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Journal of Human Evolution xxx (2017) 1–6

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Alternative methods for calculating percentage prediction error and their implications for predicting body mass in fossil taxa

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A R T I C L E   I N F O

Article history:
Received 26 April 2016
Accepted 15 March 2017
Available online xxx

Keywords:
Body size
Allometry
Scaling
Primates
Paleontology

A B S T R A C T

Since body mass covaries with many ecological aspects of an animal, body mass prediction of fossil taxa is a frequent goal of paleontologists. Body mass prediction often relies on a body mass prediction equation (BMPE): a bivariate relationship between a predictor variable (e.g., molar occlusal area, femoral head breadth) and body mass as observed in extant taxa. A variety of metrics have been used to assess the reliability of BMPEs, including percentage prediction error (%PE), which involves predicting body masses of a test sample comprising individuals with associated masses. A mean %PE can be calculated in two ways: 1) as the mean %PE of multiple individual predictions (%MPE), or 2) as the %PE of mean body mass generated from the mean predictor value of multiple individuals (here termed %PEM). Differences between these two approaches have never been formally examined and no formal protocols have been recommended. Using a large sample of cercopithecoid primates (406 individuals from 50 species/subspecies) with associated body masses, body mass is predicted with six previously published interspecific BMPEs. Both %MPE and %PEM are calculated and compared. For all BMPEs, the distributions of differences between %MPE and %PEM exhibit positive skew and have medians significantly greater than zero, indicating that the examined prediction equations are more accurate at predicting mean body mass when they are applied to mean predictor values. The decreased predictive accuracy of %MPE relative to %PEM likely stems from changing the unit of analysis from mean values (in the reference sample) to individual values (in the test sample) when calculating %MPE. Empirical results are supported with a simulated dataset. Implications for body mass prediction in fossil species are discussed.

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1. Introduction

Because an animal's body mass covaries with many aspects of its ecology, physiology, and behavior (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984), predicting body mass is a frequent goal in comparative biology and paleontology (e.g., Gingerich et al., 1982; Conroy, 1987; Dagosto and Terranova, 1992; Delson et al., 2000; Ruff, 2003). While some studies focus exclusively on issues surrounding body mass prediction, it is often a component of broader descriptions of fossil material (e.g., Kay and Simons, 1980; Meldrum and Kay, 1997; Bloch et al., 1998; Sears et al., 2008; Boyer et al., 2013; Bertrand et al., 2016). The most common method for predicting body mass uses the observed relationship between body mass and a particular predictor variable. Popular predictor variables for paleontological application include molar dimensions (Kay and Simons, 1980; Gingerich et al., 1982; Conroy, 1987), cranial dimensions (Aiello and Wood, 1994; Kappelman, 1996; Spocter and Manger, 2007; Silcox et al., 2009), and limb bone articular surface and diaphyseal dimensions (Ruff et al., 1991; Dagosto and Terranova, 1992; Grine et al., 1995; Egi, 2001; Ruff, 2003; Yapuncich et al., 2015). Using a robust reference sample, these relationships are typically modeled with ordinary least squares (OLS) linear regression of logarithmically transformed variables, although reduced major axis linear regression has also been used (see Warton et al., 2006; Smith, 2009).

Different predictor variables (i.e., dental versus postcranial) can have profound effects on the inferred body mass of fossil taxa. For example, molar dimensions of the Eocene omomyiform *Hemiacodon gracilis* suggest a body mass between 640 and 1150 g (Conroy, 1987; Dagosto and Terranova, 1992; Jones et al., 2014), while predictions from tarsal dimensions are much lower (250–400 g; Dagosto and Terranova, 1992). Since these values fall on either side of “Kay's threshold” of 500 g, researchers using a particular predictor variable could reach divergent conclusions regarding the primary source of protein for *Hemiacodon*. As many

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http://dx.doi.org/10.1016/j.jhevol.2017.03.001
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Please cite this article in press as: Yapuncich, G.S., Alternative methods for calculating percentage prediction error and their implications for predicting body mass in fossil taxa, Journal of Human Evolution (2017), http://dx.doi.org/10.1016/j.jhevol.2017.03.001

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paleoecological inferences rely on predicted body masses, it is crucial that researchers are able to identify which values are most reliable. These preferences are often determined by evaluating the precision and accuracy of the underlying body mass prediction equations (BMPEs) using statistical metrics such as the coefficient of determination, mean square error, and standard error of the estimate (Gingerich, 1990; Smith, 2002; Yapuncich et al., 2015). For assessing predictive accuracy, Smith (1980, 1984) suggested calculating the percentage prediction error (%PE) for each data point with the following formula:

$$([\text{Observed} - \text{Predicted}]/\text{Predicteed})*100 = \%\text{PE}$$

A mean percentage prediction error (%MPE) can then be calculated by averaging absolute values of the %PE of each observation. Percentage prediction error has been used as an accuracy metric in many subsequent BMPE studies (Supplementary Online Material [SOM] Table S1).

