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RESEARCH ARTICLE

Can body mass and skull morphology predict seed and fruit ingestion potential for mammal species? A test using extant species and its application to extinct species

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Abstract

1. Larger animals are assumed to ingest larger seeds and consume larger fruits, but empirical studies reveal inconsistent trends between body mass and the average size of fruits and seeds ingested. Furthermore, no studies have explored seed size relationships with morphological traits, such as skull dimensions. Such characteristics might provide more reliable estimates of ingestion ability and allow for accurate predictions of seed dispersal capacity in species for which we lack empirical data, especially extinct species. To determine whether (i) mammalian skull dimensions are better predictors of the maximum size of ingested seeds and fruits, compared to body mass and (ii) body mass are the better predictors of mean fruit and seed sizes, we studied these relationships across three mammalian orders: Chiroptera, Primates and Carnivora.
2. We collected novel data on skull dimensions and collated available data on body mass and maximum and mean sizes of ingested fruits and seeds for mammals ($N = 100$) across the Neotropics, Asia, Africa and Madagascar. We explored the relationships between anatomical traits and fruit and seed sizes of extant species and made predictions for five extinct species.
3. Our results revealed that body mass and skull dimensions are essential determinants of ingested fruit and seed size in mammals. The latter traits can generate predictions for extinct species, especially coronoid height and maximum jaw gape. Nevertheless, body mass predicted larger ingested fruits and seeds than skull dimensions and explained a greater part of the variance for both maximum and mean sizes in our dataset.

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4. Our results show how body mass and cranial anatomy constrain seed size and reinforce the importance of maintaining functional diversity in seed dispersers to maintain tropical forest structure. We also show that scientists can use morphological characteristics to predict the seed dispersal potential of extinct mammals allowing better inferences on past and future consequences of frugivore extinctions within tropical forests.

KEYWORDS
bats, body mass, carnivores, frugivores, primates, seed dispersal, skull, tropical forests

1 | INTRODUCTION

Most trees and woody lianas in tropical forests depend on animals for seed dispersal (zoochory). Many trees produce fruits that are attractive to animals (Buitrón-Jurado & Ramírez, 2014; Howe, 2014; Howe & Smallwood, 1982; Jordano, 2000). Frugivores disperse seeds by consuming the fruit pulp and spitting out the seeds (synzoochory; Corlett & Lucas, 1990; Howe & Vande Kerckhove, 1981; Lobova et al., 2009), or they ingest fruits whole, and the seeds are found intact in their faeces (endozoochory; Beaune et al., 2013; Shilton et al., 1999; Tobler et al., 2010). According to the Janzen–Connell hypothesis, the deposition of seeds away from the parent tree is often advantageous for the plant because the establishment and the survivorship of seedlings are affected by negative density-dependent processes such as intraspecific competition and the presence of herbivores or pathogens near the parent tree (Bell et al., 2006; Connell, 1971; Janzen, 1970; Mangan et al., 2010; Swamy et al., 2011).

Plant and animal traits influence the interactions between plants and frugivores (Dehling et al., 2016). Many animal traits influence the quantity and quality of seed dispersal and consequently, impact the seed dispersal effectiveness (Beckman & Rogers, 2013; Schupp et al., 2010). It is widely accepted that a positive relationship between body size and consumed fruit size occurs in all taxa (Lim et al., 2020; Muñoz et al., 2017). However, according to a broad-scale study (Chen & Moles, 2015), the relationship between body mass (BM) and the average size of ingested seeds follows various scenarios. Birds show a robust positive relationship while mammals follow different patterns (i.e. none, positive or negative) due to more diverse seed-handling behaviours and digestive systems (e.g. ruminants). Moreover, bill size and wing morphology influence fruit handling and manoeuvrability for fruit access (Dehling et al., 2016), while gape width is an important driver of the ingested seed and fruit sizes in birds (Godínez-Alvarez et al., 2020; Lord, 2004). Nevertheless, no studies have explored the link between comparable morphological traits in mammals, such as skull dimensions, with the size of ingested fruits and seeds that they consume. Yet, we might expect skull dimensions, especially jaw gape, to show different relationships with the maximum size of the ingested fruits and seeds than BM, given that jaw gape is a direct limitation of the size of the item that can be swallowed by an animal.

The loss of species has critical consequences on behavioural (e.g. habitat selection), ecological (e.g. seed dispersal) and evolutionary (e.g. phenotypic changes) processes (Galetti & Dirzo, 2013). While exploring relationships between morphology and seed dispersal potential in extant mammals, inferences on extinct species might be achievable (Lim et al., 2020). Reconstructing the lifestyle and ecology of extinct species has become possible through modern palaeoecological and eco-morphological research tools. Several features such as diet, behaviour and BM of extinct species can be predicted using stable isotopes, cranial or dental morphology, and fossil skeletons (Dumont et al., 2011; Godfrey et al., 2005). However, predictions on the seed dispersal capacities of extinct mammal species have been little explored (Pires et al., 2014).

