	4.48	3.31	5.27	3.5	4.01
Tockus deckeni USNM431796	1.94	1.36	2.32	1.41	1.89
Penelopides panini manillae USNM613075	2.83	2.17	3.07	2.2	2.31
Momotus momotus aequatorialis USNM428784	1.72	1.2	2.08	1.56	2.16
Choriotis/Ardeotis kori USNM491382	9.54	7.01	11.57	6.19	9.94
Neotis cafra/denhami USNM322694	8.31	5.54	8.94	4.34	7.54
Chlamydotis undulata macqueenii USNM430485	5.08	3.42	5.66	2.93	4.59
Eupodotis senegalensis USNM500301	3.65	2.9	3.97	2.6	3.85
Bubo bubo USNM610383	7.53	6.21	8.57	7.6	10.44
Struthio camelus (juv) teaching collections	23.57	17.08	26.64	13.71	20.72
Pica hudsonia teaching collections	1.63	1.3	1.81	1.32	1.94

Species	P2H3	P3L1	P3DTD	P3L3A	P3L4
Megapodius freycinet duperrigi AMNH1389	3.22	12.47	0.43	10.7	12.39
Alectura lathami AMNH522bis	3.59	12.18	0.54	10.4	11.74
Crax rubra AMNH6272	4.17	20.85	0.45	18.63	20.71
Crax/Mitu mitu AMNH3815	3.51	18.61	0.26	16.78	18.83
Penelope pileata AMNH3798	3	16.66	0.2	15.02	16.66
Nothocrax urumutum AMNH6043	2.73	13.82	0.16	12.69	14.02
Ortalis canicollis AMNH25628	2.03	13.62	0.01	12.87	13.65
Coracopsis vasa AMNH2307	1.93	14.72	0.11	13.31	14.94
Carpococcyx renauldi AMNH12164	2.23	11.8	0.14	10.81	12.08
Geococcyx velox AMNH2167	1.31	8.41	0.11	7.73	8.43
Crotophaga ani AMNH5343	1.12	8.64	0.02	8.2	8.87
Piaya cayana AMNH5174	0.95	7.91	0.07	7.69	8.01
Cuculus sparveroides AMNH23219	1.06	7.91	0.05	7.65	8.07
Coccyzus melacoryphus AMNH23920	0.73	6.13	0.05	5.96	6.19
Pharomacrus mocinno AMNH5890	1.13	7.01	0.07	6.56	7.03
Grus antigone AMNH11428	4.6	26.09	0.53	23.1	25.02
Grus/Bugeranus carunculatus AMNH10218	4.54	19.67	1.06	18.05	19.65
Anthropoides virgo AMNH9177	2.95	12.67	0.64	11.1	12.28
Anthropoides paradisea AMNH1716	3.77	18.4	0.34	15.94	17.56
Cariama cristata AMNH1392	3.11	11.32	0.25	9.36	11.29
Chunga burmeisteri AMNH4250	3.15	13.73	0.72	11.97	13.65
Tinamus major robustus AMNH5283	1.78	6.66	0.09	5.93	6.66
Crypturellus tataupa AMNH6903	1.1	5.46	0.11	4.93	5.4
Nothoprocta ornata AMNH6503	1.89	8.43	0.41	7.24	8.35
Nothura maculosa AMNH3540	1.18	5.46	0	4.83	5.52
Nothura boraquira AMNH25427	1.28	6.27	0.11	5.77	6.38
Eudromia elegans AMNH26842	1.59	5.86	0.03	4.78	5.6
Apteryx australis AMNH4437	4.2	14.95	0.14	12.76	15.63
Casuarius unappendiculatus AMNH2729	7.77	22.46	0.37	19.53	22.4
Casuarius casuarius AMNH3870	8.98	28.34	0.51	24.53	27.88
Pterocnemia pennata AMNH12892	7.86	18.29	0.59	13.43	16.47
Callipepla squamata AMNH21530	1.17	7.52	0.16	6.91	7.4
Tragopan satyra AMNH614	2.92	19.7	0.22	17.92	19.15
Tragopan caboti AMNH16364	2.1	13.74	0.13	13.09	14.33
Coturnix japonica AMNH26503	1.16	6.69	0.1	6.3	6.82
Alectoris graeca chukar AMNH2769	1.69	9.69	0.14	8.78	9.63
Tetraogallus himalayensis AMNH25536	3.44	15.88	0.53	13.21	14.89
Arborophila torqueola AMNH2554	1.81	10.58	0.11	9.5	10.35
Gallus gallus AMNH4031	4	17.51	0.39	16.32	17.5
Numida meleagris AMNH23327	3.03	11.96	0.24	10.55	12.02
Guttera edouardi schoutedeni AMNH6045	2.78	13.75	0.22	12.26	13.85
Harpia harpyja AMNH2041	5.83	27.83	0.6	25.67	29.55
Aquila chrysaetos AMNH2038	6.17	28.63	0.23	26.03	30.12
Falco rusticolus AMNH2003	3.52	19.95	0.49	18.38	20.73
Rallus longirostris AMNH24509	1.43	12.56	0.14	11.87	12.63
Athene noctua AMNH25249	1.49	9.22	0.17	7.9	9.13

Species	P2H3	P3L1	P3DTD	P3L3A	P3L4
Tyto alba AMNH16544	2.75	17.51	0.67	14.72	16.04
Morococcyx erythropygus AMNH4578	0.98	6.81	0.04	6.53	6.84
Clamator levaillantii AMNH16891	0.95	8.16	0.05	7.91	8.18
Corvus brachyrhynchos AMNH17603	1.44	11.85	0.13	10.8	11.54
Tinamus solitarius AMNH21983	2.1	7.6	0.26	6.79	8.16
Rhea americana USNM19915	9.43	17.03	0.34	12.22	14.47
Casuarius casuarius (juv) USNM18217	8.63	24.13	1.02	19.85	23.17
Centropus goliath USNM557168	2.04	13.1	0.19	11.97	13.31
Geococcyx californianus USNM430251	1.43	9.11	0.12	8.41	9.18
Megapodius freycinet USNM557000	5.4	12.34	0.05	10.8	12.62
Sagittarius serpentarius USNM322093	4.87	14.04	0.98	11.9	13.61
Tinamus tao tao USNM345738	2.13	8.63	0.11	7.68	8.87
Strix varia USNM502622	2.51	18.36	0.77	15.67	18.95
Meleagris gallopavo USNM556351	4.84	20.19	0.25	18.48	20.43
Cariama cristata USNM555731	3.42	12.64	0.29	11.02	12.59
Grus grus USNM610381	3.32	19.98	0.24	18.36	19.97
Tetrao urogallus USNM500264	3.12	17.49	0.44	16.33	17.47
Cathartes aura USNM621368	3.16	20.13	0.28	18.15	19.79
Dromaius novaehollandiae teaching collections	9.07	24.98	0.03	21.27	24.95
Coua ruficeps ruficeps USNM432195	1.48	8.69	0.14	8.25	8.72
Guira guira USNM428557	1.16	9.27	0.12	8.83	9.53
Eudynamis scolopacea chinensis USNM292053	1.4	11.01	0.11	10.32	11.11
Rhamphococcyx curvirostris harringtoni USNM562043	1.02	9.95	0.2	9.28	10.02
Aburria pipile USNM345799	2.43	15.17	0.25	14.15	15.39
Dendrortyx leucophrys USNM343477	1.76	12.79	0.14	11.92	12.76
Tympanuchus cupido USNM576678	2.08	11.36	0.08	10.44	11.37
Lagopus lagopus USNM622649	1.84	7.65	0.35	6.68	7.54
Ara chloroptera USNM623234	2.91	19.04	0.09	17.3	19.43
Vultur gryphus USNM346633	7.15	28.75	0.81	24.26	27.77
Gymnogyps californianus USNM489359	5.65	28.3	0.52	25.17	28.1
Cyanocorax cyanomelas USNM227413	1.36	11.22	0.28	10.67	11.23
Talegalla jobiensis USNM146774	3.42	13.22	0.15	11.92	13.35
Macrocephalon maleo USNM225130	3.13	12.46	0.04	11.59	12.74
Chamaepetes unicolor USNM613282	2.59	15.67	0.11	14.59	15.98
Ithaginis cruentus geoffrayi USNM319178	2.04	13.36	0.16	12.06	13.03
Tragopan temminckii USNM553832	2.26	14.97	0.37	13.81	14.85
Lophophorus impeyanus USNM347359	3.31	16.85	0.3	14.97	16.83
Rollulus rouloul USNM344458	1.36	8.35	0.07	7.74	8.39
Francolinus coqui USNM347708	1.43	5.83	0.13	5.32	5.8
Crossoptilon auritum USNM430712	2.77	15.19	0.17	13.96	15.28
Cyanocitta stelleri USNM555365	1.05	8.63	0.02	8.17	8.62
Zenaida aurita zenaida USNM292525	1.24	5.98	0.04	5.61	6.11
Leucosarcia melanoleuca USNM345193	1.6	9.73	0.06	8.99	9.74
Phaps chalcoptera USNM322219	1.52	6.12	0.07	5.73	6.3
Philemon argenticeps USNM227839	0.85	8.22	0.06	7.98	8.21
Ptilonorhynchus violaceus USNM559121	1.16	10.93	0.12	10.57	10.91

