

Morphometric models for estimating bite force in *Mus* and *Rattus*: mandible shape and size do better than lever-arm ratios.

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Abstract

Morphological traits are frequently used as proxies for functional outputs such as bite force performance. This allows researchers to infer and interpret the impacts of functional variation, notably in adaptive terms. Despite their mechanical bases, the predictive power of these proxies for performance is not always tested. In particular, their accuracy at the intraspecific level is rarely assessed, and they have sometimes been shown to be unreliable. Here, we compare the performance of several morphological proxies in estimating *in vivo* bite force, across five species of murine rodents, at the interspecific and intraspecific levels. Proxies used include the size and shape of the mandible, as well as individual and combined muscular mechanical advantages (temporal, superficial masseter and deep masseter). Maximum voluntary bite force was measured in all individuals included. To test the accuracy of predictions allowed by the proxies, we combined linear regressions with a leave-one-out approach, estimating an individual bite force based on the rest of the dataset. The correlations between estimated values and the *in vivo* measurements were tested. At the interspecific and intraspecific levels, size and shape were better estimators than mechanical advantages. Mechanical advantage showed some predictive power at the interspecific level, but generally not within species, except for the deep masseter in *Rattus*. In few species, size and shape did not allow us to predict bite force. Extrapolations of performance based on mechanical advantage should therefore be used with care, and are mostly unjustified within species. In the latter case, size and shape are preferable.

Introduction

For decades, deductions of functional outputs from morphology have been routinely used in an adaptationist framework to infer the potential selective advantage of phenotypic variation (Gould and Lewontin, 1979; Mayr, 1983). However, this evaluation was often done without measuring functional performance until the integration of functional morphology within evolutionary biology (Arnold, 1983). Since then, some of the best examples of adaptation and adaptive radiation have been illustrated using this integrative approach (*e.g.* Grant and Grant, 2002; Herrel et al., 2005, 2009). Yet, relationships between morphology and function vary at different scales (*e.g.* inter-specific, intra-specific or intra-population), and only a precise quantification of the links between morphological and functional variation can avoid the pitfalls of a pan-adaptationist approach (Gould and Lewontin, 1979; Mayr, 1983).

In the diversified clade of rodents, links between skull or mandible morphology and diet or ecology have been reported for several groups and at different taxonomic scales (Michaux et al., 2007; Samuels, 2009; Hautier et al., 2009, 2011, 2012; Cox et al., 2012). The influence of skull and mandible morphology on *in vivo* bite force performance also has been directly tested, using various anatomical variables (*e.g.* Freeman and Lemen, 2008; Ginot et al., 2018). The use of biomechanical models (*i.e.* combining muscle PCSA and lines of action) or mechanical descriptors (combinations of mandibular measurements) in these articles allowed the accurate estimation of bite force (compared to *in vivo* data) at the interspecific level. However, Ginot et al. (2018) showed that these estimates of bite force were less precise at the intraspecific level. Furthermore, this approach requires the accurate dissection of muscles, to dissolve them and measure fiber length for individual muscle strands, and is therefore time-consuming and inapplicable to specimens for which muscles have not been preserved. Therefore, other osteological proxies, such as morphometric data or mechanical advantages (*i.e.* muscular lever-arms ratios) are often used to estimate bite force (Greaves, 1983; Kiltie, 1984; Thomason, 1991; Christiansen and Adolfssen, 2005; Ellis et al., 2008).

Here, we estimate bite force using osteological proxies in five species of murine rodents (*Mus musculus* Linnaeus, 1758, *M. cervicolor* Hodgson, 1845, *M. caroli* Bohnote, 1902, *Rattus exulans* Peale, 1848, and *R. tanezumi* Temminck, 1844), for which *in vivo* measurements were also taken. Several osteological proxies are tested and compared: mandible size and shape, the mechanical advantage of the temporalis muscle, the mechanical advantage of the superficial masseter muscle and the mechanical advantage of the deep masseter muscle, as well as the combination of the three mechanical advantages. Although mechanical advantage makes mechanical sense and has previously been used as a proxy for function (*e.g.* Thorington and

Darrow, 1996; Velhagen and Roth, 1997; Swiderski and Zelditch, 2010; Blanco et al., 2013; Casanovas-Vilar and van Dam, 2013; Gomes Rodrigues et al., 2016; Fabre et al., 2017; Renaud et al., 2015, 2018a,b; Parmenter et al., 2019; Souquet et al., 2019), its relationship with bite force has never been formally tested. The mechanical expectation is that individuals with larger values of mechanical advantages will show larger bite forces. The tighter this relationship, the more precise our estimates should be, producing a stronger correlation (i.e. closer to 1) between estimated and *in vivo* bite force. However, shape may be a better predictor because the complexity of shape variation as quantified by geometric morphometrics may be more integrative than the limited number of scalars obtained from lever arm mechanical advantage. Notably, the strong allometric component of shape variation means that shape also integrates a large part of the signal linked to size. Although it is expected that more complex methods, using muscular characteristics to estimate forces, will give much better estimations (see Ginot et al., 2018), the aim of this paper is to verify and compare the validity of osteological proxies which are easy to access (allowing large sample sizes), already in use in the literature, and available even when soft tissues are absent (e.g. paleontology).

