

1 Clade-wide variation in bite-force
2 performance is determined primarily by
3 size not ecology.

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12 **Abstract**

13 Performance traits are tightly linked to the fitness of organisms. However,
14 because studies of variation in performance traits generally focus on just
15 one or several closely-related species, we are unable to draw broader
16 conclusions about how and why these traits vary across clades. One
17 important performance trait related to many aspects of an animal's life
18 history is bite-force. Here we use a clade-wide phylogenetic comparative
19 approach to investigate relationships between size, head dimensions and
20 bite-force among lizards and tuatara (lepidosaurs), using the largest
21 bite-force dataset collated to date for any taxonomic group. We test four
22 predictions: that bite-force will be greater in larger species, and for a
23 given body size, bite-force will be greatest in species with acrodont tooth
24 attachment, herbivorous diets, and non-burrowing habits. We show that
25 bite-force is strongly related to body and head size across lepidosaurs
26 and, as predicted, larger species have the greatest bite-forces. Contrary to
27 our other predictions, tooth attachment, diet and habit have little
28 predictive power when accounting for size. Herbivores bite more
29 forcefully simply because they are larger. Our results also highlight
30 priorities for future sampling to further enhance our understanding of
31 broader evolutionary patterns.

32 **Keywords: biteforce, diet, lizard, tuatara, Lepidosauria**

33 Introduction

34 Performance traits are of vital importance for activities that influence
35 organism survival, such as food acquisition, predator avoidance, and mate
36 acquisition.¹⁻⁴ Due to the direct links between performance and fitness,
37 we expect these traits to be under strong selection;^{4,5} however, relatively
38 few studies of natural selection in the wild have focused on performance
39 traits^{4,6} and, due to limited time and resources, most studies focus on just
40 one or several species, limiting our ability to draw broader conclusions
41 about how and why performance traits vary across clades.⁴ Bite-force is
42 an important performance trait with close ties to ecology and life
43 history.⁷⁻¹¹ Greater bite-force may reduce prey handling times and
44 increase dietary breadth,^{7,12-15} can increase the likelihood of success in
45 territory defence and male-male combat,^{1,3,16,17} and boost reproductive
46 success.^{3,11,17} Crucially, bite-force data are relatively simple to collect;
47 voluntary *in vivo* bite-force has been successfully measured in a wide
48 range of taxa, including sharks, frogs, lizards, crocodylians, rodents, and
49 bats (e.g.^{7,9,10,18-21}). To date, however, large scale analyses of variation in
50 bite-force and its relationship to key traits such as diet, body size, and
51 habit are lacking. Most bite-force studies instead focus on a single species
52 (e.g.¹⁷) or a set of closely related species (e.g.¹⁵). A clade-wide
53 comparative approach is required to understand how and why bite-force
54 varies among species and to test related hypotheses.

55 In this study we use a clade-wide comparative approach to investigate
56 variation in bite-force within lizards and tuatara (i.e. Lepidosauria minus
57 Serpentes for which very little bite-force data exists) in relation to species'

58 morphological and ecological traits. We use lepidosaurs because most
59 studies of bite-force have focused on these species due to their
60 experimental tractability and the key importance of bite-force to many
61 aspects of their ecology and life history.^{7,10} Lepidosaurs are also an ideal
62 group on which to test many hypotheses about variation in bite-force
63 because they are diverse in terms of species richness (7,262 species²²),
64 diet,²³ food processing,²⁴ life habit,²⁵ muscle anatomy,^{26,27} tooth
65 attachment,²⁸ and skull shape.²⁹ Here we test the following predictions
66 about variation in bite-force within lizards and tuatara using the largest
67 dataset of existing *in vivo* bite-force data collated to date, and phylogenetic
68 generalised least squares (PGLS) analyses.

- 69 1. *Larger species, in terms of body and head size, will have greater bite-forces.*
70 Bite-force tends to show positive allometric scaling with
71 morphological traits, as larger individuals will have more muscle
72 mass and presumably a greater bite-force,^{1,12,30-32} but this has not
73 been tested across a broad taxonomic group. Independent of
74 differences in overall body size, head dimensions are also strongly
75 associated with bite-force performance,^{33,34} as animals with larger or
76 wider heads are assumed to accommodate more jaw musculature
77 which results in a greater bite-force.^{7,16}
- 78 2. *Species with acrodont tooth implantation will have greater bite-force than*
79 *those with non-acrodont tooth implantation for a given size.* Acrodonty,
80 where the teeth attach to the crest of the jaw bone rather than the
81 inside of the jaw,³⁵ has long been associated with greater anchorage
82 and greater loading (e.g.^{35,36}) and recent analyses appear to support
83 that association.²⁸ However, an analysis accounting for phylogeny

84 has yet to be attempted.

85 3. *Herbivorous species will have the greatest bite-forces for a given size.*

86 Herbivorous species of lizard are often considered to have greater
87 bite-forces than carnivores and omnivores due to the forces required
88 to process fibrous plant material.^{7,12,23,29,37} However, a relationship
89 between bite-force and diet across lepidosaurs more broadly has
90 never been tested, and some studies suggest carnivores, especially
91 species that feed upon hard-shelled prey (e.g. shelled molluscs,
92 crabs etc.), may exhibit greater maximum bite-forces (e.g.³⁸).