We explore relationships between BM and skull dimensions with ingested seed and fruit sizes across three mammal orders: Chiroptera, Primates and Carnivora, with predominantly frugivorous diets. Frugivorous bats are represented by the Pteropodidae of the Old World (Africa, Asia, Oceania) and the Phyllostomidae of the New World (America). They can carry up to 1.5 times their BM in fruit (Mahandran et al., 2018), and some can ingest and defecate many tiny seeds (Lobova et al., 2009). Frugivorous primates are represented by strepsirrhines, platyrrhines (New World monkeys) and catarrhines (Old World monkeys and apes). They constitute up to 25%–40% of the biomass of frugivorous animals in tropical forests (Chapman, 1995). These taxa show high interspecific variability in terms of seed treatment and, therefore, in seed dispersal efficiency (Gross-Camp & Kaplin, 2011; Lambert, 1999). Frugivorous carnivores are mainly represented by the Viverridae in the Old World and the Procyonidae in the New World. Viverrids represent the third largest group of frugivorous mammals in the Indo-Himalayan region (Kitamura et al., 2002). Even if they are much less studied than primates and bats, frugivorous carnivores are recognized as essential dispersers (Alves-Costa & Eterovick, 2007; Nakabayashi et al., 2016; Zhou et al., 2008). They consume a wide variety of fruits, of which they disperse a significant number of intact seeds (Alves-Costa & Eterovick, 2007; Chakravarthy & Ratnam, 2015).

Using the available global data on fruit and seed size, BM and original data on cranial morphology for extant mammals from the Neotropics, Asia, Africa and Madagascar, this study aimed to quantify the relationship between BM and skull dimensions with the mean and maximum size of consumed fruits and ingested seeds. Specifically, we test the following hypotheses: (1) that the mean size of ingested seeds and fruits is positively correlated with BM; (2) that the maximum size of ingested seeds and fruits is positively correlated with the skull dimensions, especially, the jaw gape, as it is a direct determinant of what can be ingested by the frugivores. In a novel application of the relationships obtained, we present the mean and maximum seed and fruit sizes estimates for three extinct lemurs and two extinct platyrrhine species, three of which are assumed to have acted as seed dispersers (Albert-Daviaud et al., 2020; Godfrey et al., 2005).

2 | MATERIALS AND METHODS

2.1 | BM and skull dimensions

We carried out skull measurements of primates, carnivores and bats from the comparative anatomy collections of the Natural History Museums of Paris (MNHN) and London (NHM). All measurements (Figure 1) were made with an accuracy of 0.01 cm using digital callipers. Measurements of jaw length (A) and the jaw gape (B) allow us to estimate approximately the maximum opening of the jaw. The bicondylar width (C) and the projected jaw length (D) correlate with the animal's size and estimate the shape of the mandible. Canine overlap (E) has been suggested to explain the maximal opening of the jaw and thus the size of the food that can be ingested (Hylander, 2013). The jaw width (F) and the distance between molars (G) estimate the oral and pharyngeal tract size. The coronoid height (H) reflects the size of the temporalis muscles and provides insights into bite force, which may also be related to the fruit and seeds ingested. The frequent absence of teeth on specimens' skulls resulted in all measurements being taken at the base of the teeth. Where possible, the skulls of two adult males and two adult females were measured for each species, and juveniles were excluded. BM data were derived from the open-access database of the Encyclopedia of Life (2018) which lists the adult male and female BM (https://eol.org/) for all species included in our study.

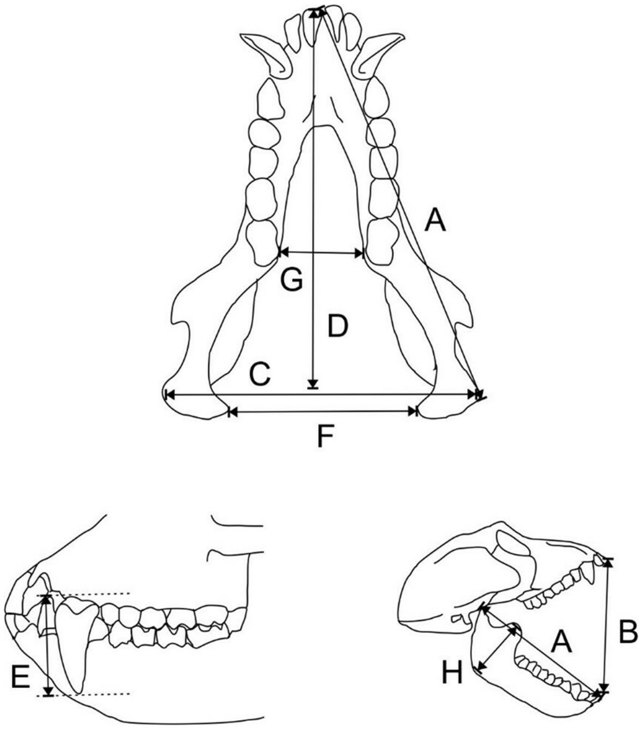

FIGURE 1 Diagram of measurements carried out on mammalian skulls. A, jaw length; B, jaw gape; C, bicondylar width; D, jaw length; E, canine overlap; F, jaw width; G, distance between molars; H, coronoid height; modified from Hylander (2013).

