communications biology

A Nature Portfolio journal

https://doi.org/10.1038/s42003-025-09334-8

Breeding male mole-rats (*Fukomys*) use strong bites to defend reproductive monopoly

Radim Šumbera[1] ✉, Andrea Kraus[1], Ondřej Mikula[1,2], Jan Okrouhlík[1], John Measey[3], Sabine Begall[4], Nigel C. Bennett[5], Markus Zöttl[6,7], Anthony Herrel[8] & Matěj Lövy[1]

Bite force is a simple trait indicating an animal's performance related to foraging, social dominance, and defence, all of which influence individual reproductive success. We examine the effect of breeding status on bite force in four social species of *Fukomys*, a genus of subterranean African rodents (*Bathyergidae*). These species are cooperative breeders, where reproduction is limited typically to a breeding pair. We collected in vivo bite force data, head width, and upper incisors width from 404 individuals from 75 families and tested whether breeders exhibit stronger bite force. We reveal that breeding males of all four species outperform non-breeders, with bite force in non-breeding males and females being 12% and 22% lower, respectively. In contrast, breeding females underperform relative to other categories, with bite force approximately 31% lower than in breeding males, and many are reluctant to bite. Head width and upper incisors width corroborate these findings. We propose that breeding males require a stronger bite force because of repeated competition with non-related males that may try to enter the family. In contrast, there is much less competition for the breeding position among females, as females rarely intrude into established families.

In social vertebrates, especially those with remarkable reproductive skew, the chances of reproduction depends on many factors including body condition, age, and experience. Breeding individuals must usually defend their position because they face challenges from rivals within, or outside of their society[1–5].

Among the various ways to achieve and defend the reproductive privilege, aggressive encounters and combats are among the most common behavioural strategies. These interactions usually involve sparring and biting rivals using their prominent extrabuccal incisors[6]. An often-used proxy for success in such encounters is bite force[7,8] which is highly correlated with body mass in vertebrates, as well as the morphology and efficiency of the masticatory apparatus in mammals[9–11]. Although relevant primarily for digging and subsequent food acquisition and processing in mole-rats e.g.[12–16], bite force is also a strong predictor of social dominance and reproductive success[7,17–19]. Moreover, bite force is heritable[20] and under selection[21].

African mole-rats (Bathyergidae) are ideal mammalian models for investigating biting performance. This rodent family is renowned for its exceptional adaptations to a subterranean lifestyle and displays remarkable diversity in social organisation, ranging from strictly solitary through to highly social, cooperatively breeding species[22,23]. All African mole-rats excavate extensive underground burrow systems using their incisors to access both food resources – primarily subterranean storage organs of plants – and potential mates. While the solitary genus *Bathyergus* employs scratch-digging, the remaining five genera (solitary *Heliophobius* and *Georychus*, social *Heterocephalus*, *Cryptomys* and *Fukomys*) are highly specialised chisel-tooth diggers that excavate by loosening the soil with their incisors[23,24].

Several characteristics make social African mole-rats especially relevant for the study of bite force. Their bite force can reach extremely high values for mammals of their sizes such as 15 N in a 40 g naked mole-rat[25], rivalling mammals with the highest bite forces, bone-cracking hyenas[26,27]. Their digging behaviour requires a robust masticatory apparatus and considerable bite force to penetrate often consolidated soils[25,28,29]. Additionally, aggressive encounters frequently involve tooth-locking and biting[22,23],

---

[1]Department of Zoology, Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic. [2]Institute of Vertebrate Biology, Czech Academy of Sciences, Brno, Czech Republic. [3]Centre for Invasion Biology, Department of Botany & Zoology, Stellenbosch University, Stellenbosch, South Africa. [4]Department of General Zoology, Faculty of Biology, University of Duisburg-Essen, Essen, Germany. [5]Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa. [6]Department of Biology and Environmental Science, Centre for Ecology and Evolution in Microbial Model Systems (EEMIS), Linnaeus University, Kalmar, Sweden. [7]Kalahari Research Centre, Kuruman River Reserve, Van Zylsrus, South Africa. [8]Département Adaptations du Vivant, UMR 7179 MECADEV C.N.R.S/M.N.H.N., Paris, France. ✉e-mail: sumbera@prf.jcu.cz

further emphasising the functional importance of bite force. In social African mole-rats, we might expect an additional driver of higher bite force in some family members. Although social bathyergids typically live in natal families based on cooperative monogamy[30], where usually only a pair of the oldest, genetically unrelated individuals reproduce and the rest are their offspring, numerous studies have revealed immigration of unrelated animals into these families, and have demonstrated their participation in reproduction, and even extrapair paternity from other families[31–36]. Such infiltration into family groups implies intense competition for reproductive status, in which bite force may play a key role.

In this study, we investigated differences in in vivo bite force between breeders and non-breeders across four species of northern common mole-rats of the genus *Fukomys*. This genus inhabits savanna habitats across a broad geographic range, extending from the southern margins of the Kalahari to the Sahelo-Sudanian zone[37]. *Fukomys* species are cooperative breeders with high reproductive skew, but capture-recapture and genetic studies have revealed the presence of unrelated, usually male, immigrants, as well as documented cases of extrapair and extrafamilial paternity[34–36,38], which likely pose a serious threat to the fitness of established breeding males. Conversely, breeding *Fukomys* females exhibit higher tenure and greater variance in lifetime reproductive success[36,39], which may also indicate high intrasexual competition among females. Higher male-male competition is supported by evidence of faster growth, wider heads, and larger incisors in *F. damarensis*[39,40], as well as generally larger male body mass in many *Fukomys* species[41]. In contrast, reduced skull growth in *F. damarensis* females after acquiring a breeding position may indicate a reduced bite force[42,43] and overall lower competition. Since head width and upper incisors width are traits known to contribute to biting performance in vertebrates[27,44,45], and together with bite force scale allometrically with body mass[39] we analysed them in relation to body mass.

If bite force is driven by intraspecific competition, we predict it to be higher in breeding males than in breeding females and non-breeders. If non-breeders exhibit similar or higher bite force than breeders, its primary function is therefore likely related to burrow excavation and maintenance, which is performed predominantly by non-breeders[46–50]. We reveal that breeding males exhibit higher bite force than non-breeders, whereas breeding females show lower bite force compared to other categories. These patterns were supported by measures of head width and upper incisors width. We propose that breeding males require a stronger bite force due to repeated competition with unrelated males attempting to enter the family. In contrast, competition for the breeding position among females is much less intense, as females rarely intrude into established families.

Results

Bite force, head width, and upper incisors width increased with body mass across all four studied species (Fig. 1). Mean bite force was lowest in the relatively smaller species *F. micklemi* (28.8 ± 14.6 N) and *F. darlingi* (36.0 ± 12.8 N), but higher in *F. damarensis* (57.4 ± 31.7 N), and highest in the largest species, *F. mechowii* (81.6 ± 51.4 N). Similar patterns were observed for head width (*F. micklemi* 24.0 ± 3.2 mm, *F. darlingi* 27.4 ± 2.9 mm, *F. damarensis* 30.0 ± 4.2 mm, and *F. mechowii* 39.0 ± 7.7 mm) and upper incisors width (*F. micklemi* 4.3 ± 0.7 mm, *F. darlingi* 5.0 ± 0.6 mm, *F. damarensis* 5.9 ± 1.1 mm, and *F. mechowii* 6.3 ± 1.4 mm). In all species, breeding males were typically the largest individuals and exhibited the highest values in all three parameters (Fig. 1 and Table 1). In contrast, breeding females did not reach such high values. For instance, in breeding females of *F. darlingi*, both head and upper incisors width showed no clear association with body mass (Fig. 1 and Supplementary Table 1).

Model comparison (Table 1) was used to evaluate how bite force varies across all combinations of sex and reproductive category, while accounting for differences among *Fukomys* species in a combined analysis (see Supplementary Table 2 for model specifications and Supplementary Fig. 1 for diagnostic plots for all models). The "full factorial" model was identified as the best-fitting one (see Table 2 for summary). A nearly equivalent level of support was found for the "full additive" model, with ΔWAIC = 2.1 and a scaled ΔELPD = −0.46 (ΔELPD/SE = −1.1/2.4). This means that pointwise log predictive densities are very similar when all four groups are constrained to share the same allometric scaling. Models ranked 3rd to 7th performed significantly worse in terms of ΔWAIC (from 5.6 to 9.5), although less so in terms of scaled ΔELPD (from −0.78 to −1.30). These included all three "specific" models, where one slope differed from the other two, and "fm-breeders factorial" and "fm-breeders additive" models, in which non-breeders of both sexes were combined into a single category. A shared feature of the seven top-ranking models was that estimated bite force (i.e. the predicted value of bite force at average body mass) differed between breeding males and breeding females, but also from that of non-breeding individuals—or from those of non-breeding males and females when these were modelled separately. The remaining models performed substantially worse than the best-fitting model (ΔWAIC > 21, scaled ΔELPD > −2).