Mean percentage prediction error can be calculated using the predicted values of all observations in the equation's reference sample (e.g., Aiello and Wood, 1994; Kappelman, 1996; Spocter and Manger, 2007; Squyres and Ruff, 2015; Tsubamoto et al., 2015) or a subset of the reference sample (Payseur et al., 1999). However, this procedure does not reveal the predictive accuracy of a BMPE when applied to new observations. Therefore, many BMPE studies (SOM Table S1) utilize a separate test sample—observations not used to generate the prediction equation—to calculate %MPE. Similarly, some researchers have used novel test samples to evaluate the predictive accuracy of previously published BMPEs (e.g., Ruff, 2000; Ruff et al., 2005; Elliott et al., 2014, 2016; Yapuncich et al., 2015). Since the workflow for calculating prediction error is analogous to predicting fossil body masses, evaluating BMPEs with a test sample has an intuitive and straightforward appeal.

Among those studies with test samples, two versions of %MPE have been calculated. First, the predictor value of each individual specimen has been used to predict an individual's body mass, which is then compared to that individual's observed body mass. Mean percentage prediction error is then calculated as the average of the absolute values of all individual %PEs. When test samples comprise specimens with associated body masses, this has been the preferred method for calculating %MPE (e.g., Ruff, 2000, 2003; Delson et al., 2000; Halenar, 2011; Elliott et al., 2014, 2016). Alternatively, the sample mean of the predictor values can be used to predict a sample mean body mass, and then tested against an observed sample mean body mass. This second method has been used less frequently with test samples (Dagosto and Terranova, 1992; Biknevicius, 1999; De Estaban-Trivigno et al., 2008), although studies that compute %PE from a species mean reference sample implicitly follow this approach (including many of the studies in SOM Table S1).

Van Valkenburgh (1990:197) highlighted both alternatives for calculating prediction error, but did not advocate a particular option: “Prediction errors could probably be lowered if body mass and length data were compared for the same individual, or averages of skeletal measures and mass based on large samples were used.” These procedures, averaging the %PEs for all individuals (hereinafter referred to as %MPE) versus averaging predictor values before calculating a mean %PE (subsequently referred to as the percentage prediction error of the mean or %PEM), treat the same data differently and may describe the predictive accuracy of BMPEs differently. If there were a systematic difference between these methods, it would be inappropriate to compare the prediction errors from studies utilizing alternative approaches. More critically, as the application of prediction equations to test samples replicates application to fossil taxa, any systematic difference may inform the best procedure to reduce prediction error for fossils. However, as these approaches have not been formally examined, no consistent protocol for calculating prediction error has been developed.

This study evaluates the effect of %MPE and %PEM on reported prediction error. Body masses are predicted from dental dimensions for a large sample of primates with associated body masses. Both %MPE and %PEM are calculated and compared for several published BMPEs. Results from empirical data are supported using simulated data (SOM File 1). As a null hypothesis, this study assumes that workflow differences do not result in significantly different assessments of predictive accuracy. This hypothesis generates the following predictions:

P_1: Per-taxon differences between %MPE and %PEM will be normally distributed. Skew in the distribution of differences would indicate that one approach might modestly reduce prediction error for most taxa, while substantially increasing prediction error for one or two species.
P_2: The mean (or median) of the distribution of per-taxon differences between %MPE and %PEM will not be significantly different from 0. A shift in the mean (or median) would indicate that one approach has less error in the majority of test cases.

If either of these predictions is not met, it should be possible to recommend a preferred method for calculating prediction error, at least in conditions similar to those of this study.

2. Methods and materials

Maximum mesiodistal length and buccolingual breadth of the first mandibular (M_1) and maxillary (M^1) molars and maximum mesiodistal length of the second mandibular molar (M_2) were measured on 406 individuals from 50 cercopithecoid primate taxa with associated body masses (SOM Table S2) at the National Museum of Natural History (Washington, DC). All taxa were represented by at least two individuals. Occlusal area (the product of the two linear dimensions) was natural log-transformed and used to predict body mass with the primate M^1 and M_1 equations of Gingerich et al. (1982), and the male primate, anthropoid, and “monkey” M_1 equations of Conroy (1987). Additionally, M_2 length was $\log_{10}$-transformed and used to predict body mass using the primate M_2 equation of Kay and Simons (1980).