93 4. *Burrowing species will have lower bite-forces than non-burrowing species of*
94 *a given size.* Bite-force may also vary with substrate (or life habit) due
95 to selection pressures and constraints imposed on feeding apparatus
96 such as the skull structure (e.g.³⁹). Burrowing can restrict head
97 width⁴⁰ and may, in turn, restrict relative jaw muscle volume. We
98 predict that these constraints will result in lower bite-forces in
99 burrowing species.

100 **Materials and Methods**

101 **Data collection**

102 **Bite-force and morphological data**

103 We surveyed all studies published between 1999 (when the first in vivo
104 bite-force data were collected for lizards) and 2020, reporting empirical

105 data on *in vivo* bite-force performance in lizards and tuatara, using the
106 VolBif bite-force database¹⁰ supplemented with Google Scholar searches
107 with search terms: bite, force, performance, transducer, and Kistler. We
108 excluded studies where the bite-force and morphological data came from
109 different animals, where only residual or size corrected bite-force data
110 were provided, or where bite-force was provided without body size data.
111 These requirements left us with 53 published studies (out of 111) that had
112 bite-force data for one or more species, comprising 164 species in total.

113 We collated mean maximum bite-force \pm standard error (N) from each of
114 the 53 studies with appropriate data, for each species within the
115 publication, and for females and males separately where possible. The
116 majority of studies did not specify bite location,¹⁰ but in lizards bite-force
117 is generally taken from the front of the jaw as it can be difficult to get bites
118 from further back. Where multiple bites from different locations were
119 specified we used bite-forces extracted from the tips of the jaw to ensure
120 our data were as comparable as possible. When there was more than one
121 population with bite-force data available for a species within a
122 publication, we used the population with the greatest bite-force. For each
123 bite-force record we recorded the (1) species name; (2) sex; (3) age (adult
124 or juvenile); (4) sample size for bite-force data; (5) snout-vent length (SVL;
125 mm); (6) head width (mm); (7) head length (mm); (8) head height (mm);
126 and (9) sample size for morphometric data. For the morphological
127 measurements we collected the mean \pm standard error values.

128 **Ecological and phylogenetic data**

129 For prediction 2, all Acrodonta and the tuatara were classified as acrodont
130 and the rest of the species were classified as non-acrodont. Trogonophidae
131 are sometimes classified as acrodont,²⁸ so we repeated the analyses with
132 this family in the acrodont category. We used diet and substrate data
133 provided in Meiri,²⁵ with additional data from Metzger and Herrel²⁹ and
134 Cooper and Vitt.²³ Diets were classified as carnivorous, herbivorous, or
135 omnivorous based on whether animals, plants or both made up the
136 greatest proportion of the diet (prediction 3²⁵). Three species (*Anolis*
137 *singularis*, *Pygomeles braconnieri* and *Scelotes montispectus*) had no diet data
138 and were excluded from the diet analyses. The substrate/life habit data²⁵
139 consisted of 14 different categories, so we created a fossorial variable
140 (Fossorial versus all other categories) to test prediction 4. We also
141 explored whether saxicolous (crevice dwelling) or arboreal species had
142 significantly different bite-forces for their size using two new variables:
143 arboreal (Arboreal versus all other categories), and saxicolous
144 (Arboreal/Saxicolous, Arboreal/Terrestrial/Saxicolous, Saxicolous,
145 Terrestrial/Saxicolous versus all other categories). We also investigated
146 differences across clades, using the classification of Burbrink *et al.*⁴¹ to
147 define eight more inclusive clades (Acrodonta, Anguimorpha, Dibamia,
148 Gekkota, Lacertoidea, Pleurodonta, Rhynchocephalia and Scincoidea).

149 For the phylogenetic generalised least squares (PGLS) analyses (see
150 below) we used the dated molecular phylogeny of Wright *et al.*⁴² and
151 pruned it to the species in our dataset. Eight species were in our dataset
152 but missing from the tree. We added five of these species to the tree using
153 information from other published phylogenies to determine where they

154 fitted into the tree (Table S1) and an arbitrary branch length of 0.1. Note
155 that we repeated all analyses using only the species in the original tree to
156 ensure this procedure did not bias our results. We were unable to find
157 data on the phylogenetic relationships of three species (*Aspidoscelis*
158 *sonorae*, *Diplolaemus leopardinus* and *Tropidurus semitaeniatus*) leaving 161
159 species in the phylogeny.

160 **Data cleaning and processing**

161 Prior to analyses we cleaned the data using the tidyverse package⁴³ in R.⁴⁴
162 We removed juveniles and sub-adults from the dataset and corrected
163 species binomial names and family names using The Reptile Database.²²

164 Maximum values are the most appropriate measure for comparing
165 performance.^{45,46} For each species, we therefore selected the study with
166 the highest maximum bite-force. If two or more studies of the same
167 species had the same maximum bite-force value, we used the study with
168 the most complete data for the other variables. Note that we used the
169 morphological data associated with the study that had the maximum
170 bite-force for each species to ensure these data came from the same
171 animals. Finally we also created datasets that included only females or
172 only males. All raw and cleaned data are available on the NHM Data
173 Portal (<https://doi.org/10.5519/dkrhpxjh>⁴⁷).

