Bite force in the strictly subterranean rodent family of African mole-rats (Bathyergidae): The role of digging mode, social organization and ecology

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Abstract

1. Bite force is an ecologically relevant performance trait that has been measured to better understand the adaptations to diet and habitat use. Moreover, bite force is relevant in understanding reproductive success, as well as inter- and intraspecific competition.
2. African mole-rats (Bathyergidae, Rodentia) are a unique clade of mammals that use different digging strategies, show different types of social organization and occur in ecologically diverse savanna habitats in sub-Saharan Africa. Whereas previous studies have suggested these animals have exceptionally high bite forces, the ecological and other proximate and ultimate drivers of variation in bite force in the group remain unstudied.
3. In the present study we measured in vivo bite force of 394 adult specimens from 10 African mole-rat species including all genera within the family.
4. Our results show that in African mole-rats digging mode is a major driver of variation in bite force, with chisel-tooth diggers being stronger biters than scratch diggers. Moreover, species living in habitats characterized by low and irregular precipitation patterns and in soils with a high content of coarse particles have a higher bite force than species occupying habitats with a regular rainfall pattern and fine soil types.
5. This suggests that bite force in bathyergids has evolved in concert with rainfall and soil characteristics of different savanna habitats, which have contributed to the successful radiation of these subterranean mammals across sub-Saharan Africa.

Keywords: African mole-rats, bite force, burrowing, evolution, soil and food characteristics

1 INTRODUCTION

In mammals, the diversification of the masticatory apparatus is extremely high and has played a key role during their evolution. The modification of chewing muscles and associated skull structures, such as the shape of the mandible, position of the condylar process to the cheek-tooth row, shape and size of teeth, allow them to occupy various environmental niches and to exploit a diversity of food resources (Turnbull, 1970; Ungar, 2010). The arrangement and size of chewing muscles together with skull morphology is therefore a good proxy for a species ecology such as habitat utilization, dietary breadth and feeding strategies. An ecologically relevant performance trait associated with the ability of mammals to exploit different resources is bite force (e.g. Aguirre et al., 2003; Anderson et al., 2008; Herrel et al., 2008). Bite force is a performance trait which can be assessed in vivo (e.g. Erickson et al., 2004; Zablocki Thomas et al., 2018) or indirectly based on measurements of selected morphological characteristics of the skull, teeth and muscles (e.g. Christiansen & Wroe, 2007; Herrel et al., 2008). However, bite force estimation using CT scan-based biomechanical models may underestimate in vivo data (i.e. up to three times less than in vivo bite force, see Curtis et al., 2010).

Apart from an animal's diet, bite force in vertebrates is determined by body mass (Aguirre et al., 2002; Freeman & Lemen, 2008). However, other factors such as sociality (Damasceno et al., 2013; Magalhães et al., 2020) and sex can play a role as well (Herrel et al., 2007; Thomas et al., 2015). A strong bite may further be at a premium during aggressive encounters (e.g. in territorial and colony defence, or competition for sexual mates) and therefore it is also a good predictor of dominance and reproductive success in many animals (Husak et al., 2006; Lailvaux et al., 2004).

Subterranean rodents belong to the most specialized mammals and are well adapted to the underground ecotope. They spend virtually all of their life in complexes of self-excavated burrows, in which they forage and search for sexual partners, and some species even disperse below the ground (Nevo, 1999). The excavation of burrows is energetically very costly (Lovegrove, 1989; Vleck, 1979), which has resulted in the evolution of a well-developed digging apparatus allowing to overcome the mechanical resistance of soil (e.g. Stein, 2000). Despite their general morphological uniformity, there is a surprisingly wide diversity of lifestyles in subterranean rodents, which are related mainly to the degree of adaptation to subterranean life, digging strategies and phylogenetic origin (Stein, 2000).

There are two main strategies of digging in subterranean rodents: chisel-tooth and scratch digging. Chisel-tooth diggers use their procumbent incisors as a chisel to break up, loosen and dig through the soil, whereas scratch diggers use their forearms with robust claws to scratch away the soil (Hildebrand, 1985; Nevo, 1999). Due to the need for loosening of hard soils, chisel-tooth diggers need a high bite force which can thus be expected to be higher than in other mammals of comparable body mass (Becerra et al., 2013). This property is enabled by stronger neck and masticatory muscles, and curved incisors for better force transmission (Becerra et al., 2013; McIntosh & Cox, 2016). However, both types of burrowing can be present in many species and even strict chisel-tooth diggers often use scratch digging (Stein, 2000). The proportion of each type of digging mode can thus be expected to impact bite force according to the soil characteristics of a respective habitat (Kubiak et al., 2018).

African mole-rats (Bathyergidae, Rodentia) are an ideal group to study the factors affecting bite force in subterranean mammals. Their masticatory musculature is well-developed (e.g.

enlarged temporalis and masseter, see Cox et al., 2020; van Daele et al., 2009), which in the case of the naked mole-rat *Heterocephalus glaber* can make up to 25% of its entire muscle mass (Sherman et al., 1992). This makes them, in relation to their body size, comparable in biting performance to bone-crushing mammals such as hyaenas and the Tasmanian devils (Hite et al., 2019; van Daele et al., 2009). Moreover, bathyergids occupy habitats differing strongly in soil parameters, precipitation patterns and food resources (Lövy et al., 2012). They further show considerable variation in body mass, ranging from ~35 g in the naked mole-rat up to almost 2,000 g in the Cape dune mole-rat *Bathyergus suillus*. Importantly, this family includes both chisel-tooth and scratch diggers, and both solitary and highly social species (Bennett & Faulkes, 2000). Living in family groups and sharing the costs for digging may release the selection on the need of extremely effective burrowing apparatus and thus a strong bite force compared to solitary bathyergids (as indicated, for instance, by a more effective working metabolism in a solitary compared to a social species, Zelová et al., 2010).

In the present study, we measured in vivo bite force in 394 individuals of 10 species from all six genera of African mole-rats. We then tested the proximate and ultimate drivers of variation in bite force including body mass, sociality, mode of burrow excavation and sex. We predicted higher bite forces in chisel-tooth than in scratch diggers and in solitary compared to social species. In addition, we also tested the influence of climatic variation (annual precipitation and seasonality, annual mean temperature and the number of months per year with >25 mm of precipitation) and soil characteristics (bulk density, clay, sand and coarse fragment contents, and organic carbon density) as predictors of bite force variation. We predicted that higher bite forces have evolved in species inhabiting relatively denser soils with a higher amount of clay and coarse fragments of stones, and in species living in regions characterized by a prolonged dry season and generally a lower amount of annual precipitation, causing soils to be harder.