Body masses predicted with the Gingerich et al. (1982) and Conroy (1987) equations were converted from the logarithmic scale and corrected for bias using published quasi-maximum likelihood estimates (Smith, 1993). A correction factor was not available for the Kay and Simons (1980) equation. For individual %PEs, body mass was predicted for each individual and compared to that individual's associated body mass. Mean percentage prediction error was then calculated as the mean of the absolute values of all individual %PEs. For %PEM, molar occlusal area was averaged at the species/subspecies level and used to predict a mean species/subspecies body mass. An observed mean body mass was computed as the average of associated body masses for all specimens. For each taxon, the difference between %MPE and %PEM was calculated; positive values indicate lower prediction error for %PEM. Normality was evaluated using a Shapiro–Wilk test. Depending on the results of the normality test, a *t*-test or a Wilcoxon rank sum test was used to check if the mean or median of the distribution was significantly different than zero.

All individuals ($k = 406$) from all species/subspecies ($n = 50$) were input into the Gingerich et al. (1982) and Kay and Simons (1980) equations, while only male individuals ($k = 194$) from those species/subspecies with at least two male individuals ($n = 36$) were input into the Conroy (1987) equations.

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Table 1
Medians, standard deviations (StDev), skewness, and statistical tests for distributions of the difference between mean prediction error (%MPE) and prediction error of the mean (%PEM).

Reference	Prediction equation	%MPE − %PEM			Shapiro-Wilk		Wilcoxon rank sum		
		Median	StDev	Skew	W	p	W	p	Different from 0?
Gingerich et al. (1982)	M_1 area	1.55	6.71	1.49	0.8088	<0.001	1108	<0.001	Yes
Gingerich et al. (1982)	M^1 area	1.12	5.32	1.37	0.8257	<0.001	1091	<0.001	Yes
Conroy (1987)	Monkey M_1 area	1.14	4.15	1.15	0.8155	<0.001	591	<0.001	Yes
Conroy (1987)	Anthropoid M_1 area	1.26	4.03	1.21	0.8089	<0.001	595.5	<0.001	Yes
Conroy (1987)	Primate M_1 area	1.57	3.71	1.15	0.8496	<0.001	570	<0.001	Yes
Kay and Simons (1980)	M_2 length	1.47	5.99	2.09	0.7021	<0.001	1151.5	<0.001	Yes

Measurements and associated body masses for each individual are presented in SOM Table S3.

3. Results

Mean percentage prediction error and %PEM are reported for all taxa and all equations in SOM Tables S4–S6. Summary statistics and statistical test results for the per-taxon differences between %PEM and %MPE are presented in Table 1. All BMPEs exhibit the same pattern. All distributions of differences in prediction error are non-normal and positively skewed, which can be readily observed when %MPE is plotted against %PEM (Fig. 1). Wilcoxon rank sum tests reveal that the medians of all distributions are significantly different from zero (Table 1). On a per-taxon basis, %PEM is consistently less than %MPE. Neither of the predictions of this study is met.

Though certain biological factors (i.e., phylogeny, degree of sexual dimorphism) may explain why %PEM consistently returns less error than %MPE, there is no clear pattern in the taxa that exhibit the atypical pattern of %PEM > %MPE (SOM Tables S4–S6). Both cercopithecines and colobines are represented in these taxa; they show both high levels of body size dimorphism (e.g., *Nasalis larvatus*) and are relatively monomorphic (e.g., *Presbytis melaphos melaphos*). Additionally, they are both included in and absent from the reference samples of the equations being evaluated. The most evident factor uniting taxa in which %PEM > %MPE is the number of individuals sampled, with relatively few individuals sampled in these cases. Low but significant positive correlations were recovered between the number of individuals (k) used to generate the mean predictor value and the difference between %MPE and %PEM ($r = 0.25$, $p < 0.001$; Fig. 2),[1] and a significant negative correlation was recovered between %PEM and k ($r = -0.17$, $p = 0.036$), suggesting that predictions become more accurate when the predictor value represents a more robust sample mean. No significant correlations were recovered between %MPE and k.