Materials and methods

Specimens

Four species were caught in the wild with no control for age: *M. cervicolor* (n=65), *M. caroli* (n=13), *R. exulans* (n=42) and *R. tanezumi* (n=29). All were caught with live traps (either handmade local cage traps, or Sherman traps) over two field sessions (2015 and 2016) during the dry season (February-March) in several localities across Northern, Eastern and North-Eastern Thailand. Sampled sites were around the towns of Tha Wang Pha, Nan Province; Sakaerat, Nakhon Ratchasima Province; Mahasarakham, Mahasarakham Province; and Sahatsakhan, Kalasin Province. *Mus musculus* specimens (n=51), were raised in the lab at the University of Montpellier and are descendants from wild ancestors captured in the Orkney islands (Scotland). These individuals all had their bite forces measured at 68 days and were subsequently euthanized. Males and females were pooled to improve the sample size on which the predictive bite force models were built (see below).

Bite force measurements

Shortly after capture we measured the voluntary bite force at the incisors of each individual using a piezoelectric force transducer (Kistler, type 9203, range 0-500 N, accuracy 0.01–0.1 N; Amherst, NY, USA; calibrated by the constructor at 25 °C and 36% humidity) attached to a handheld charge amplifier (Kistler, type 5995, Amherst, NY, USA; Herrel et al., 1999). The force transducer was mounted between two steel bite plates as described in Herrel et al. (1999). We

adjusted the distance between the bite plates by measuring it with a caliper, and by increasing or decreasing it via the micrometer head, so that each individual bit at a consistent gape angle of $\sim 30^\circ$. All animals bit directly onto steel at the same spot on the plates (*i.e.* at the tip), to ensure a consistent out-lever length. We recorded three trials in a row for each individual, and the maximal score was used in the analyses. All measurements were taken by one user (SG) to avoid inter-user variation.

Animals were treated in accordance with the guidelines of the American Society of Mammalogists, and within the European Union legislation guidelines (Directive 86/609/EEC). Approval notices for trapping and investigation of rodents on the field (Thailand) were provided by the Ethical Committee of Mahidol University, Bangkok, Thailand, number 0517.1116/661, for the CERoPath protocols (project ANR 07 BDIV 012). All lab procedures were under the Approval No. A34-172-042 (Hérault Prefecture).

Morphometric analyses

All mandibles were skeletonized manually, after which they were photographed in a standardized way (camera at a fixed distance, mandible positioned flat with the lingual side down) using a Pentax K200D reflex camera, with a 45mm focal distance. In total, 17 landmarks were placed on each mandible (Fig. 1) using tpsDig2.x software to represent shape, and to calculate the length of lever arms. Additionally, we computed centroid size of the mandible to be used as our measure of size. The coordinate data were imported in R (R Core Team, 2018) and scaled, centered and superimposed using Procrustes analyses routines from Claude (2008). In order to avoid possible overparametrisation of statistical predictive models, shape data were submitted to principal component analyses for variable reduction, and the principal components (PCs) representing a total of 90% of variation were kept. Mechanical advantages for the temporal, superficial masseter and deep masseter were obtained by computing their respective inlever/outlever ratios (Fig. 1). In the case of the superficial masseter, two different inlever measurements were used, corresponding to the ventral-most insertion point and posterior-most insertion point (following Velhagen and Roth, 1997; Swiderski and Zelditch, 2010). Only the incisor outlever was used, as our *in vivo* measurements were restricted to incisive bites.

Bite force estimations

Using \log_{10} mechanical advantage (individually and all combined), \log_{10} centroid size or shape (PCs including 90% of shape variation) data, we fitted linear models of \log_{10} *in vivo* bite force either within species or combining the entire dataset (*i.e.* using all individual values). The model combining all mechanical advantages was built by simply using them all as explanatory variables in the same model. Interaction effects were checked and found to be non-significant, and

were therefore dropped. To test the precision of these models, we used a leave-one-out validation approach. To do so, we took out one individual from the dataset, fitted the model, then used the 'predict' function in R to compute a bite force estimate for this individual. After iterating this process for all individuals, we compared estimated and *in vivo* bite force using one-tailed Pearson's correlation coefficient in which the alternative hypothesis was that the correlation was greater than 0, because estimations should be positively correlated with *in vivo* measures. We also computed linear models of estimated against *in vivo* bite forces, to obtain the adjusted \bar{R}^2 values to quantify and compare the precision of the estimations.

Results

At the interspecific level (Fig. 2A, Table 1), all morphometric estimations of bite force are significantly and positively correlated with *in vivo* bite force. The superficial masseter mechanical advantage is, however, only predictive when using the ventral insertion point (i.e. B-F in Fig. 1). Considering the correlation coefficients and \bar{R}^2 values (Table 1), it is clear that size and shape of the mandible are better estimators than the individual or combined mechanical advantages. Despite this, the latter two do show some predictive power. Shape differences related to bite force variation basically represent differences between small mice, with longer and more slender mandibles, and large rats, with shorter, more robust mandibles, a larger angular process and posteriorly developed coronoid process (Fig. 2C). It can be noted that intraspecifically (especially in *Mus* species; Figs 2B, 3A,B), some slopes appear strongly negative, which is necessarily artefactual: if the model (significant or not) has a negative slope, and morphology is less variable than the measured bite force, the leave-one-out prediction based on this model will simply follow the regression line, despite representing very little morphological variation.