2.2 | Extant mammal species

The species of bats, primates and carnivores selected for this study include at least 50% of fruit in their diet in some localities and throughout most of the year. Indeed, depending on the availability of resources, even highly frugivorous species may include insects, other plant material or even vertebrates in their diet. Diet data are derived from observations or experiments (average dry mass of faeces or stomach contents) available in the literature (Chivers & Hladik, 1984; Gautier-Hion et al., 1980; Wilson, 1973; Appendix S5). We took the availability of skulls in museum collections, and we also considered the size of ingested seeds and fruits in literature in the species selection. Our final dataset encompassed eight families of Primates, including 46 species, two families of Chiroptera, including 42 species, and two families of Carnivora, including 12 species (*N* = 100 species; see Appendices S5 and S6).

2.3 | Fruit and seed sizes

We mainly obtained information on the ingested seeds and fruits from existing databases (Forget et al., 2007; Bretagnolle et al. unpubl.), journal articles and book chapters (see Appendix S6), unpublished and published theses (Djossa, 2007; Gompper, 1994; Nakabayashi, 2015; Thomas, 1982), as well as with the help of collaborators (see acknowledgements). Seeds found intact in the faeces were considered ingested and, therefore, dispersed by endozoochory. The dimensions measured on seeds and fruits are length and width (mm). Sometimes, these data are available for the same species at different locations. Thus, we used data from the locality where we found the maximum information on seed and fruit sizes and where the species ingested the largest seeds because we were interested in the maximal seed or fruit size that an animal could eat. The list of consumed plant species is not complete due to the lack of some seed or fruit measures. We used the mean and the maximum length and width of ingested fruits and seeds to minimize a potential sampling bias.

2.4 | Extinct mammal species

We used the quantitative associations between anatomy, fruit and seed sizes to make predictions for five extinct primate species (i.e. *Hadropithecus stenognathus*, *Archaeolemur majori*, *Archaeolemur edwardsi*, *Paralouatta varonai* and *Antillothrix bernensis*). The extinct species were alive between the late Pleistocene and Holocene. BM data were derived from the literature, and published images (Table S1 in Appendix S1) were used to quantify the cranial morphology of the extinct species. The images were analysed using the ImageJ software (Schneider et al., 2012) to obtain the skull dimensions. However, 'Jaw gape (B)' was difficult to measure from the pictures of fossil crania, we thus used the strong correlation found between jaw gape and jaw length ($R^2 = 0.97$) in our dataset of extant species, to estimate the jaw gape of the extinct species. Where possible, an average of the skull dimensions of multiple individuals was used (Table S1).

2.5 | Statistical analysis

To identify potential relationships between morphological data (BM and skull dimensions) and seed and fruit sizes (mean and maximum length and width), we used the 'two-block partial least squares' (2B-PLS) approach (Rohlf & Corti, 2000). This method quantifies the degree of association between two matrices of data, recorded for the same species. It is a descriptive multivariate analysis robust to multicollinearity between variables and therefore suitable for the use of morphometric and dietary variables. These analyses generate axes that explain the covariance between two matrices. A PLS correlation coefficient (R_{pls}) and the percentage of covariance for each axis were obtained using the function 'pls2b' in R from the Morpho library (Schlager, 2013). Significance is tested by running 1000 permutations of the dataset. A distribution of PLS coefficients is obtained by resampling. The p_{95} value is calculated by comparing the observed PLS coefficient with those obtained after resampling. The significance of each linear combination is assessed by comparing the singular value (PLS coefficient) with those obtained from permuted blocks. If the PLS coefficient is higher than those obtained from permutated blocks, its associated p_{95} value is significant. PLS vectors are generated for each variable which provides each variable's weight in the covariation (Table S4.1). We generated a graph and histograms of the variables for each significant analysis using the 'Geomorph' library (Adams & Otárola-Castillo, 2013). Each 2B-PLS is cross-validated using the leave-one-out cross-validation implemented in the Morpho library. Moreover, to identify potential variations in our results due to the statistical method, we performed redundancy analyses (i.e. RDA) using the same two blocks of variables. RDA analyses were generated using the easyCODA (Greenacre, 2018) and vegan (Oksanen et al., 2018) packages.

Species share a part of their evolutionary history and therefore cannot be treated as independent data points. Thus, we conducted these analyses (phylogenetic 2B-PLS) while considering the phylogenetic relationships between species. We used the 'phylo.integration' function (Adams et al., 2014) from the Geomorph library. This function allowed us to quantify the degree of covariance of two data tables but under a Brownian motion model of evolution (Adams et al., 2014). The blocks are phylogenetically corrected, and the PLS coefficient (R_{pls}) between the two blocks is evaluated.