2 MATERIALS AND METHODS

Study animals

In vivo bite force was measured in 10 species of African mole-rats differing in body mass, digging mode and level of sociality (for details see Table S1, for graphical visualization of the characteristics of mole-rats relevant for this study see Figure 1): the social Ansell's mole-rat *Fukomys anselli*, the Damaraland mole-rat *Fukomys damarensis*, *Fukomys* 'Nsanje' (taxonomic status of this mole-rat population is awaiting detailed phylogenetic analysis, however, according to our preliminary results it belongs to *F. darlingi*), the giant mole-rat, *Fukomys mechowii*, Micklem's mole-rat, *Fukomys micklemi*, the common mole-rat *Cryptomys hottentotus hottentotus* and the naked mole-rat *Heterocephalus glaber*; the solitary Cape dune mole-rat *Bathyergus suillus*, the Cape mole-rat *Georychus capensis* and the silvery mole-rat *Heliophobius argenteocinereus*. Only adults and non-breeding individuals were included in the study.
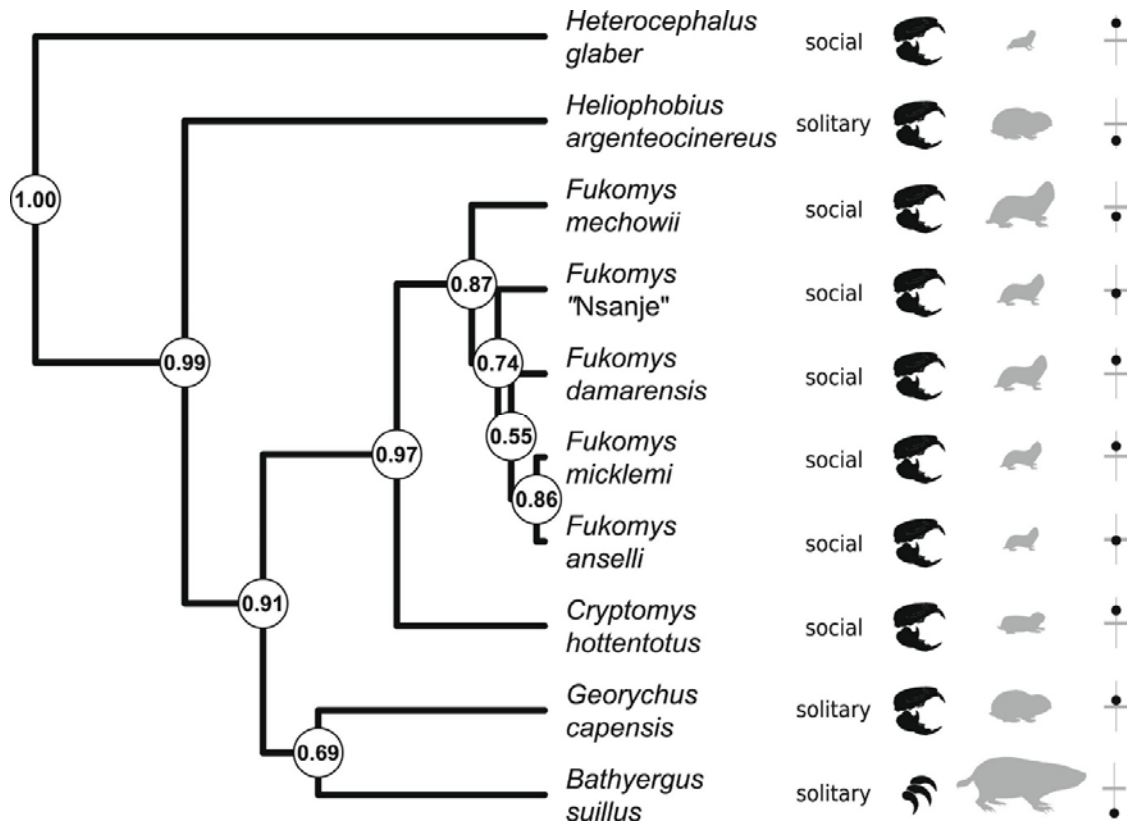
FIGURE 1. Phylogeny of the 10 species of African mole-rats studied (for the details of the phylogenetic analysis see Figure S1). Social system, digging style, body size, and body-mass corrected bite forces are also depicted. Chisel-tooth diggers and the only scratch digger are marked by a skull and claw symbols, respectively; relative body mass is indicated by the size of the body silhouettes. The last column demonstrates corrected bite force, where the horizontal line indicates the expected values based on the species' body masses and the black dot shows the measured value for each species.

All individuals of *Fukomys*, *H. glaber* and *H. argenteocinereus* had been in captivity for a long time, either at the Kuruman River Reserve in the Northern Cape in South Africa (*F. damarensis*, temperature: 21–24°C, humidity: 40%–50%, no light) or at the University of South Bohemia in České Budějovice, Czech Republic (temperature: 25°C, additional heating plates for *H. glaber*, humidity: 40%–50%, photoperiod 12L:12D). The captive animals were fed ad libitum with vegetables (such as carrots, potatoes, sweet potatoes, beetroot, apple, cucumbers) and rodent dry food mix. All animals were given the possibility to carry out their natural digging behaviour either in sand (*F. damarensis*), wood shavings (*H. glaber*) or peat (remaining species) and were given extra enrichment such as tree branches and plastic tubes for gnawing. *Cryptomys h. hottentotus*, *B. suillus* and *G. capensis* were captured shortly before measuring bite force at the Waylands farm, Darling, South Africa (33°23′S, 18°25′E). They were sexed, weighed and kept in plastic containers with saw dust bedding, a plastic tube as a shelter and enrichment and fed with sweet potatoes (fresh grass was provided to *B. suillus*, whose diet consists predominantly of above-ground vegetation, Bennett et al., 2009) until bite force measurements could be obtained (typically within several days after capture).

The study was approved by the ethic committee of the University of Pretoria (Permits EC-69-16, EC069-17 and AUCC-040702/015) and of the University of South Bohemia (Permit

MSMT-35731/2019-4) and the capture of the wild African mole-rats was acted out under the permission of the Western Cape Nature Conservation Board (Permits 0056-AAA041-00169 and CN13-31-2488).