174 **Analyses**

175 All statistical analyses used R version 4.0⁴⁴ and reproducible R scripts are
176 available on GitHub
177 (<https://github.com/nhcooper123/lepidosaur-biteforce>; Zenodo DOI:
178 10.5281/zenodo.5838511). All continuous variables were natural
179 log-transformed prior to analyses. Results were visualised using *ggtree*⁴⁸
180 and *ggplot2*.⁴⁹

181 **Dataset coverage**

182 We calculated the total numbers and percentage coverage of all 164
183 species in our dataset from each family recognised in Uetz *et al.*²² and
184 clade,⁴¹ and for lizards and tuatara as a whole. We explored the
185 distribution of raw bite-force (i.e. bite-force values before correcting for
186 size differences) across clades and families, and within tooth attachment,
187 diet and substrate categories, and visualised the differences in bite-force
188 and the four size measures in the full dataset, and the data for females
189 and males separately.

190 **Predicted correlates of bite-force**

191 We used phylogenetic generalised least squares (PGLS) models (with
192 maximum likelihood estimates of Pagels λ) to test our predictions. PGLS
193 models account for the non-independence of trait values in close relatives
194 by incorporating information about phylogenetic relationships into the
195 error term of the model. This approach deals with the problem of

196 phylogenetic pseudoreplication.⁵⁰ We fitted PGLS models using the R
197 package *caper*,⁵¹ and performed standard model checks for GLS models
198 (Q-Q plot, histogram of residuals, residuals versus linear predictors,
199 response versus fitted values) to assess model fit.

200 First we used PGLS models to investigate the relationship between
201 maximum bite-force and size, using SVL ($n = 161$), head width ($n = 142$),
202 head height ($n = 136$), or head length ($n = 136$), to represent size
203 (prediction 1). Next we fitted PGLS models testing whether the
204 relationship between maximum bite-force and size (SVL, head width,
205 head height, or head length) varied with (i) tooth attachment (prediction
206 2); (ii) diet (prediction 3); (iv) whether species were purely fossorial or not
207 (prediction 4). We additionally tested whether the relationship between
208 maximum bite-force and size varied with clade, whether species were
209 purely arboreal or not, and whether species were saxicolous or not. For
210 the clade analyses we excluded Anguimorpha, Gekkota and
211 Rhynchocephalia because they had fewer than 10 species in the dataset,
212 and for females and males separately we also excluded Scincoidea
213 because we had only one sexed skink species. Finally, we Bonferroni
214 corrected our p-values to account for multiple comparisons.

215 In many species of lizards, males have larger heads than females and thus
216 we expect some sexual dimorphism in bite-force.^{13,52} We initially used
217 data from both sexes combined, but repeated each analysis using just
218 females, and just males (except for the fossoriality analyses where only
219 one fossorial species had known sex). We also ran each analysis using the
220 original 156 species tree without the five added taxa to ensure this
221 difference in sampling did not bias our results.

222 **Results**

223 **Dataset coverage**

224 The final cleaned dataset contained bite-force data for 164 species overall,
225 112 species when only data from females were used and 132 when only
226 data from males were used. Body size (SVL) ranged from 31.62 mm to 425
227 mm.

228 Overall, our dataset included only 2.26% of 7,262 extant lizard and tuatara
229 species,²² and these were extremely skewed phylogenetically and
230 taxonomically (Figure 1, Figure S1, Tables S2-3). Over 45% of our species
231 sample (74 species) are members of Pleurodonta. However, these 74
232 species represent only around 6% of the diversity of Pleurodonta. No
233 family had more than 25% species coverage, except Sphenodontidae
234 which contains only one extant species and had 100% coverage (Figure 1,
235 Table S2). 24 of the 44 families (54.5%; Figure 1, Table S2), and one clade
236 (Dibamia; Figure S1, Table S3) had no species with bite-force data we
237 could use in this study.

238 Raw bite-force, i.e. bite-force values before correcting for size differences,
239 ranged from 0.12 N to 534.24 N, and varied among clades, families, and
240 within tooth attachment, diet, and substrate categories (Figures S2-S3;
241 Table S4). Overall, females have lower bite-forces and slightly smaller
242 body and head dimensions than males (Figure S4).

243 **Predicted correlates of bite-force**

244 We were unable to place three species (*Aspidoscelis sonorae*, *Diplolaemus*
245 *leopardinus* and *Tropidurus semitaeniatus*) within the phylogeny, meaning
246 that the analyses used only 161 species. Each analysis contained slightly
247 different numbers of species (due to the three species without diet data,
248 the 19 species without head width data and the 25 species without head
249 length or head height data).

250 All analyses of all subsets of the data show strong, significant, positive
251 correlations among bite-force and all measures of size (prediction 1;
252 Figure 2; Tables S5-S6). The large negative outliers on the plots showing
253 the relationship between bite-force and SVL are skinks (Scincoidea; Figure
254 2A). The skinks in our dataset have long bodies relative to their head size
255 in comparison with other lizards. This difference in body shape results in
256 some skinks appearing to have much lower bite-force than other groups
257 given their SVL, but this effect disappears if we use head dimensions as
258 proxies for size instead (Figure 2B-D).