Species	P2H3	P3L1	P3DTD	P3L3A	P3L4
Gymnorhina tibicen USNM612723	1.34	11.38	0.04	10.6	11.2
Paradisea raggiana salvadorii USNM489056	1.3	12.02	0.15	11.39	12.04
Pteroglossus aracari USNM347341	1.5	10.79	0.14	10.24	10.94
Rupicola peruviana sanguinolenta USNM428736	1.19	10.48	0.28	9.83	10.36
Asio flammeus flammeus USNM18960	2.21	14.74	0.54	13.11	14.7
Lepidogrammus/Phaenicophaeus cumingi USNM6130	1.23	9.49	0.11	9	9.82
Dasylophus/Phaenicophaeus superciliosus cagayensis	0.95	8.34	0.1	8.09	8.56
Tapera naevia USNM623126	0.73	6.99	0.24	6.69	7.1
Casuarius bennetti USNM346989	8.09	29.85	1.24	26.15	30
Casuarius unappendiculatus USNM489302	9.68	29.45	1.22	23.97	28.94
Struthio camelus molybdophanes USNM346697	16.56	34.46	1.74	27.73	31.6
Falco tinnunculus USNM610371	1.4	9.59	0.27	8.8	9.97
Pandion haliaetus USNM499429	5.62	23.47	0.7	21.93	24.03
Penelope superciliaris jacupemba USNM345795	2.68	16.19	0.08	14.89	16.8
Penelope marail USNM621703	2.16	13.25	0.33	12.44	13.52
Crax fasciolata USNM428612	3.57	18.58	0.26	17.25	19.1
Ceryle/Megaceryle maxima USNM560529	1.37	7.16	0.19	6.56	7.71
Chloroceryle amazona USNM559478	0.95	5.82	0.14	5.63	6.01
Turdus philomelos clarki USNM498650	0.7	7.26	0.12	6.82	7.13
Cephalopterus ornatus USNM346051	1.58	14.1	0.26	13.58	14.24
Gymnoderus foetidus USNM612074	1.21	9.81	0.14	9.14	9.43
Campephilus rubricollis USNM562222	1.21	11.63	0.18	10.36	11.56
Chrysocolaptes lucidus guttacristatus USNM343518	1.25	11.1	0.2	10.1	11.24
Ramphastos sulfuratus USNM612338	1.57	12.22	0.29	11.5	12.53
Saurothera vetula longirostris USNM225866	1.03	7.62	0.11	7.42	7.83
Centrocercus urophasianus USNM17991	2.52	13.37	0.22	11.93	13.56
Pavo muticus USNM343982	3.65	18.45	0.25	17.37	18.28
Polyplectron bicalcaratum USNM561448	2.04	12.96	0.22	12.22	13.37
Ceratogymna atrata USNM291326	2.18	16.33	0.02	15.82	16.22
Buceros bicornis USNM19336	3.68	24.55	0.2	23.77	24.51
Aceros/Rhyticeros plicatus USNM558296	2.83	19.1	0.3	18.29	19.1
Tockus deckeni USNM431796	1.13	8.29	0.06	8.22	8.32
Penelopides panini manillae USNM613075	1.62	12.01	0.19	11.53	11.99
Momotus momotus aequatorialis USNM428784	1.07	7.1	0.15	6.71	7.23
Choriotis/Ardeotis kori USNM491382	5.04	11.82	0.29	8.36	9.87
Neotis cafra/denhami USNM322694	3.68	9.13	0.05	6.5	8.01
Chlamydotis undulata macqueenii USNM430485	1.98	7.28	0.54	6.12	7.38
Eupodotis senegalensis USNM500301	2.09	5.08	0.14	4.45	5.42
Bubo bubo USNM610383	5.2	27.24	1.18	23.89	27.84
Struthio camelus (juv) teaching collections	10.64	19	0.08	16.59	17.39
Pica hudsonia teaching collections	0.96	7.92	0.03	7.49	7.93