Bite force measurements

In vivo bite forces were measured with an isometric force transducer (type 9203; range 0–5,000 N, error 0.1 N; Kistler Inc. Switzerland), for details of the experimental set-up, see Herrel et al. (1999). The bite plates were covered with a thin protective coating made of cloth or duct tape, to avoid damage to the incisors of the animal and to improve grip. Each measured individual was held around the neck with one hand and prompted with the transducer device. Mole-rats were induced to bite at least three times (usually five measurements were taken) and the maximum bite force in Newtons (N) of each individual was kept and used as an estimate of its maximal bite performance. Animals were weighed on a digital scale (0.1 g).

Statistical approach

Bite force is expected to scale with body mass (e.g. Aguirre et al., 2002; Freeman & Lemen, 2008) and we corrected for this effect before testing our hypotheses. The scaling is expected to be allometric and thus we worked on a decadic logarithmic scale, that is, with log-transformed body mass and log-transformed bite force, which makes the expected relationship linear (Huxley, 1932).

For the allometric correction, we used a linear mixed-effects model with log-transformed body mass as a predictor, log-transformed bite force as the response variable and species as a random term. We considered three such models, either with a random intercept, a random slope or both, and selected the best model according to Akaike information criterion (AIC, Akaike, 1974). We used the best random effects allometric model to obtain individual residuals (=corrected bite force) for the final analyses. They were obtained as residuals from each intraspecific allometric trend added to the residual of the respective species mean from the interspecific allometric trend. In the allometric corrections, all species were included, which introduces circularity into the analysis. Therefore, we used a simple jackknife procedure to assess the robustness of the estimated interspecific allometric scaling. We replicated the best of our three random-effects models 100 times with different subsets of species. These subsets included seven to nine species, whose sampling with respect to body mass was as balanced as possible. The correction was considered robust as the fixed effect coefficients were close to the median of their jackknife distributions (see Section 3).

The allometric correction could be biased by confounding effects of sexual dimorphism and phylogenetic relationships. We therefore addressed them in initial tests. First, we tested for the difference between males and females in every species using a series of additive linear models with sex and body mass as predictors and we applied the Holm adjustment (Holm, 1979) to the resulting p values to account for multiple testing. Then, we conducted an analysis testing for the interference of phylogenetic and allometric effects. We regressed species mean bite force to species mean body mass (both log-transformed) using generalized least squares with phylogenetic (Brownian motion) structure of error covariance and different specification of the strength of the phylogenetic signal using Pagel's

(Pagel, 1999). First, was set to zero, which is equivalent to omitting the phylogenetic effect. Then,

was optimized during the model fit, which makes it an additional parameter to be estimated. These models were compared using likelihood ratio test and if there is no significant difference, the use of non-phylogenetic model is justified. For this analysis, we inferred phylogeny of 10 studied species as a species tree in StarBEAST 2 (Ogilvie et al., 2017). It was inferred from published sequences of one mitochondrial (*CYTB*) and three nuclear markers (*GHR*, *IRBP* and *VWF*), see Figure S1, Table S2 for details.

The corrected bite force was analysed in two ways. First, we tested whether corrected bite force differs among the 10 studied species. The factor 'species' was used as a single predictor in the general linear model and its significance was tested by an *F* test. Then we used Tukey pairwise comparisons to assess which of the species differed significantly from each other (Tukey, 1949). Second, we replaced the factor 'species' by seven predictors characterizing the species, namely species mean body mass, digging mode (chisel teeth and scratch digger), sociality (solitary and social) and four ecological variables. These ecological variables were the first four principal components (PCs) from a PCA analysis performed to cope with high correlations among the five soil and four climatic variables chosen for this study (Table S3, for correlation matrices among these variables see Table S4). The model selection procedure started from the full model with all seven predictors and proceeded with their backward stepwise elimination until only significant terms remained in the final model. The significance of the terms was tested by *F* tests.

The soil variables were bulk density (bulk density of the fine earth fraction oven-dry, g/cm^3), clay (0–2 μm) and sand (50–2,000 μm) contents (gravimetric contents in the specific fine earth fraction of the soil, g/kg), coarse fragment content (volumetric content of fragments >2 mm in the whole soil, cm^3/dm^3) and soil organic carbon density (g/dm^3); the climate variables were the annual sum of precipitation (mm), precipitation seasonality (coefficient of variation), the annual mean temperature (°C) and the number of months per year with >25 mm of precipitation. The latter variable corresponds to the estimated amount of precipitation necessary to soften the soil and thus to make it workable at the depth of most foraging burrows of mole-rats (see Jarvis et al., 1994). Values of the soil variables were obtained from the SoilGrid™ database v. 2.0 (Poggio et al., 2021, www.soilgrids.org) and values of the climatic variables from the Worldclim database (Fick & Hijmans, 2017, www.worldclim.org). For each species, they were calculated as mean over the range as presented by the IUCN Red List (iucnredlist.org). For *G. capensis*, two isolated populations occurring in KwaZulu Natal Province and Mpumalanga Province were not included in the range, as they represent very localized isolates occupying small and isolated patches of montane grasslands and/or mesic grasslands (Bennett et al., 2006). All variables entering the PCA were log-transformed, centred and standardized to have zero mean and unite variance.

The statistical analyses were performed, and graphical outputs were created in r (R Core Team, 2020) using packages mass (Venables & Ripley, 2002), nlme (Pinheiro et al., 2020), ape (Paradis & Schliep, 2019) and vioplot (Adler & Kelly, 2020).

3 RESULTS

The analyses revealed no effect of sex in any species (all corrected $p \geq 0.95$) and thus we pooled together sexes in all subsequent analyses. The phylogenetic (λ optimized) and non-phylogenetic ($\lambda+0$) models were not significantly different ($\rho + 0.96$) and the estimate of λ was close to zero (-0.04) with a wide 95% confidence interval (-1.70, 1.62). This implies no detectable phylogenetic dependence in our data and the phylogenetic effect was therefore not further considered.

