Body mass and skull dimensions predict seed dispersal capacity in bats, primates and carnivores from tropical forests

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Abstract

Endozoochory is an essential plant-animal interaction in tropical forests, involving the swallowing and defecation of seeds. To better understand whether anatomical traits (i.e. body mass and skull dimensions) are good predictors of seed dispersal in mammals we studied the relationships between morphology, fruit and seed size and seed dispersal distance across three orders: Chiroptera, Primates, and Carnivora. Our results revealed that body mass is an important driver of the size of ingested seeds for all orders and of the seed dispersal distance produced by Primates. In addition, the distance between the molars, jaw length, and jaw gape are good predictors of the size of ingested seeds. These results show how body mass and cranial anatomy constrain ingested seed size and dispersal distance across mammals and reinforce the importance of maintaining functional diversity in seed dispersers to maintain tropical forest structure and regeneration.

Introduction

Most trees and woody lianas in tropical forests depend on animals for seed dispersal (zoochory), with many trees producing fruits that are attractive to animals (Howe & Smallwood 1982; Jordano 2000; Buitrón-Jurado & Ramírez 2014; Howe 2014). Frugivores disperse seeds by consuming the fruit pulp and spitting out the seeds after cleaning them from their pulp (synzoochory) (Howe & Kerckhove 1981; Corlett & Lucas 1990; Lobova *et al.* 2009), or they ingest fruits whole and the seeds are found intact in their feces (endozoochory) (Shilton *et al.* 1999; Tobler *et al.* 2010; Beaune *et al.* 2013). According to the Janzen-Connell hypothesis, the deposition of seeds away from the parent tree could be advantageous for the plant because the establishment and the survivorship of seedlings is affected by negative density dependent processes such as intraspecific competition, herbivores or pathogens (Janzen 1970; Connell 1971; Bell *et al.*2006; Mangan *et al.* 2010; Swamy *et al.* 2011). When endozoochory occurs, seed dispersal distances mostly depend on the transit time of the seed in the digestive tract and the movement of the animal (Traveset *et al.* 2007). Large-sized dispersers, like elephants for example, show long-distance movements and long gut retention times, thus generating a more diverse, long-distance dispersal pattern than smaller dispersers (Jordano *et al.* 2007 ; Nathan *et al.* 2008; Campos-Arceiz & Blake 2011; Bueno *et al.* 2013; O'Farrill *et al.* 2013; Gonzalez & Stevenson 2014; Fuzessy *et al.* 2017). Thus, body mass can be expected to be an important driver of seed dispersal distance.

The outcomes of interactions between plants and frugivores are influenced by both plant and animal traits

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(Dehling *et al.* 2016). Many traits of animals influence the quantity and quality of seed dispersal and consequently impact the seed-dispersal effectiveness (Schupp *et al.* 2010; Beckman & Rogers 2013). Avian body mass determines energy requirements, affecting foraging behaviour and consequently may constrain the size of fruit that can be ingested (Jordano 2000; Kitamura *et al.* 2002). Moreover, bill size or wing morphology in birds influence fruit handling and manoeuvrability for fruit access (Dehling *et al.* 2016). Nevertheless, no studies have explored the link between body mass or skull dimensions with the size of ingested seeds in mammals. Yet, body size and gape limitations can be expected to be important drivers of these relationships as they are for birds (Lord 2004; Godinez-Alvarez *et al.* 2020).

Here, we focus on mammals with a predominantly frugivorous diet across three orders: Chiroptera, Primates, and Carnivora. Frugivorous bats are represented by the Pteropodidae family of the Old World (Africa, Asia, Oceania) and Phyllostomidae of the New World (America). They are able to carry up to 1.5x their body mass in fruit (Mahandran *et al.* 2018) and some can ingest and defecate a large amount of small 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 (Lambert 1999; Gross-Camp & Kaplin 2011). 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 important dispersers (Alves Costa & Eterovick 2007; Zhou *et al.* 2008; Nakabayashi *et al.* 2016). 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 global data including Neotropics, Asia, Africa and Madagascar, we tested the following questions:

1. Do body mass and skull dimensions predict the size of ingested seeds and fruits? We expected a positive relationship between body mass and cranial dimensions with the size of consumed fruits and ingested seeds.