In the "full factorial" model, bite force increased with body mass, but the strength of this relationship varied across the four sex-by-breeding-status categories, i.e. breeding females, breeding males, non-breeding females, and non-breeding males (Table 2). In this model, the intercept can be interpreted as the estimated bite force for an individual with average body mass within each category, while the slope describes allometric scaling, i.e. how much bite force increases with increasing body mass in each category (Fig. 2). Since the credible intervals for all slope pairwise contrasts included zero (Fig. 3), the rate at which bite force scales with body mass was comparable across categories. Therefore, we focus primarily on differences in intercepts (Table 2), which reflect systematic differences in bite force between categories regardless of body mass. Accordingly, breeding males consistently exhibited the highest bite force, followed by non-breeding males (12% lower for an individual of average body mass in our sample) and non-breeding females (22% lower), whereas breeding females showed the lowest bite force, which was 31% lower than that of breeding males and 12% lower than that of non-breeding females (Fig. 3; credible intervals for all pairwise intercept contrasts excluded zero, supporting the robustness of these differences). The importance of estimated bite force differences was further supported by the second-best "full additive" model, in which the four animal categories differed in expected bite force while sharing a common allometric slope (Supplementary Fig. 2).

Separate "full factorial" models for each *Fukomys* species revealed similar patterns to those found in the combined dataset. Evidence for differences in how strongly bite force increased with body mass across the four sex-by-breeding-status categories was again limited (Supplementary Fig. 3). Also, the estimated bite force in each group followed the same ranking as in the overall analysis of three out of four categories (breeding males > non-breeding females > breeding females), with the only inconsistency involving non-breeding males. While in *F. damarensis* and *F. micklemi* the estimated bite force of non-breeding males was close to that of non-breeding females (as in the overall analysis), in *F. mechowii* it was closer to breeding males, and in *F. darlingi* it was even the highest (Supplementary Fig. 4).

For head width, the "full factorial" model was identified as the best-supported one (Supplementary Table 3). Two other models ("non-breeders specific" and "fm-breeders factorial") had scaled ΔELPD close to 2.00, but their ΔWAIC > 26; all remaining models performed substantially worse according to both criteria (Supplementary Table 3 and Supplementary Fig. 5 for diagnostic plots for all models). In the "full factorial" model, head width increased with body mass across all sex-by-breeding-status categories, but allometric scaling varied slightly across the four sex-by-breeding-status categories (Table 3, Fig. 4A, B). However, the only supported difference in allometric scaling was a shallower increase in head width in breeding females than in non-breeding males (the credible interval for this contrast excluded zero; Supplementary Table 4), providing only limited evidence for variation in how strongly head width scaled with body mass among the four categories. A similar pattern was found for the estimated head width regardless of body mass, with the only supported difference being wider heads in breeding males than in breeding females (the credible interval for this contrast excluded zero; Supplementary Table 4).

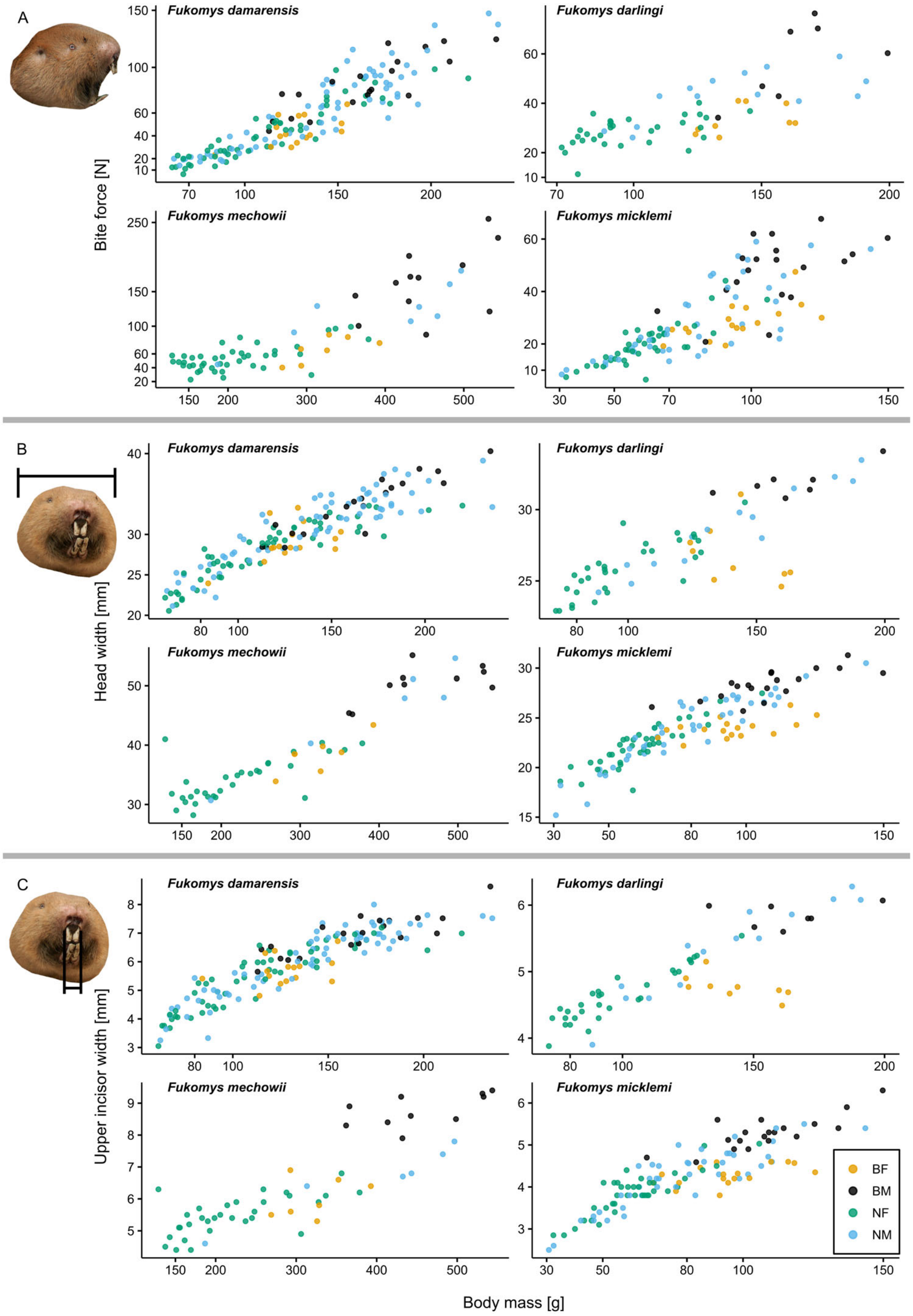

Fig. 1 | Relationships between body mass and bite force, head width, and upper incisors width in all combinations of sex and breeding status in four *Fukomys* mole-rat species. Bite force (**A**), head width (**B**), an upper incisors width (**C**) as a function of body mass in breeding and non-breeding individuals of both sexes. Abbreviations: BF—breeding females (orange), BM—breeding males (black), NF—non-breeding females (green), NM—non-breeding males (blue); raw data are plotted.

For upper incisors width, two models ("fm-breeders factorial" and "non-breeders specific") exhibited nearly identical predictive performance (scaled ΔELPD = −0.06, ΔWAIC = 0.3). All other models performed considerably worse, at least according to ΔWAIC (see Supplementary Table 5 and Supplementary Fig. 6 for diagnostic plots for all models). The two best-performing models grouped animals into three categories—breeding males, breeding females, and pooled non-breeders. In both models, upper incisors width increased with body mass, but they differed in whether allometric scaling varied between all three categories ("fm-breeders factorial" model) or only between non-breeders and breeders ("non-breeders specific" model). In the "fm-breeders factorial" model, upper incisors width increased with body mass, but differences in allometric scaling among the three categories were subtle (Fig. 4C, D and Table 2), with the only supported difference being a shallower increase in upper incisors width in breeding females than in non-breeding individuals (the credible interval for this contrast excluded zero; Supplementary Table 6). Systematic differences in estimated upper incisors width, regardless of body mass, revealed wider upper incisors in breeding males than both non-breeders and breeding females, whose estimated values were lower and mutually comparable (Supplementary Table 6). In the second-best "non-breeders specific" model, upper incisors width scaled similarly with body mass in breeding males and females, but the relationship was steeper in non-breeders.

Discussion

In this study, we discovered that breeding males exhibited a higher bite force compared to non-breeders of both sexes, and especially compared to the breeding females, across all four species of northern common mole-rats of the genus *Fukomys*. The particularly low biting performance of breeding

Table 1 | Bite force model comparison

Rank	Model	ΔELPD	SE	ΔELPD/SE	ΔWAIC
1	full factorial	0.0			0.0
2	full additive	−1.1	2.4	−0.46	2.1
3	non-breeders specific	−2.8	3.6	−0.78	5.6
4	m-breeders specific	−2.9	3.6	−0.81	5.8
5	fm-breeders factorial	−3.6	3.5	−1.03	7.2
6	fm-breeders additive	−4.4	3.8	−1.16	8.7
7	f-breeders specific	−4.8	3.7	−1.30	9.5
8	m-breeders factorial	−10.8	5.2	−2.08	21.5
9	m-breeders additive	−11.7	5.2	−2.25	23.3
10	f-breeders factorial	−12.3	6.1	−2.02	24.6
11	f-breeders additive	−12.4	6.1	−2.03	24.7
12	allometric	−25.7	7.8	−3.29	51.3

Comparison of twelve models describing bite force in a combined dataset comprising four *Fukomys* mole-rat species. The models are listed in order of decreasing performance, based on differences in expected log predictive density (ΔELPD) and Watanabe–Akaike information criterion (ΔWAIC), both expressed relative to the best-performing model (“full factorial”). The ΔELPD is also shown scaled by its standard error (ΔELPD/SE).