The allometric model with both random intercept and slope was clearly preferred against the alternatives ($\Delta AIC = 60$ and 78 relatively to the slope-only and intercept-only model respectively). In other words, there is a common interspecific trend of bite force increasing with body mass ($F = 80.3$, $p < 0.001$), but it scales differently for species (see Table 1 for coefficients describing species-specific relationships between bite force and body mass, Figure S2). The estimate of the interspecific trend (intercept = -0.743, slope = 1.099) proved to be robust: the intercept represents 0.45 quantile and the slope 0.57 quantile of the corresponding jackknife distributions (Figure 2). The model was therefore used for the allometric correction, and the residuals obtained from this model served as the input dataset for the subsequent analyses of the corrected bite force.

TABLE 1. Mean maximal bite force and parameters characterizing the increase in maximal bite force in response to increasing body mass in 10 African mole-rat species (intercept and slope estimates originate from the allometric model with both random intercept and slope on a log–log scale)

| Species (*n*)	Maximal bite force in N (range)	Intercept	Slope
B. suillus (46)	99.8 ± 43.7 (33.2–197.7)	−0.327	0.851
C. hottentotus (15)	23.0 ± 9.0 (13.3–45.9)	−0.617	1.096
F. anselli (10)	24.9 ± 7.4 (15.4–36.9)	−0.922	1.181
F. damarensis (122)	60.6 ± 29.9 (9.7–147.3)	−2.068	1.785
F. 'Nsanje' (26)	33.0 ± 9.4 (20.8–59.0)	−0.347	0.894
F. mechowii (56)	79.8.0 ± 39.0 (25.5–182.9)	−1.071	1.193
F. micklemi (23)	39.8 ± 16.0 (15.3–79.1)	−1.234	1.384
G. capensis (58)	48.5 ± 16.8 (25.5–92.9)	−0.449	0.987
H. argenteocinereus (7)	40.0 ± 11.1 (25.5–53.6)	−0.303	0.824
H. glaber (31)	14.7 ± 3.3 (9.4–20.8)	−0.092	0.794
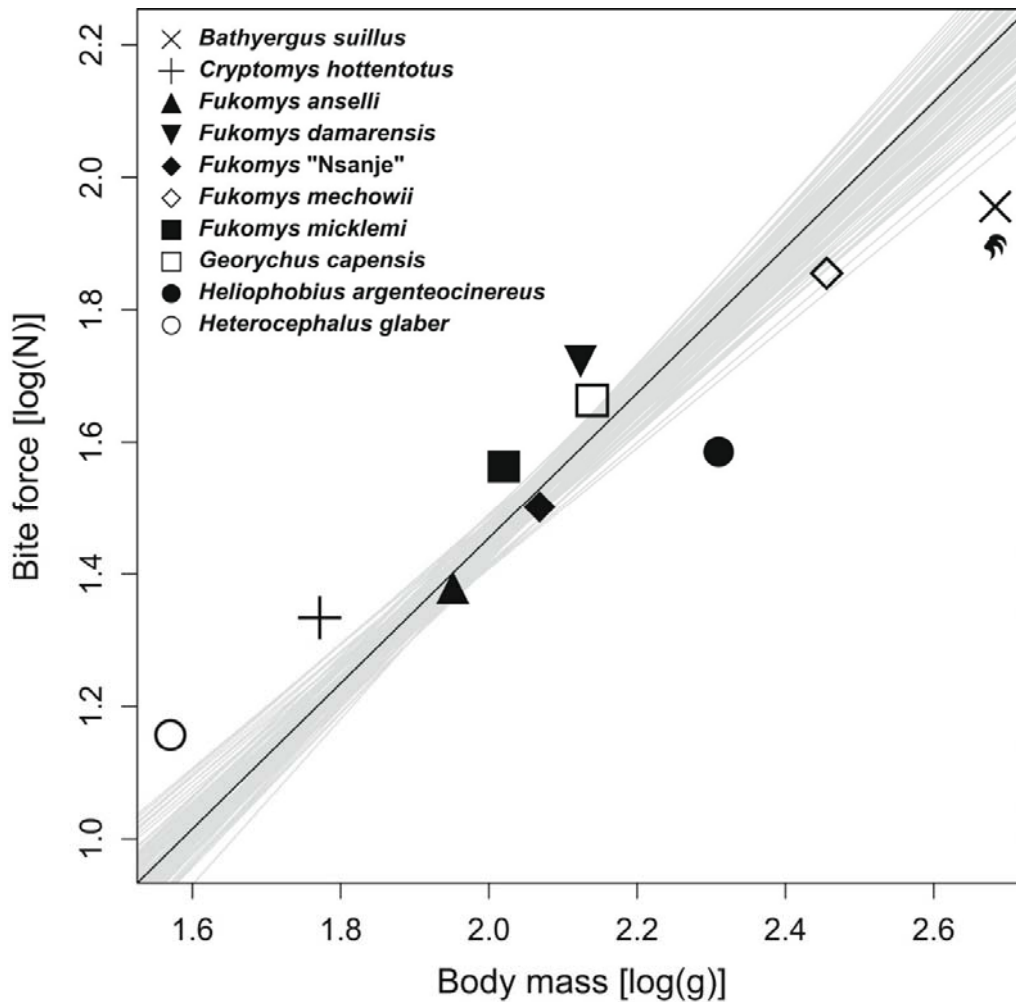
FIGURE 2. Robustness of the estimated inter-specific allometry in bite force. Thin grey lines represent jackknife estimates, while the thick black line is the estimate from the full data set. The scratch-digger *Bathyergus suillus* is indicated by a claw symbol.