Species	P3W1	P3W2	P3W3	P3H1	P3H2
Megapodius freycinet duperrigi AMNH1389	4.1	3.37	4.63	3.28	5.38
Alectura lathami AMNH522bis	5.03	3.82	5.48	3.42	4.82
Crax rubra AMNH6272	4.66	3.41	5.82	3.89	5.57
Crax/Mitu mitu AMNH3815	4.02	3.4	5.11	3.66	5.43
Penelope pileata AMNH3798	3.45	2.79	3.92	3.39	4.37
Nothocrax urumutum AMNH6043	3.59	2.64	4.21	2.75	4.31
Ortalis canicollis AMNH25628	2.24	1.84	2.72	2.47	3.2
Coracopsis vasa AMNH2307	2.65	2.12	3.1	2.87	3.5
Carpococcyx renauldi AMNH12164	2.64	2.14	2.95	2.19	3.35
Geococcyx velox AMNH2167	1.75	1.49	2.24	1.77	2.31
Crotophaga ani AMNH5343	1.51	1.21	1.74	1.55	1.85
Piaya cayana AMNH5174	1.33	1	1.6	1.29	1.78
Cuculus sparveroides AMNH23219	1.15	0.92	1.55	1.4	1.61
Coccyzus melacoryphus AMNH23920	0.78	0.62	0.99	0.89	1.13
Pharomacrus mocinno AMNH5890	1.44	1.09	1.77	1.77	1.82
Grus antigone AMNH11428	6.22	5.36	7.91	4.6	7.53
Grus/Bugeranus carunculatus AMNH10218	5.46	4.84	7.27	5.16	7.38
Anthropoides virgo AMNH9177	4.18	3.26	5.07	3.5	4.75
Anthropoides paradisea AMNH1716	4.94	4.34	6.44	4.03	6.27
Cariama cristata AMNH1392	4.7	3.92	4.94	3.01	5.07
Chunga burmeisteri AMNH4250	5.02	4.01	5.82	3.5	5.23
Tinamus major robustus AMNH5283	2.27	1.86	2.86	1.73	2.85
Crypturellus tataupa AMNH6903	1.4	1.08	2.01	1.25	2.22
Nothoprocta ornata AMNH6503	2.7	2	3.44	2.36	3.35
Nothura maculosa AMNH3540	1.82	1.38	2.5	1.38	2.34
Nothura boraquira AMNH25427	1.96	1.42	2.29	1.61	2.33
Eudromia elegans AMNH26842	2.75	1.89	3.21	1.79	2.87
Apteryx australis AMNH4437	5.88	4.95	6.1	4.8	7.35
Casuarius unappendiculatus AMNH2729	11.49	10.45	13.79	8.28	10.37
Casuarius casuarius AMNH3870	14.06	13	17.32	8.43	13.1
Pterocnemia pennata AMNH12892	14.43	14.43	14.89	9.83	12.42
Callipepla squamata AMNH21530	1.89	1.25	2.05	1.54	2.22
Tragopan satyra AMNH614	4.41	3.24	4.82	2.79	4.94
Tragopan caboti AMNH16364	2.98	2.21	3.4	2.08	3.48
Coturnix japonica AMNH26503	1.57	1.31	1.85	1.08	2.05
Alectoris graeca chukar AMNH2769	2.45	1.68	2.82	1.87	3.01
Tetraogallus himalayensis AMNH25536	5.47	3.85	5.91	3.3	5.89
Arborophila torqueola AMNH2554	2.61	2	2.89	2.03	3.23
Gallus gallus AMNH4031	5.67	4.16	6.64	3.08	5.77
Numida meleagris AMNH23327	4.28	3.4	4.5	2.83	4.84
Guttera edouardi schoutedeni AMNH6045	3.64	2.84	4.33	2.49	4.34
Harpia harpyja AMNH2041	7.71	7.19	8.74	5.53	9.46
Aquila chrysaetos AMNH2038	7.84	6.63	8.44	6.58	7.99
Falco rusticolus AMNH2003	4.42	3.96	5.35	4.28	5.01
Rallus longirostris AMNH24509	1.84	1.77	2.22	1.43	2.5
Athene noctua AMNH25249	2.34	2.34	2.96	2.06	3.04

Species	P3W1	P3W2	P3W3	P3H1	P3H2
Tyto alba AMNH16544	3.33	3.58	4.02	4.02	4.62
Morococcyx erythropygus AMNH4578	1.4	0.95	1.35	1.29	1.48
Clamator levaillantii AMNH16891	1.27	1.04	1.55	1.27	1.58
Corvus brachyrhynchos AMNH17603	2.43	2.04	2.79	2.09	2.84
Tinamus solitarius AMNH21983	2.86	2.3	3.77	2.01	3.34
Rhea americana USNM19915	12.7	13.47	14.05	10.05	12.13
Casuarius casuarius (juv) USNM18217	13.02	12.82	16.06	8.74	12.05
Centropus goliath USNM557168	3.13	2.68	3.5	2.83	3.67
Geococcyx californianus USNM430251	2.03	1.75	2.54	1.88	2.46
Megapodius freycinet USNM557000	3.7	3.01	4.18	3.03	5.13
Sagittarius serpentarius USNM322093	7.62	6.36	7.42	4.7	7.38
Tinamus tao tao USNM345738	2.62	1.88	2.92	2.11	3.52
Strix varia USNM502622	4.07	3.81	5.02	4.1	5.37
Meleagris gallopavo USNM556351	6.93	5.22	8.73	4.84	7.61
Cariama cristata USNM555731	5.12	4.16	5.33	3.59	5.23
Grus grus USNM610381	4.55	3.96	5.71	3.66	6.17
Tetrao urogallus USNM500264	4.51	3.19	5.2	2.87	5.2
Cathartes aura USNM621368	4.33	3.1	4.69	3.98	5.47
Dromaius novaehollandiae teaching collections	18.05	15.41	19.85	9.94	14.35
Coua ruficeps ruficeps USNM432195	2.13	1.62	2.44	1.83	2.32
Guira guira USNM428557	1.6	1.27	1.94	1.47	2.06
Eudynamis scolopacea chinensis USNM292053	1.88	1.43	1.96	1.74	2.25
Rhamphococcyx curvirostris harringtoni USNM562043	1.46	1.18	1.71	1.47	1.86
Aburria pipile USNM345799	3.24	2.4	3.52	2.8	3.62
Dendrortyx leucophrys USNM343477	2.29	1.85	2.58	2.16	3.2
Tympanuchus cupido USNM576678	2.54	1.94	3.02	1.77	3.49
Lagopus lagopus USNM622649	2.54	1.92	2.82	1.8	2.95
Ara chloroptera USNM623234	4.08	3.12	4.33	3.65	4.7
Vultur gryphus USNM346633	9.14	7.8	10.16	7.7	11.63
Gymnogyps californianus USNM489359	6.99	6.11	8.14	6.29	9.25
Cyanocorax cyanomelas USNM227413	1.88	1.46	2.07	1.63	2.15
Talegalla jobiensis USNM146774	3.64	3.06	4.44	3.12	4.8
Macrocephalon maleo USNM225130	4.21	3.22	4.87	2.92	4.8
Chamaepetes unicolor USNM613282	3.18	2.48	3.56	3.4	4
Ithaginis cruentus geoffrayi USNM319178	2.86	2.19	3.43	2.56	3.56
Tragopan temminckii USNM553832	3.41	2.31	3.88	2.11	3.67
Lophophorus impeyanus USNM347359	3.83	3.68	5.35	3.49	5.54
Rollulus rouloul USNM344458	2.1	1.53	2.15	1.61	2.49
Francolinus coqui USNM347708	1.98	1.42	2.21	1.27	2.44
Crossoptilon auritum USNM430712	3.6	3.01	4.39	3.01	4.53
Cyanocitta stelleri USNM555365	1.43	1.05	1.56	1.36	1.81
Zenaida aurita zenaida USNM292525	1.32	1.03	1.57	1.13	1.8
Leucosarcia melanoleuca USNM345193	2.02	1.5	2.53	1.66	2.43
Phaps chalcoptera USNM322219	1.67	1.34	2.02	1.45	2.22
Philemon argenticeps USNM227839	1.32	0.95	1.47	1.18	1.61
Ptilonorhynchus violaceus USNM559121	1.9	1.28	1.93	1.63	2.26