Table 2 | Summaries of the two best bite force models

Predictors	Estimate (±SE)	90% CI	*%PP*
The best model (full factorial):			
Intercept (BF)	−0.24 ± 0.19	[−0.53, 0.05]	32.17
sBmass	0.74 ± 0.26	[0.30, 1.15]	94.66
BM	0.54 ± 0.11	[0.37, 0.71]	94.02
NF	0.17 ± 0.09	[0.01, 0.32]	30.28
NM	0.32 ± 0.09	[0.17, 0.46]	71.36
sBMmass: BM	0.11 ± 0.15	[−0.14, 0.34]	99.45
sBMass: NF	0.11 ± 0.14	[−0.11, 0.34]	99.52
sBMass: NM	0.19 ± 0.15	[−0.04, 0.44]	99.70
The second-ranking model (full additive):			
Intercept (BF)	−0.26 ± 0.20	[−0.56, 0.04]	6.61
sBMass	0.87 ± 0.26	[0.42, 1.25]	99.24
BM	0.57 ± 0.10	[0.41, 0.74]	94.83
NF	0.17 ± 0.09	[0.02, 0.32]	24.81
NM	0.35 ± 0.09	[0.20, 0.50]	71.09

Summary statistics of the best-performing “full factorial” and the second-best “full-additive” model comparing bite force among sex-by-breeding-status categories in four *Fukomys* mole-rat species. Shown are posterior means with standard errors (SE), 90% credibility interval (CI), and the maximum quantile of posterior probability away from zero (*%PP*). In this parametrization, the baseline intercept corresponds to breeding females. Coefficients for other three groups represent differences in intercepts relative to this baseline, and the associated *%PP* values refer to these differences. *sBMass* standardized body mass, *BF* breeding females, *BM* breeding males, *NF* non-breeding females, *NM* non-breeding males.

females was further corroborated by a substantial number of individuals refusing to bite (Supplementary Table 7). The observed differences in head and upper incisors width generally aligned well with the bite force results. For head width, substantial differences were observed only between breeders, with breeding males possessing wider heads than breeding females. Moreover, head width increased less with body mass in breeding females than in non-breeding males. The main difference in upper incisors width was between breeding males that possessed broader incisors than the other groups.

Our results further indicate that the relationship between body mass and bite force in all sex-by-breeding-status categories of *Fukomys* mole-rats exhibits positive allometry, meaning that bite force increases disproportionately more than body mass (Fig. 2). Similar, though weaker, patterns were observed for both head and upper incisors widths (Fig. 4). However, the differences in allometric scaling among the categories were subtle, with the 90% credible intervals for all groups including the isometric expectation, indicating uncertainty in the precise scaling relationships. Moreover, the overall statistical support for slope differences among the four categories was low (see Results).

A positive allometry in bite force has previously been reported across 10 species in the family *Bathyergidae*, with species-specific allometric slopes ranging from 0.79 in the naked mole-rat to 1.79 in the Damaraland mole-rat[25]. In comparison, studies on mammals (eg. slope 0.59[27], ~0.62[51] recalculated from a graph) or in non-passerine birds (e.g. slope 0.69[52]) have typically found slopes close to isometry. On the other hand, strongly positive allometry was found in passerines (slope 1.38)[52]. The highly positive allometry observed in bathyergids thus likely reflects a disproportionate investment in the development of a powerful biting apparatus, consistent with the extreme ecological and morphological demands of a subterranean lifestyle. This suggests that allometric scaling of bite performance is itself an adaptive feature within burrowing rodents.

In social mammals, bite force has been found to be related to sex and social status[53–55]. Although stronger biting in males can result simply from their larger body mass[44,51,56,57], it likely evolves into formidable weaponry under conditions of intense intrasexual competition. For example, in New World monkeys, sexual dimorphism in canine size increases with male competition as monogamous and polyandrous species have the lowest canine dimorphism, while polygynous species with male dominance hierarchies have the largest dimorphism[58]. In grey wolves, broader male skulls suggesting a higher bite force are useful during territorial aggressive behaviour[59]. In meerkats, dominant females are larger and have wider skulls compared to subordinate females[60] due to regular challenges by females within the group for reproductive monopoly[3]. The role of intrasexual competition is demonstrated by the absence of sex differences in bite force in socially monogamous canids[61]. Our results suggest that bite force in *Fukomys* is also influenced by intrasexual competition for breeding opportunities, with different selection pressures on males and females.

All *Fukomys* species studied to date have a similar social structure and mean family size (see Supplementary Table 8). Families are typically established when two unrelated individuals of opposite sex meet and begin to reproduce[36,38,48,62–64]. This breeding pair must initially dig a sufficiently long burrow system to secure food and defend both their territory and breeding opportunity against intruders, tasks for which well-developed chewing muscles and high bite force are essential. As the family grows, these

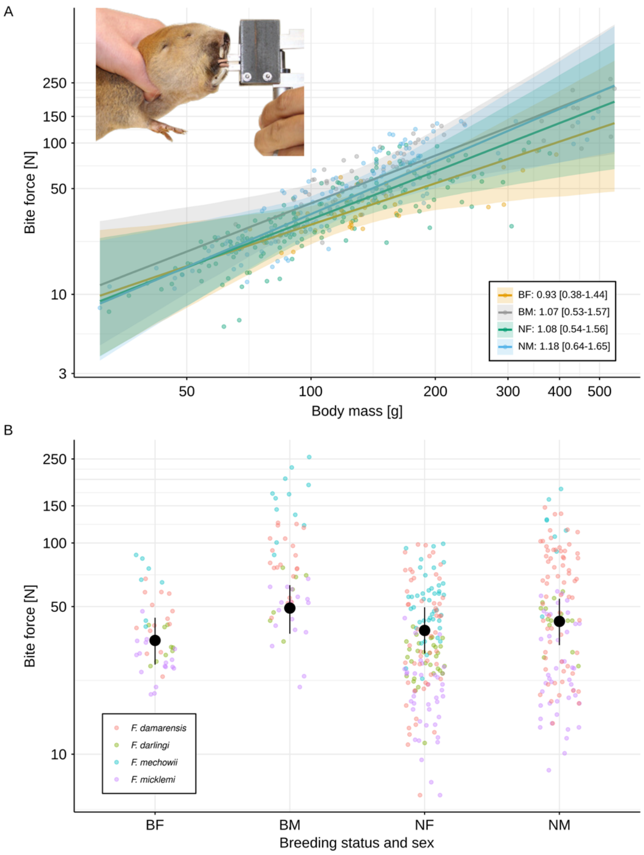

Fig. 2 | Predicted bite force in relation to body mass and all combinations of sex and breeding status in four *Fukomys* mole-rat species. For each combination of sex and breeding status, predicted bite force from the best-performing model is shown in relation to body mass (**A**) and at the mean body mass (**B**). Bite force was back-transformed from standardised values and is plotted on a log–log scale. In (**A**), lines represent posterior mean estimates from a Bayesian mixed-effects model, shaded ribbons indicate 90% credible intervals around the posterior mean and scaling coefficients (slopes) with their 90% credible intervals (in brackets) for each combination of sex and breeding status are shown in the legend box. In (**B**), black points and error bars represent population-level posterior mean estimates and 90% credible intervals for each combination of sex and breeding status, respectively, while semi-transparent coloured points show individual raw data values for each species: *F. damarensis* (red), *F. darlingi* (green), *F. mechowii* (cyan) and *F. micklemi* (purple). Abbreviations for combinations of sex and breeding status and their colour coding in (**A**): BF ($n = 48$)—breeding females (orange), BM ($n = 58$)—breeding males (grey), NF ($n = 166$)—non-breeding females (green) and NM ($n = 132$)—non-breeding males (blue).

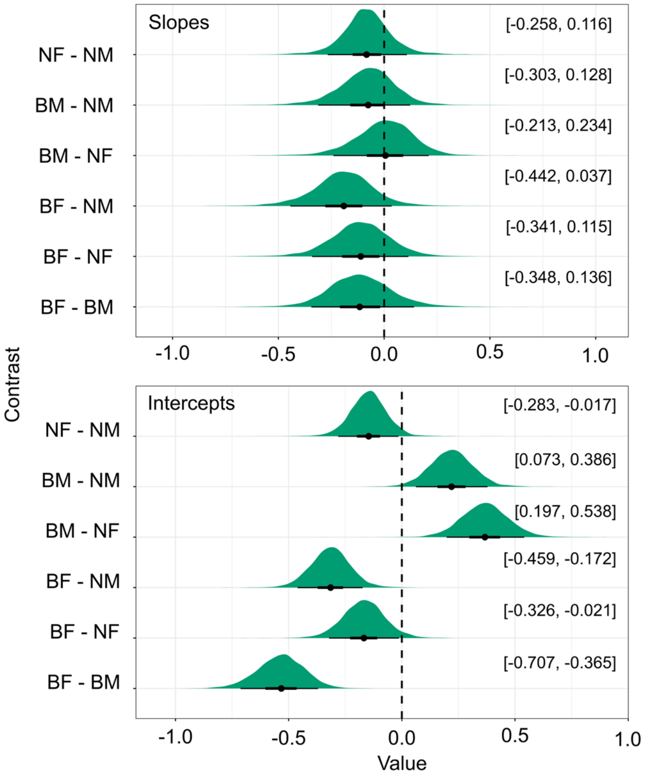

Fig. 3 | Differences in bite force slopes and intercepts between all combinations of sex and breeding status in four *Fukomys* mole-rat species. Summary of pairwise contrasts for slopes and intercepts comparing bite force among breeding females (BF), breeding males (BM), non-breeding females (NF), non-breeding males (NM) (for each contrast, 90% credible intervals are provided in parentheses). Posterior distributions of pairwise differences are depicted. Black points indicate posterior means of each pairwise difference; horizontal lines represent 50% and 90% credible intervals.