Ten mole-rat species differed substantially in their corrected bite force ($F = 85.6$, $p < 0.0001$, the distributions of the corrected bite force are shown in Figures 1 and 3). *Bathyergus suillus* had a lower corrected bite force than all other mole-rats, apart from *H. argenteocinereus*, which had similar corrected bite force as *F. mechowii*. *Fukomys mechowii* had the comparable corrected bite force to both *F.* 'Nsanje' and *F. anselli*. *Fukomys anselli* had a similar corrected bite force as both *G. capensis* and *F. micklemi*. *Cryptomys hottentotus*, *F. damarensis* and *H. glaber* had the strongest corrected bite force among all studied mole-rats (see Table S5 for all post-hoc comparisons).
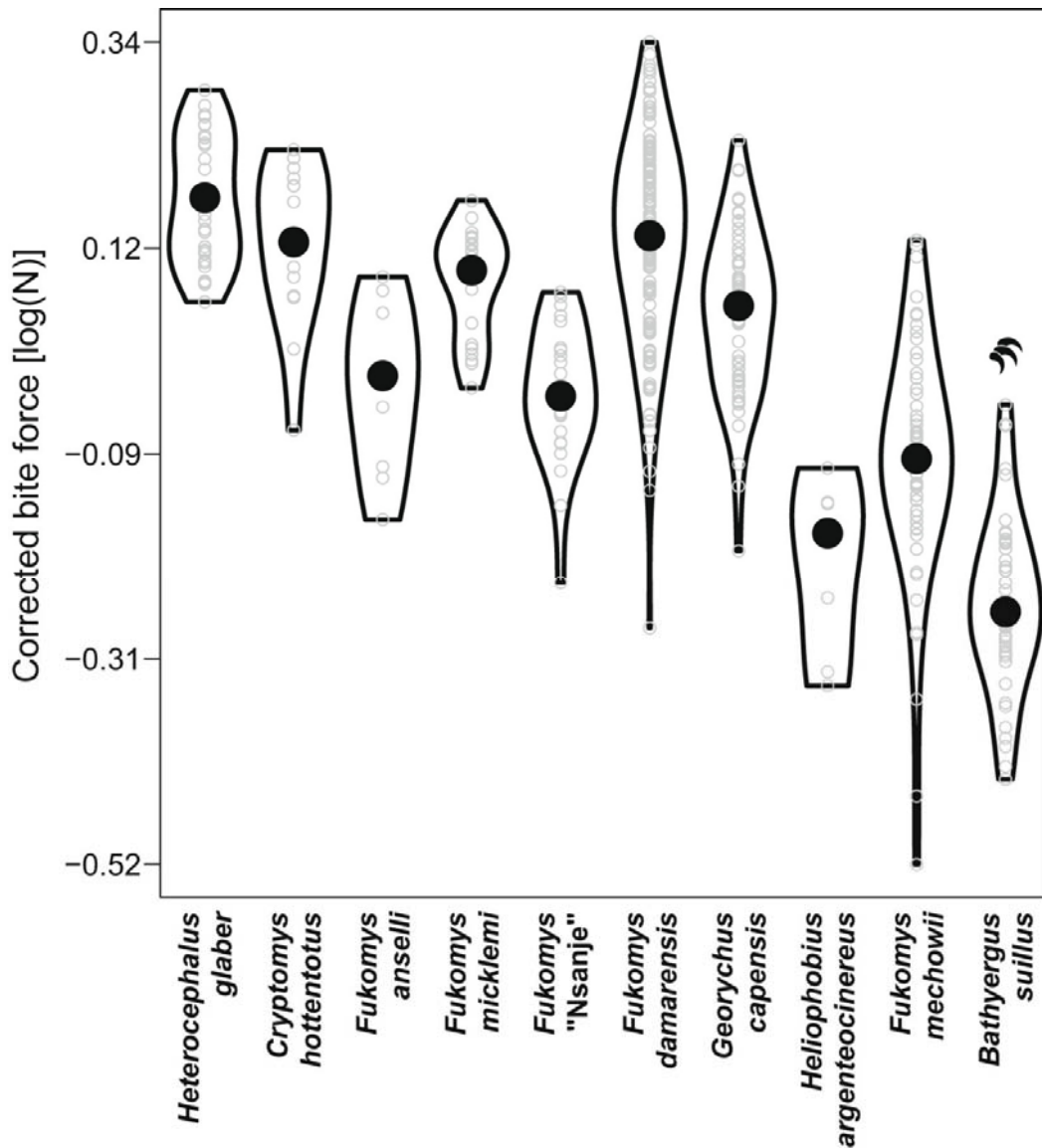
FIGURE 3. Species-specific distributions of the corrected bite force. The species are sorted in the order of increasing body mass. The scratch-digger *Bathyergus suillus* is indicated by a claw symbol.

The first four principal components (PC1–4) of the analysis performed on soil and climatic variables explained 96.6% of the variation (Figure S3). PC1 explained 46.6% of the variation and it was mainly determined by bulk density, annual mean temperature and precipitation seasonality against organic carbon content and the number of months with >25 mm of precipitation. PC2 (25.7%) was mainly determined by sand content contrasted with contents of clay, coarse fragments and organic carbon. PC3 (19.6%) was mainly determined by mean annual precipitation, the number of months with >25 mm of precipitation, organic carbon content and clay content, all these standing in contrast with coarse fragment content and bulk density. PC4 (4.7%) was primarily determined by annual mean temperature (for details of PC loadings, see Figure S4).

The backward elimination procedure resulted in a final model showing that the corrected bite force decreased with species mean body mass, it was lower in scratch diggers compared to chisel-tooth diggers and was influenced by PC3, and to a lesser extent to PC2 (see Table 2 and Figure 4; PC1 and PC4 were eliminated from the final model). PC3 predicted the corrected bite force to decrease mainly with annual precipitation and the number of months with >25 mm of precipitation, but to increase with the content of coarse fragments (Figure 4). PC2 was included in the model due to increasing sufficiently the overall likelihood ($F = 101$, $p < 0.0001$), although the difference of its regression coefficient from zero was only marginally significant ($p = 0.106$) and its effect was weak (Figure 4).

TABLE 2. Summary of the stepwise backward elimination method to assess predictors of the corrected bite force in 10 African mole-rat species. Results of F tests show all terms were estimated as significantly contributing to overall likelihood. Estimates of the coefficient values are reported with their standard errors and p values indicating significance of their difference from zero