2. Do body mass and skull dimensions influence seed dispersal distance? We expect a positive relationship between body mass and seed dispersal distance in relation to digestion times, with longer transit times resulting in greater seed dispersal distances.

Materials and Methods

Body mass 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 (see Appendix S1 in supporting information) were made with an accuracy of 0.01 cm using digital calipers. 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) are correlated with the size of the animal and give an estimate of 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) provide an estimate of the size of the food passage (size of the oral and pharyngeal tract). The coronoid height (H) indicates the size of the temporalis muscles and provides insights on bite force which may also be related to the size of the fruit and seeds ingested. The regular absence of teeth on the skulls of the specimens resulted in all measurements being taken at the base of the teeth. As far as possible, the skulls of two adult males and two adult females were measured for each species. Body mass data were derived from the open access database of the Encyclopedia of Life which lists the adult male and female body mass (https://eol.org/).

Species

The species of bats, primates and carnivores selected for this study include at least 50 percent of fruit in their diet in some localities and throughout most of the year. Indeed, depending on the availability of resources,

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even highly frugivorous species may include insects, other plant material or other vertebrates into their diet. Our data are derived from the results of observations or experiments (average dry mass of feces or stomach contents) presented in the literature (see Appendix S2). Our data set encompassed eight families of Primates including 48 species, two families of Chiroptera including 43 species and two families of Carnivora including 13 species (N = 104 species) (see Appendix S2).

Fruit and seed sizes

The fruit and seed sizes of the plants consumed by the three taxa studied were compiled to relate them to their morphology and the seed dispersal capacities. Seeds found intact in the feces are considered to be dispersed by endozoochory. These data were mainly obtained from existing databases (Forget *et al.* 2007; Bretagnolle *et al.*unpub.), a book (Lobova *et al.* 2009), journals (see Appendix S2), theses (Gompper 1994; Nakabayashi 2015) and through the help of M. Norconk, T. Gregory, D. Chakravarthy, A. Blackburn, O. Razafindratsima and M. Gompper. 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, data from the locality where the species ingests the larger seeds were used because we were interested in the maximal seed or fruit size that can be ingested by an animal.

Seed dispersal data

In order to explore the seed dispersal capacities of the species studied, we compiled data on transit times and seed dispersal distances. Unfortunately, these parameters are only variably present in the literature, thus we were not able to compile enough data for bats and carnivores. We obtained data for 16 species of Primates (see Appendix S2). We compiled average and maximum transit times of the food ingested but also the average and maximum seed dispersal distances estimated in the literature. For two species (i.e. *Leontocebus nigrifrons* and *Saguinus mystax*), only medians of seed dispersal distances were available instead of averages. The average transit time is the average of the measured durations between the ingestion of a food and its first defecation. The maximum transit time is the time to the defecation of the last element.

Statistical analysis

In order to identify potential relationships between morphological data (body mass and skull dimensions) on one hand and seed and fruit sizes and seed dispersal distance data on the other hand we used a "two-block partial least squares" (2B-PLS) approach (Rohlf & Corti 2000). This method makes it possible to quantify the degree of association between two tables 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 data tables. A PLS correlation coefficient (R_{pls}) and the covariance percentage for each axis produced are obtained using the function "pls2b" in R from the Morpho library (Schlager 2013). The result comes from a set of 1000 permutations. Next, a sampling distribution of coefficients is obtained by resampling. The P $_{95}$-value is calculated by comparison of the observed PLS coefficient to those obtained after resampling. The significance of each linear combination is assessed by comparing the singular value (PLS coefficient) to those obtained from permuted blocks. If the PLS coefficient is higher than those obtained from permutated blocks, then its associated P $_{95}$-value is considered as significant. For each significant analysis, a graph and histograms of the variables are generated by using the Geomorph library (Adams *et al.* 2013).

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

As body mass is known to impact morphology, we ran Spearman correlation tests (non-parametric) and linear regressions of each of the skull dimensions as a function of body mass and extracted the residuals.