energetically demanding activities can be adopted by other members. It has been found that acquiring breeding status in *Fukomys* influences their behaviour, such as the amount of activity[47–50,65,66], as well as morphology, for instance elongation of body and narrowing of skull in breeding females[43,67]. In *Fukomys*, we found relatively small differences in bite force between non-breeding males and females, which confirms other studies on bathyergids[25,65]. It indicates their bite force is primarily determined by burrowing demands rather than by competitive engagements. In breeders, strong selection pressure towards effective burrowing can be relaxed, theoretically resulting in lower bite force in both sexes after they start to reproduce and acquire breeding status. Indeed, Hite and colleagues[26] reported generally higher bite force in subordinate than in dominant naked mole-rats. However, our findings contradict this, as we observed the highest biting performance in male breeders. This may indicate different selection pressures on bite force between breeders and non-breeders in the naked mole-rat and members of the genus *Fukomys*. Upon attaining breeding status, male naked mole-rats typically lose body mass[68] and are less involved in colony maintenance or risky activities, such as family defence e.g.[69], suggesting lower demands for biting performance compared to those of male *Fukomys* breeders. Thus, the distinct evolutionary trajectories related to biting performance between breeding males and females in *Fukomys* mole-rats are intriguing and deserve further explanations.

This study found relatively narrower upper incisors and, to a lesser extent, skulls in breeding females of the tested *Fukomys* species, which resulted in lower bite force. Similarly, Young & Bennett[39], found relatively narrower skulls and incisors in female wild *F. damarensis*. We propose that the relatively low biting performance in breeding females (31% lower than in breeding males) relates to lower competition with other females for breeding position and to the costs of breeding. Since pregnancy and lactation are energetically very expensive[70], breeding females need to allocate more energy to reproduction and therefore invest more time in resting instead of working, as described for several *Fukomys* species - *F. damarensis*[47,48], *F. mechowii*[71,72], *F. micklemi*[65,73]. They also invest less energy into overall body growth, which is evident in reduced skull growth in *F. damarensis*[42,43]. Since skull characteristics are important for anchoring incisors during burrowing, the relatively narrow heads and incisors may be related to their lower bite force – i.e. the wider and taller the skull, the stronger the bite force; see refs. 27,45. Interestingly, breeding females of *F. damarensis* lose bone growth potential, resulting in thinner femurs with a higher risk of fracture[67]. These aspects suggest that females' willingness to engage in risky activities such as fights is very low, and they usually stay close to the nest[50,66].

Previous studies suggest that the risk of takeover by another female in *Fukomys* is probably very low due to several reasons. Non-breeding individuals, especially females (see below), are usually descendants of a family pair, and *Fukomys* do not breed with relatives[74,75]. As in other cooperative

Table 3 | Summaries of the best head and upper incisors width models

Predictor	Estimate (±SE)	90% CI	%*PP*
Head width (full factorial)			
Intercept (BF)	−0.26 ± 0.18	[−0.53, 0.03]	6.76
sBMass	0.62 ± 0.18	[0.31, 0.88]	99.48
BM	0.44 ± 0.16	[0.17, 0.70]	86.85
NF	0.23 ± 0.16	[−0.02, 0.49]	43.45
NM	0.23 ± 0.16	[−0.06, 0.46]	42.40
sBMmass: BM	0.23 ± 0.19	[−0.05, 0.54]	99.80
sBMass: NF	0.16 ± 0.18	[−0.11, 0.47]	99.80
sBMass: NM	0.38 ± 0.18	[0.11, 0.70]	99.92
Incisors width (fm-breeders factorial)			
Intercept (BF)	−0.21 ± 0.31	[−0.68, 0.30]	21.45
sBMass	0.39 ± 0.24	[−0.00, 0.77]	94.95
BM	0.58 ± 0.26	[0.16, 0.98]	91.11
N	0.14 ± 0.26	[−0.31, 0.51]	39.12
sBMass: BM	0.29 ± 0.23	[−0.10, 0.66]	99.33
sBMass: *N*	0.56 ± 0.22	[0.20, 0.92]	99.92

Summary statistics of the best-performing models describing head and upper incisors widths among sex-by-breeding-status categories in four *Fukomys* mole-rat species. The models compare breeding females (BF), breeding males (BM), non-breeding females (NF), and non-breeding males (NM) in *Fukomys* mole-rats; in the best-performing upper incisors-width model, the latter two categories were pooled into a single non-breeder group (*N*). The table includes posterior means with standard errors (SE), 90% credibility intervals (CI), and the maximum quantile of posterior probability out of zero (%*PP*). In this parametrization, the baseline intercept corresponds to breeding females, and coefficients of other groups represent differences in intercepts relative to this baseline. The associated %*PP* values refer to these differences.
sBMass standardized body mass.

breeders, daughters are probably also reluctant to challenge the reproductive status of their mother[76]. The presence of female immigrants within an unrelated family is extremely rare[34,36,62,64], and at least in *F. damarensis* from the extreme southern Kalahari, females in a recently studied population may settle alone in their new burrow systems, even for several years, before being joined by males[38]. Similar indications of solitary female settlement have been reported in *F. anselli*[36] and *F. mechowii*[63]. In addition, if territory inheritance occurs in *Fukomys*, it is a female non-breeder who inherits the breeding position, as observed in *F. damarensis* (rare inheritance in[64]; 30% of breeding females inherited in ref. 38). Indeed, no breeding-female turnover was found among 16 families of *F. anselli*[36]. Although in experiments with intruders, breeding *Fukomys* females are aggressive towards other females[74,77,78], this behaviour may not necessarily occur outside the laboratory. In free-living conditions, breeding females are likely rarely challenged by other females due to a relatively lower female dispersal rate, higher philopatry and because breeding females are usually located around the nest and probably protected by relatives. Along with the high cost of reproduction, this could explain the relatively low bite force in breeding females in *Fukomys* mole-rats.

The ways by which *Fukomys* males compete with each other and how they attain breeding positions may result in selection for a stronger bite force, differing from selection shown in females (see above). Although genetically related family members are unlikely to compete with their parents for breeding, the situation may change dramatically when an unrelated male immigrates into an established family, or if intruders from neighbouring families, seek extrafamilial copulations[31]. In some *Fukomys* mole-rats, dispersal is male biased[64,79], with males more likely to join existing families[31,34,38,62], and such males may replace the resident male breeder[34,36,62,64]. The existence of large male floaters who can also challenge breeding monopoly has been suggested (Bennett and Jarvis pers. obs., cited in ref. 79).

Noteworthy in this context is an observation from the Ansell's mole-rat (which is included in this study within *F. micklemi*). In approximately 30% of their families, older offspring were sired by males who were not present, which indicates breeding male turnover[36]. The same was found also in one of two genotyped families of *F. mechowii*[63]. This suggests that intruders either killed or expelled the former breeding male or, alternatively, a new male was accepted into the family and began to breed after the original male deceased. Their acceptance may by facilitated by the fact that in *F. damarensis* dispersing males are not yet sexually mature[64]. Once these males grow bigger and become sexually mature, they may challenge the breeder, or take over the breeding position in a group which has lost its breeder[41]. Higher male bite force may also be advantageous for defending the reproductive monopoly of the breeding male during brief encounters with males from neighbouring families.

The question thus arises as to why such unrelated males and potential rivals are accepted into the family. Unrelated immigrants may be accepted in families of other cooperatively breeding vertebrates as secondary helpers to assist with raising offspring, protecting the group from predators, or defending the territory[80,81]. In subterranean rodents, the most energy-consuming activity is burrowing and transporting excavated soil[82]. It is possible that in African mole-rats, accepting secondary helpers may be particularly relevant in families shortly after establishment, due to the lack of their own offspring (i.e., primary helpers) or when ecological conditions are so adverse that a larger workforce is required to reach food resources.

Our study has revealed that sexual differences in in vivo bite force are related to breeding status in four social species of northern common mole-rats. While there are only subtle sex differences in non-breeders, breeding individuals show dramatic differences in their bite force performance. Breeding males have the highest bite force, whereas breeding females perform poorly, with many females refusing to bite. The head width and upper incisors width further corroborate these findings. We suggest that this dichotomy is related to the probability of being challenged for the male breeding role by genetically unrelated individuals. The breeding position of females is probably not challenged from inside or outside the family as female immigration into established families is low e.g.[34,83]. Conversely, higher male immigration into established families and the risk of extrapair copulations by unrelated males suggest that breeding males are more likely to be challenged for their breeding position. For future studies, it would be interesting to study the postnatal development of bite force over a longer period and focus on how bite force in individuals changes after the establishment of breeding pairs from a non-breeding status. It might also be of interest to carry out a similar study on another social mole-rat genus *Cryptomys*, where we would predict higher bite force in males due to a very high level of immigration and extrapair paternity[31], as well as the most pronounced male biased sexual size dimorphism among African mole-rats[41].