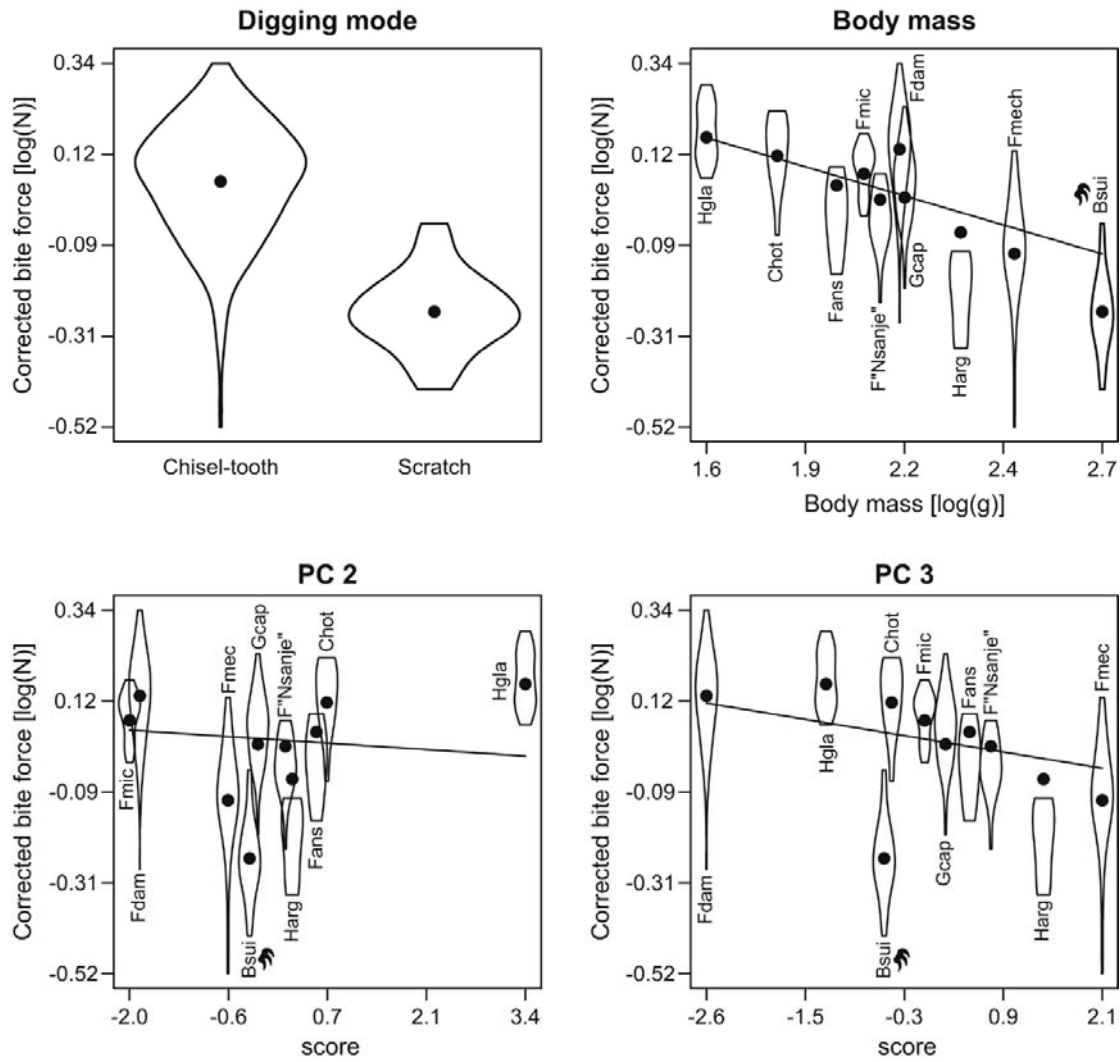| Predictors	$F_{4,389}$	p (F test)	Estimate	SE	p (coeff. test)
Intercept			0.542	0.106	
Species mean body mass	505	<0.0001	−0.239	0.050	<0.0001
Digging mode	37	<0.0001	−0.158	0.035	<0.0001
PC2	101	<0.0001	−0.011	0.007	0.106
PC3	35	<0.0001	−0.033	0.006	<0.0001

FIGURE 4. Predictions of the best performing model plotted against the values of its four predictors. For the three continuous predictors (body mass, PC2 and PC3), black dots mark species-specific predictions of the corrected bite force and black line is the trend predicted for chisel-tooth diggers when the other continuous predictors are kept constant at their means. In the background the corrected bite force (=response variable) is shown by means of violin plots (Hgla—*Heterocephalus glaber*, Chot—*Cryptomys hottentotus*, Fans—*Fukomys anselli*, Fmic—*Fukomys micklemi*, Fdam—*Fukomys damarensis*, Gcap—*Georychus capensis*, Harg—*Heliophobius argenteocinereus*, Fmech—*Fukomys mechowii*, Bsui—*Bathyergus suillus*, the claw symbol indicates its scratch digging mode).

4 DISCUSSION

The maximal bite force varied among the species of African mole-rats as a function of body mass, digging mode and some of the soil and climate characteristics. Interestingly, the effect of social organization (social vs. solitary) was not statistically significant. The analysis was based on a sample of 394 adult individuals from 10 species, which is substantially more than in most in vivo studies, where around 10–30 individuals are usually included (e.g. Erickson et al., 2004; Thomas et al., 2015, but see Senawi et al., 2015, Zablocki-Thomas et al., 2021, for comparable sample size).

Sex and phylogeny

Two other potentially confounding effects were excluded in preliminary analyses. First, bite force did not differ between sexes in any of the species. This was surprising given the clear examples of sexual dimorphism in species with different social organizations and vastly different body sizes. Namely, the males of the large and solitary *B. suillus* are about 20% larger than females (Bennett et al., 2009) and both breeding and non-breeding adult males of the small and social *F. anselli* displayed larger skulls relative to body size than females, along with an expansion of the facial portion of the cranium, which indicates male intrasexual competition (Caspar et al., 2021). It should also be noted, however, that this dataset was not designed to analyse bite force variation at the intraspecific level, as we included only non-breeding individuals in social species. Therefore, we cannot conclude that some level of sexual dimorphism in bite force does not exist.

Based on the comparison of simple allometric models with and without phylogenetic correlation of residuals we concluded that species can be treated as independent observations. This implies that the phylogenetic effect is not large and consistent enough to change performance of the model when considered. However, our result does not imply that the cranial morphology, masticatory musculature or bite force itself bears no phylogenetic signal. It just shows no important deviations from the allometric relationship when phylogeny is taken into account. In some studies, effect of phylogeny on bite force has been demonstrated (e.g. Sakamoto et al., 2010).

Body mass

Body mass is the most universal determinant of bite force in vertebrates (e.g. Aguirre et al., 2002; Freeman & Lemen, 2008), including African mole-rats (Hite et al., 2019; van Daele et al., 2009). In African mole-rats, its effect is twofold. First, bite force scales allometrically with body mass at both intraspecific and interspecific levels. Second, even after accounting for allometry, the corrected bite force is significantly dependent on the species mean body mass. This is possible due to the interference of the interspecific allometry (fixed effect of the model) and intraspecific allometries (random effect). The dependence was negative: larger species had lower corrected bite forces (Figure 1). This suggests that in the large-bodied mole-rats, body size itself ensures their bite is strong enough, whereas in the small-bodied species this must be achieved by increased bite force for their size. To the best of our knowledge, such a phenomenon has not been described in any study dealing with biting performance in vertebrates and it deserves further investigation. This is, however, a common intraspecific phenomenon where juveniles perform relatively well for their size as they are in an absolute competitive disadvantage when competing for the same resources as adults (Herrel & Gibb, 2006).