Species	P3W1	P3W2	P3W3	P3H1	P3H2
Gymnorhina tibicen USNM612723	2.28	1.46	2.37	1.89	2.85
Paradisea raggiana salvadorii USNM489056	2.08	1.52	2.17	1.75	2.52
Pteroglossus aracari USNM347341	1.93	1.69	2.13	1.99	2.6
Rupicola peruviana sanguinolenta USNM428736	1.76	1.11	1.9	1.6	2.13
Asio flammeus flammeus USNM18960	2.69	2.47	3.41	3.06	3.61
Lepidogrammus/Phaenicophaeus cumingi USNM6130	1.72	1.4	2.06	1.69	2.07
Dasylophus/Phaenicophaeus superciliosus cagayensis	1.37	1.13	1.54	1.29	1.7
Tapera naevia USNM623126	0.97	0.8	1.29	1	1.26
Casuarius bennetti USNM346989	14.02	11.5	15.9	9.25	13.21
Casuarius unappendiculatus USNM489302	14.84	12.53	18.21	10.92	14.42
Struthio camelus molybdophanes USNM346697	30.7	27.49	30.72	16.09	23.85
Falco tinnunculus USNM610371	2.08	1.87	2.45	2.05	2.57
Pandion haliaetus USNM499429	4.66	3.4	5.61	6.06	7.24
Penelope superciliaris jacupemba USNM345795	3.46	2.47	3.92	2.83	3.92
Penelope marail USNM621703	2.8	2.05	3.15	3.03	3.51
Crax fasciolata USNM428612	4.7	3.3	4.65	3.45	5.44
Ceryle/Megaceryle maxima USNM560529	1.8	1.28	2.16	1.7	2.4
Chloroceryle amazona USNM559478	1.03	0.75	1.37	1.11	1.45
Turdus philomelos clarki USNM498650	1.32	0.8	1.48	1.21	1.36
Cephalopterus ornatus USNM346051	2.41	1.43	2.45	2.01	2.77
Gymnoderus foetidus USNM612074	1.6	0.96	1.87	1.55	1.94
Campephilus rubricollis USNM562222	1.85	1.18	1.79	2.09	2.76
Chrysocolaptes lucidus guttacristatus USNM343518	1.84	1.22	1.75	1.88	2.5
Ramphastos sulfuratus USNM612338	2.23	1.82	2.49	2.12	2.98
Saurothera vetula longirostris USNM225866	1.41	1.08	1.65	1.32	1.62
Centrocercus urophasianus USNM17991	3.62	2.81	3.9	2.18	4.32
Pavo muticus USNM343982	4.73	3.62	5.87	3.66	6.15
Polyplectron bicalcaratum USNM561448	2.52	1.9	2.86	2.01	3.3
Ceratogymna atrata USNM291326	3.24	2.6	3.16	2.66	3.12
Buceros bicornis USNM19336	4.99	3.52	5.35	5.07	5.21
Aceros/Rhyticeros plicatus USNM558296	3.52	2.75	4.2	3.25	3.71
Tockus deckeni USNM431796	1.66	1.29	1.94	1.44	1.75
Penelopides panini manillae USNM613075	2.53	1.99	2.43	2.34	2.32
Momotus momotus aequatorialis USNM428784	1.58	1.23	1.99	1.69	1.93
Choriotis/Ardeotis kori USNM491382	9.44	9.88	10.26	5.26	7.8
Neotis cafra/denhami USNM322694	7.87	7.72	8.51	3.7	6.02
Chlamydotis undulata macqueenii USNM430485	4.92	4.01	4.88	2.12	3.52
Eupodotis senegalensis USNM500301	3.74	3.62	3.77	2.19	3.19
Bubo bubo USNM610383	6.18	5.89	7.41	6.6	8.12
Struthio camelus (juv) teaching collections	18.48	16.24	18.49	10.09	13.69
Pica hudsonia teaching collections	1.24	1.14	1.36	0.96	1.69

Species	P3H3	Feeding	Phylogeny	Behavior
Megapodius freycinet duperrigi AMNH1389	3.08	T	GM	C2
Alectura lathami AMNH522bis	3.35	T	GM	C2
Crax rubra AMNH6272	3.2	A	GC	C2
Crax/Mitu mitu AMNH3815	3.29	A	GC	A2
Penelope pileata AMNH3798	2.62	A	GC	A2
Nothocrax urumutum AMNH6043	2.5	T	GC	C2
Ortalis canicollis AMNH25628	1.82	A	GC	A2
Coracopsis vasa AMNH2307	1.83	A	PP	A1
Carpococcyx renauldi AMNH12164	2.06	T	CCP	C2
Geococcyx velox AMNH2167	1.21	T	CCN	C1
Crotophaga ani AMNH5343	1.05	M	CCC	M
Piaya cayana AMNH5174	0.93	A	CCP	A1
Cuculus sparveroides AMNH23219	1.15	A	CCU	A1
Coccyzus melacoryphus AMNH23920	0.68	A	CCP	A2
Pharomacrus mocinno AMNH5890	1.23	A	TT	A1
Grus antigone AMNH11428	4.14	T	RG	C1
Grus/Bugeranus carunculatus AMNH10218	3.9	T	RG	C1
Anthropoides virgo AMNH9177	2.37	T	RG	C1
Anthropoides paradisea AMNH1716	3.56	T	RG	C1
Cariama cristata AMNH1392	2.59	TR	RC	C1
Chunga burmeisteri AMNH4250	2.89	TR	RC	C1
Tinamus major robustus AMNH5283	1.71	T	IT	C1
Crypturellus tataupa AMNH6903	1.12	T	IT	C1
Nothoprocta ornata AMNH6503	1.81	T	IT	C1
Nothura maculosa AMNH3540	1.13	T	IT	C1
Nothura boraquira AMNH25427	1.31	T	IT	C1
Eudromia elegans AMNH26842	1.52	T	IT	C1
Apteryx australis AMNH4437	4.35	T	SA	C1
Casuarius unappendiculatus AMNH2729	7.02	T	SC	C1
Casuarius casuarius AMNH3870	7.63	T	SC	C1
Pterocnemia pennata AMNH12892	9.16	T	SR	C1
Callipepla squamata AMNH21530	1.13	T	GO	C2
Tragopan satyra AMNH614	2.76	M	GP	M
Tragopan caboti AMNH16364	1.92	M	GP	M
Coturnix japonica AMNH26503	0.92	T	GP	C1
Alectoris graeca chukar AMNH2769	1.68	T	GP	C1
Tetraogallus himalayensis AMNH25536	3.03	T	GP	C1
Arborophila torqueola AMNH2554	1.81	T	GP	C2
Gallus gallus AMNH4031	3.31	T	GP	C1
Numida meleagris AMNH23327	2.79	T	GN	C1
Guttera edouardi schoutedeni AMNH6045	2.38	T	GN	C2
Harpia harpyja AMNH2041	4.22	R	FA	A1
Aquila chrysaetos AMNH2038	4.25	R	FA	A1
Falco rusticolus AMNH2003	2.67	R	FF	A1
Rallus longirostris AMNH24509	1.33	T	RR	C1
Athene noctua AMNH25249	1.19	R	OS	A1