Methods

Study animals

In vivo bite force was measured in four species of the social Northern common mole-rats of the genus *Fukomys* (Bathyergidae, Rodentia), which differed in body mass (for details see Supplementary Table 8): the Damaraland mole-rat *Fukomys damarensis*, the Mashona mole-rat *Fukomys darlingi*, the giant mole-rat *Fukomys mechowii*, and the Micklem's mole-rat *Fukomys micklemi*. In the dataset on *F. micklemi*, we included bite force data from another traditionally recognised species, the Ansell's mole-rat *Fukomys anselli*. This inclusion is based on previous molecular genetic phylogenies using the genus-wide cytochrome *b* e.g.[84,85] and a pilot study using thousands of nuclear loci (Mikula et al. in prep.), both indicating that these putative species form a single taxonomic unit. Most individuals had been in captivity for an extended period. *Fukomys damarensis* was housed in artificial systems made from transparent plastic tubes and boxes in the laboratory at the Kuruman River Reserve in the Northern Cape, South Africa (26 °59′S 21°49′E, temperature: 21–24 °C, humidity: 40%–50%, constant darkness).

The remaining species were kept in glass terraria at the University of South Bohemia in České Budějovice, Czech Republic, or the University of

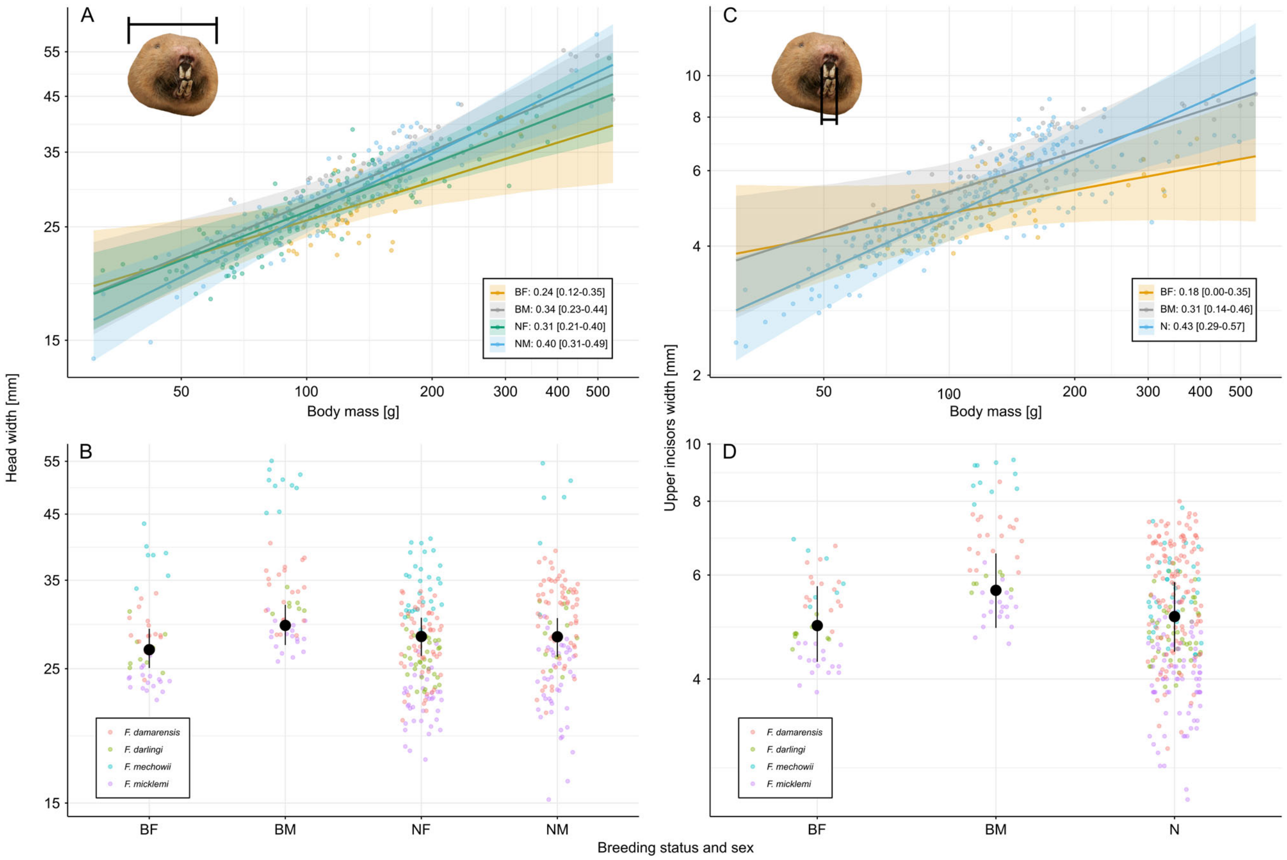

Fig. 4 | Predicted head width and upper incisors width in relation to body mass and all combinations of sex and breeding status in four *Fukomys* mole-rat species. For each combination of sex and breeding status, predicted head width and upper incisors width from the respective best-performing models, are shown in relation to body mass (**A**, **C**, respectively) and at the mean body mass (**B**, **D**, respectively). Head width and upper incisors width were back-transformed from standardised values. In (**A**, **C**), widths are plotted on a log–log scale, lines represent posterior mean estimates from a Bayesian mixed-effects model, shaded ribbons indicate 90% credible intervals around the posterior mean and scaling coefficients (slopes) with their 90% credible intervals (in brackets) for each combination of sex and breeding status are given in the legend box. In (**B**, **D**), black points and error bars represent population-level posterior mean estimates and 90% credible intervals for each combination of sex and breeding status, respectively, while semi-transparent coloured points show individual raw data values for each species: *F. damarensis* (red), *F. darlingi* (green), *F. mechowii* (cyan) and *F. micklemi* (purple). Abbreviations for combinations of sex and breeding status and their colour coding in **A**, **C**: BF ($n = 48$)—breeding females (orange), BM ($n = 56$)—breeding males (grey), NF ($n = 154$)—non-breeding females (green in **A**), NM ($n = 130$)—non-breeding males (blue) and *N* ($n = 284$)—pooled non-breeders (green in **C**).

Duisburg-Essen, Germany, under similar conditions (temperature: 25 °C, humidity: 40%–50%, photoperiod 12 L:12D). All captive animals were fed *ad libitum* with vegetables (such as carrots, potatoes, sweet potatoes, beetroot, apple, cucumbers) and a rodent dry food mix. All animals were given the opportunity to carry out their natural digging behaviours, either in red Kalahari sand (Kuruman River Reserve), wood shavings (Essen), or peat (České Budějovice), and were provided extra enrichment such as tree branches and plastic tubes for gnawing. The study used captive mole-rats and no wild animals were captured for this research. The animals were sourced from three independent and well established laboratory colonies (at the institutions listed above). After data collection, all animals remained in their respective colonies and continued to be cared for according to institutional standards.

In total, 612 individuals from 75 actively breeding *Fukomys* families were available for this study. These families consisted of both breeders and at least one non-breeding individual. As *Fukomys* families typically comprise a breeding pair and their offspring (which remain in the natal group due to delayed dispersal), and given the strong taboo of incest when mole-rats do not breed with their relatives in captivity[75], breeders could be reliably identifiable. We focused exclusively on adults (assessed based on body mass, see Supplementary Table 8) and excluded some individuals primarily due to health issues (e.g., broken incisors, overall poor body condition) or a clear lack of motivation to bite (i.e., unusually low bite force values compared to individuals of similar body mass, same sex, and species). Consequently, the final dataset included 404 individuals. We paid particular attention to the breeding females, as they were at various stages of pregnancy and consistently showed the lowest biting tendency among the animals tested. To avoid any potential adverse effects of the bite force measurement on the pregnancy and/or newborn pups, breeding females considered to be in a late stage of pregnancy and those after recent delivery were not measured. We analysed 69 females, as six were not measured due to advanced pregnancy and health issues. Out of 69 breeding females, 13 refused to bite (three were pregnant, and four had pups younger than 3 months) and eight were reluctant to bite. Consequently, these breeding females were removed from the dataset (for details see Supplementary Table 7), and the remaining 48 breeding females were included in the analyses.

We have complied with all relevant ethical regulations for animal use. The study was approved by the ethics committee of the University of Pretoria (Permits EC-69-16, EC069-17, EC050-16, and AUCC-040702/015) and the University of South Bohemia (Permit MSMT-35731/2019-4).

Bite force and head and incisors widths measurements

In vivo bite force was measured with an isometric force transducer (type 9203; range 0–5000 N, error 0.1 N; Kistler Inc., Switzerland; for details of the experimental set-up, see refs. 25,57. The bite plates were covered with a thin protective coating made of cloth or duct tape to avoid damage to the animal's incisors. Each measured individual was held around the neck with one hand and the mouth was approached with the transducer device thus prompting the animal to bite into the bite plates[25]. Mole-rats were induced to bite at least three times, and the maximum bite force in Newtons (N) of each individual was recorded as an estimate of its maximal bite performance. All specimens were weighed to the nearest 0.1 g, and head width (the widest distance on the head between zygomatic arches) and upper incisors width, i. e. the widest point across the incisor pair (following[39]) were measured to the nearest 0.01 mm with a digital calliper. The skull size and incisor characteristics are good estimators of in vivo bite force and/or social dominance[9,44,86,87].