4. Discussion

For the vast majority of taxa in this study, prediction errors calculated from the sample mean predictor value are less than prediction errors calculated as the average %PE of a sample of individuals. This pattern holds across all six examined prediction equations (Table 1, Fig. 1). Additionally, increasing the number of individuals used to estimate sample means (of body mass and predictor variables) is correlated with a greater difference between these two prediction error methods (Fig. 2), caused primarily by a decrease in %PEM. Since the raw data do not change in these comparisons, differences between %MPE and %PEM must be driven by the data processing workflow. It is reasonable to ask why the %PEM < %MPE pattern is so pervasive.

4.1. Interspecific versus intraspecific scaling relationships

All of the BMPEs evaluated here use interspecific scaling relationships and have reference samples comprising species or sex-specific mean values. With the notable exception of fossil hominins, fossil primate body masses have been most frequently predicted with this type of BMPE (e.g., Gingerich et al., 1982; Conroy, 1987; Dagosto and Terranova, 1992; Payseur et al., 1999; Delson et al., 2000; Ruff, 2003; Egi et al., 2004; Bajpai et al., 2008; Halenar, 2011). However, when individual body masses are predicted with interspecific equations, the unit of analysis changes from a mean to an individual value. As highlighted by Smith (2002:281), an interspecific BMPE will return predicted body masses with the “expected values of … *species* whose mean [predictor values] are those values” (emphasis in original). Any predictor value serving as input for an interspecific BMPE will return the predicted body mass for a species with that value, even if the original value represents an individual.

There is a rich literature commenting on differences between inter- and intraspecific scaling relationships (Gould, 1971, 1975; McMahon, 1975; Clutton-Brock and Harvey, 1979; Smith, 1980, 1981, 1984; Steudel-Numbers, 1981; Martin and Harvey, 1985; Pagel and Harvey, 2001), which include differences in slopes, ranges, and correlation coefficients (SOM Table S7). For body mass prediction in a paleontological context (rather than archaeological or forensic contexts), it is important to recognize that having one relationship well characterized does not necessarily provide information about the other. While individuals with associated body masses may serve as raw data for generating interspecific BMPEs, the covariation of body mass and the predictor variable at the individual level is lost when values are averaged. Thus, when interspecific BMPEs are used to predict the body masses of individuals, the change in the unit of analysis will often decrease the predictive accuracy of the equation. Ideally, test samples should have the same units of analysis as the reference sample.

4.2. Applying interspecific BMPEs to fossil taxa

The results of this study strongly suggest that fossil body masses should be predicted using the mean of available predictor values to avoid changing the unit of analysis. However, studies often predict a set of “individual” body masses from interspecific BMPEs, then estimate species mean body mass by averaging the “individual” predicted values (SOM Table S8). A more accurate mean body mass can be predicted using a robust mean predictor value (estimated by averaging all available predictor values [as in Kay and Simons, 1980; Gingerich et al., 1982; Simons and Kay, 1983; Dagosto and Terranova, 1992; Payseur et al., 1999]).

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[1] Because the Gingerich et al. (1982) and Conroy (1987) equations have overlapping reference samples and thus generate non-independent sets of prediction errors, correlations between prediction error and sample size were restricted to the Gingerich et al. (1982) equations and the Kay and Simons (1980) equation.

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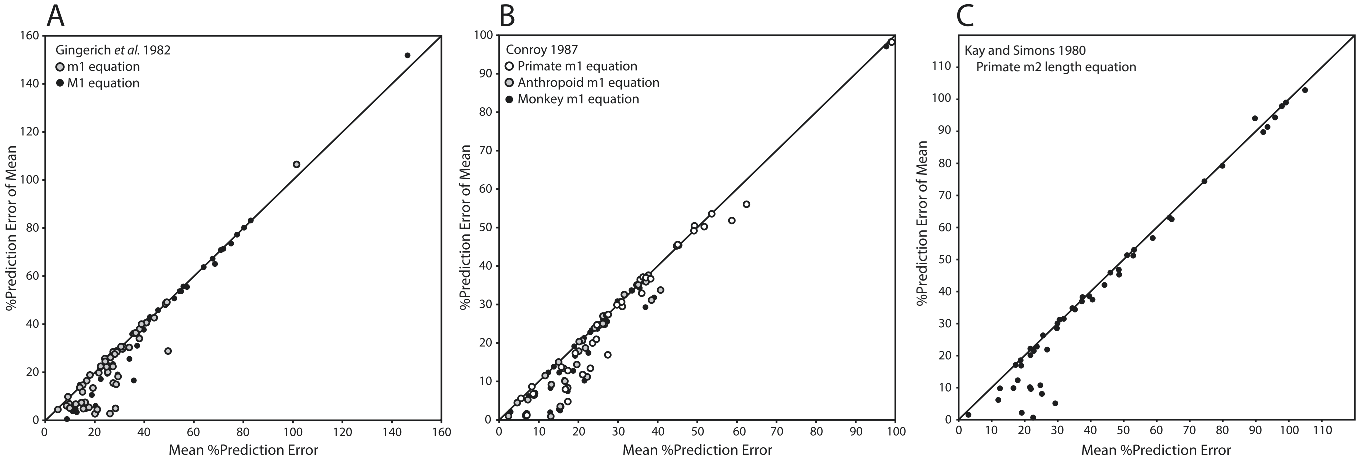