Species	P3H3	Feeding	Phylogeny	Behavior
Tyto alba AMNH16544	2.03	R	OT	A1
Morococcyx erythropygus AMNH4578	0.95	T	CCN	C2
Clamator levaillantii AMNH16891	0.97	A	CCU	A2
Corvus brachyrhynchos AMNH17603	1.67	M	AC	M
Tinamus solitarius AMNH21983	1.94	T	IT	C1
Rhea americana USNM19915	9.67	T	SR	C1
Casuarius casuarius (juv) USNM18217	8.37	T	SC	C1
Centropus goliath USNM557168	1.95	M	CCE	M
Geococcyx californianus USNM430251	1.45	T	CCN	C1
Megapodius freycinet USNM557000	2.77	T	GM	C2
Sagittarius serpentarius USNM322093	3.59	TR	FA	C1
Tinamus tao tao USNM345738	2	T	IT	C1
Strix varia USNM502622	2.34	R	OS	A1
Meleagris gallopavo USNM556351	4.28	T	GP	C2
Cariama cristata USNM555731	2.92	TR	RC	C1
Grus grus USNM610381	3.16	T	RG	C1
Tetrao urogallus USNM500264	2.87	M	GT	M
Cathartes aura USNM621368	3.35	T	FC	C2
Dromaius novaehollandiae teaching collections	8.41	T	SC	C1
Coua ruficeps ruficeps USNM432195	1.52	T	CCP	C2
Guira guira USNM428557	1.15	T	CCC	C2
Eudynamis scolopacea chinensis USNM292053	1.35	A	CCU	A1
Rhamphococcyx curvirostris harringtoni USNM562043	1.03	A	CCP	A1
Aburria pipile USNM345799	2.36	A	GC	A1
Dendrortyx leucophrys USNM343477	1.53	A	GO	A2
Tympanuchus cupido USNM576678	1.7	T	GT	C2
Lagopus lagopus USNM622649	1.69	T	GT	C2
Ara chloroptera USNM623234	2.56	A	PP	A1
Vultur gryphus USNM346633	6.76	T	NC	C2
Gymnogyps californianus USNM489359	5	T	NC	C2
Cyanocorax cyanomelas USNM227413	1.31	A	AC	A2
Talegalla jobiensis USNM146774	2.78	T	GM	C2
Macrocephalon maleo USNM225130	2.69	T	GM	C2
Chamaepetes unicolor USNM613282	2.59	A	GC	A2
Ithaginis cruentus geoffrayi USNM319178	1.98	M	GP	M
Tragopan temminckii USNM553832	2.01	A	GP	A2
Lophophorus impeyanus USNM347359	3.3	T	GP	C2
Rollulus rouloul USNM344458	1.31	T	GP	C2
Francolinus coqui USNM347708	1.28	T	GP	C2
Crossoptilon auritum USNM430712	2.61	T	GP	C2
Cyanocitta stelleri USNM555365	1.01	A	AC	A2
Zenaida aurita zenaida USNM292525	1	M	UC	M
Leucosarcia melanoleuca USNM345193	1.2	T	UC	C2
Phaps chalcoptera USNM322219	1.34	T	UC	C2
Philemon argenticeps USNM227839	1.07	A	AM	A1
Ptilonorhynchus violaceus USNM559121	1.32	M	AP	M

Species	P3H3	Feeding	Phylogeny	Behavior
Gymnorhina tibicen USNM612723	1.36	T	AA	C2
Paradisea raggiana salvadorii USNM489056	1.33	A	AR	A1
Pteroglossus aracari USNM347341	1.5	A	HR	A1
Rupicola peruviana sanguinolenta USNM428736	1.14	A	AO	A1
Asio flammeus flammeus USNM18960	1.98	R	OS	A2
Lepidogrammus/Phaenicophaeus cumingi USNM6130	1.22	A	CCP	A1
Dasylophus/Phaenicophaeus superciliosus cagayensis	0.98	A	CCP	A2
Tapera naevia USNM623126	0.67	M	CCN	M
Casuarius bennetti USNM346989	8.27	T	SC	C1
Casuarius unappendiculatus USNM489302	8.42	T	SC	C1
Struthio camelus molybdophanes USNM346697	15.46	T	SS	C1
Falco tinnunculus USNM610371	1.27	R	FF	A1
Pandion haliaetus USNM499429	3.59	R	FP	A1
Penelope superciliaris jacupemba USNM345795	2.45	A	GC	A2
Penelope marail USNM621703	1.81	A	GC	A2
Crax fasciolata USNM428612	3.36	T	GC	C2
Ceryle/Megaceryle maxima USNM560529	1.46	A	EC	A1
Chloroceryle amazona USNM559478	1.04	A	EC	A1
Turdus philomelos clarki USNM498650	0.92	M	AT	M
Cephalopterus ornatus USNM346051	1.54	A	AO	A1
Gymnoderus foetidus USNM612074	1.26	A	AO	A1
Campephilus rubricollis USNM562222	1.46	A	HP	A1
Chrysocolaptes lucidus guttacristatus USNM343518	1.23	A	HP	A1
Ramphastos sulfuratus USNM612338	1.7	A	HR	A1
Saurothera vetula longirostris USNM225866	1	A	CCP	A1
Centrocercus urophasianus USNM17991	2.3	T	GP	C1
Pavo muticus USNM343982	3.44	T	GP	C1
Polyplectron bicalcaratum USNM561448	1.74	T	GP	C2
Ceratogymna atrata USNM291326	2.3	A	EB	A2
Buceros bicornis USNM19336	4.19	A	EB	A2
Aceros/Rhyticeros plicatus USNM558296	3.08	A	EB	A2
Tockus deckeni USNM431796	1.28	M	EB	M
Penelopides panini manillae USNM613075	1.81	A	EB	A2
Momotus momotus aequatorialis USNM428784	1.11	A	EM	A2
Choriotis/Ardeotis kori USNM491382	5.44	T	RO	C1
Neotis cafra/denhami USNM322694	4.01	T	RO	C1
Chlamydotis undulata macqueenii USNM430485	1.82	T	RO	C1
Eupodotis senegalensis USNM500301	2.1	T	RO	C1
Bubo bubo USNM610383	3.61	R	OS	A1
Struthio camelus (juv) teaching collections	9.27	T	SS	C1
Pica hudsonia teaching collections	0.95	T	AC	C2

APPENDIX B

MEASUREMENTS OF NON-AVIAN THEROPODS

Species	Femur_d	P1L1	P1LDTD	P1L3A	P1L4	P1W1
MOR_cast_Bambiraptor_feinbergi_FIP_001	9.43	30.71	0.71	30.13	30.22	6.81
Troodon_formosus_MOR563	19.81	38.85	0.96	35.48	37.46	13.47
Saurornitholestes_Cast_MOR	.	48.85	1.28	47.21	51.28	13.66
Deinonychus_antirrhopus_MOR747_L_foot	.	49.58	2.18	45.31	51.83	17.54
Troodon_748	27.61	48.39	1.58	42.55	44.79	20.4
Albertosaurus_MOR_657	127.45	143.05	5.23	137.6	134.52	79.93
Elmisaurus_elegans_MOR752	.	33.55	1.62	32.62	33.33	10.98
Lambeosaur_MOR471	47.28	71.19	2.78	66.13	67.88	55.69
Oryctodromeus_MOR1642	20.57	36.66	1.93	34.92	36.84	17.89
Allosaurus_MOR693	73.08	125.53	3.24	109.99	127.64	56.36
Daspletosaurus_MOR590	95.16	122.57	5.5	117.19	127.58	86.22
Brachylophosaurus_MOR794	75.03	137.36	2.7	130.25	139.52	124.53
Tyrannosaurus_rex_MOR555	129.52	218.23	16.92	221.23	233.18	130.34