259 The relationship between bite-force and size did not vary significantly
260 with tooth attachment (prediction 2), for all four measures of size (Table 1;
261 Figure S5), for the full dataset and for females and males separately
262 (Tables S7-S8). The results were qualitatively similar when Trogonophidae
263 were categorised as acrodont (Table S9).

264 The relationship between bite-force and size varied significantly with diet
265 (prediction 3), but only when using head width as the measure of size for
266 the full dataset (Table 1; Figure 3), and head width or head length using
267 only females (Tables S7-S8). This result reflects a very small, but

268 significant difference between the intercepts of carnivores and omnivores.
269 Herbivores did not differ significantly from carnivores or omnivores, but
270 were larger on average than the other two dietary groups (Figure S6; mean
271 SVL herbivores = 192.8 mm; mean SVL of non-herbivores = 86.85 mm).

272 There was a significant effect of fossoriality on the relationship between
273 bite-force and size for all size measures except SVL (prediction 4; Table 1;
274 Figure 4). Fossorial species had higher bite-forces for their head
275 dimensions compared to non-fossorial species, though the slope of the
276 relationship was not significantly different (Table 1; Figure 4). Note that
277 because only one fossorial species was sexed we were unable to run
278 separate models for females and males.

279 The relationship between bite-force and size did not vary significantly
280 with clade, whether species were purely arboreal or not or whether
281 species were saxicolous or not. This was the case using all four measures
282 of size (Table S10; Figure 2, Figures S7-S8), for the full dataset and for
283 females and males separately (Tables S7-S8).

284 Results using the original 156 species tree are in the Supplementary
285 Materials (Tables S6 and S11) but were qualitatively identical to those
286 using the full 161 species tree.

287 **Discussion**

288 Bite-force was strongly positively correlated with snout-vent length and
289 head dimensions across the 161 species in our analyses. This relationship
290 varied with some aspects of species ecology; for certain head

291 measurements carnivorous species had greater bite-forces compared to
292 omnivores, and fossorial species had higher bite-forces for their head
293 dimensions compared to non-fossorial species. There was no significant
294 variation with clade, tooth attachment, or whether species were purely
295 arboreal or not, or saxicolous or not. These results support some of our
296 predictions, but not all, as discussed below.

297 Despite the great variety of morphologies and ecologies represented by
298 the lepidosaurs in our sample, size always appeared to be the most
299 important variable in explaining variation among species. The strong
300 correlations among size measures and bite-force matches that found in
301 mammals, turtles, and crocodylians.^{9,20,30,53} This pattern also parallels
302 results from other lepidosaur studies of narrower taxonomic
303 breadth.^{1,31,32,34} The only group for which this pattern was less clear was
304 Scincoidea. However, many skinks have long bodies in relation to their
305 head size (e.g.⁵⁴), meaning their bite-force was lower than expected in
306 relation to their snout-vent length, but scaled more similarly to other
307 taxonomic groups for their head dimensions. The close relationship
308 between bite-force and size is almost certainly due to the close
309 relationship between size and jaw muscle cross-sectional area. Muscles
310 with greater cross-sectional area are generally able to generate greater
311 force,^{55,56} thus providing more forceful bites. Large animals are usually
312 able to bite more forcefully than smaller animals regardless of other
313 factors such as head shape or diet.

314 We did not find support for our second prediction, that species with
315 acrodont tooth implantation would have greater bite-force than those with
316 non-acrodont tooth implantation. There are several lizards with forceful

317 bites that are not acrodont which may explain this result. In addition, our
318 two tooth attachment categories may not adequately represent the range
319 of tooth implantation anatomy in extant Lepidosauria. Non-acrodonty
320 encompasses a range of variation that includes teeth with deep lingual
321 roots and minimal alveolar bone and teeth with shallow lingual roots and
322 extensive alveolar bone.^{35,57,58} Given the spectrum of variation known in
323 tooth attachment in lepidosaurs,⁵⁹ and that tooth implantation can also
324 vary along the tooth in some taxa, tooth attachment may be related to the
325 direction (compression and tension) and magnitude of local loading
326 conditions during biting behaviour rather than overall bite-force capacity
327 *per se*.

328 Our results also do not support our third prediction, that herbivorous
329 species would have the greatest bite-forces (though note that our data are
330 limited to larger herbivorous species; see below). Previous studies have
331 suggested that herbivorous lepidosaurs have greater bite-forces, on
332 average, than carnivores or omnivores due to their larger jaw muscles for
333 processing plant material.^{7,12,23,29,37,52,60} These suggestions were based
334 on comparisons among a few species (e.g.^{12,60}) or within a genus (e.g.⁶¹),
335 so our taxonomic sample is much broader here and highlights the benefit
336 of a clade-wide comparative approach. Our results confirm that
337 herbivores did tend to have greater bite-forces, but this result reflects the
338 fact that herbivores were larger on average, in both snout-vent length and
339 head dimensions, than their carnivorous or omnivorous counterparts, and
340 size was the strongest predictor of bite-force. Plant consumption in
341 lepidosaurs has been linked to increased size,^{23,29,60} perhaps because of
342 the lower mass-specific metabolic requirements of larger individuals, or

343 the increased space for the digestive system allowing more efficient
344 digestion of tough plant material in larger individuals.^{60,62} Our results,
345 however, showed that herbivores did not have significantly greater
346 bite-forces than expected given their size. This result suggests that
347 herbivores tend to bite more forcefully merely because they are larger, not
348 because of any specialised adaptations for herbivory.