Figure 1. A) %MPE relative to %PEM for predicted body masses of 50 cercopithecoid taxa using equations of Gingerich et al. (1982). B) %MPE relative to %PEM for predicting body masses of males representing 36 cercopithecoid taxa using Conroy's (1987) equations. C) %MPE relative to %PEM for predicted body masses of 50 cercopithecoid taxa using equation of Kay and Simons (1980). Solid lines depict the line $y = x$.

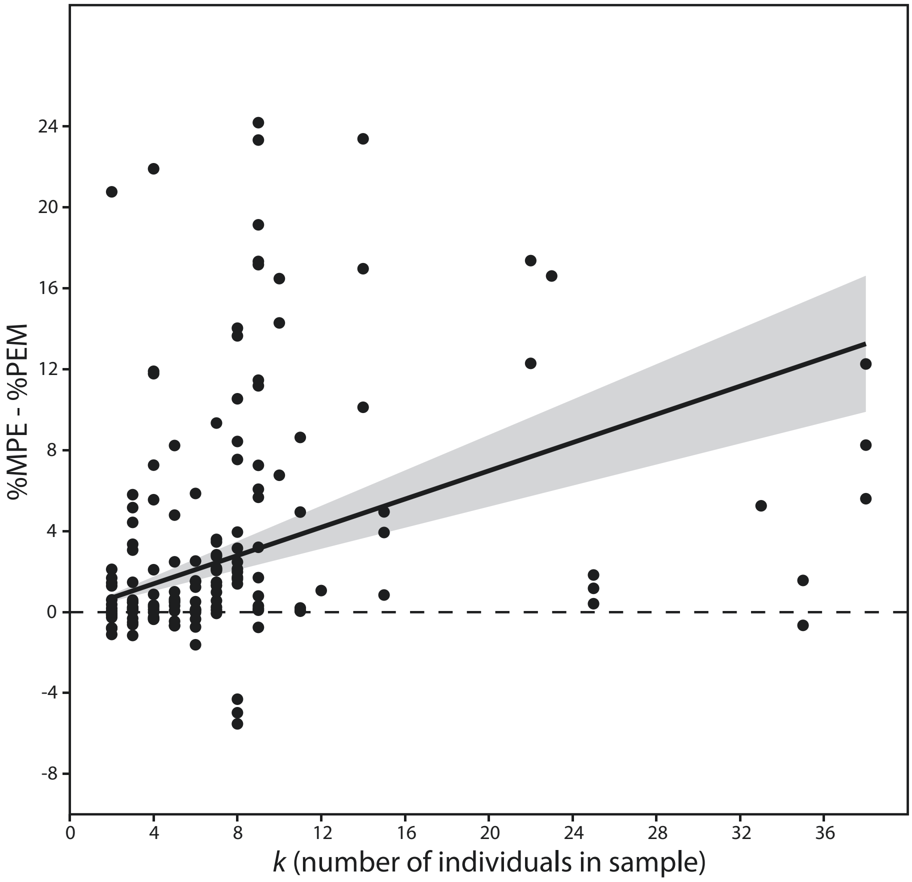

Figure 2. Ordinary least squares regression of the number of individuals in sample (k) and the difference in predictive accuracy (%MPE-%PEM) for all taxa across the restricted set of equations ($n = 150$, including both Gingerich et al. [1982] equations and the Kay and Simons [1980] equation). Though the correlation is low ($r = 0.25$), the relationship is significant ($p < 0.001$). Since there can be no prediction error when $k = 0$, the regression has been forced through the origin. The gray area indicates the 95% confidence interval. The relationship remains significant ($p < 0.001$) when the line is not forced through the origin.