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These were then used for 2B-PLS and phylogenetic 2B-PLS analyses to explore covariation between skull dimensions and fruit and seed size without the confounding effect of body mass.

We used R statistical environment (R core team (2019), version 3.5.2) for these analyses. All data were Log_{10}-transformed before analyses to assure normality and homoscedascity.

Phylogeny

In order to integrate the phylogeny of the species into our analyses, we used the phylogenetic tree produced by Bininda-Emonds in 2007. It contains a significant number of mammalian species and it is the most complete tree to date (Bininda-Emonds *et al.* 2007). We checked the presence of our species in this tree with the function "treedata" and we reduced this tree by keeping only the species studied, using the geiger (Pennell *et al.* 2014) and ape (Paradis & Schliep 2018) libraries in R.

Results

Body mass and skull dimensions with fruit and seed sizes

Our analysis revealed significant covariations (R_{pls}=0.31; P=0.008) between morphology and seed and fruit size ingested. We can observe that body mass drives the covariation with ingested seed and fruit sizes (average and maximum length and width) (see Fig. 1).

Spearman correlation tests showed that skull dimensions are strongly correlated to body mass (R > 0.9; P $<<<0.001$). Consequently, we reran our 2BphyloPLS analyses using residual data. These analyses showed that the distance between molars, the canine overlap, the projected and effective jaw length, and jaw gape covaried significantly with seed sizes. Moreover, the coronoid height, jaw width and bicondylar width covaried with fruit sizes (R_{pls}=0.44; P=0.001) (see Fig. 2).

To explore whether the overall pattern held within each clade we repeated this phylogenetic 2B-PLS analysis between seed and fruit sizes and residual skull dimensions for primates only and did not find any significant covariation (R_{pls} = 0.42; P = 0.06). A similar 2B-PLS phylogenetic analysis was also performed for the Chiroptera group and showed significant covariations (R_{pls}=0.66; P=0.001). The distance between molars, the canine overlap, the projected and effective jaw length, and the jaw gape covaried with the dimensions of the ingested seeds. Also, the coronoid height, jaw width and bicondylar width covaried with fruit sizes (see Fig. 3). For the carnivores the 2B-PLS analysis did not reveal any covariation (R_{pls}=0.6; P=0.2) likely due to the small sample size.

Body mass, skull dimensions and seed dispersal distances

Our analysis for primates only (N=16) detected significant covariation between body mass and seed dispersal distances and transit times, respectively (R_{pls}=0.73; P=0.01; Fig. 4). Small primates like e.g. tamarins (*Leontocebus nigrifrons* 11 Previously *Saguinus fuscicollis* (see Rylands *et al.*2016)) have short retention times and seed dispersal distances, while large primates such as gorillas (*Gorilla gorilla*) have a long retention time and disperse seeds further.

An analysis excluding the body mass revealed significant co-variations between the skull dimensions and seed dispersal distances (R_{pls}=0.78; P=0.03). Coronoid height, the distance between molars, the projected and effective jaw length covaried with the transit times and seed dispersal distances (see Fig. 5).

Discussion

Our data revealed a strong link between the average and maximum seed and fruit sizes consumed and the body mass of frugivorous mammals (see Fig.1). These data thus indicate that larger mammals generally consume larger fruits and ingest larger seeds. 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. Furthermore, seed size does not necessarily correlate with fruit size, e.g. *Annona muricata* , as large fruits can contain numerous small seeds.

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Skull dimensions including jaw gape, jaw length, canine overlap, and the distance between molars also appear good predictors of the size of ingested seeds (see Fig.2). These measurements mainly reflect the food passage and maximal jaw opening (Hylander 2013). Consequently, cranial dimensions, especially those linked with food passage size constrain the size of seeds ingested. Moreover, coronoid height and jaw width appear predictors of the size of ingested fruits. These dimensions reflect the food passage and the bite force of the species. Nevertheless, these data suggest that the size of consumed fruits is less predictable than the size of seeds. Large-sized fruits can be broken into pieces or eaten without being detached from their support by some bats (Morrison 1980; Singaravelan & Marimuthu 2008). Carnivores sometimes drop large fruit to the ground to break it up (Howe 1986), while the dexterity of primates enables them to consume fruit larger than their gape (Peckre*et al.* 2019).