In addition, we used the function 'pgls' from the 'caper' library to explore in greater detail those relationships. We also checked lambda profiles to estimate the strength of the phylogenetic signal in the analyses. We found out that the size of our dataset was not sufficient to decide whether phylogenetic generalized least squares (PGLS) were better to use than simple ordinary least squares (OLS). Thus, we report the results of both OLS models (i.e. the equivalent of PGLS with lambda set to 0) and the PGLS model with lambda set to 1 (i.e. equivalent to independent contrasts). First, we performed simple OLS and PGLS with BM as a single explanatory variable for mammals. Second, we performed both analyses with the size-corrected skull dimensions and reported only significant relationships. Predictions on five extinct mammal species were made using the equation of each significant relationship to calculate predicted seed and fruit sizes. Error inflation of the P value was corrected using a 'Bonferroni' correction with the 'p.adjust' function.

All data were Log_{10}-transformed before analyses to assure normality and homoscedasticity. We used the phylogenetic tree produced by Upham et al. (2019). We checked the presence of the extant species and reduced the tree using the Geiger (Pennell et al., 2014) and ape (Paradis & Schliep, 2018) libraries. Phylogenetic size corrections were performed using the 'phyl.resid' function from the 'phytools' package (Revell, 2012) on skull dimensions as they were strongly correlated to the BM of the mammal species. We used R statistical environment (R Core Team, 2019, version 3.5.2) for all analyses.

3 | RESULTS

3.1 | Relationships of BM with fruit and seed sizes

The 2B-PLS analysis between BM and skull dimensions and the seed and fruit size ingested (Figures S2.1 and S2.2) revealed significant covariation regardless of whether ($R_{\text{pls}} = 0.67$; $p = 0.001$) or not the phylogeny was incorporated ($R_{\text{pls}} = 0.48$; $p < 0.001$) into the analyses. PLS vectors showed that BM is the principal variable driving the covariation with both the maximum and mean seed sizes in the non-phylogenetic analysis, further confirmed by the redundancy analysis (Figure S3.1). In contrast, only the mean length and the maximum length and width of fruits appeared to covary with BM in the phylogenetic analysis.

Ordinary least squares and PGLS models confirmed the observed trends in the multivariate analyses (Table 1). OLS models showed greater coefficients and smaller intercepts for all seed dimensions, especially for the averages than those of PGLS models.

TABLE 1 Equations based on (a) the ordinary least square (OLS) procedure and (b) phylogenetic generalized least squares (PGLS) from extant mammals using body masses (BM). Type I error at 5% is corrected using the 'Bonferroni' method.

Seed and fruit dimensions	Intercept	BM	R^2 adj	*p* (Bonferroni corr.)
(a) OLS ($\lambda = 0$)				
Seed length	0.007 ±0.083	0.239 ±0.027	0.425	**<<0.001**
Seed width	−0.185 ±0.077	0.246 ±0.025	0.476	**<<0.001**
Max. seed length	0.294 ±0.111	0.262 ±0.037	0.332	**<<0.001**
Max. seed width	0.107 ±0.108	0.264 ±0.035	0.349	**<<0.001**
Fruit length	1.587 ±0.053	−0.013 ±0.017	−0.004	1.000
Fruit width	1.170 ±0.049	0.057 ±0.016	0.102	**0.005**
Max. fruit length	1.727 ±0.097	0.093 ±0.032	0.070	**0.035**
Max. fruit width	1.191 ±0.080	0.182 ±0.026	0.317	**<<0.001**
(b) PGLS ($\lambda = 1$)				
Seed length	0.518 ±0.803	0.070 ±0.115	−0.006	1.000
Seed width	0.634 ±0.686	−0.032 ±0.098	−0.009	1.000
Max. seed length	1.107 ±1.056	−0.014 ±0.151	−0.010	1.000
Max. seed width	0.874 ±0.927	0.003 ±0.133	−0.010	1.000
Fruit length	0.539 ±0.346	0.346 ±0.049	0.324	**<<0.001**
Fruit width	1.055 ±0.283	0.094 ±0.040	0.042	0.176
Max. fruit length	0.374 ±0.744	0.550 ±0.106	0.204	**<<0.001**
Max. fruit width	0.905 ±0.549	0.276 ±0.078	0.102	**0.005**

In contrast, PGLS models demonstrated greater coefficients for BM and smaller intercepts for fruit dimensions than those in the OLS models.

3.2 | Relationships of skull dimensions with fruit and seed sizes

Size-corrected skull dimensions also revealed strong relationships in both phylogenetic ($R_{pls} = 0.47$; $p = 0.001$) and non-phylogenetic 2B-PLS ($R_{pls} = 0.67$; $p = 0.001$) analyses. Phylogenetic 2B-PLS analysis showed that maximum jaw gape (MJG), canine overlap (CO) and coronoid height (CH) positively drive the covariation with the maximum and mean seed sizes and the maximum fruit sizes (Figure 2). In contrast to the phylogenetic analysis, the non-phylogenetic 2B-PLS showed that bicondylar width (BW), jaw width (JW) and CH positively drive the covariation with the maximum and mean seed sizes and the maximum fruit sizes (Figure S2.3). In contrast, the distance between molars, projected jaw length and jaw length (PJL and JL) negatively drive the covariation, again confirmed by the redundancy analysis (Figure S3.2). Overall, the maximum fruit and seed sizes performed better than mean sizes, but generally, the seed sizes are predicted better than fruit sizes.