Species	P1W2	P1W3	P1H1	P1H2	P1H3	P2L1
MOR_cast_Bambiraptor_feinbergi_FIP_001	4.78	8.35	6.98	8.91	4.33	17.93
Troodon_formosus_MOR563	7.5	14.6	12.03	17.16	8.24	26.62
Saurornitholestes_Cast_MOR	8.84	13.52	13.06	16.72	7.95	.
Deinonychus_antirrhopus_MOR747_L_foot	13.02	22.25	16.86	22.85	10.4	32.33
Troodon_748	14.11	21.58	16.3	24.95	11.66	29.75
Albertosaurus_MOR_657	54.41	91.74	58.49	77.27	34.81	104.33
Elmisaurus_elegans_MOR752	7.18	13.38	9.82	12.69	6.39	23.01
Lambeosaur_MOR471	50.64	66.59	28.65	33.72	19.8	23.58
Oryctodromeus_MOR1642	13.61	22.11	14.38	17.49	9.84	27.21
Allosaurus_MOR693	41.96	67.44	40.63	66.74	38.58	93.4
Daspletosaurus_MOR590	50.22	82.76	50.58	83.26	34.85	93.27
Brachylophosaurus_MOR794	96.29	142.43	70.3	101.89	55.44	69.5
Tyrannosaurus_rex_MOR555	81.95	143.05	101.57	148.25	61.5	166.53

Species	P2DTD	P2L3A	P2L4	P2W1	P2W2	P2W3
MOR_cast_Bambiraptor_feinbergi_FIP_001	0.32	16.86	19.12	6.18	4.15	6.37
Troodon_formosus_MOR563	1.18	24.44	28.36	11.29	8.48	12.88
Saurornitholestes_Cast_MOR	.	.	.	.	.	.
Deinonychus_antirrhopus_MOR747_L_foot	1.29	30.52	36.67	16.2	12.32	18.16
Troodon_748	0.62	27.62	.	16.93	13.85	.
Albertosaurus_MOR_657	8.41	87.21	107.42	67.75	47.72	80.51
Elmisaurus_elegans_MOR752	1.33	19.74	23.26	9.67	7.84	11.31
Lambeosaur_MOR471	4.41	18.62	19.4	52.14	53.5	54.43
Oryctodromeus_MOR1642	1.99	24.24	28.84	15.12	12.74	17.81
Allosaurus_MOR693	3.47	80.02	95.08	45.99	33.62	57.66
Daspletosaurus_MOR590	2.42	76.5	101.8	62.14	44.7	67.14
Brachylophosaurus_MOR794	4.6	48.71	58.49	119.83	113.63	115.42
Tyrannosaurus_rex_MOR555	7.97	144.06	169.03	110.35	72.56	127.61

Species	P2H1	P2H2	P2H3	P3L1	P3DTD	P3L3A
MOR_cast_Bambiraptor_feinbergi_FIP_001	6.02	6.78	3.53	17.69	0.7	16.57
Troodon_formosus_MOR563	9.13	13.54	6.49	24.37	1.14	22.62
Saurornitholestes_Cast_MOR	.	.	.	30.07	1.28	26.66
Deinonychus_antirrhopus_MOR747_L_foot	14.56	17.17	9.16	31.27	1.43	27.19
Troodon_748	13.32	.	9.48	23.6	1.27	19.85
Albertosaurus_MOR_657	43.22	59.4	30.51	81.6	5.29	69.82
Elmisaurus_elegans_MOR752	8.95	11.15	6.33	24.68	1.28	21.42
Lambeosaur_MOR471	29.14	30.05	28.45	17.5	1.07	14.19
Oryctodromeus_MOR1642	11.79	15.65	8.25	23.77	0.87	19.79
Allosaurus_MOR693	32.68	45.78	26.59	74.86	3.73	58.89
Daspletosaurus_MOR590	40.48	54.73	32.49	76.92	1.56	62.53
Brachylophosaurus_MOR794	52.87	68.61	46.3	54.02	3.16	36.14
Tyrannosaurus_rex_MOR555	68.08	105.93	47.11	140.77	8.94	123.41

Species	P3L4	P3W1	P3W2	P3W3	P3H1	P3H2
MOR_cast_Bambiraptor_feinbergi_FIP_001	17.83	4.99	3.61	5.97	5.4	5.93
Troodon_formosus_MOR563	25.88	9.97	7.18	10.22	9.19	11.55
Saurornitholestes_Cast_MOR	29.9	9.02	6.99	11.57	10.61	12.42
Deinonychus_antirrhopus_MOR747_L_foot	31.13	12.65	10.33	15.77	14.44	15.21
Troodon_748	21.85	15.39	13.74	15.12	12.19	15.38
Albertosaurus_MOR_657	79.05	53.73	45.49	65.63	40.23	45.03
Elmisaurus_elegans_MOR752	25.5	8.09	6.4	9.6	7.97	10.65
Lambeosaur_MOR471	16.03	37.26	42.34	45.14	22.51	23.45
Oryctodromeus_MOR1642	25.02	15.06	12.16	15.48	9.69	13.22
Allosaurus_MOR693	70.86	31.78	28.48	43.23	28.12	34.29
Daspletosaurus_MOR590	79.54	46.99	37.89	56.97	34.65	40.36
Brachylophosaurus_MOR794	53.27	81.13	84.91	93.01	45.27	50.74
Tyrannosaurus_rex_MOR555	145.1	87.87	63.6	97.8	59.82	76.73

Species	P3H3
MOR_cast_Bambiraptor_feinbergi_FIP_001	3.18
Troodon_formosus_MOR563	5.96
Saurornitholestes_Cast_MOR	6.14
Deinonychus_antirrhopus_MOR747_L_foot	9.15
Troodon_748	9.89
Albertosaurus_MOR_657	30.29
Elmisaurus_elegans_MOR752	6.1
Lambeosaur_MOR471	22.16
Oryctodromeus_MOR1642	8
Allosaurus_MOR693	21.5
Daspletosaurus_MOR590	25.03
Brachylophosaurus_MOR794	44.7
Tyrannosaurus_rex_MOR555	42.06

APPENDIX C

EIGENVALUES AND EIGENVECTORS FOR PCA RUNS ON FEMUR DIAMETER SCALED DATA

Eigenvalues of the Covariance Matrix

	Eigenvalue	Difference	Proportion	Cumulative
1	3.32258646	2.33098830	0.7112	0.7112
2	0.99159815	0.83630774	0.2123	0.9235
3	0.15529041	0.03149324	0.0332	0.9567
4	0.12379717	0.10735807	0.0265	0.9832
5	0.01643911	0.00400295	0.0035	0.9867
6	0.01243616	0.00458889	0.0027	0.9894
7	0.00784727	0.00175030	0.0017	0.9911
8	0.00609697	0.00077917	0.0013	0.9924
9	0.00531780	0.00077469	0.0011	0.9935
10	0.00454312	0.00104478	0.0010	0.9945
11	0.00349834	0.00043429	0.0007	0.9952
12	0.00306405	0.00010637	0.0007	0.9959
13	0.00295767	0.00053946	0.0006	0.9965
14	0.00241821	0.00058499	0.0005	0.9971
15	0.00183322	0.00010038	0.0004	0.9974
16	0.00173284	0.00017965	0.0004	0.9978
17	0.00155319	0.00006745	0.0003	0.9982
18	0.00148574	0.00043421	0.0003	0.9985
19	0.00105153	0.00009545	0.0002	0.9987
20	0.00095608	0.00011605	0.0002	0.9989
21	0.00084004	0.00008386	0.0002	0.9991
22	0.00075617	0.00003226	0.0002	0.9992
23	0.00072391	0.00010897	0.0002	0.9994
24	0.00061494	0.00011264	0.0001	0.9995
25	0.00050230	0.00005910	0.0001	0.9996
26	0.00044320	0.00001301	0.0001	0.9997
27	0.00043019	0.00011889	0.0001	0.9998
28	0.00031130	0.00003960	0.0001	0.9999
29	0.00027170	0.00002279	0.0001	0.9999
30	0.00024891		0.0001	1.0000