The same analysis was carried out only for Chiroptera and revealed co-variations similar to the multi-taxon analysis (see Fig. 2 and 3). Thus, also within Chiroptera the morphology of the cranium appears to limit the size of the seeds that can be ingested and dispersed. This pattern is relatively strong and reveal few different behaviours in the treatment of seeds by Chiroptera. Bats consume the pulp of the fruits, swallow small seeds, or drop them if they are too large to be swallowed (Forget *et al.* 2007; Lobova *et al* 2009). However, the same analysis was not significant for Primates. Although many of them swallow seeds, some primates consistently spit large seeds (Lambert 1999). It suggests that taxa with diverse handling behaviour (swallowing versus spitting) might not be well represented by this model.

Our analysis exploring relations between transit times, seed dispersal distances and body mass of primates did reveal covariation (see Fig. 4). Gorillas dispersed seeds further than tamarins, for example, showing that body mass is the principal driver of these covariations. This reflects the strong relationship between body mass and seed retention times suggested in previous studies (Wotton & Kelly 2012; Yoshikawa*et al.* 2019).

Our analysis exploring relationships between skull dimensions, seed dispersal distances and transit times of primates was significant. However, the covariations were quite variable and dependent on the species involved. A possible explanation can be the difference in group size among primate species. There is a positive correlation between primate body mass and group size (Clutton-Brock & Harvey 1977). Primates living in large groups travel further than species in small groups (Wrangham *et al.* 1993). Nevertheless, further studies exploring how primates and other mammals manipulate fruits and seeds are needed to better understand these relationships. Our limited database does not allow to test for this relationship at the moment, but this is an obvious issue for future studies.

Oral behaviours related to food acquisition and ingestion are reflected in the form of the skull, jaws and teeth. Consequently, based on cranial morphology, several examples show the possibility to infer feeding or dietary behaviour to museum specimens (Dumont 1997; Bargo 2001; Jungers*et al.* 2002). In addition, evidence shows that body size can be used as a strong indicator of seed retention time of extinct animals. This is suggested by a study using body mass of extinct Mesozoic dinosaurs to deduce their seed retention times that determines the spatial pattern of seed dispersal (Yoshikawa *et al.* 2019). The strong covariations that we observed, indicate that seed size ingested, retention times and seed dispersal distance could be inferred in extinct animals based on morphological measurements.

Significant gaps in our understanding of the diet in frugivorous carnivores were apparent. For example, data on seeds ingested by the binturong (*Arctictis binturong)* are based on a single individual (Nakabayashi *et al.* 2017). Consequently, we were able to gather data on ingested seeds for only a small number of species (N=13). 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).

Our results demonstrate a tight link between seed traits and the skull dimensions and body mass in frugivorous mammals. In harvested forests for timber, the average seed size decreases because plants with large seeds (hardwood, commercial species) are often harvested (Markl *et al.* 2012) which can, in turn, impact

large-bodied frugivores by modifying the availability of their food resources. Conversely, if large dispersers go extinct, e.g. through hunting, average seed size will also decrease given that size and cranial morphology appear tightly correlated to seed size dispersed. This is 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 (Pacheco & Simonetti 2000; Carvalho *et al.* 2016). Thus, the absence of seed dispersers does not only result in phenotypic changes but also affects allelic frequencies of plants, with unknown effects on the long-term persistence of plant species and entire communities.

In this study, we have shown that large mammals are essential for dispersing the seeds of large-seeded plants. Our results underline the importance of maintaining functional diversity in seed dispersers to maintain tropical forest structure and regeneration, because of morphological constraints on seed sizes consumed by different species. In addition, we have shown that morphological characteristics can be used to predict seed dispersal patterns of recent or extinct mammals which also provide a basis for predicting the consequences of frugivore extinction within tropical forests.