Phylogenetic generalized least squares and OLS models confirmed the 2B-PLS trends with fruit and seed sizes (Table 2). Overall, the coefficients and intercepts of CH were smaller in OLS models than the coefficients of MJG in PGLS models for seed and fruit dimensions. None of the other skull dimensions covaried in the phylogenetic 2B-PLS (i.e. CO, CH) was significant in PGLS models. In contrast, JW and BW were other significant explanatory variables in OLS models.

Overall, OLS models always generated greater correlation coefficients than the PGLS models. The R_{pls} of 2B-PLS were also greater for the non-phylogenetic analyses. In addition, models using BM generated higher R^2 and coefficients than models using CH or MJG.

3.3 | BM, CH and jaw gape as predictors of fruit and seed sizes in extinct species

Using the aforementioned OLS and PGLS models, we estimated the size of the ingested seeds and fruits of five extinct primate species. Overall, using BM, the predictions revealed larger maximum ingested seed sizes (±10 mm on average) and consumed fruit sizes (±13 mm on average) than when using only CH or MJG in the OLS predictions (Table 3a,c). Moreover, PGLS tends to overestimate fruit size (i.e. length up to 750 mm) using BM as a predictor (Table 3b). Nevertheless, *Hadropithecus stegnognathus* is predicted to ingest the largest seeds and fruits based on BM (i.e. up to 30.6 and 141.2 mm long). In contrast, based on CH in OLS models, *Archaeolemur edwardsi* is expected to swallow the largest seeds and fruits (i.e. up to 22.4 and 130.8 mm long), whereas based on MJG in PGLS models, *Paralouatta varonai* is expected to swallow the largest seeds (i.e. up to 18.1 mm long) and consume the largest fruits (i.e. up to 100 mm long).

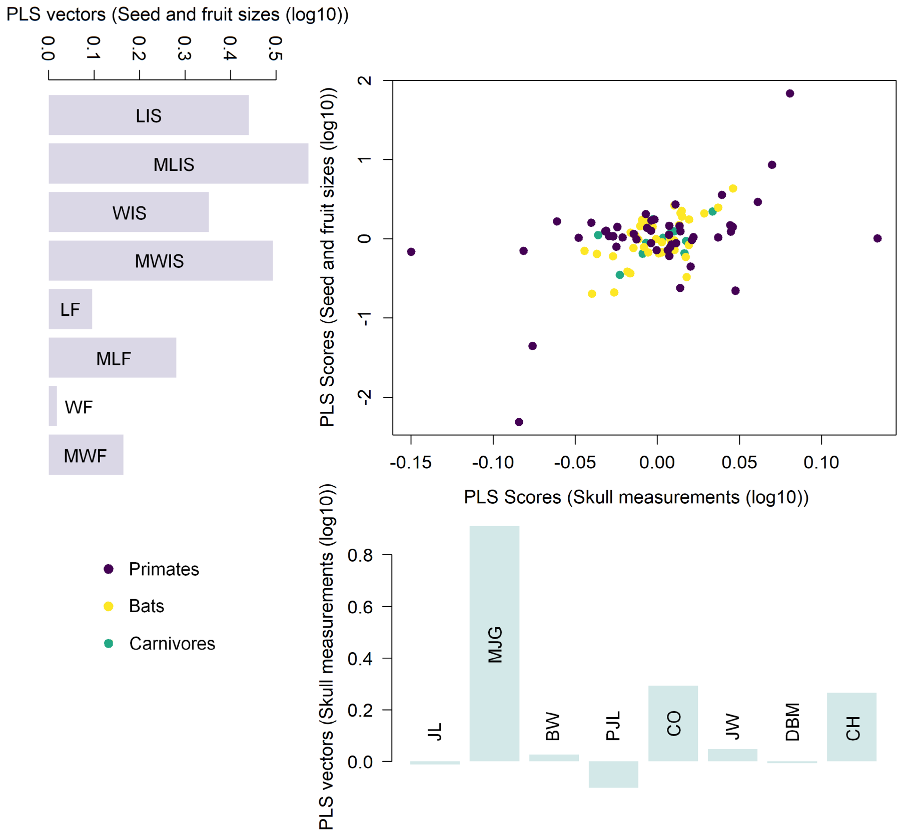

FIGURE 2 Phylogenetic two block-partial least square (PLS) between the size-corrected skull dimensions and the size of consumed fruits and ingested seeds. Scatter plot of the PLS axis describing the covariation between the residual skull measurements and the size of fruits and seeds. Seed and fruit sizes (MLF/LF, maximum and mean length of fruits; MLIS/LIS, maximum and mean length of ingested seeds; MWF/WF, maximum and mean width of fruits; MWIS/WIS, maximum and mean width of ingested seeds) associated with the skull measurements are represented by the histogram at the left side of the scatterplot (light purple). The skull measurements (BW, bicondylar width; CH, coronoid height; CO, canine overlap; DBM, distance between molars; JL, jaw length; JW, jaw width; MJG, maximum jaw gape; PJL, projected jaw length) associated with the size of fruits and seeds are represented by the histogram at the bottom of the scatterplot (light green).