Eigenvectors of the Covariance Matrix

	Comp.1	Comp.2	Comp.3	Comp.4
P1H1	-0.0255423886	-0.04233364	0.059671020	-0.204773546
P1H2	-0.0037637768	-0.03160956	0.131681912	-0.353615720
P1H3	-0.0147275872	-0.04110510	0.072196559	-0.129682068
P1L1	-0.1992695024	0.44703909	-0.233945228	-0.184567483
P1L3A	-0.2003853852	0.44508352	-0.265901527	-0.155315256
P1L4	-0.2235706456	0.45218795	-0.249392738	-0.128576388
P1LDTD	-0.0148758381	-0.03270915	0.012559425	-0.045438676
P1W1	-0.0106259075	-0.05406126	0.121119013	-0.271921518
P1W2	-0.0144906315	-0.05892523	0.074187660	-0.203560376
P1W3	-0.0119570661	-0.05686469	0.089549934	-0.398047620
P2DTD	-0.0083166197	-0.02011030	0.014432248	-0.029495900
P2H1	-0.0243866220	-0.06632318	0.047303412	-0.176606957
P2H2	-0.0226909536	-0.05262830	0.100927577	-0.243071183
P2H3	-0.0086821746	-0.02867496	-0.027765342	-0.127495057
P2L1	-0.3129065874	0.15023850	0.449953008	0.130114508
P2L3A	-0.3114545441	0.17978595	0.382648757	0.171593333
P2L4	-0.3211446651	0.10934497	0.488875556	0.067972417

P2W1	-0.0041033009	-0.04641093	0.069793522	-0.212400052
P2W2	-0.0062597575	-0.03763922	0.013383402	-0.181562986
P2W3	-0.0104709417	-0.02832983	0.081370291	-0.246080451
P3DTD	-0.0031178392	-0.01302006	0.009957715	-0.024992272
P3H1	-0.0321204418	-0.07374236	0.008247311	-0.112777158
P3H2	-0.0311977589	-0.05777201	0.035414243	-0.181812356
P3H3	-0.0136571399	-0.02219887	0.012748462	-0.053206571
P3L1	-0.4319269689	-0.32538425	-0.172247423	-0.007625926
P3L3A	-0.4307647121	-0.28182870	-0.236077212	0.075133350
P3L4	-0.4412106120	-0.32386219	-0.221294383	-0.009469923
P3W1	-0.0001404487	-0.03338877	0.043327763	-0.171567776
P3W2	0.0108121358	-0.03035754	0.056877437	-0.194122735
P3W3	-0.0032572554	-0.03347997	0.062329180	-0.215481580

Eigenvalues of the Correlation Matrix

	Eigenvalue	Difference	Proportion	Cumulative
1	13.6150114	6.6907979	0.4538	0.4538
2	6.9242135	4.3880104	0.2308	0.6846
3	2.5362031	1.3449152	0.0845	0.7692
4	1.1912879	0.2073776	0.0397	0.8089
5	0.9839103	0.2225053	0.0328	0.8417
6	0.7614050	0.1224040	0.0254	0.8671
7	0.6390010	0.0567876	0.0213	0.8884
8	0.5822134	0.1540332	0.0194	0.9078
9	0.4281802	0.0716671	0.0143	0.9220
10	0.3565132	0.0290690	0.0119	0.9339
11	0.3274441	0.0101198	0.0109	0.9448
12	0.3173244	0.0849100	0.0106	0.9554
13	0.2324144	0.0233475	0.0077	0.9632
14	0.2090669	0.0199873	0.0070	0.9701
15	0.1890796	0.0474308	0.0063	0.9764
16	0.1416488	0.0279465	0.0047	0.9812
17	0.1137024	0.0121433	0.0038	0.9850
18	0.1015591	0.0148754	0.0034	0.9883
19	0.0866837	0.0131943	0.0029	0.9912
20	0.0734894	0.0184955	0.0024	0.9937
21	0.0549939	0.0056969	0.0018	0.9955
22	0.0492970	0.0140077	0.0016	0.9972
23	0.0352894	0.0084243	0.0012	0.9983
24	0.0268650	0.0178353	0.0009	0.9992
25	0.0090298	0.0033561	0.0003	0.9995
26	0.0056736	0.0015429	0.0002	0.9997
27	0.0041308	0.0017537	0.0001	0.9999
28	0.0023770	0.0012975	0.0001	0.9999
29	0.0010796	0.0001674	0.0000	1.0000
30	0.0009122		0.0000	1.0000

Eigenvectors of the Correlation Matrix

	Comp.1	Comp.2	Comp.3	Comp.4
P1H1	-0.24595221	-0.025352132	-0.016011553	-0.157906788
P1H2	-0.16879944	0.086018862	-0.176500156	-0.373557661
P1H3	-0.17934487	0.011672063	0.071813749	-0.020527063
P1L1	0.01636435	-0.300233185	-0.346599224	-0.050354719
P1L3A	0.02003966	-0.302175990	-0.340870883	-0.028470532
P1L4	0.01370876	-0.312852504	-0.320287960	-0.014314478

P1LDTD	-0.17955312	-0.061614537	0.243123577	-0.160738077
P1W1	-0.22750115	0.101088227	-0.153818335	-0.023414584
P1W2	-0.24193976	0.069896052	-0.004753287	-0.032043535
P1W3	-0.21586608	0.094222042	-0.154691774	-0.113120491
P2DTD	-0.15388715	-0.041461894	0.250230144	-0.330612830
P2H1	-0.25164812	-0.001698675	0.131989461	-0.047147757
P2H2	-0.23113880	0.013239303	-0.011814365	-0.289705965
P2H3	-0.18118815	0.029485430	0.041220142	0.270757643
P2L1	-0.08174860	-0.337409096	-0.084340098	-0.048845867
P2L3A	-0.06775362	-0.345022046	-0.099053764	-0.029404751
P2L4	-0.10014015	-0.328108901	-0.058087068	-0.063520643
P2W1	-0.21835411	0.133977026	-0.163910389	0.139184540
P2W2	-0.22155667	0.106920152	-0.124356834	0.237148744
P2W3	-0.22071078	0.076604100	-0.247738157	-0.002115706
P3DTD	-0.14832869	0.023932245	0.169181618	-0.344566971
P3H1	-0.22388168	-0.055907834	0.221566493	0.190821396
P3H2	-0.23914551	-0.048995819	0.093949232	-0.030256860
P3H3	-0.18738635	-0.062581900	0.065793254	0.430887825
P3L1	-0.15679449	-0.261859995	0.200962192	0.122340381
P3L3A	-0.14415906	-0.275457312	0.188303128	0.151451590
P3L4	-0.15523334	-0.264223613	0.200900463	0.129506133
P3W1	-0.19716290	0.147553856	-0.179984556	0.184635386
P3W2	-0.16600757	0.210358975	-0.198013496	0.095204902
P3W3	-0.22021872	0.125933118	-0.182337612	0.011005478