349 Finally our fourth prediction was also not supported by our results; in fact
350 fossorial species bite more forcefully than expected given their head
351 dimensions. Previous studies have suggested a trade-off between
352 burrowing and bite-force: greater head width accommodates larger jaw
353 muscles but also increases the cross-sectional area that must displace
354 burrowing medium (e.g. soil, sand, plant matter).^{40,63} In the fossorial
355 skink *Acontias percivali*, narrow-headed individuals were able to dig into
356 the substrate much faster than broader-headed individuals, but bite-force
357 was greater in individuals with relatively wider heads⁴⁰ (although see⁶⁴).
358 Similarly, in the amphisbaenid *Leposternon microcephalum*, the energetic
359 costs associated with burrowing increase exponentially with body and
360 head size.⁶³ Our results suggest that, at least for the species in our dataset,
361 fossorial lepidosaurs are able to overcome this trade-off and bite more
362 forcefully than their head dimension alone would predict. This result may
363 suggest that fossorial species require greater bite-force than non-fossorial
364 lizards whether it be due to the range of prey that they encounter or the
365 importance of biting when gape is limited (and thus swallowing prey
366 whole is not possible). However, 11 of the 12 fossorial species available to
367 our analyses were skinks (the remaining species is the amphisbaenian
368 *Trogonophis wiegmanni*). Therefore, the result may reflect differences

369 particular to Scincoidea rather than burrowing lepidosaurs in general.
370 There are no obvious differences in jaw mechanism or jaw muscle
371 arrangement known for Scincoidea that might increase bite-force capacity
372 (e.g.^{26,27}), but future studies should pay greater attention to details of jaw
373 muscle pennation structure. Alternatively skinks may be particularly
374 aggressive and/or cooperative for bite-force data collection, or perhaps
375 bite-force was collected in a slightly different manner for these 11 species.
376 Data from additional non-fossorial scincoids or other fossorial lepidosaurs
377 should help address this issue. The longer bodies relative to head size in
378 skinks also explains why we did not find a significant effect of fossoriality
379 on the relationship between snout-vent length and bite-force because, as
380 described above, skinks have a lower bite-force than expected given their
381 snout-vent length.

382 Although there have been over 100 studies of bite-force on lizards and
383 tuatara, many species remain unexamined. Some of these species are
384 either too small (e.g. *Brookesia* sp.) or are uncooperative (e.g. *Ophisaurus*
385 sp.; MEHJ *pers. obs.*). Our dataset encompassed only 2.26% of the 7,262
386 existing lizard and tuatara species,²² and this sample was heavily skewed
387 towards certain clades and ecologies. Despite including an order of
388 magnitude more species than previous studies, we still had no data from
389 any species within Dibamia or within 24 lizard families, and only had
390 data for 11 herbivores. Usable data for small herbivores (for example
391 various species within Liolaemidae; average SVL < 100mm⁶²) are
392 conspicuously missing from the bite-force literature. Additionally, our
393 dataset was limited not only by the number of species that have been
394 investigated for bite-force, but by the availability of these data in the

395 literature. Of the 111 published studies we collated, less than half ($n = 53$)
396 contained openly accessible/usable data. This issue prevents larger
397 comparative studies being undertaken. Future studies should provide
398 their raw individual bite-force and morphological measurement data to
399 enable future studies to build on previous work. This study represents the
400 first rigorous step in examining bite-force across an entire clade while
401 accounting for phylogenetic relationships among species, providing a
402 framework for future work.

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408 **Data accessibility**

409 Data are available from the NHM Data Portal
410 (<https://doi.org/10.5519/dkrhpxjh>⁴⁷). R code is available from GitHub
411 (<https://github.com/nhcooper123/lepidosaur-biteforce>; Zenodo DOI:
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623 **Tables**

Table 1: Results from phylogenetic generalised least squares (PGLS) models of bite-force as a function of size, one of three covariates (tooth attachment type, diet, fossorial or not) and their interaction term. Size was snout vent length (SVL; mm), head width (HW; mm), head length (HL; mm), or head height (HH; mm). Significant p values are highlighted in bold. Bonferroni corrected p values (bonf p) are provided for all terms except the size term for which Bonferroni corrected p values were always < 0.001 . res df = residual degrees of freedom. df = degrees of freedom. λ = Pagel's λ .