4 | DISCUSSION

We show here significant relationships between BM and skull dimensions with ingested fruit and seed sizes in mammals. In accordance with our first hypothesis, BM generated models with greater correlation coefficients, especially for the mean seed sizes, and predicted larger ingested seed and fruit sizes than skull dimensions. However, contrary to our expectations, jaw gape does not necessarily predict the maximum sizes of the ingested fruits and seeds better than BM. These findings suggest that BM might provide better predictions than skull dimensions (i.e. CH, MJG). Nevertheless, using mammal BM or skull morphology as predictors of seed dispersal capacity provides a sound basis for future research. For extinct species, BM data are not available (although they can be inferred based on skeletal proxies) and as such the skull dimensions may provide solid and direct predictors of ingested fruit and seed size.

4.1 | Relationships of BM with fruit and seed sizes

Our data revealed that BM is primarily correlated to the mean seed sizes in the non-phylogenetic analyses, which is in line with our first hypothesis. These data confirmed the general assumptions that larger mammals generally ingest larger seeds, on average (Jordano, 2000; Lord, 2004). However, these findings contrasted with the global study of Chen and Moles (2015), where they found a negative relationship between BM and average seed sizes when including all mammal groups. It is important to note that the largest seeds can only be ingested by large mammals (Forget et al., 2007), but the opposite is not true; large mammals can ingest many small seeds as well. Nevertheless, our study only included mammals with at least 50% of fruits in their diet and from groups described as efficient dispersers which may explain part of the discrepancy between the two studies.

In contrast to our expectations, maximum seed sizes were strongly correlated to BM, yet most of the fruit dimensions were only weakly correlated. Indeed, our data suggest that the size of consumed fruits is less predictable than the mean and maximum size of the seeds. Seed size does not necessarily correlate with fruit size (e.g. *Annona muricata*) as large fruits can contain numerous small seeds. Furthermore, large-sized fruits can be broken into pieces or eaten without being detached from their support by some bats (Morrison, 1980; Singaravelan & Marimuthu, 2008).

TABLE 2 Equations based on (a) the ordinary least square (OLS) procedure using coronoid height (CH) and on (b) phylogenetic generalized least squares (PGLS) using maximum jaw gape (MJG) from extant mammals. Type I error at 5% is corrected using the 'Bonferroni' method.

Seed and fruit dimensions	**Intercept**	**CH**	**R^2 adj**	***p* (Bonferroni corr.)**
(a) OLS ($\lambda = 0$)				
Seed length	0.674 ± 0.033	1.302 ± 0.183	0.333	**<<0.001**
Seed width	0.501 ± 0.032	1.309 ± 0.175	0.355	**<<0.001**
Max. seed length	1.024 ± 0.042	1.497 ± 0.234	0.287	**<<0.001**
Max. seed width	0.844 ± 0.042	1.448 ± 0.231	0.277	**<<0.001**
Fruit length	1.551 ± 0.019	−0.077 ± 0.109	−0.004	1.000
Fruit width	1.329 ± 0.018	0.363 ± 0.099	0.110	**0.003**
Max. fruit length	1.989 ± 0.036	0.586 ± 0.197	0.073	**0.029**
Max. fruit width	1.700 ± 0.029	1.113 ± 0.163	0.313	**<<0.001**
Seed and fruit dimensions	**Intercept**	**MJG**	**R^2 adj**	***p* (Bonferroni corr.)**
(b) PGLS ($\lambda = 1$)				
Seed length	0.715 ± 0.624	3.42 ± 0.549	0.276	**<<0.001**
Seed width	0.542 ± 0.551	2.659 ± 0.485	0.266	**<<0.001**
Max. seed length	1.066 ± 0.824	4.436 ± 0.725	0.268	**<<0.001**
Max. seed width	0.885 ± 0.733	3.749 ± 0.645	0.248	**<<0.001**
Fruit length	1.503 ± 0.379	0.741 ± 0.334	0.038	0.231
Fruit width	1.318 ± 0.266	0.129 ± 0.234	−0.007	1.000
Max. fruit length	1.904 ± 0.726	2.204 ± 0.640	0.071	**0.006**
Max. fruit width	1.673 ± 0.512	1.328 ± 0.451	0.098	**0.032**

Carnivores sometimes drop large fruit to the ground to break them (Howe, 1986), while the dexterity of primates enables them to consume fruit larger than their gape (Peckre et al., 2019).

4.2 | Relationships of skull dimensions with fruit and seed sizes

Contrary to our expectations, the jaw gape was not the only skull dimension linked to the seed and fruit dimensions. Indeed, CH and CO, on the one hand, and BW and JW, on the other hand, were also linked to both the mean and maximum size of ingested seeds. The fact that jaw gape is not the only predictor of seed sizes suggests that other traits related to fruit and seed processing are equally important. Moreover, as we measured the jaw gape as the maximum distance between the upper and lower jaw in skeletal preparation, this may overestimate the in vivo gape which is constrained by the architecture and size of the jaw muscles (Hylander, 2013). Ideally, this dimension should be taken on living individuals to obtain more precise measurements (Hartstone-Rose et al., 2015). Nevertheless, the other dimensions reflect the maximal jaw opening capacity and the size of the temporalis muscles and thus provide a proxy for bite force (Hylander, 2013). Consequently, cranial dimensions, especially those linked with the opening of the jaw and the size of the temporalis muscle, appear to be good indicators of the size of seeds ingested. Our results also showed that we can predict the mean and maximum seed sizes that mammals can disperse by endozoochory. This result mirrors the strong link between the mean and maximum size of ingested seeds, meaning that bigger mammals tend to also consume bigger seeds on average. To a lesser extent, we can also predict fruit sizes, but the correlation coefficients are much lower and reflect the fruit consumption variability mentioned above.