Statistical analysis

The effects of sex and breeding status on bite force were evaluated by comparing a series of multilevel regression models. All models used standardized log-transformed bite force as the response variable and standardized, log-transformed body mass as a predictor. The log-transformation of both bite force and body mass linearised their expected allometric relationship, while standardization to zero mean and unit variance facilitated prior specification and made sampling from posterior distribution easier. The models differed in how they incorporated sex-by-breeding-status predictors distinguishing specific combinations of sex and breeding status (listed in Supplementary Table 9) and their interactions with body mass. Each model also included random terms, which modelled the effect of species (random intercept) and species-specific effects of body mass, sex-status and their interactions (random slope). These species-specific effects were represented by random terms of the same structure as the fixed terms and nested within species. The random intercepts and slopes were assumed mutually uncorrelated.

We fitted twelve candidate models (see Supplementary Table 2). The baseline model included body mass as the only predictor, capturing the general allometric relationship. The following nine models explored the hypothesis whether either female breeders, male breeders, or both groups deviated from the common non-breeder pattern. These models distinguished the three groups (female breeders, male breeders, and non-breeders) but constrain their intercepts and allometric slopes differently. Three "additive" models shared a common allometric slope but allowed for different intercepts for each group. Either one of the groups has an intercept from the other two or all three intercepts are different (i.e. "fm-breeders additive" model). Three "factorial" models differed in both their intercepts and allometric slopes. Three "specific" models considered the possibility that all three groups have different intercepts and one of the groups differ in its allometric slope from the other two (i.e. it has "specific" slope). Finally, two models distinguished female and male non-breeders, resulting in four groups for comparison, with either different intercepts ("full additive") or both intercepts and allometric slopes ("full factorial").

Model fitting was performed within a Bayesian inferential framework as implemented in the statistical programming language Stan interfaced to R[88] using *brms* package[89]. The Bayesian approach was chosen to accommodate the relatively small and imbalanced sample sizes across the examined species, which frequently caused the lack of convergence in maximum likelihood fit of models with complex random effects. The analyses used priors for (i) regression coefficients of the fixed term predictors (a normal prior with mean zero and standard deviation of one) and (ii) standard deviations of random effects (an exponential prior with a rate parameter set to one). Posterior probability distribution of parameter values was sampled by Hamiltonian Monte Carlo chain (for details see ref. 90) with 3000 iterations (1000 of them being a warm-up). Four independent chains were run for each model and their convergence assessed by rank-normalized potential scale reduction factor[91] ('Rhat' in brms notation), which should be close to 1 at convergence. For each parameter, we also assessed whether the effective sample size was sufficient (>1000) in both the bulk of the posterior probability density distribution, i. e. around its mean, ('Bulk_EES') and at its tail ('Tail_EES')[91].

Relative fit of the twelve models was assessed by two measures based on pointwise log-likelihoods, the expected log predictive density (ELPD) and Watanabe-Akaike information criterion (WAIC), whose optimization approximates minimization of Kullback-Leibler divergence[92]. The ELPD is a sum of pointwise log predictive densities, i.e., log-likelihoods of new data points integrated over estimated posterior distribution of parameters. In the *brms* package, it is estimated by a leave-one-out cross validation (LOO), approximated by Pareto smoothed importance sampling[93]. The reliability of the approximation was examined by checking that individual Pareto k values are typically < 0.5 in a given model[94]. The significance of ΔELPD, i.e., the difference from the best (maximum) ELPD, is judged against the standard error of differences between pointwise log predictive densities in the compared models. As a rule of thumb, a model is favoured over another if ΔELPD is at least twice its standard error ($\Delta\text{ELPD} \geq 2 * \text{SE}_{\Delta\text{ELPD}}$), which corresponds to limits of an approximate normal-based confidence interval[94]. The magnitude of ΔWAIC, i.e., the difference from the best (minimum) WAIC, can be interpreted in terms of relative likelihoods of the compared models[95]. It means that if WAIC of two models differ by ~5.89, their relative likelihoods are 0.95 and 0.05.

Absolute fit of the models was tested by means of graphical predictive posterior check[96]. It provides visual comparison of response variable values (standardized log-transformed bite force) that were actually observed and those that were simulated from given model. The simulations were based on the observed predictor values and 100 different sets of sampled parameter values. If the simulated values are far from the observed ones, the model is inadequate irrespective of its relative fit compared to other models.

Predictive power of each predictor in the selected models was evaluated by considering posterior probability density of the corresponding parameter (intercept or slope). First, we checked whether 90% credibility interval (CI) of the parameter overlap with zero. Next, we calculated the quantile of the density below or above zero, whichever was greater. Post-hoc comparisons of intercepts and/or slopes among the given categories were made using the 'emtrends' and 'emmeans' functions in the package *emmeans*[97]. All analyses were performed in R version 4.4.1[88].

Following the analysis of bite force, the same modelling approach was applied to test differences in head and upper incisors width, using standardized log-transformed values of these traits as response variables in these models.

Finally, the optimal bite force model based on the pooled dataset (with species included as a random term) was refitted separately for each of the four studied *Fukomys* species to further test whether the differences among sex-by-breeding-status categories exhibited a consistent pattern across them.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The raw data (Supplementary Data 1 and Supplementary Data 2) used to calculate the results and generate the figures presented in this study are available in the Figshare repository, as part of this record: https://doi.org/10.6084/m9.figshare.29423288[98].

Code availability

The R code (Supplementary Data 3) used to calculate the results and generate the figures presented in this study is available in the Figshare repository, as part of this record: https://doi.org/10.6084/m9.figshare.29423288[98].

Received: 10 December 2024; Accepted: 25 November 2025;

References

1. Palanza, P., Mainardi, D., Brain, P. F. & Parmigiani, S. Male and female competitive strategies of wild house mice pairs (*Mus musculus domesticus*) confronted with intruders of different sex and age in artificial territories. *Behaviour* **133**, 863–882 (1996).