covariate	size	size						covariate				interaction			
		res df	λ	r^2	df	F	p	df	F	p	bonf p	df	F	p	bonf p
tooth attachment	SVL	157	0.946	0.723	1.000	416.8	< 0.001	1.000	0.767	0.382	1.000	1.000	3.187	0.076	1.000
tooth attachment	HW	138	0.982	0.741	1.000	403.6	< 0.001	1.000	0.053	0.818	1.000	1.000	3.049	0.083	1.000
tooth attachment	HL	132	0.96	0.709	1.000	330.1	< 0.001	1.000	0.764	0.384	1.000	1.000	1.270	0.262	1.000
tooth attachment	HH	132	0.703	0.822	1.000	622.9	< 0.001	1.000	0.344	0.558	1.000	1.000	1.230	0.269	1.000
diet	SVL	152	0.953	0.714	1.000	393.4	< 0.001	2.000	0.706	0.495	1.000	2.000	1.008	0.367	1.000
diet	HW	133	1.000	0.806	1.000	546.8	< 0.001	2.000	13.75	< 0.001	< 0.001	2.000	1.150	0.320	1.000
diet	HL	127	0.967	0.704	1.000	316.9	< 0.001	2.000	1.026	0.362	1.000	2.000	0.328	0.721	1.000
diet	HH	127	0.681	0.822	1.000	613.5	< 0.001	2.000	0.900	0.409	1.000	2.000	0.603	0.549	1.000
fossorial	SVL	157	0.949	0.741	1.000	445.3	< 0.001	1.000	7.493	0.007	0.387	1.000	7.760	0.006	0.366
fossorial	HW	138	0.968	0.769	1.000	451.6	< 0.001	1.000	16.48	< 0.001	0.005	1.000	3.502	0.063	1.000
fossorial	HL	132	0.900	0.745	1.000	381.1	< 0.001	1.000	14.89	< 0.001	0.010	1.000	1.444	0.232	1.000

fossorial	HH	132	0.446	0.852	1.000	760.7	< 0.001	1.000	16.53	< 0.001	0.005	1.000	0.014	0.906	1.000
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624 **Table 1:** Results from phylogenetic generalised least squares (PGLS)
625 models of bite-force as a function of size, one of three covariates (tooth
626 attachment type, diet, fossorial or not) and their interaction term. Size was
627 snout vent length (SVL; mm), head width (HW; mm), head length (HL;
628 mm), or head height (HH; mm). Significant p values are highlighted in
629 bold. Bonferroni corrected p values (bonf p) are provided for all terms
630 except the size term for which Bonferroni corrected p values were always
631 < 0.001 . res df = residual degrees of freedom. df = degrees of freedom. λ
632 = Pagel's λ .

633 **Figure legends**

634 **Figure 1:** Family-level coverage of the bite-force dataset (n = 164 species).
635 The left-hand panel shows the family level phylogeny, the central panel
636 shows the number of species from each family in our dataset, and the
637 right-hand panel shows the percentage of species from that family from²²
638 that are in our dataset. Sphenodontidae (Rhynchocephalia) contains only
639 one species, *Sphenodon punctatus*, and has 100% coverage so was removed
640 from the right-hand panel to prevent it from compressing the x-axis.
641 Colours indicate clades.

642 **Figure 2:** The relationship between bite-force and each of the four size
643 measures, with points coloured to identify clades. (A) snout vent length
644 (SVL; n = 161); (B) head width (n = 142); (C) head length (n = 136); and
645 (D) head height (n = 136). Points are slightly transparent to show where
646 they overlap. The lines are taken from phylogenetic generalised least
647 squares (PGLS) models of bite-force as a function of size (Table S5). There
648 were no significant differences among clades (Table 1).

649 **Figure 3:** The relationship between bite-force and each of the four size
650 measures for species with different diets. (A) snout vent length (SVL; n =
651 158); (B) head width (n = 139); (C) head length (n = 133); and (D) head
652 height (n = 133). Points are slightly transparent to show where they
653 overlap. The lines in (B) are taken from a phylogenetic generalised least
654 squares (PGLS) model of bite-force as a function of head width and diet,
655 where different diets have significantly different intercepts (Table 1).
656 There were no significant differences among diets for the other three size
657 measures (Table 1).

658 **Figure 4:** The relationship between bite-force and each of the four size
659 measures for species that are purely fossorial and those that are not. (A)
660 snout vent length (SVL; $n = 161$); (B) head width ($n = 142$); (C) head length
661 ($n = 136$); and (D) head height ($n = 136$). Points are slightly transparent to
662 show where they overlap. The lines in (B-D) are taken from phylogenetic
663 generalised least squares (PGLS) models of bite-force as a function of size
664 and fossoriality, where fossorial and non-fossorial species have
665 significantly different intercepts (Table 1). There were no significant
666 differences among fossorial and non-fossorial species for SVL (Table 1).