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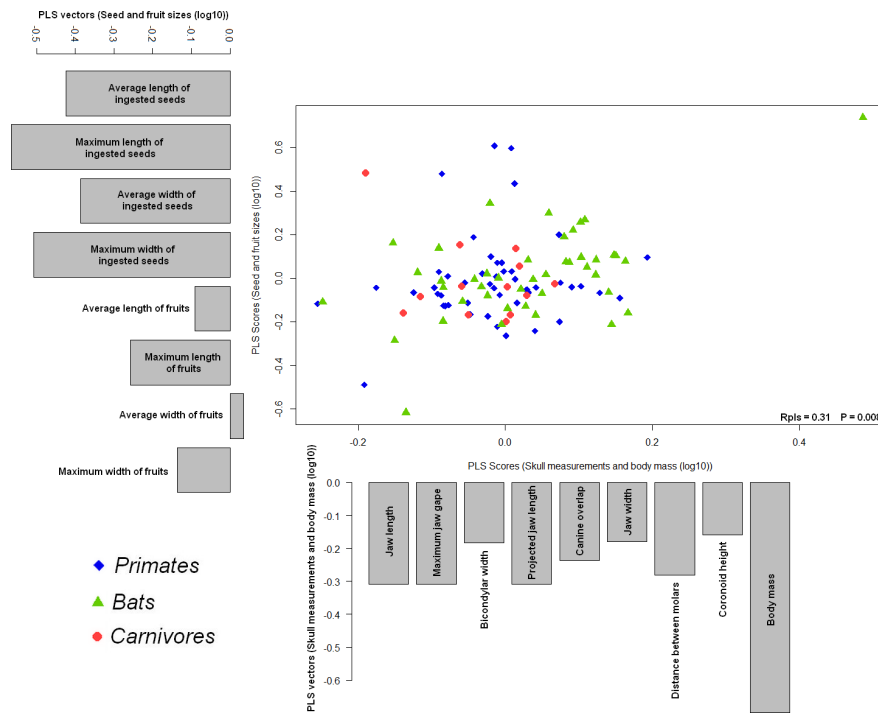
Fig.1: Phylogenetic Two Block-Partial Least Squares analysis between the skull measurements, body mass and the size of consumed fruits and ingested seeds. Scatter plot of the PLS axis describing the co-variation between the morphology data and the size of fruits and seeds. Seed and fruit sizes associated with the morphological data are represented by the histogram at the left side of the scatterplot. The morphology data associated with the size of fruits and seeds are represented by the histogram at the bottom of the scatterplot.
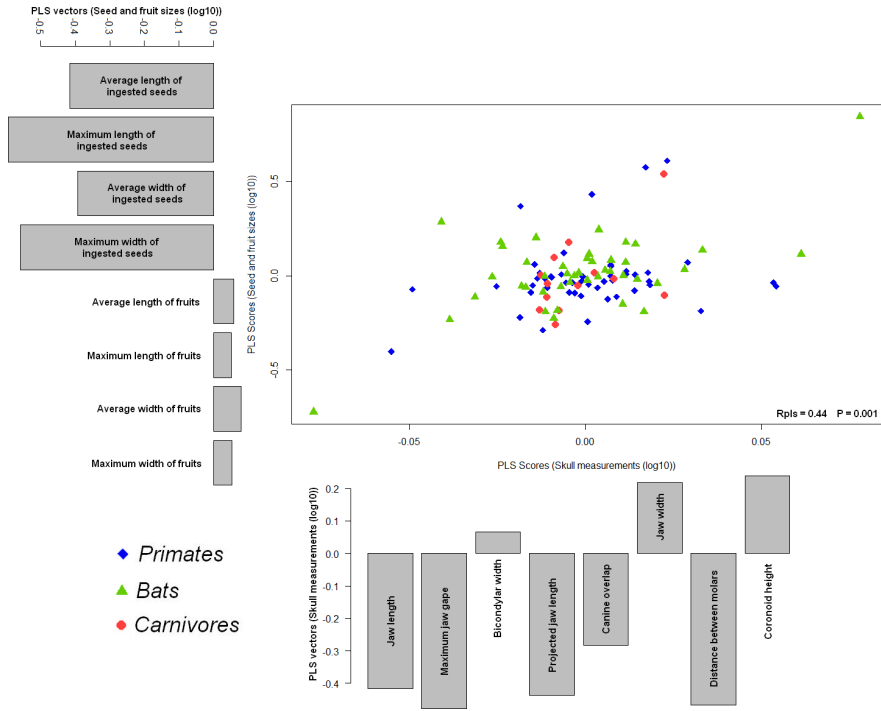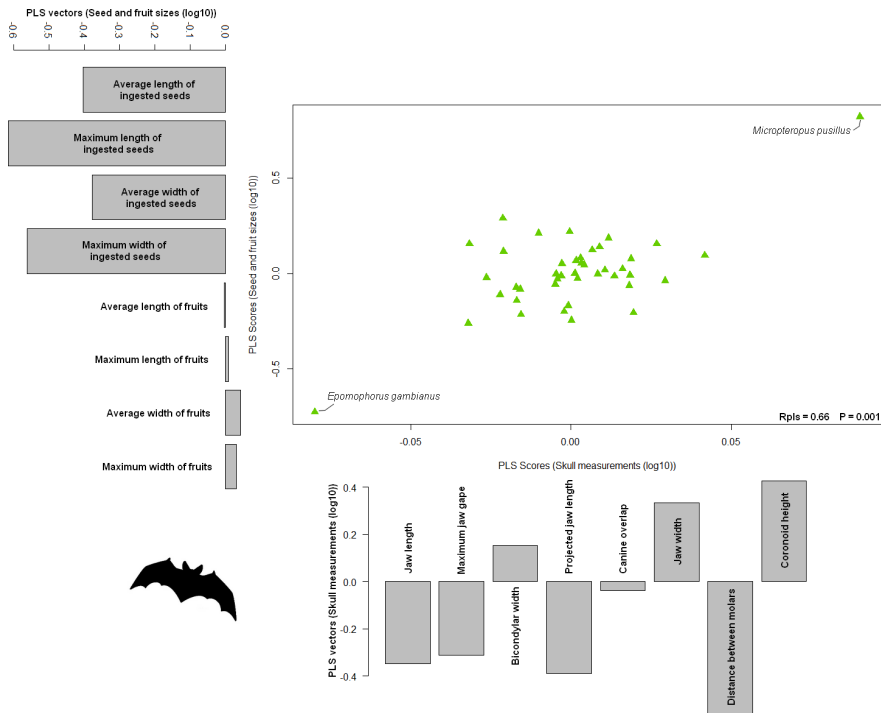
Fig. 2: Phylogenetic Two Block-Partial Least Square between the residual skull measurements and the size of consumed fruits and ingested seeds. Scatter plot of the PLS axis describing the co-variation between the residual skull measurements and the size of fruits and seeds. Seed and fruit sizes associated with the skull measurements are represented by the histogram at the left side of the scatterplot. The skull measurements associated with the size of fruits and seeds are represented by the histogram at bottom of the scatterplot.