2. Packer, C. & Pusey, A. E. Adaptations of female lions to infanticide by incoming males. *Am. Nat.* **121**, 716–728 (1983).
3. Clutton-Brock, T. H. et al. Intrasexual competition and sexual selection in cooperative mammals. *Nature* **444**, 1065–1068 (2006).
4. Emlen, S. T. Predicting family dynamics in social vertebrates. in *Behavioural Ecology: an Evolutionary Approach* (eds Krebs, J. R. & Davies, N. B.) 228–253 (Blackwell Scientific, 1997).
5. Sharp, S. P. & Clutton-Brock, T. H. Competition, breeding success and ageing rates in female meerkats: competition and senescence in meerkats. *J. Evol. Biol.* **24**, 1756–1762 (2011).
6. Krebs, J. R. & Davies, N. B. Fighting and assessment. in *An Introduction to Behavioural Ecology* (eds Krebs, J. R. & Davies, N. B.) 147–174 (Blackwell Scientific Publication, 1993).
7. Husak, J. F., Kristopher Lappin, A., Fox, S. F. & Lemos-Espinal, J. A. Bite-force performance predicts dominance in male venerable collared lizards (*Crotaphytus antiquus*). *Copeia* **2006**, 301–306 (2006).
8. Lailvaux, S. P., Herrel, A., VanHooydonck, B., Meyers, J. J. & Irschick, D. J. Performance capacity, fighting tactics and the evolution of life–stage male morphs in the green anole lizard (*Anolis carolinensis*). *Proc. R. Soc. Lond. B Biol. Sci.* **271**, 2501–2508 (2004).
9. Anderson, R. A., Mcbrayer, L. D. & Herrel, A. Bite force in vertebrates: opportunities and caveats for use of a nonpareil whole-animal performance measure. *Biol. J. Linn. Soc.* **93**, 709–720 (2008).
10. Herrel, A., De Smet, A., Aguirre, L. F. & Aerts, P. Morphological and mechanical determinants of bite force in bats: Do muscles matter?. *J. Exp. Biol.* **211**, 86–91 (2008).
11. van der Meijden, A., González-Gómez, J. C., Pulido-Osorio, M. D. & Herrel, A. Measurement of voluntary bite forces in large carnivores using a semi-automated reward-driven system. *J. Exp. Biol.* **226**, jeb245255 (2023).
12. Aguirre, L. F., Herrel, A., Van Damme, R. & MatThysen, E. The implications of food hardness for diet in bats. *Funct. Ecol.* **17**, 201–212 (2003).
13. Christiansen, P. & Wroe, S. Bite forces and evolutionary adaptations to feeding ecology in carnivores. *Ecology* **88**, 347–358 (2007).
14. Maestri, R., Patterson, B. D., Fornel, R., Monteiro, L. R. & De Freitas, T. R. O. Diet, bite force and skull morphology in the generalist rodent morphotype. *J. Evol. Biol.* **29**, 2191–2204 (2016).
15. Santana, S. E., Dumont, E. R. & Davis, J. L. Mechanics of bite force production and its relationship to diet in bats. *Funct. Ecol.* **24**, 776–784 (2010).
16. Verwaijen, D., Van Damme, R. & Herrel, A. Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. *Funct. Ecol.* **16**, 842–850 (2002).
17. Gowan, T. A., Mcbrayer, L. D. & Rostal, D. C. Seasonal variation in testosterone and performance in males of a non-territorial lizard species. *Physiol. Behav.* **100**, 357–363 (2010).
18. Husak, J. F., Lappin, A. K. & Van Den Bussche, R. A. The fitness advantage of a high-performance weapon. *Biol. J. Linn. Soc.* **96**, 840–845 (2009).
19. Lappin, A. K. & Husak, J. F. Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *Am. Nat.* **166**, 426–436 (2005).
20. Zablocki-Thomas, P., Lailvaux, S., Aujard, F., Pouydebat, E. & Herrel, A. Maternal and genetic correlations between morphology and physical performance traits in a small captive primate, *Microcebus murinus*. *Biol. J. Linn. Soc.* **134**, 28–39 (2021).
21. Herrel, A. et al. Do adult phenotypes reflect selection on juvenile performance? A comparative study on performance and morphology in lizards. *Integr. Comp. Biol.* **56**, 469–478 (2016).
22. Begall, S., Burda, H. & Šumbera, R. *Graumulle: Cryptomys und Fukomys* (VerlagsKG Wolf, 2018).
23. Bennett, N. C. & Faulkes, C. G. *African Mole-Rats—Ecology and Eusociality* (Cambridge University Press, 2000).
24. Rodrigues, H. G., Šumbera, R., Hautier, L. & Herrel, A. Digging up convergence in fossorial rodents: insights into burrowing activity and morpho-functional specializations of the masticatory apparatus. in *Convergent Evolution: Animal Form and Function* (eds Bels, V. L. & Russell, A. P.) 37–63. https://doi.org/10.1007/978-3-031-11441-0_3 (Springer International Publishing, 2023).
25. Kraus, A. et al. Bite force in the strictly subterranean rodent family of African mole-rats (Bathyergidae): the role of digging mode, social organization and ecology. *Funct. Ecol.* **36**, 2344–2355 (2022).
26. Hite, N. J. et al. The better to eat you with: bite force in the naked mole-rat (*Heterocephalus glaber*) is stronger than predicted based on body size. *Front. Integr. Neurosci.* **13**, 70 (2019).
27. van Daele, P. A. A. G., Herrel, A. & Adriaens, D. Biting performance in teeth-digging African mole-rats (*Fukomys*, Bathyergidae, Rodentia). *Physiol. Biochem. Zool.* **82**, 40–50 (2009).
28. Gomes Rodrigues, H. & Damette, M. Incipient morphological specializations associated with fossorial life in the skull of ground squirrels (Sciuridae, Rodentia). *J. Morphol.* **284**, e21540 (2023).
29. Hildebrand, M. Digging of Quadrupeds. in *Functional Vertebrate Morphology* (eds Hildebrand, M., Bramble, D. M., Liem, K. F. & Wake, D. B.) 89–109 (Harvard University Press, 1985).
30. Burda, H., Honeycutt, R. L., Begall, S., Locker-Grutjen, O. & Scharff, A. Are naked and common mole-rats eusocial and if so, why?. *Behav. Ecol. Sociobiol.* **47**, 293–303 (2000).
31. Bishop, J. M., Jarvis, J. U. M., Spinks, A. C., Bennett, N. C. & O'Ryan, C. Molecular insight into patterns of colony composition and paternity in the common mole-rat *Cryptomys hottentotus hottentotus*. *Mol. Ecol.* **13**, 1217–1229 (2004).
32. Braude, S. Dispersal and new colony formation in wild naked mole-rats: evidence against inbreeding as the system of mating. *Behav. Ecol.* **11**, 7–12 (2000).
33. Braude, S., Hess, J. & Ingram, C. Inter-colony invasion between wild naked mole-rat colonies. *J. Zool.* **313**, 37–42 (2021).
34. Burland, T. M., Bennett, N. C., Jarvis, J. U. M. & Faulkes, C. G. Colony structure and parentage in wild colonies of co-operatively breeding Damaraland mole-rats suggest incest avoidance alone may not maintain reproductive skew. *Mol. Ecol.* **13**, 2371–2379 (2004).
35. Mynhardt, S., Harris-Barnes, L., Bloomer, P. & Bennett, N. C. Spatial population genetic structure and colony dynamics in Damaraland mole-rats (*Fukomys damarensis*) from the southern Kalahari. *BMC Ecol. Evol.* **21**, 221 (2021).
36. Patzenhauerová, H., Šklíba, J., Bryja, J. & Šumbera, R. Parentage analysis of Ansell's mole-rat family groups indicates a high reproductive skew despite relatively relaxed ecological constraints on dispersal. *Mol. Ecol.* **22**, 4988–5000 (2013).
37. Monadjem, A., Taylor, P. J., Denys, C. & Cotterill, F. P. D. *Rodents of Sub-Saharan Africa: a Biogeographic and Taxonomic Synthesis*. (De Gruyter, 2015).
38. Thorley, J., Bensch, H. M., Finn, K., Clutton-Brock, T. & Zöttl, M. Damaraland mole-rats do not rely on helpers for reproduction or survival. *Evol. Lett.* **7**, 203–215 (2023).
39. Young, A. J. & Bennett, N. C. Intra-sexual selection in cooperative mammals and birds: why are females not bigger and better armed? *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **368**, 20130075 (2013).
40. Zöttl, M., Thorley, J., Gaynor, D., Bennett, N. C. & Clutton-Brock, T. Variation in growth of Damaraland mole-rats is explained by competition rather than by functional specialization for different tasks. *Biol. Lett.* **12**, 20160820 (2016).
41. Caspar, K. R., Müller, J. & Begall, S. Effects of sex and breeding status on skull morphology in cooperatively breeding Ansell's mole-rats and an appraisal of sexual dimorphism in the Bathyergidae. *Front. Ecol. Evol.* **9**, 638754 (2021).
42. Thorley, J., Katlein, N., Goddard, K., Zöttl, M. & Clutton-Brock, T. Reproduction triggers adaptive increases in body size in female mole-rats. *Proc. R. Soc. B Biol. Sci.* **285**, 20180897 (2018).