Mus musculus

In the lab-reared mice (Fig. 2B), age was controlled, and all specimens in this study were 68 days old. We found a significant positive relationship between shape-estimated bite force and *in vivo* bite force ($r = 0.32$, $t = 2.40$, $df = 49$, $P = 0.01$). On the other hand, the estimations based on mechanical advantage or centroid size were not significantly and positively correlated with *in vivo* data (Table 1).

Mus caroli

In this wild species (Fig. 3A), although we had fewer specimens than in others, we found significant correlation between shape estimates of bite force and *in vivo* bite force ($r = 0.51$, $t = 1.96$, $df = 11$, $P = 0.03$). Size estimations were not significantly related to *in vivo* measurements ($r = 0.47$, $t = 1.75$, $df = 11$, $P = 0.054$). However, this may simply be due to the small sample size, and the relationship may in fact be significant with more measurements. Again, the mechanical-advantage-based estimations were not significantly related to *in vivo* bite force data (Table 1).

Mus cervicolor

Our sample was larger than for *M. caroli* and shape-estimated bite force values were again significantly positively correlated to *in vivo* data in this wild mouse species ($r = 0.26$, $t = 2.13$, $df = 63$, $P = 0.019$, Fig. 3B). Here, size was a better estimator than shape ($r = 0.36$, $t = 3.073$, $df = 63$, $P = 0.0016$). However, the mechanical advantage estimates were not correlated to *in vivo* values (Table 1, Fig. 3B).

Rattus exulans

For *R. exulans* both size and shape estimations were correlated to *in vivo* bite forces (Fig. 4A), with a stronger correlation for size ($r = 0.55$, $t = 4.16$, $df = 40$, $P < 0.001$) than for shape estimates ($r = 0.41$, $t = 2.84$, $df = 40$, $P = 0.0035$). In this species, the deep masseter mechanical advantage also had some significant predictive power, although less than size or shape ($r = 0.36$, $t = 2.46$, $df = 40$, $P = 0.0092$). Both the superficial masseter and temporal mechanical advantages estimates of bite force were not significantly correlated with *in vivo* bite force (Table 1). The combination of all mechanical advantages yielded a significant correlation between estimated and *in vivo* bite force, although it was less than for the deep masseter estimate ($r = 0.33$, $t = 2.20$, $df = 40$, $P = 0.017$).

Rattus tanezumi

Contrary to all other species, the shape estimated bite force did not correlate significantly with *in vivo* data ($r = 0.16$, $t = 0.86$, $df = 27$, $P = 0.20$, Fig. 4B). However, there were positive correlations between the deep masseter mechanical advantage ($r = 0.55$, $t = 3.44$, $df = 27$, $P = 0.00095$) and size estimates and *in vivo* bite force ($r = 0.49$, $t = 2.93$, $df = 27$, $P = 0.0034$). The combined mechanical advantage estimations were also correlated to *in vivo* bite force, although less than size or deep masseter estimations ($r = 0.46$, $t = 2.66$, $df = 27$, $P = 0.0065$). The other mechanical advantage estimates did not show significant positive correlations with *in vivo* bite force (Table 1).

Discussion

Our results show that despite being commonly used as functional proxies (e.g. Thorington and Darrow, 1996; Velhagen and Roth, 1997; Swiderski and Zelditch, 2010; Blanco et al., 2013; Casanovas-Vilar and van Dam, 2013; Gomes Rodrigues et al., 2016; Fabre et al., 2017; Renaud et al., 2015, 2018a, b; Parmenter et al., 2019; Souquet et al., 2019), mechanical advantages generally do not appear to be accurate estimators of *in vivo* bite force, at least for incisor bites, and across our sample of species. In particular, the temporal mechanical advantage bite force estimates were never significantly related to *in vivo* bite force at the intraspecific level. Additionally, the superficial masseter mechanical advantage estimates were never significantly related to *in vivo* bite force when using the posterior-most insertion points, and only had predictive power in *R. tanezumi* when using the ventral-most insertion point (Fig. 4B). At the interspecific level, the superficial masseter mechanical advantage only allowed us to make correct predictions of *in vivo* bite force when using the ventral-most insertion, and the temporal mechanical advantage also showed some predictive power (although both had low \bar{R}^2 values, Table 1). On the other hand, the deep masseter mechanical advantage did better, with significant correlations between estimated and *in vivo* data at the interspecific level, as well as in both rat species studied here (*R. exulans* and *R. tanezumi*). These results may appear, at first sight, surprising when considering the typical role assigned to individual muscles during incision in rodents (e.g. Hiiemae, 1971; Cox and Jeffery, 2015). The temporal and superficial masseter are usually cited as major actors in gnawing (i.e. biting at the incisors), while the deep masseter and its different sub-parts are typically associated with chewing (i.e. masticating at the molars), although some authors have also found that it is positively involved in gnawing (Druzinsky, 2010). When taken as a whole, our results seem to suggest that the deep masseter may have a larger impact on *in vivo* bite force than the temporal or superficial masseter (Table 1). However, it must be kept in mind that our measurements of *in vivo* bite force represent maximum voluntary bite force, during which all muscles are contracting (McBrayer and White, 2002). Therefore, it cannot be taken to be functionally identical to either chewing or gnawing. Intraspecifically, the temporal mechanical advantage had little or no predictive power for *in vivo* bite force, including in both rat species (Fig. 4), and had the lowest predictive power of all studied variables interspecifically. Although the muscular properties of the temporalis may reveal another pattern, our results confirm that this muscle, which is reduced in murids compared to the masseter, and not well positioned to produce high forces at low gapes, does not have a major role in force production at the incisor. The temporalis may therefore be acting more as a control for lateral jaw movements as suggested by some authors (Hiiemae, 1971; Cox and Jeffery, 2015 and references therein). The superficial masseter mechanical advantage was also generally not a great predictor of