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Fig. 3: Phylogenetic Two Block-Partial Least Square between the residual skull measurements and the size of consumed fruits and ingested seeds of bats. Scatter plot of the PLS axis describing the co-variation between the residual skull measurements and the size of fruits and seeds. Seed and fruit sizes associated with the residual skull measurements are represented by the histogram at the left side of the scatterplot. The residual skull measurements associated with the size of fruits and seeds are represented by the histogram at bottom of the scatterplot.
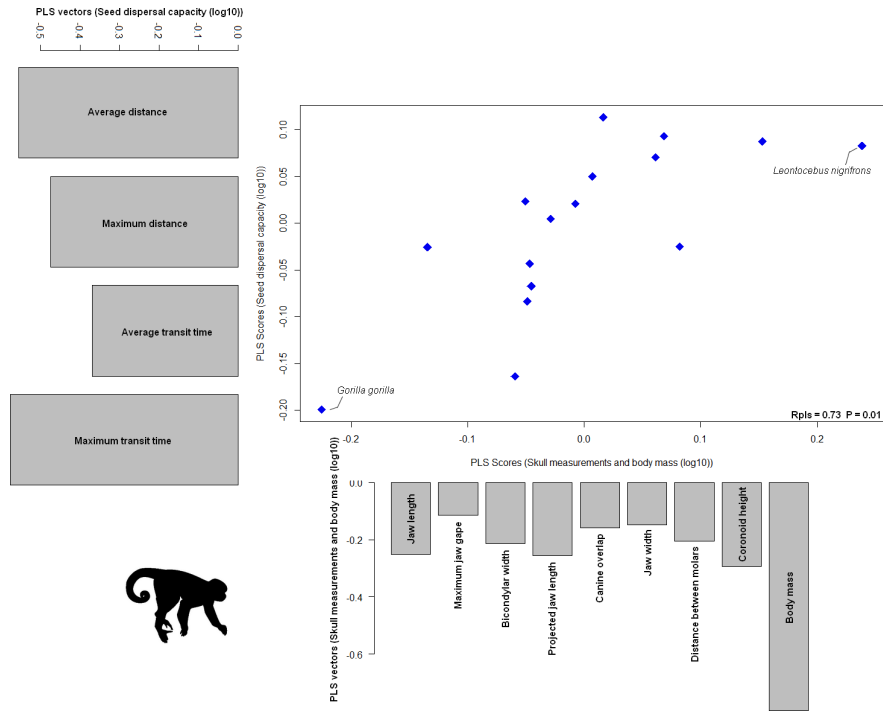