43. Young, A. J. & Bennett, N. C. Morphological divergence of breeders and helpers in wild Damaraland mole-rat societies. *Evolution* **64**, 3190–3197 (2010).
44. Freeman, P. W. & Lemen, C. A. A simple morphological predictor of bite force in rodents. *J. Zool.* **275**, 418–422 (2008).
45. McIntosh, A. F. & Cox, P. G. Functional implications of craniomandibular morphology in African mole-rats (Rodentia: Bathyergidae). *Biol. J. Linn. Soc.* **117**, 447–462 (2016).
46. Bennett, N. C. Behaviour and social organization in a colony of the Damaraland mole-rat *Cryptomys damarensis*. *J. Zool.* **220**, 225–247 (1990).
47. Francioli, Y., Thorley, J., Finn, K., Clutton-Brock, T. & Zöttl, M. Breeders are less active foragers than non-breeders in wild Damaraland mole-rats. *Biol. Lett.* **16**, 20200475 (2020).
48. Houslay, T. M., Vullioud, P., Zöttl, M. & Clutton-Brock, T. H. Benefits of cooperation in captive Damaraland mole-rats. *Behav. Ecol.* **31**, 711–718 (2020).
49. Lövy, M., Šklíba, J. & Šumbera, R. Spatial and temporal activity patterns of the free-living giant mole-rat (*Fukomys mechowii*), the largest social Bathyergid. *PLoS ONE* **8**, e55357 (2013).
50. Šklíba, J., Lövy, M., Burda, H. & Šumbera, R. Variability of space-use patterns in a free living eusocial rodent, Ansell's mole-rat indicates age-based rather than caste polyethism. *Sci. Rep.* **6**, 37497 (2016).
51. Wroe, S., McHenry, C. & Thomason, J. Bite club: comparative bite force in big biting mammals and the prediction of predatory behaviour in fossil taxa. *Proc. R. Soc. B Biol. Sci.* **272**, 619–625 (2005).
52. Deeming, D. C., Harrison, S. L. & Sutton, G. P. Inter-relationships among body mass, jaw musculature and bite force in birds. *J. Zool.* **317**, 129–137 (2022).
53. Herrel, A., Mcbrayer, L. D. & Larson, P. M. Functional basis for sexual differences in bite force in the lizard *Anolis carolinensis*. *Biol. J. Linn. Soc.* **91**, 111–119 (2007).
54. Rebol, E. J. & Anderson, D. J. Sex-specific aging in bite force in a wild vertebrate. *Exp. Gerontol.* **159**, 111661 (2022).
55. Thomas, P. et al. Sexual dimorphism in bite force in the grey mouse lemur. *J. Zool.* **296**, 133–138 (2015).
56. Becerra, F., Echeverría, A., Vassallo, A. I. & Casinos, A. Bite force and jaw biomechanics in the subterranean rodent Talas tuco-tuco (*Ctenomys talarum*) (Caviomorpha: Octodontoidea). *Can. J. Zool.* **89**, 334–342 (2011).
57. Herrel, A., Spithoven, L., Van Damme, R. & De Vree, F. Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. *Funct. Ecol.* **13**, 289–297 (1999).
58. Kay, R. F., Plavcan, J. M., Glander, K. E. & Wright, P. C. Sexual selection and canine dimorphism in new world monkeys. *Am. J. Phys. Anthropol.* **77**, 385–397 (1988).
59. Morris, J. S. & Brandt, E. K. Specialization for aggression in sexually dimorphic skeletal morphology in grey wolves (*Canis lupus*). *J. Anat.* **225**, 1–11 (2014).
60. Russell, A. F., Carlson, A. A., McIlrath, G. M., Jordan, N. R. & Clutton-Brock, T. Adaptive size modification by dominant female meerkats. *Evolution* **58**, 1600–1607 (2004).
61. Magalhães, A. R., Damasceno, E. M. & Astúa, D. Bite force sexual dimorphism in Canidae (Mammalia: Carnivora): Relations between diet, sociality and bite force intersexual differences. *Hystrix* **31**, 1–6 (2020).
62. Jarvis, J. U. M. & Bennett, N. C. Eusociality has evolved independently in two genera of bathyergid mole-rats—but occurs in no other subterranean mammal. *Behav. Ecol. Sociobiol.* **33**, 253–260 (1993).
63. Šumbera, R. et al. Burrow architecture, family composition and habitat characteristics of the largest social African mole-rat: The giant mole-rat constructs really giant burrow systems. *Acta Theriol.* **57**, 121–130 (2012).
64. Torrents-Ticó, M., Bennett, N. C., Jarvis, J. U. M. & Zöttl, M. Sex differences in timing and context of dispersal in Damaraland mole-rats (*Fukomys damarensis*). *J. Zool.* **306**, 252–257 (2018).
65. van Daele, P. A. A. G., Desmet, N., Šumbera, R. & Adriaens, D. Work behaviour and biting performance in the cooperative breeding Micklem's mole-rat *Fukomys micklemi* (Bathyergidae, Rodentia). *Mamm. Biol.* **95**, 69–76 (2019).
66. Rotics, S., Bensch, H. M., Resheff, Y. S., Clutton-Brock, T. & Zöttl, M. Workload distribution in wild Damaraland mole-rat groups. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **380**, 20230276 (2025).
67. Johnston, R. A. et al. Morphological and genomic shifts in mole-rat 'queens' increase fecundity but reduce skeletal integrity. *eLife* **10**, e65760 (2021).
68. Jarvis, J. U. M., O'Riain, M. J. & McDaid, E. Growth and factors affecting body size in naked mole-rats. in *The Biology of the Naked Mole-Rat* (eds Sherman, P. W., Jarvis, J. U. M. & Alexander, R. D.) 358–383. https://doi.org/10.1515/9781400887132-015 (Princeton University Press, 1991).
69. Lacey, E. A. & Sherman, P. W. Social organization of naked mole-rat colonies: Evidence for divisions of labor. in *The Biology of the Naked Mole-rat* (eds Sherman, P. W., Jarvis, J. U. M. & Alexander, R. D.) 275–336. https://doi.org/10.1515/9781400887132-013 (Princeton University Press, 1991).
70. Speakman, J. R. The physiological costs of reproduction in small mammals. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **363**, 375–398 (2008).
71. Dammann, P., Šumbera, R., Massmann, C., Scherag, A. & Burda, H. Extended longevity of reproductives appears to be common in Fukomys mole-rats (Rodentia, Bathyergidae). *PloS ONE* **6**, e18757 (2011).
72. Wallace, E. D. & Bennett, N. C. The colony structure and social organization of the giant Zambian mole-rat, *Cryptomys mechowi*. *J. Zool.* **244**, 51–61 (1998).
73. Dammann, P. & Burda, H. Sexual activity and reproduction delay ageing in a mammal. *Curr. Biol.* **16**, R117–R118 (2006).
74. Begall, S., Bottermann, L. & Caspar, K. R. Self-domestication underground? Testing for social and morphological correlates of animal personality in cooperatively-breeding Ansell's mole-rats (*Fukomys anselli*). *Front. Ecol. Evol.* **10**, 862082 (2022).
75. Burda, H. Individual recognition and incest avoidance in eusocial common mole-rats rather than reproductive suppression by parents. *Experientia* **51**, 411–413 (1995).
76. Sharp, S. P. & Clutton-Brock, T. H. Reluctant challengers: why do subordinate female meerkats rarely displace their dominant mothers? *Behav. Ecol.* **22**, 1337–1343 (2011).
77. Cooney, R. Colony defense in Damaraland mole-rats, *Cryptomys damarensis*. *Behav. Ecol.* **13**, 160–162 (2002).
78. Jacobs, D. S., Reid, S. & Kuiper, S. Out-breeding behaviour and xenophobia in the damaraland mole-rat, *Cryptomys damarensis*. *South Afr. J. Zool.* **33**, 189–194 (1998).
79. Hazell, R. W. A., Bennett, N. C., Jarvis, J. U. M. & Griffin, M. Adult dispersal in the co-operatively breeding Damaraland mole-rat (*Cryptomys damarensis*): a case study from the Waterberg region of Namibia. *J. Zool.* **252**, 19–25 (2000).
80. Griffin, A. S. et al. A genetic analysis of breeding success in the cooperative meerkat (*Suricata suricatta*). *Behav. Ecol.* **14**, 472–480 (2003).
81. Nelson-Flower, M. J., Hockey, P. A. R., O'Ryan, C. & Ridley, A. R. Inbreeding avoidance mechanisms: Dispersal dynamics in cooperatively breeding southern pied babblers. *J. Anim. Ecol.* **81**, 876–883 (2012).
82. Šumbera, R. Thermal biology of a strictly subterranean mammalian family, the African mole-rats (Bathyergidae, Rodentia) - a review. *J. Therm. Biol.* **79**, 166–189 (2019).

83. Patzenhauerová, H., Šklíba, J., Bryja, J. & Šumbera, R. Parentage analysis of Ansell's mole-rat family groups indicates a high reproductive skew despite relatively relaxed ecological constraints on dispersal. *Mol. Ecol.* **22**, 4988–5000 (2013).
84. Šumbera, R. et al. The biology of an isolated Mashona mole-rat population from southern Malawi, with implications for the diversity and biogeography of the genus Fukomys. *Org. Divers. Evol.* **23**, 603–620 (2023).
85. van Daele, P. A. A. G., Verheyen, E., Brunain, M. & Adriaens, D. Cytochrome *b* sequence analysis reveals differential molecular evolution in African mole-rats of the chromosomally hyperdiverse genus *Fukomys* (Bathyergidae, Rodentia) from the Zambezian region. *Mol. Phylogenet. Evol.* **45**, 142–157 (2007).
86. Borges, L. R. et al. The role of soil features in shaping the bite force and related skull and mandible morphology in the subterranean rodents of genus *Ctenomys* (Hystricognathi: Ctenomyidae). *J. Zool.* **301**, 108–117 (2017).
87. Ginot, S., Herrel, A., Claude, J. & Hautier, L. Skull size and biomechanics are good estimators of in vivo bite force in murid rodents. *Anat. Rec.* **301**, 256–266 (2018).
88. R Core Team. *R: A Language and Environment for Statistical Computing*. https://www.R-project.org/ (Vienna, 2024).
89. Bürkner, P. Bayesian item response modeling in R with brms and Stan. *J. Stat. Softw.* **100**, 1–54 (2021).
90. Neal, R. MCMC using Hamiltonian dynamics. In *Handbook of Markov Chain Monte Carlo* (eds Brooks, S., Gelman, A., Jones, G. L. & Meng, X.-L.) 116–62 (Chapman & Hall/CRC Press, 2011).
91. Vehtari, A., Gelman, A., Simpson, D., Carpenter, B. & Bürkner, P.-C. Rank-normalization, folding, and localization: an improved $\hat{R}$ for assessing convergence of MCMC (with discussion). *Bayesian Anal.* **16**, 667–718 (2021).
92. Gelman, A., Hwang, J. & Vehtari, A. Understanding predictive information criteria for Bayesian models. *Stat. Comput.* **24**, 997–1016 (2014).
93. Vehtari, A., Simpson, D., Gelman, A., Yao, Y. & Gabry, J. Pareto smoothed importance sampling. *J. Mach. Learn. Res.* **25**, 1–58 (2024).
94. Vehtari, A., Gelman, A. & Gabry, J. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat. Comput.* **27**, 1413–1432 (2017).
95. Burnham, K. P. & Anderson, D. R. *Model Selection and Multimodel Inference: a Practical Information-Theoretical Approach* (Springer, 2002).
96. Gabry, J., Simpson, D., Vehtari, A., Betancourt, M. & Gelman, A. Visualization in Bayesian workflow. *J. R. Stat. Soc. A* **182**, 389–402 (2019).
97. Lenth, R. emmeans: estimated marginal means, aka least-squares means. *R Package Version 1.10.4* https://CRAN.R-project.org/package=emmeans (2024).
98. Šumbera, R. et al. Breeding males, but not females, of *Fukomys* mole-rats use stronger bites to defend reproductive monopoly. [Data set]. *Figshare* https://doi.org/10.6084/m9.figshare.29423288 (2025).

Acknowledgements

We thank Helder Gomes Rodrigues, David Gaynor and Kyle Finn for help with data collection and logistics, and Radka Pešková for taking care of experimental animals. We are grateful to Tim H. Clutton-Brock for access to Damaraland mole-rats in the facility at the Kuruman River Reserve supported by European Research Council under the European Union's 2020 research and innovation programme (Grants No. 742808 and 294494). This study was supported by the Czech Science Foundation project no. 20-10222S.

Author contributions

R.Š., A.K. and M.L. conceptualized the study. R.Š., A.K., J.O. and M.L. carried out the investigation, and R.Š., A.K. and M.L. curated the data. O.M. performed the formal analyses and, together with M.L., developed the methodology and prepared the figures. R.Š., A.K., J.M., S.B., N.C.B., M.Z. and A.H. provided resources. R.Š. and M.L. wrote the original draft. All authors reviewed and edited the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s42003-025-09334-8.

Correspondence and requests for materials should be addressed to Radim Šumbera.

Peer review information *Communications Biology* thanks Frederik Püffel and Helder Gomes Rodrigues for their contribution to the peer review of this work. Primary Handling Editor: Michele Repetto. A peer review file is available.

Reprints and permissions information is available at http://www.nature.com/reprints