in vivo bite force, except in *R. tanezumi* and at the interspecific level when using the ventral insertion point. This suggests that the expansion of the ventral border of the angular process may be more functionally significant than its tip. However, our results do not contradict its role as the main protractor of the mandible. Its action during gnawing may be more related to the maintenance of the mandible in a forward position, against the posterior reaction forces induced by the bitten material (Hiimeae, 1971). Finally, the deep masseter, despite performing fairly badly, was the best of the mechanical advantage proxies (Table 1). One notable point is that it had (some) predictive power in both rat species as well as interspecifically, but in none of the mice species. Although this may be due to biased sampling in the field and other noise sources, this may also hint at evolutionary differences in anatomy between *Rattus* and *Mus* (e.g. rats may increase the force output of the deep masseter by modifying lever-arms, while mice may vary more in terms of muscular PCSA). It is also notable that the combination of mechanical advantages did not perform better than the deep masseter mechanical advantage in both species of rats, while it did perform better than individual mechanical advantage at the interspecific level (Table 1). Although lever arms and mechanical advantages are often used, probably due to the ease of measuring them, their weak performances as proxies for bite force is not entirely surprising. They are extremely simplified approximations of any muscular system, and notably do not account for the facts that i) muscles insert on areas rather than on single points, ii) rodents have multi-layered masticatory muscles, and iii) muscular action has three dimensions rather than two (the transverse axis is ignored). More difficult to obtain, the moment arms of muscles (i.e. the line running from the joint, perpendicularly to the muscle line of action) may be better proxies, but require the cranium and mandible to be in articulation. Of course, even more precise estimations of bite force can be obtained by using physiological cross-sectional area (PCSA) to calculate muscle forces (Ginot et al., 2018). However, the aim of the paper was specifically to test and compare ‘simplistic’ morphological estimators that are currently used by the community, rather than trying to obtain the most precise estimation possible.

Both mandible size and shape appeared to be reasonably accurate estimators of *in vivo* bite force, with a better performance for size in most cases, with the exceptions of *M. caroli* and *M. musculus* (Table 1). This is not surprising for size, which is generally the major correlate with bite force, including in humans (Raadsheer et al., 1999). Yet, neither of these morphometric estimators was perfect, and both had no predictive power in at least one species of our sample (*M. musculus* for size and *R. tanezumi* for shape, Table 1). The lack of predictive power of size in *M. musculus* may be explained by the limited size variation since all selected mice were of the same age (68 days). However, the same kind of explanation does not seem to fit for shape in *R. tanezumi*, since its shape variance was the second highest. At the interspecific level, the shape differences associated

with *in vivo* bite force variation basically reflect differences between a large rat (here *R. tanezumi*), and a small mouse, with a stronger bite being linked to a shorter mandible with enlarged anterior ramus, ventrally extended angular process, longer masseteric ridge and posteriorly extended coronoid process (Fig. 2A). These shape changes therefore integrate aspects that are also reflected in lever-arms ratios (i.e. mechanical advantages) of the various muscles, alongside multiple morphological parameters, which may explain the more robust and accurate predictions of shape-estimated bite force compared to mechanical-advantage based estimations. One caveat that must be noted is that spurious relationships between bite force and shape may appear due to ‘pinocchio effects’ (i.e. when most shape variation is limited to one or few landmarks), which may not be the case for mechanical advantages (Rohlf and Slice, 1990).

Overall, in most species, it appears that mandible size or shape are better *in vivo* incisor bite force estimators than mechanical advantages, with stronger correlations between estimated and *in vivo* bite force. However, our results also suggest that this depends on the group studied, since deep masseter mechanical advantage estimates were related to *in vivo* data in both rats, but in none of the mice. Although our results partly warrant the use of mandible morphology and mechanical advantages as proxies for performance interspecifically (Fig. 1A, Table 1), for example in reconstructions of (sub) fossil function and ecology, they also reveal important imprecisions in the estimated values at the intraspecific level, as was found for estimates based on muscular data (Ginot et al., 2018). The large difference in the amount of variation between the intra and interspecific levels certainly results in weaker correlations within species. Yet, bite force is also clearly under the influence of multiple factors intraspecifically, so that morphological variation may only partly explain performance variation. Among such factors, sex (Ginot et al., 2017), age (which was mostly uncontrolled in our wild species sample), behaviour (notably motivational state), hormones, social status, health status, inbreeding or genetics, as well as a general plasticity of *in vivo* bite force depending on abiotic environmental conditions (e.g. temperature, food availability), might play an important role. Furthermore, many-to-one mapping implies that optimal bite force may be attained by various anatomical configurations (Wainwright et al., 2005), therefore linear relationships between morphology and performance need not be always assumed.