Due to the change in the unit of analysis, true individual body masses are not obtainable from interspecific BMPEs. Of course, with many fossil taxa, a single specimen may comprise the entire available sample. In these cases, Smith (2002) delineated two possibilities (and advocated for the second): 1) consider a single specimen as representative of the species mean, or 2) consider the predictions to be limited to that particular specimen. These alternatives can be tested by calculating %PEs with both associated masses and the sample mean mass as each individual's “observed” body mass, taking the per-taxon differences between these prediction errors and analyzing the distribution with the same statistical tests as above. For the Gingerich et al. (1982) dental equations, these distributions are not normally distributed (M_1: Shapiro–Wilk $W = 0.9026$, $p = 5.86\text{e-}04$; M^1: $W = 0.8759$, $p = 8.44\text{e-}05$) and exhibit positive skew. For the M^1

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equation, the median is not significantly different from zero. For the M_1 equation, the median is significantly different from zero (Wilcoxon rank sum $W = 873$, $p = 0.02$), indicating that predictions are more accurate when the sample mean mass is the "observed" body mass. Simulations provide further support for these results (SOM File 1). Though further testing would be informative, it is possible that individual predictor values are, on average, more accurate at predicting a mean body mass than an individual's associated body mass in interspecific BMPEs. Therefore, it may be more reasonable (though not strictly statistically appropriate) to regard body mass predictions made from an individual as a rough approximation of species mean body mass.

Finally, the importance of being able to estimate a robust species mean predictor value should inform subsequent efforts to generate BMPEs. Elements that are relatively abundant and can be confidently attributed to fossil taxa (teeth, potentially tarsals) will provide more robust estimates of species mean predictor values. An ideal predictor variable would be well represented in the fossil record and exhibit the same scaling relationship within species as between species, so that intra- and interspecific allometries were equivalent. However, such a predictor variable may not exist, and there may be a trade-off between employing very precise BMPEs (such as those generated from weight-bearing elements) and the ability to estimate a robust sample mean for the predictor variable.

5. Conclusions

Previous studies have evaluated the predictive accuracy of BMPEs with two subtly different metrics: %MPE, mean percentage prediction error of a sample of individual predictions, and %PEM, percentage prediction error of the mean predictor value. Van Valkenburgh (1990) highlighted both as potential approaches to minimize prediction error. However, for the interspecific BMPEs evaluated in this study, %PEM is consistently and significantly lower than %MPE. Because %MPE alters the unit of analysis from means to individuals, it reduces predictive accuracy. To maintain consistency, %MPE is most appropriately applied to intraspecific BMPEs in which reference samples are composed of individuals (more common in archaeological or forensic contexts). In contrast, %PEM is most appropriately used to evaluate interspecific BMPEs in which reference samples are mean values (more common in paleontological contexts).

These results have clear implications for applying interspecific BMPEs to fossil taxa. All available predictor values should be averaged and a single species mean body mass predicted. When only a single specimen is known, initial results suggest that the predicted body mass may be considered a rough approximation of the species mean body mass, as individual predictor values entered into interspecific BMPEs are slightly more accurate at predicting mean body mass than that individual's associated mass. This finding should be investigated more thoroughly.

The relative simplicity of using a bivariate relationship to predict body mass belies many methodological complications. This study highlights both the importance of estimating a robust sample mean of predictor variables (by increasing the number of individuals sampled) and the importance of maintaining the units of analysis during the evaluation and application of interspecific BMPEs. Given the ecological importance of body mass and the prevalence of interspecific BMPEs, it is vital that these analytical tools are used as effectively as possible.

Acknowledgments

This work was supported by the National Science Foundation (NSF BCS 1540421 to GSY and Doug M. Boyer). Chris Ruff provided helpful comments on an early draft of this paper that greatly improved the final manuscript. Two anonymous reviewers also provided helpful comments. Eric Delson provided access to NMNH cercopithecoid body mass data. Conversations with Mary Silcox, Jon Bloch, J.D. Pampush, and Doug Boyer aided immensely in developing this study. Many thanks to Paul E. Morse for the kind use of his initials.

Supplementary Online Material

Supplementary online material related to this article can be found at http://dx.doi.org/10.1016/j.jhevol.2017.03.001.

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Please cite this article in press as: Yapuncich, G.S., Alternative methods for calculating percentage prediction error and their implications for predicting body mass in fossil taxa, Journal of Human Evolution (2017), http://dx.doi.org/10.1016/j.jhevol.2017.03.001