Overall, phylogenetic analyses (i.e. PGLS) revealed smaller correlation coefficients than simple regression analyses (i.e. OLS) but still showed significant results. This demonstrates that the life history of the mammal species included here does not explain all of the variability of our dataset. Rather, part of the relationships between body and skull size and fruit and seed size is because closely related species resemble each other and often also eat similar food items, thus reducing the explanatory power of the phylogenetic models. In addition, BM revealed greater correlation coefficients and thus, explained a larger part of the variance than the size-corrected skull dimensions (i.e. CH, MJG). Nevertheless, skull dimensions are still a good alternative for museum specimens for which we have access to the skulls but often no information on BM.

4.3 | BM, CH and jaw gape as predictors of fruit and seed sizes in extinct species

Oral behaviours related to food acquisition and ingestion are reflected in the form of the skull, jaws and teeth. Thus, dietary

TABLE 3 Predictions (mm) for five extinct mammal species based on (a) the ordinary least square (OLS) equations using body mass (BM), (b) phylogenetic generalized least squares (PGLS) equations using body mass (BM) and (c) the ordinary least square (OLS) equations using coronoid height (CH), (d) phylogenetic generalized least squares (PGLS) equations using maximum jaw gape. A blank case means that the relationship was not significant. Therefore, we did not use the equation to make predictions.

Extinct species	Seed length	Seed width	Max. seed length	Max. seed width	Fruit length	Fruit width	Max. fruit length	Max. fruit width
(a) Estimated by BM (OLS)								
Hadropithecus stenognathus	12.4	8.5	30.6	20.3		26.8	141.2	104.4
Archaeolemur majori	10.5	7.2	25.7	17.0		25.8	132.7	92.5
Archaeolemur edwardsi	11.5	8	28.3	18.8		26.4	137.5	99.0
Paralouatta varonai	7.9	5.4	18.7	12.4		24.1	118.8	74.4
Antillothrix bernensis	7.6	5.2	18.0	11.9		23.9	117.0	72.3
(b) Estimated by BM (PGLS)								
Hadropithecus stenognathus					129.7		751.5	144.7
Archaeolemur majori					103.0		521.4	120.4
Archaeolemur edwardsi					117.3		640.8	133.6
Paralouatta varonai					68.1		269.8	86.5
Antillothrix bernensis					64.4		247.2	82.84
(c) Estimated by CH (OLS)								
Hadropithecus stenognathus	5.9	3.9	13.7	9.0		22.7	108.8	61.0
Archaeolemur majori	6.6	4.4	15.5	10.1		23.4	113.5	66.9
Archaeolemur edwardsi	9.0	6.1	22.4	14.4		25.5	130.8	87.6
Paralouatta varonai	6.6	4.5	15.7	10.2		23.5	114.1	67.5
Antillothrix bernensis	5.3	3.5	12.2	8.0		22.0	103.1	55.7
(d) Estimated by MJG (PGLS)								
Hadropithecus stenognathus	4.9	3.3	10.8	7.2			77.5	46.1
Archaeolemur majori	3.5	2.6	7.2	5.1			63.2	40.8
Archaeolemur edwardsi	7.1	4.4	17.5	10.8			98.3	53.2
Paralouatta varonai	7.3	4.5	18.1	11.1			100	53.8
Antillothrix bernensis	4.0	2.8	8.5	5.8			68.4	42.8

behaviour can be inferred based on cranial morphology (Bargo, 2001; Dumont, 1997; Jungers et al., 2002). We tested our models by estimating the mean and maximum sizes of ingested seeds and fruits of several extinct species using BM, CH and jaw gape as our predictors. Our results showed variation depending on whether we used BM, CH or jaw gape as the predictor. Generally, BM suggested larger maximum ingested seed sizes (±10 mm long) than the other predictors, whereas jaw gape predicted the smallest fruit and seed sizes. According to the correlation coefficients, we propose that BM can be used to predict the mean and maximum size of ingested seeds and to a lesser extent the fruit sizes, in extant or extinct mammal species. To a lesser extent, although the estimated sizes were smaller, the CH would be another good predictor, especially for extinct species for which body size data are not available.