667 **Figures**

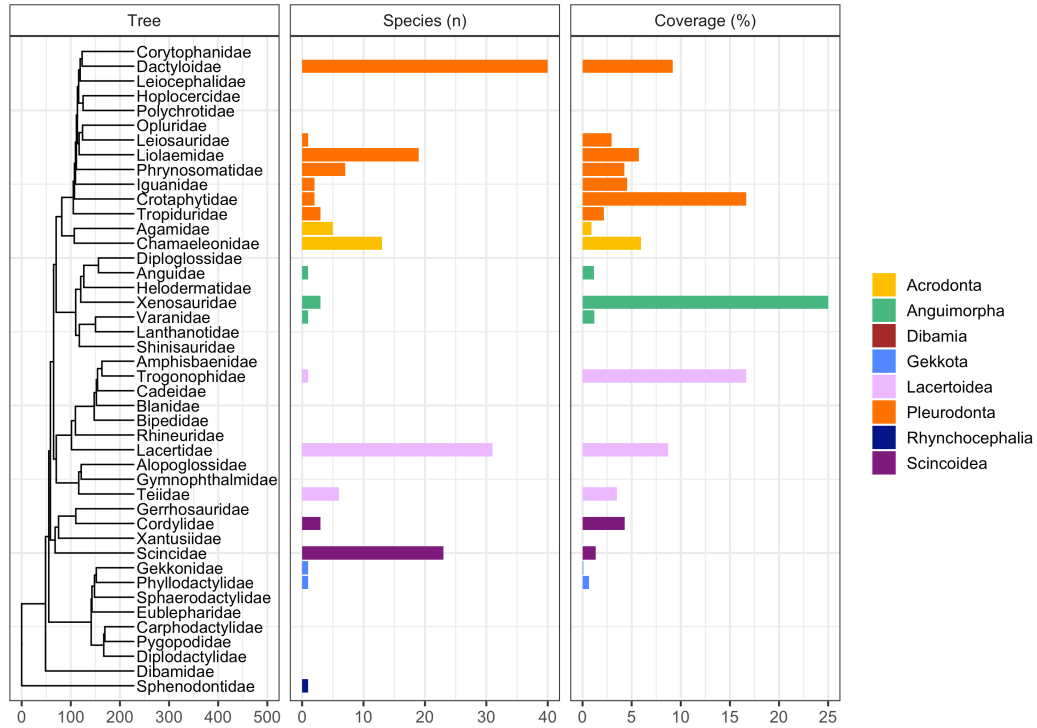


Figure 1: Family-level coverage of the bite-force dataset (n = 164 species). The left-hand panel shows the family level phylogeny, the central panel shows the number of species from each family in our dataset, and the right-hand panel shows the percentage of species from that family from²² that are in our dataset. Sphenodontidae (Rhynchocephalia) contains only one species, *Sphenodon punctatus*, and has 100% coverage so was removed from the right-hand panel to prevent it from compressing the x-axis. Colours indicate clades.

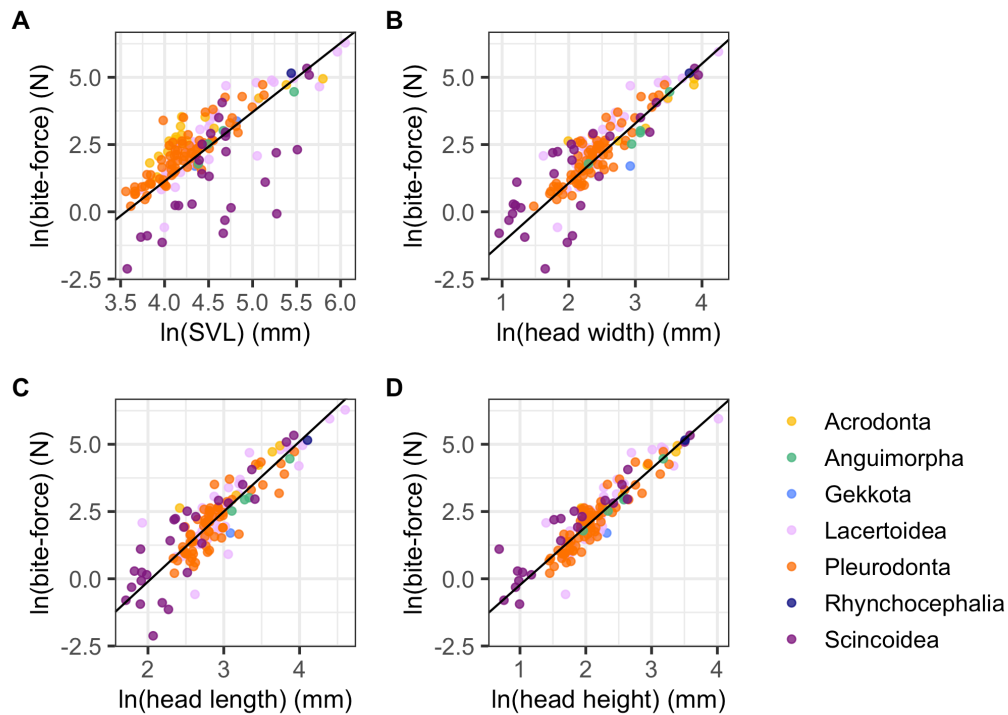


Figure 2: The relationship between bite-force and each of the four size measures, with points coloured to identify clades. (A) snout vent length (SVL; $n = 161$); (B) head width ($n = 142$); (C) head length ($n = 136$); and (D) head height ($n = 136$). Points are slightly transparent to show where they overlap. The lines are taken from phylogenetic generalised least squares (PGLS) models of bite-force as a function of size (Table S5). There were no significant differences among clades (Table 1).