Sociality

A lack of differences between the three solitary and seven social species in bite force is surprising, as they differ substantially in many aspects of their biology and lifestyle (Bennett & Faulkes, 2000). While social mole-rats could divide burrowing workload among family members, solitary mole-rats must rely on themselves. Thus, we expected bite force to be at a premium in solitary species. Interestingly, Zelová et al. (2010) found the solitary *H. argenteocinereus* is a more efficient digger (spending less energy for burrowing per distance burrowed in the same soil type) than the social *F. mechowii*, despite both occupying habitats

with a similar soil and food characteristics (Šumbera et al., 2012). Note, however, that the masticatory musculature does not differ between the solitary and social genera (Cox et al., 2020). This suggests that mole-rats have adapted to solitary digging by other means, for example, by increased metabolic efficiency, but not by increased bite force. It is also true, however, that the low number of solitary mole-rat species and the presence of the only scratch diggers among them could cause bias in the estimated difference.

Digging mode

Chisel-tooth diggers, except for *H. argenteocinereus*, were more forceful biters than the scratch digger *B. suillus* (only the genus *Bathyergus* contains scratch diggers and its second representative *B. janetta* was not available for this study). The significant effect of digging mode was expected because life activities of chisel-tooth diggers depend more crucially on biting. Similarly, among octodontids, the degu *Octodon degus*, which is a non-specialized scratch digger, shows a lower bite force than the chisel-tooth digging cururo (Gomes Rodrigues et al., in press). The difference in digging mode and bite force mainly relates to occupying different habitats because scratch diggers usually live in more workable (i.e. loose, less dense) soils. This was demonstrated by Borges et al. (2017) who found that the estimated bite force (estimated from incisor width and length) is driven by habitat utilization in 24 species of the genus *Ctenomys*. Whereas weaker biters occur in low-density soils, the species with high and medium estimated bite forces live in more consolidated substrates. Interestingly, the mutual correlation of habitat characteristics, bite force and the prevailing digging mode was found even at the intraspecific level. Kubiak et al. (2018) found that populations of tiny tuco-tucos *Ctenomys minutus* from harder soils showed a higher proportion of chisel-tooth digging compared to a population from the sand dunes and their incisor traits suggested stronger bite forces.

The only scratch digging bathyergid genus, *Bathyergus*, diverged from its chisel-tooth digging sister genus, *Georychus*, approximately 7 million years (Ma) ago (Uhrová et al., 2022). It follows that the most recent common ancestor of the extant bathyergids was probably a chisel-tooth digger living probably in Oligocene (23–34 Ma; Barbière & Marivaux, 2015, Upham & Patterson, 2015), an epoch of global cooling and aridification (Hutchinson et al., 2021). It can be assumed that increased prevalence of dry hard soils with energy-rich geophytes, which evolved as a response to increased aridification and seasonality (Nevo, 1999), imposed selective pressures that gave rise to tooth digging. Concurrently, strong bite forces likely evolved due to ongoing adaptive changes in underlying morphological traits, including enamel structure (van der Merwe & Botha, 1998) and muscle architecture (Cox et al., 2020).

Conversely, ancestors of *Bathyergus* adapted to life in less challenging soils. Indeed, *Bathyergus* differs from all other bathyergid genera in the relative proportions of masticatory muscles as it possesses an enlarged superficial masseter and relatively smaller pterygoid muscles (Cox et al., 2020) and different shapes of skull and mandible (Gomes Rodrigues et al., 2016). These adaptations may be quite old because the extinct *Bathyergus hendeyi* from an early Pliocene site of Langebaanweg is already unambiguously diagnosable as a member of the genus (Denys, 1998).

It is surprising that another mole-rat species occupying sandy habitats, that is, *F. damarensis*, is not a scratch digger with a weaker bite force. Quite the opposite, this species is one of the most powerful biters among African mole-rats (Figure 3). Such a difference is quite

intriguing, yet difficult to explain. The results of the multivariate analysis of various climatic and soil characteristics showed that soil characteristics between habitats of *Fukomys damarensis* and *Bathyergus suillus* species are different (Figure S3). The soils occupied by *F. damarensis* have higher bulk density (16%) and sand content (8%), but a lower amount of clay (17%), coarse fragments (21%) and organic carbon (75%) (Table S3). We assume that such differences cannot simply explain such a remarkable difference in bite force. However, it should be noted that according to some information, Kalahari soils can be very compacted and aggregated at deeper depths (Lovegrove & Painting, 1987), especially below 40 cm where they build their nests (Bennett & Jarvis, 2004). Only a detailed soil analysis across different soil horizons can show whether differences in soil characteristics may explain the high bite force in *F. damarensis*.

The relatively low bite forces measured for *Heliophobius argenteocinereus* is unusual, since it is a strict chisel-tooth digger, and we expected the value comparable to another chisel-tooth digger *G. capensis*. Indeed, both species share many aspects of their biology: sociality, body mass, staying in well-consolidated soils which can be temporarily very hard, etc. (Bennett et al., 2006; Šumbera et al., 2007). The length of staying in captivity may theoretically decrease bite force. As mentioned in the methods, our dataset combines wild-caught individuals with those kept in captivity for years, along with laboratory-born individuals. Although the effect of captivity on bite force is not conclusive (Erickson et al., 2004; Zablocki Thomas et al., 2018), we cannot exclude that a limited opportunity to dig through hard substrates in captivity affects bite force measurements. Nevertheless, no difference between maximum in vivo bite force between field and laboratory measurement was revealed in *Fukomys micklemi* (van Daele et al., 2019) and in mouse lemurs, diet and captive conditions did not change bite force as well (e.g. Zablocki Thomas et al., 2018). In addition, our laboratory mole-rats have the opportunity to dig in various types of substrates and uses tree branches as enrichment (see Section 2). Second, the species with the highest relative bite force, *H. glaber*, has been maintained for decades in captivity and the animals measured here are the descendants of many captive generations. Similarly, two *Fukomys* species with very high bite force, *F. damarensis* and *F. micklemi*, were also for a long time kept in captivity and most of them were even laboratory-born. In the case of *H. argenteocinereus* some other factors such as low sample size (seven individuals) and especially their age (all individuals were at least 7 years old) were probably responsible for the low bite forces.