Predictions of the five extinct species revealed great seed ingestion capacities (i.e. up to 30.6 mm long). However, they remain below the recent estimations provided by a linear model between lemur BM and observed maximum seed width ingested in Madagascar (Albert-Daviaud et al., 2020). Indeed, according to Albert-Daviaud et al. (2020), *Archaolemur* spp. and *Hadropithecus stenognathus* could potentially ingest seeds between 35.5 and 43.4 mm wide. Those results are 10–20 mm above all our predictions and likely an overestimate of the real consumed sizes. Although there are uncertainties about the habitat, diet, behaviour or home range of extinct species (Crowley et al., 2012; Crowley & Godfrey, 2019), we believe that our results demonstrate better accuracy as they are obtained based on multiple predictors and a much larger dataset. Irrespective of the exact sizes eaten, these species likely played significant roles in the seed dispersal of large-seeded plant species in tropical forests in the past. Moreover, these predictions can also allow us to make inferences about the ingestion capacities of extant species for which limited information is available (Chancellor et al., 2012;

Zhang & Zang, 2018). Unfortunately, we failed to include extinct bat and carnivore specimens despite some records on extinct fruit bats (Balseiro et al., 2009; Van Damme et al., 2018). Future studies should explore and test more fossil specimens for a deeper understanding of the lifestyle and seed dispersal capacity of extinct mammals.

4.4 | Perspectives

Overall, our results demonstrate a link between seed traits, skull dimensions and BM in frugivorous mammals. In forests harvested for timber, the mean seed size decreases because plants with large seeds (hardwood, commercial species) are often harvested first (Markl et al., 2012). Such a perturbance can, in turn, impact large-bodied frugivores by modifying the availability of their food resources. Conversely, if large dispersers go extinct, through hunting, mean seed size will also decrease given that size and cranial morphology appear tightly correlated to seed size dispersed. This is, for example, suggested by a study in South American forests, where the loss of large fruit-eaters has led to a reduction in the average seed size of *Euterpe edulis* palms (Galetti et al., 2013). Furthermore, it has been shown that defaunation also leaves its signature in the gene pool of plant populations (Carvalho et al., 2016; Pacheco & Simonetti, 2000). Thus, the absence of seed dispersers not only results in phenotypic changes, but also affects the allelic frequencies of plants, with unknown effects on the long-term persistence of plant species and entire communities.

Nonetheless, our results only demonstrated the seed dispersal potential of mammal species in terms of the capacity of seed and fruit ingestion. Animal BM may affect other aspects of the quality of seed dispersal, such as the amount of seed carried, visitation rate, the number of seeds removed and seed dispersal distance (Markl et al., 2012; Wotton & Kelly, 2012). Moreover, seed dispersal by endozoochory is influenced by a diverse array of factors beyond seed ingestion. These include digestion time, animal movement patterns and germination success. Animal movement patterns also depend on many factors such as season, resource availability and distribution, diet composition, territoriality, and social behaviour of fruit-eater vertebrates (Campos-Arceiz et al., 2008; Culot et al., 2010; Guillotin et al., 1994; Karubian et al., 2010). Thus, an important direction for future work is to combine information about animal BM and skull dimensions with the intensity of the interactions and dispersal quality.

Overall, most of our study's frugivorous primate and bat species are well studied and described as important seed disperser communities. Strikingly, significant gaps in our understanding of the diet of frugivorous carnivores are apparent. For example, data on seeds ingested by the binturong (*Arctictis binturong*) are based on a single individual (Nakabayashi et al., 2017). Consequently, we gathered data on ingested seeds for only a small number of species of carnivores ($N = 12$). Despite the few studies on carnivores, these animals have the potential to be excellent dispersers. For example, the civet (*Paradoxurus hermaphroditus*) can swallow and disperse disproportionately large seeds (Nakashima et al., 2010), and seeds can be retained for several hours in the digestive tract, during which the animal can travel several hundreds of meters (Nakashima et al., 2010).

In summary, in this study, we have shown that large mammals are essential for dispersing the seeds of large-seeded plants due to their specific cranial morphology, allowing them to ingest these seeds. Our results underscore the importance of maintaining functional diversity in seed dispersers to maintain tropical forest structure and regeneration because of the morphological constraints on seed sizes consumed by different species. In addition, we have shown that morphological characteristics can predict the seed ingestion capacities of extinct mammals, which provides the basis for predicting the consequences of frugivore extinction within tropical forests.

AUTHOR CONTRIBUTIONS

Elise Sivault performed the analyses; Anthony Herrel helped with the analyses; Elise Sivault made measurements and collected the data; Elise Sivault wrote the first draft of the manuscript; Anthony Herrel, Pierre-Michel Forget, Kim R. McConkey and Eckhard W. Heymann contributed substantially to revisions; François Bretagnolle, Eckhard W. Heymann, Joanna Lambert, Kim R. McConkey, Asmita Sengupta and Pierre-Michel Forget collected significant data.

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CONFLICT OF INTEREST STATEMENT

Anthony Herrel is an Associate Editor of Functional Ecology, but took no part in the peer review and decision-making processes for this paper. The rest of the authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.dfn2z356c (Sivault et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Prediction references.

Appendix S2. Supplementary analyses.

Appendix S3. Supplementary analyses.

Appendix S4. Additional result.

Appendix S5. Fruit database per mammal species.

Appendix S6. Seed database per mammal species.

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