Our study also suggests that, at least at the intraspecific level, testing the quality of morphological proxies of performance should be a prerequisite before making functional and adaptive inferences based on morphology in order to avoid the pitfalls of a pan-adaptationist approach (Arnold, 1983; Gould and Lewontin, 1979).

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Data availability. Morphological and bite force data is available from SG on demand.

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Table 1. Pearson correlation coefficients and adjusted R² from the various analyses run in this study.

	Size		Shape		SM		SM2		DM		T		SM2 + DM + T		df
	\bar{R}^2	r	\bar{R}^2	r	\bar{R}^2	r	\bar{R}^2	r	\bar{R}^2	r	\bar{R}^2	r	\bar{R}^2	r	
Interspecific	0.53	0.73	0.52	0.72	0.00	-0.01	0.17	0.42	0.18	0.42	0.20	0.45	0.32	0.57	1; 198
<i>Mus caroli</i>	0.15	0.47	0.19	0.51	-0.09	0.03	-0.97	0.93	0.14	-0.46	0.61	-0.80	0.72	-0.87	1; 11
<i>M. cervicolor</i>	0.12	0.36	0.05	0.26	-0.01	0.04	-0.02	-0.01	0.00	0.12	0.69	-0.84	-0.02	0.01	1; 63
<i>M. musculus</i>	-0.01	0.09	0.09	0.32	0.32	-0.58	0.06	-0.28	0.00	0.13	-0.01	-0.15	0.01	0.16	1; 49
<i>Rattus exulans</i>	0.28	0.55	0.15	0.41	-0.02	-0.08	0.00	-0.13	0.11	0.36	-0.02	-0.01	0.09	0.33	1; 40
<i>R. tanezumi</i>	0.21	0.49	-0.01	0.16	-0.03	-0.11	0.06	0.31	0.28	0.55	0.04	-0.26	0.18	0.47	1; 27

Bold values denote significance ($P < 0.05$). Abbreviations: SM = Superficial Masseter mechanical advantage (posterior-most insertion) ; SM2 = Superficial Masseter mechanical advantage (ventral-most insertion) ; DM = Deep Masseter mechanical advantage ; T = Temporal mechanical advantage.