Climate and soil characteristics

Our results indicate that in African mole-rats, bite force reflects combined effects of soil and rainfall variables (see Figure 4). We found that mole-rat species with stronger bites tend to inhabit environments characterized by lower annual rainfall, a prolonged dry season, and the presence of coarser soils (soil particles >2 mm) with less clay and organic carbon contents. In general, this finding demonstrates that the strength necessary to loosen the soil during burrowing (so-called shear strength) is given by the interaction of many soil parameters including its hardness, mechanical resistance, cohesion and water content (Carotenuto et al., 2020; Collis-George, 1959; Vleck, 1979). Previously, these characteristics have already been shown to put strong requirements on digging-related traits like working metabolism, burrowing style and bite force in subterranean mammals (e.g. Kubiak et al., 2018; Lovegrove, 1989; Vleck, 1979). Furthermore, this echoes the observation that scratch diggers are found in loose sandy soils and chisel-tooth diggers in more consolidated ones (see above).

One problematic point is that the corrected bite force was higher in mole-rat species occupying soils that are coarser, but also having less clay content, although a higher clay content makes the soil compact and digging substantially more demanding, especially when dry (Vleck, 1979). The predicted trend was not entirely consistent, however, as the clay content differed substantially between habitats of two species with extremely strong bite force. Whereas *H. glaber* inhabits soils exceptionally rich in clay, *F. damarensis* is found mainly in coarse sands (Bennett & Jarvis, 2004) containing relatively little clay (Thomas et al., 2016, Table S3). It should be noted, however, that all soils occupied by mole-rats comprise some proportion of clay (159–326 g/kg) and its effect on the soil workability can depend on the soil chemical properties, which were not studied here.

We confirmed an important role of soil water content on biting performance in African mole-rats. In seasonal savannas, the amount of rain and its distribution across the year are factors driving the whole savanna ecosystem. In general, soil moisture directly influences the hardness and structure of the soil, as it dissolves minerals and overall softens it (Marcy et al., 2013; Müller et al., 2011). It is therefore largely responsible for the ease with which the soil is worked on by mole-rats, which varies dramatically during the year (e.g. Zelová et al., 2011). We showed that not only overall annual rainfall, but also its seasonality (i.e. the number of months with rainfall higher than 25 mm) likely influence bite force. Accordingly, mole-rats with stronger bite force are usually associated with drier environments with longer dry seasons. Nevertheless, a certain amount of soil water triggers digging after a period of drought. Indeed, bursts of digging activity following heavy rains were documented in mole-rat species (e.g. Jarvis et al., 1998). On the other hand, a large amount of water can dramatically increase burrowing costs due to digging in heavy and relatively sticky and plastic soils (Collis-George, 1959).

Mole-rat species living in sympatry

The study of sites where mole-rat species occur together may further help us to disentangle the factors that influence bite force. Species coexistence is very rare in subterranean rodents (Nevo, 1999), but in southern Africa, two or even three bathyergid species can be present at the same site. One such place is the Darling area in Western Cape, where *B. suillus*, *G. capensis* and *C. h. hottentotus* occur together (Reichman & Jarvis, 1989; Robb et al., 2012). These three bathyergids do not only differ in their bite force properties, but also the degree of social organization, body mass and digging mode (Table S1). Although they are exposed to identical rainfall and temperature patterns, each species occupies different microsites in terms of soil quality and has a different diet. The largest and at the same time also the species with a higher proportion of aerial vegetation in its diet, *B. suillus*, is restricted to loose sandy soils, while *G. capensis* feeding also on aerial vegetation (but to a lesser extent) is restricted to sandy loams, alluvium and clay soils. The smallest species, *C. h. hottentotus*, feeds exclusively on geophytes and occurs mainly in the stony drier soil, that is, the soil with highest coarseness (Reichman & Jarvis, 1989; Robb et al., 2012). The presence of each species in a certain soil type of distinct quality is reflected in our bite force data, with *B. suillus* being the weakest, *G. capensis* having medium bite forces and *C. h. hottentotus* having the strongest bite force in relation to body size. We propose that due to its large size, *B. suillus* can easily monopolize its preferred habitat, despite its relatively low bite force, but its low value and large body size precludes its occurrence in more consolidated soils, as small body size was found to be an energetic advantage in hard soils for subterranean rodents (Vleck, 1979). Due to its social lifestyle and high bite force, *C. h. hottentotus* is likely able to colonize relatively harder soils with a high content of stones, which are more difficult to

colonize for solitary species (see also Uhrová et al., 2022 for discussion of coexistence of these species).

5 CONCLUSIONS

Our findings demonstrate that bite force in subterranean rodents is, except for body mass, determined by their need to overcome mechanically resistant soil during burrowing, an activity crucial for obtaining access to food, but also to acquire sexual partners and to disperse in many species. In this regard, we have provided evidence that, across the whole family, in vivo bite force is shaped mainly by the overall friability of the soil. Thus, bathyergids living in areas characterized by relatively low and irregular rainfall and higher content of coarse soil particles had higher in vivo bite forces and primarily used the chisel-tooth digging strategy compared to the scratch digger *B. suillus* occupying more easily workable sandy soils. When we put our findings into a broader context, identifying potential ecological drivers other than diet shaping biting performance in mammals and other vertebrates is rather exceptional. To date, researchers have related in vivo bite force mainly to particular aspects of foraging ecology, namely food/prey physical characteristics (e.g. Aguirre et al., 2003; Dollion et al., 2017; Herrel et al., 2001, 2004, 2006, 2018; van der Meij & Bout, 2006). To the best of our knowledge, our study is probably the first one addressing in vivo bite force to factors other than food characteristics. For future studies focused on in vivo bite force in mammals and other vertebrates, it will be interesting to continue exploring non-food related drivers of variation in bite force including agonistic interactions during both inter- and intraspecific competition (Herrel et al., 1999; Lailvaux et al., 2004).

AUTHOR CONTRIBUTIONS

ACKNOWLEDGEMENTS

CONFLICT OF INTEREST

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

DATA AVAILABILITY STATEMENT

The data are deposited in the Dryad Digital Repository https://datadryad.org/stash/dataset/doi:10.5061/dryad.ksn02v772 (Kraus et al., 2022).

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