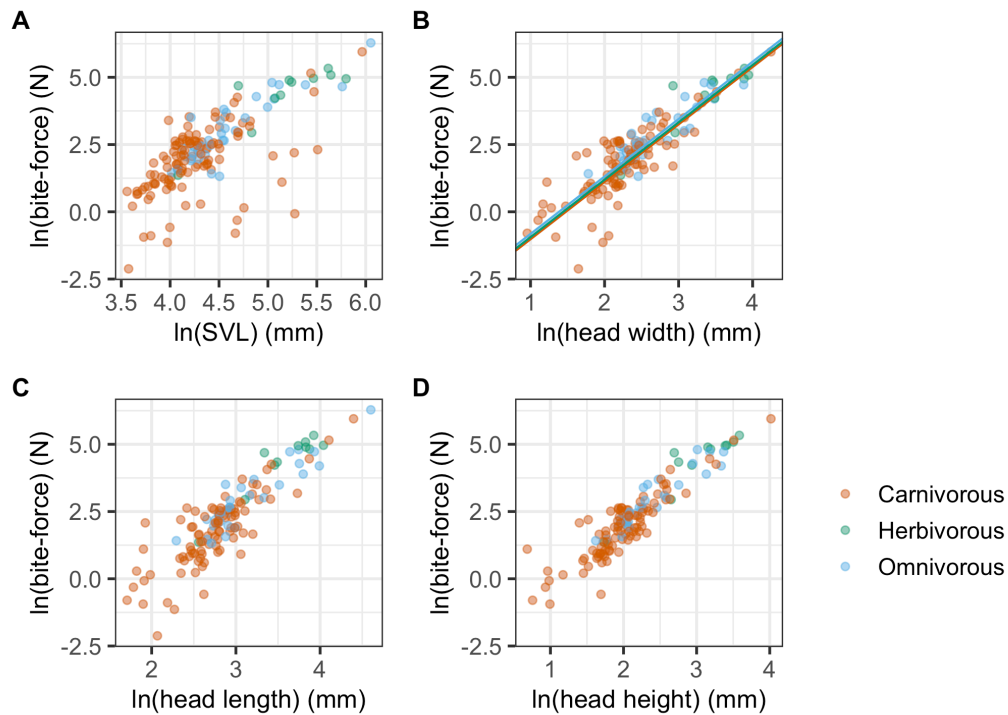


Figure 3: The relationship between bite-force and each of the four size measures for species with different diets. (A) snout vent length (SVL; $n = 158$); (B) head width ($n = 139$); (C) head length ($n = 133$); and (D) head height ($n = 133$). Points are slightly transparent to show where they overlap. The lines in (B) are taken from a phylogenetic generalised least squares (PGLS) model of bite-force as a function of head width and diet, where different diets have significantly different intercepts (Table 1). There were no significant differences among diets for the other three size measures (Table 1).

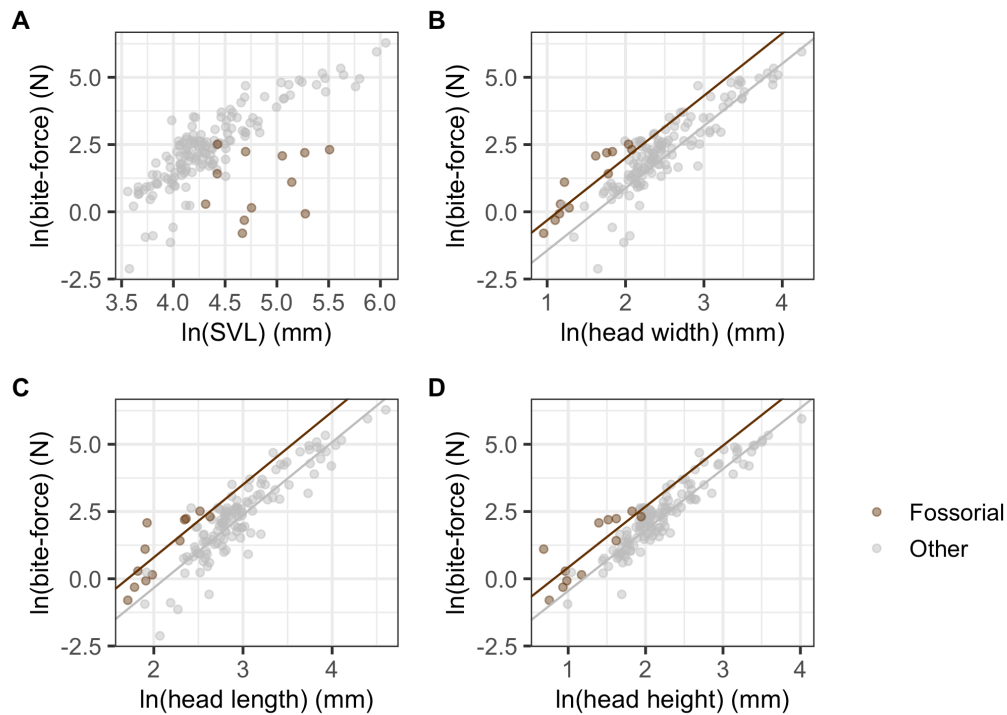


Figure 4: The relationship between bite-force and each of the four size measures for species that are purely fossorial and those that are not. (A) snout vent length (SVL; $n = 161$); (B) head width ($n = 142$); (C) head length ($n = 136$); and (D) head height ($n = 136$). Points are slightly transparent to show where they overlap. The lines in (B-D) are taken from phylogenetic generalised least squares (PGLS) models of bite-force as a function of size and fossoriality, where fossorial and non-fossorial species have significantly different intercepts (Table 1). There were no significant differences among fossorial and non-fossorial species for SVL (Table 1).