Figures

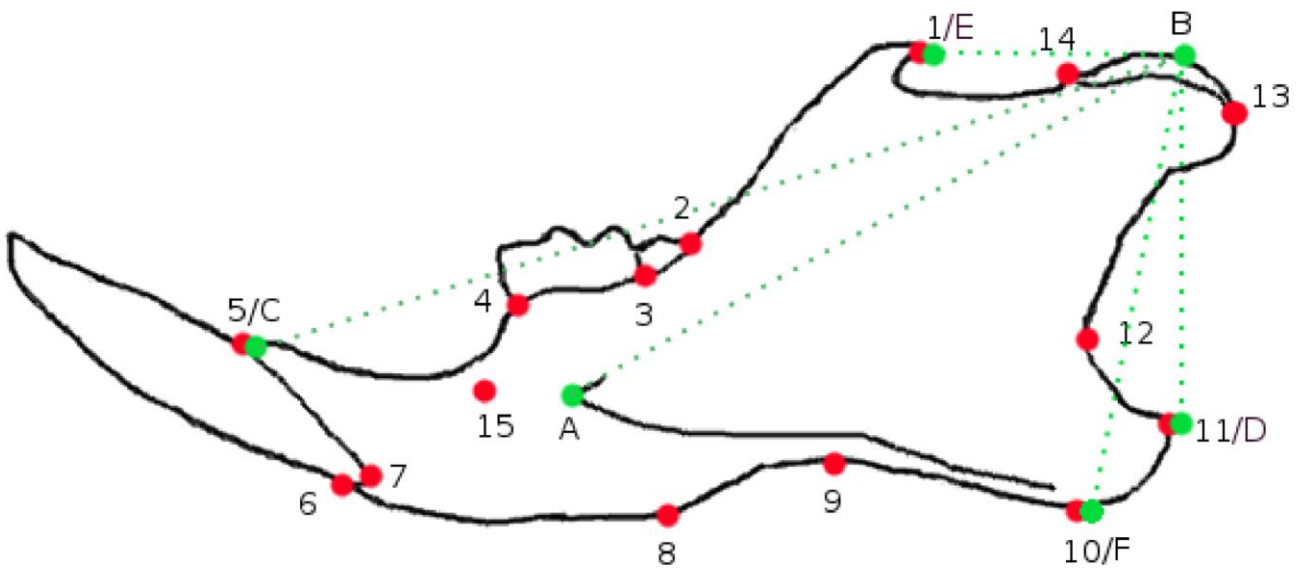
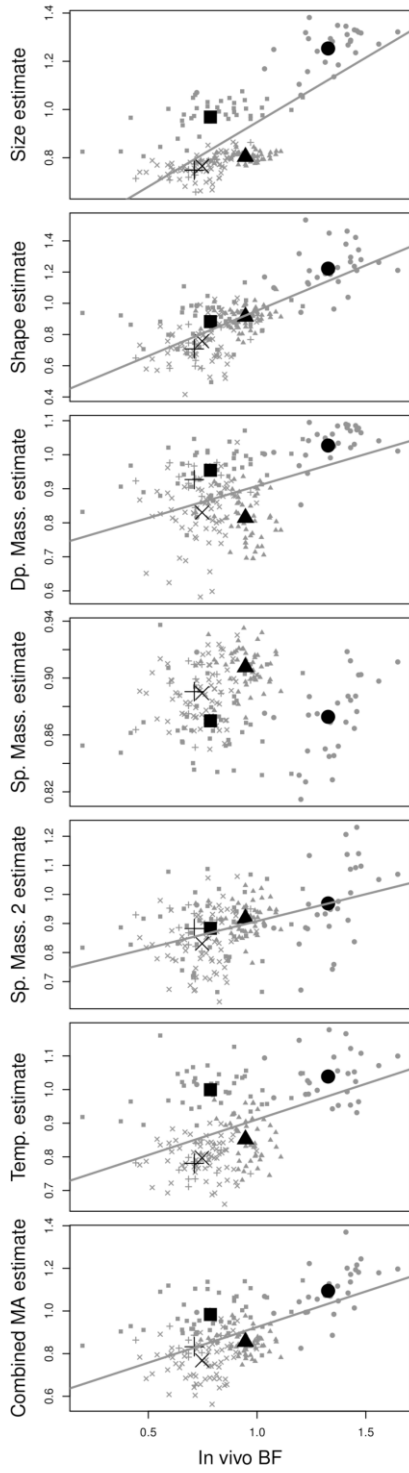
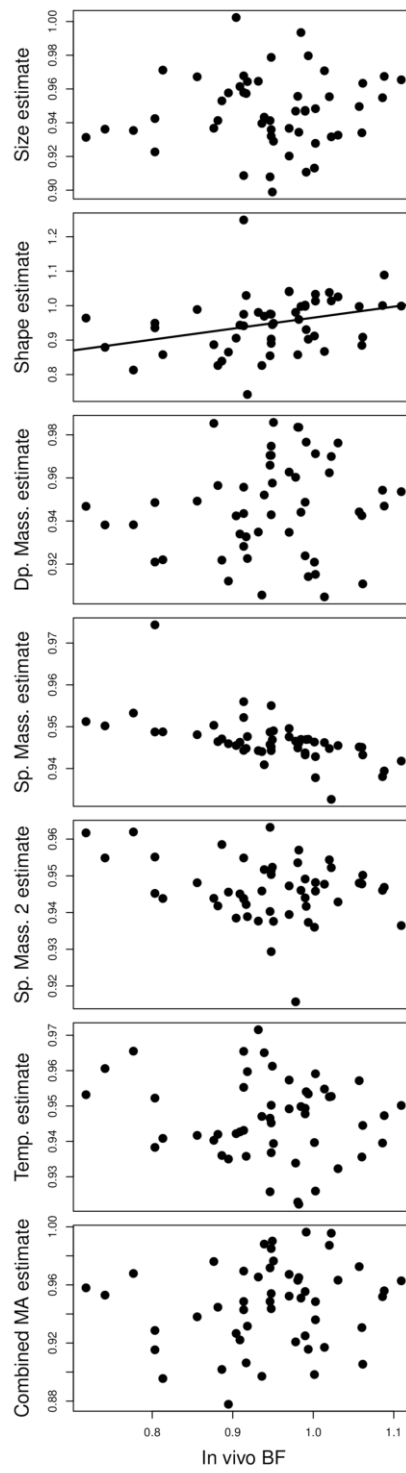


Figure 1. Mice mandible outline drawing, with the landmarks used in this study represented. Red landmarks are those used for shape analysis, and green landmarks to calculate lever arms. Shape and lever-arms were used in separate analyses. AB: Deep masseter inlever; BD: superficial masseter inlever (posterior-most); BF: superficial masseter inlever (ventral-most); BE: temporal inlever; BC: outlever.