APPENDIX D

COEFFICIENTS FOR DFA

The coefficients in Table 6 can be used to classify a new observation by calculating the result of the discriminant functions:

$$L_i = 2\ln\prod_i - 2y'\sum^{-1}\mu_i + \mu_i'\sum^{-1}\mu_i = \sum_j c_j y_j + c_0$$

where Σ is the covariance matrix, $\Sigma^{-1}\mu_i$ are the coefficients presented here and $\mu_i'\Sigma^{-1}\mu_i$ = $[C_0 - \ln(\Pi_i)]*(-2)$ where C_0 is the constant and Π_i is the prior probability of membership in that group. For this study the prior probabilities were taken to be proportional to their occurrence in the sample. The observation is assigned to the group with the highest value for the discriminant function.

Additionally the posterior probability for group assignment can be calculated using the function

$$\text{Prob}(pop_i|y) = \frac{e^{L_i}}{\sum_{j=1}^{k} e^{L_j}}$$

Where Li is the linear function for each population: $L_i = y'c_i + c_{0i}$

In this case the observation is assigned to the group with the highest posterior probability.

Table 6. Coefficients for DFA

	5 Category Raw Data				
Variable	A1	A2	C1	C2	M
Constant	-6.37226	-7.03867	-5.46097	-4.89904	-6.01166
P1H2	0.42497	-0.45416	0.95256	-0.11709	0.20694
P3H1	1.97047	1.73489	0.19945	-1.10872	-0.00833
P2L3A	0.09984	0.52003	0.12931	0.52581	0.56700
P3L3A	1.23977	1.02898	0.08153	0.25891	0.89297
P3H2	0.18831	-3.38628	3.51609	1.34574	-0.28491
P3W2	1.63905	1.72188	-0.69914	-0.64278	1.49689
P1L1	-0.48699	-0.22444	0.01825	-0.19554	-0.40722
P2H3	-1.88061	0.06434	-1.71225	0.97015	-0.68951
P2H1	-2.92810	-0.49393	-3.45701	-0.79830	-2.10622

	3 Category Raw Data		
Variable	A	C	M
Constant	-5.05393	-3.63355	-5.09210
P1L1	-0.16829	0.16257	-0.03164
P3L3A	1.06112	0.11319	0.84187
P3W2	1.09541	-1.02835	0.91226
P3H1	1.17809	-0.98587	-0.58675
P3H2	-2.54020	1.60462	-1.32207

Feeding Category Raw Data					
Variable	A	M	R	T	TR
Constant	-5.91674	-6.98616	-26.12925	-5.16945	-13.29452
P1L3A	-0.49322	-0.63602	0.00756	-0.40731	0.89958
P1W1	1.49556	-0.17535	4.72621	-1.40529	-2.17059
P1W3	-1.24777	-1.22135	4.30759	-0.84292	0.26706
P1H1	2.52758	3.75690	-1.43197	4.02048	-4.94883
P2L1	0.26920	1.32405	-3.03851	1.86310	4.75888
P2L3A	0.69123	1.20588	-3.30453	0.73532	-1.17396
P2L4	-0.40705	-1.54025	4.02423	-1.71816	-4.00534
P2W3	-1.53984	-1.14402	-7.27475	-0.40134	-0.75353
P2H1	-5.04115	-5.59210	4.90888	-4.56751	8.42771
P3L1	1.14930	0.81934	2.15240	0.12474	-0.18824
P3DTD	-1.94559	-4.21812	9.76265	-5.51907	2.19339
P3W1	2.30390	3.37536	-2.26640	1.48454	2.81047
P3H2	-0.99675	-0.12113	-0.29717	2.20697	1.84074
P3H3	2.04526	0.94874	-4.35777	0.43263	-6.50792

5 Category Scaled Data					
Variable	A1	A2	C1	C2	M
Constant	-45.18523	-41.52548	-42.24736	-46.74785	-46.30788
P1DTD	-57.37213	-43.17121	-4.87386	-8.59256	-23.67363
P1W1	-11.55589	-24.07898	-12.39982	-38.53666	-35.28100
P2L1	-8.11156	8.58163	46.21108	35.22737	27.01031
P2L4	14.19572	3.06564	-29.15226	-17.47731	-11.33912
P2W1	53.94619	60.20411	68.58835	78.18273	82.24807
P2H1	-15.13682	30.14323	-5.99204	34.14128	19.53944
P2H3	38.34653	52.31305	34.79148	54.42828	42.26761
P3DTD	-49.50039	-74.22336	-40.29974	-80.96485	-66.36102
P3L4	3.01179	-1.27638	-15.30450	-11.62362	-6.52052
P3H1	24.47366	11.37080	-9.20737	-20.13925	-1.17712
P3H2	32.66887	-2.10044	58.51605	37.22373	24.14346

3 Category Scaled Data			
Variable	A	C	M
Constant	-30.93183	-32.01904	-33.67356
P1DTD	-54.97548	-17.76800	-34.45672
P2L1	8.56143	42.04091	31.26942
P2L4	-0.52627	-27.08427	-18.00773
P3L4	-3.85718	-15.98557	-9.75516
P3H1	47.48288	19.24797	34.26727
P3H2	46.82543	86.29946	62.03511

Feeding Category Scaled Data					
Variable	A	M	R	T	TR
Constant	-58.45389	-60.02725	-89.04868	-60.26522	-79.18710
P1DTD	-44.35724	-18.70082	-70.40854	-4.55822	-13.90872
P1L3A	15.13189	15.50767	59.30502	25.75482	47.18252
P1L4	3.15479	-0.97812	-29.92315	-8.34206	-21.88876
P1W1	31.49882	13.62127	28.71669	18.04592	1.81300
P1H1	-6.81753	8.92489	-8.99047	12.28112	-36.66025
P1H3	18.21761	4.81853	51.15074	12.75892	28.02275
P2L3A	-10.04625	1.65726	-41.95743	-1.78236	-11.03460
P2W2	-61.55328	-27.73746	-112.56980	-34.99925	-32.93686
P2H1	-8.96340	-23.32283	68.01699	-29.50124	-1.71105
P3DTD	1.21048	-7.38984	60.70034	-4.02576	82.01130
P3L4	1.14572	-6.85233	17.97511	-10.89154	-8.85009
P3W1	61.43387	80.97651	-11.54814	65.99679	86.94285
P3W2	3.68856	-12.90481	111.92419	-4.76931	12.44456
P3H1	23.75537	4.89299	56.53553	-4.41522	11.16579
P3H2	15.68954	22.77740	33.14759	50.52868	74.05479
P3H3	98.58758	107.56380	-50.50073	105.76645	57.31608