Fig. 4: Phylogenetic Two Block-Partial Least Square between the body mass, cranial morphology and seed dispersal capacity. Scatter plot of the PLS axis describing the co-variation between the body mass and cranial morphology and the seed dispersal capacity. Transit times and seed dispersal distances associated with morphology are represented by the histogram at the left side of the scatterplot. The morphological traits associated with transit times and seed dispersal distances are represented by the histogram at bottom of the scatterplot.
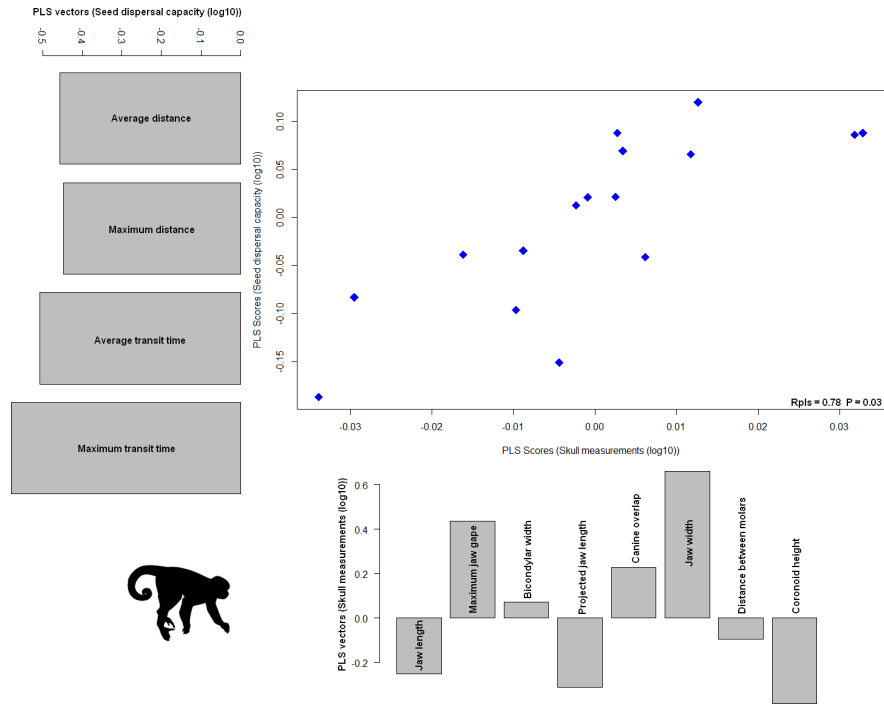
Fig. 5: Phylogenetic Two Block-Partial Least Square between cranial morphology and seed dispersal capacity. Scatter plot of the PLS axis describing the co-variation between the cranial morphology and the seed dispersal capacity. Transit times and seed dispersal distances associated with morphology are represented by the histogram at the left side of the scatterplot. The morphological traits associated with transit times and seed dispersal distances are represented by the histogram at bottom of the scatterplot.