A. Interspecific analyses



B. *Mus musculus*



C. Shape changes linked to bite force variation

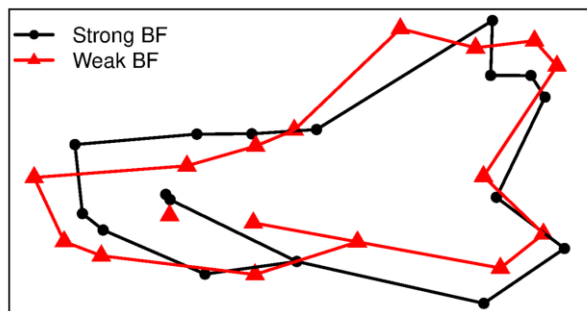
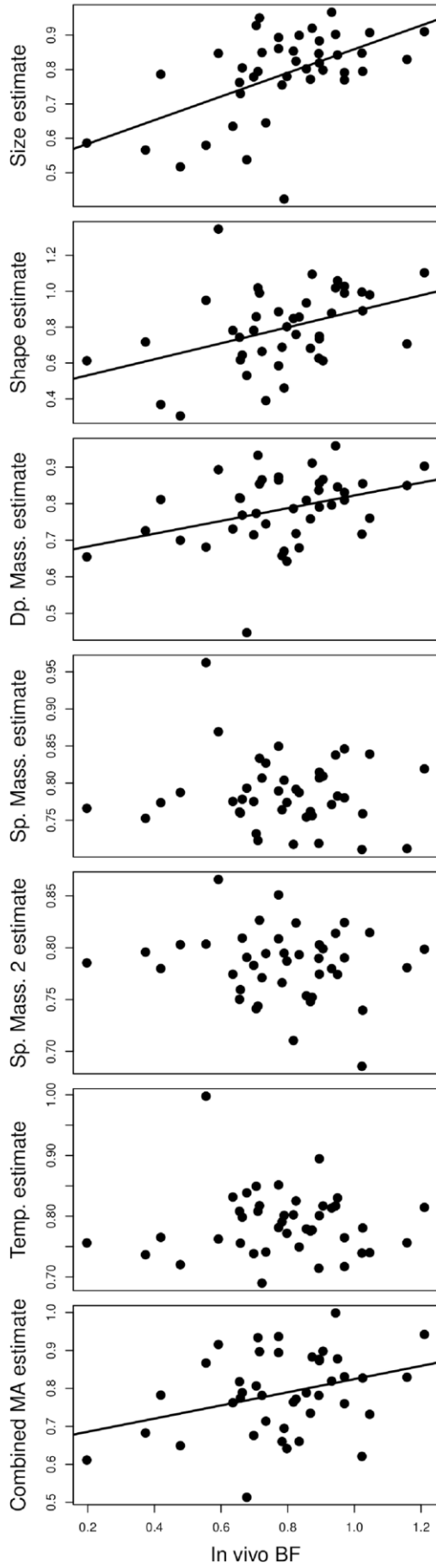


Figure 2. Bite force estimates, based on morphological variables, plotted against *in vivo* bite force at the interspecific level (n=200) (A), and intraspecific level for *Mus musculus* (n=51) raised in the lab (B). For (A), small gray points are individual values, while large black points are the species' averages. Lines represent significant ($P<0.05$) positive linear regressions (based on individual data in (A) and (B)). Note the difference in ordinates scales between (A) and (B) and Fig. 3 and 4, reflecting the difference in the amount of variation between inter and intraspecific levels. Panel (C) shows predicted shape differences for maximal (black circles) and minimal (red triangles) bite force at the interspecific level. Squares: *Rattus exulans*; circles: *R. tanezumi*; '+' symbols: *Mus caroli*; 'x' symbols: *M. cervicolor*; triangles: *M. musculus*. Abbreviations: Dp. Mass.: Deep masseter mechanical advantage; Sp. Mass.: Superficial masseter mechanical advantage; Temp.: Temporal mechanical advantage; MA: Mechanical advantage; BF: Bite force.

A. *Rattus exulans*



B. *Rattus tanezumi*

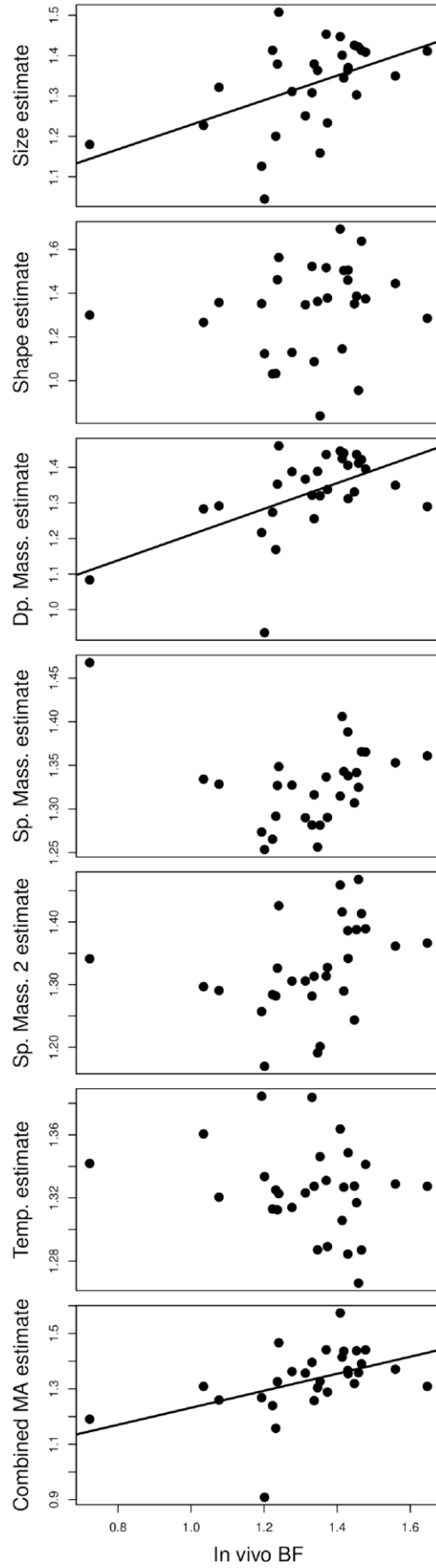


Figure 3. Bite force estimates, based on morphological variables, plotted against *in vivo* bite force at the intraspecific level for wild *Mus caroli* (n=13) (A), and wild *Mus cervicolor* (n=65) (B). Lines represent significant ($P<0.05$) positive linear regressions. Abbreviations: Dp. Mass.: Deep masseter mechanical advantage; Sp. Mass.: Superficial masseter mechanical advantage; Temp.: Temporal mechanical advantage; MA: Mechanical advantage; BF: Bite force.

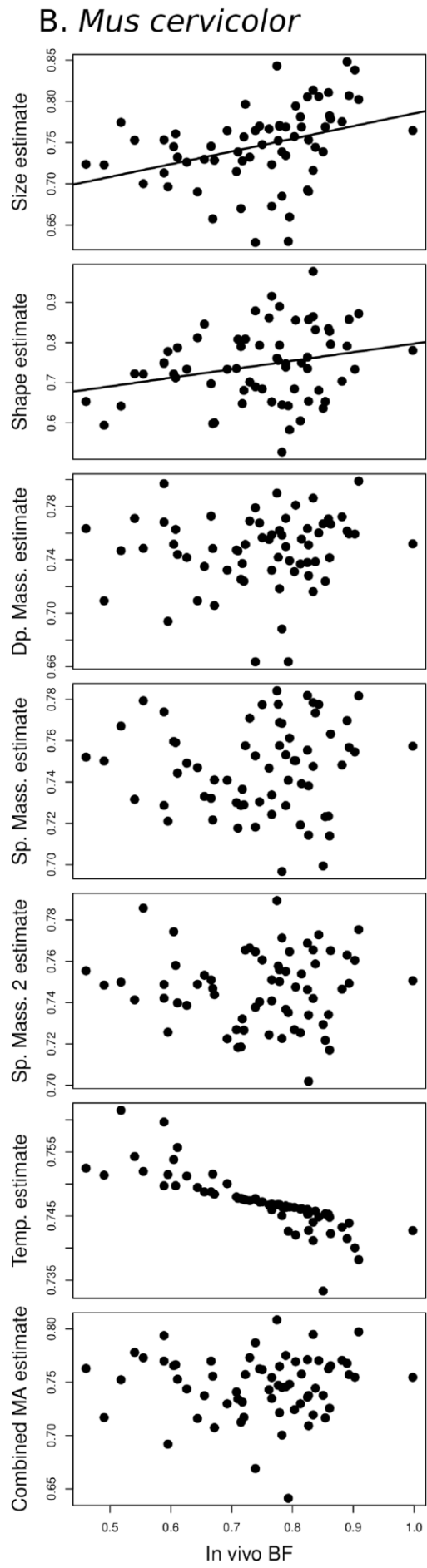
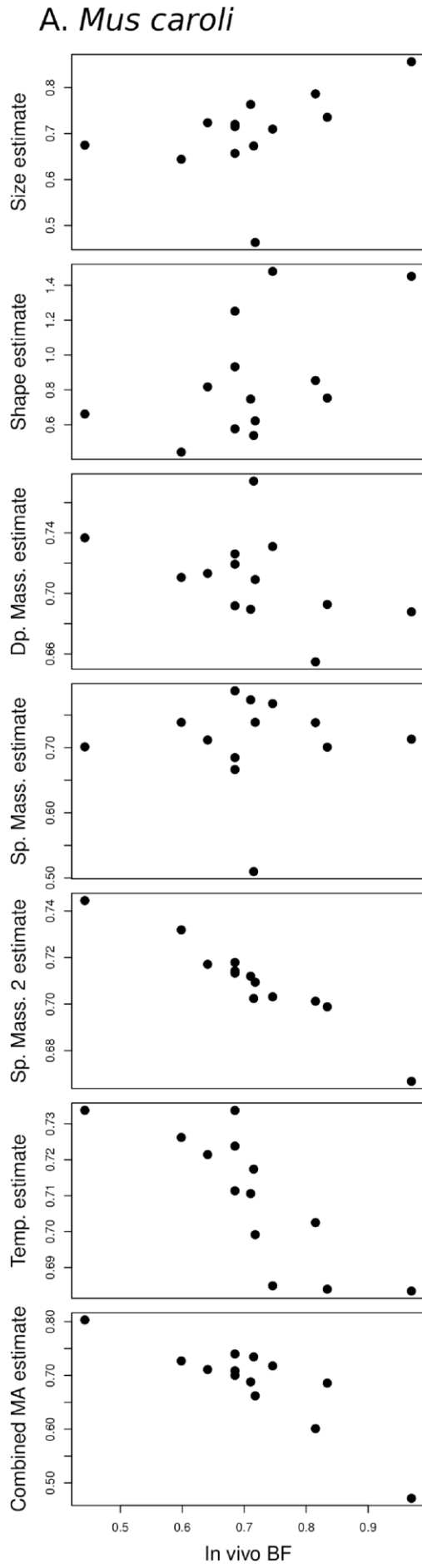


Figure 4. Bite force estimates, based on morphological variables, plotted against *in vivo* bite force at the intraspecific level for wild *Rattus exulans* (n=42) (A), and wild *R. tanezumi* (n=29) (B). Lines represent significant ($P<0.05$) positive linear regressions. Abbreviations: Dp. Mass.: Deep masseter mechanical advantage; Sp. Mass.: Superficial masseter mechanical advantage; Temp.: Temporal mechanical advantage; MA: Mechanical advantage; BF: Bite force.