Exploring the links between bite force, body mass, and exploratory behavior in the naked mole rat, *Heterocephalus glaber*.

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Abstract

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Keywords: *bite force*, *performance, body mass*, *exploratory behavior, boldness.*

Introduction

Arnold in 1983 defined performance as the ability to carry out specific tasks that directly affect survival and reproduction, serving as a crucial link between morphological traits and fitness. Therefore, natural selection acts directly on physical performance traits, making performance an essential element for animal survival (Arnold, 1983). Physical strength is frequently studied as a performance trait in evolutionary context, as it is linked to fitness (Kraus *et al.*, 2022; Christiansen & Wroe, 2007; Husak *et al.*, 2009). For instance, a higher Bite Force (BF) can provide advantages such as finding a sexual partner (Husak *et al.*, 2009) or accessing diverse food resources, as demonstrated in Darwin's finches from the Galapagos Islands (Herrel *et al.*, 2005a). During periods of drought, when only large seeds are available (Boag & Grant, 1981), individuals with larger beaks and greater biting strength are naturally selected (Herrel *et al.*, 2005a). A higher BF can also play a role in interspecific competition. Indeed, Cornette *et al.* (2015) observed that, in an insular context, the shrew species *Crocidura russula* exhibited a higher BF when *Crocidura suaveolens* was present, but a decreased one when alone. Indeed, Cornette *et al.* (2015) observed that, in an insular context, the shrew species *Crocidura russula* exhibited a higher bite force when coexisting with *Crocidura suaveolens* and a reduced one when isolated, suggesting competitive pressure. BF is a functional and ecological characteristic, that has been studied through morphological, biomechanical, or in vivo models in a broad of vertebrate, including alligators (Erickson *et al.*, 2003), lizards (Husak *et al.*, 2006; Lappin & Husak, 2005), turtles (Marshall *et al.*, 2012; Herrel *et al.*, 2017), bats (Herrel *et al.*, 2008; Nogueira *et al.*, 2009; Santana *et al.*, 2010), carnivores and other mammals (Magalhães *et al.*, 2020; Christiansen & Wroe, 2007; Sakamoto *et al.*, 2010; Law *et al.*, 2016; Cornette *et al.*, 2015; Thomason, 1991; Freeman & Lemen, 2008b) and birds (van der Meij & Bout, 2004; Herrel *et al.*, 2005a,b). It plays a crucial role in exploratory behavior, which is defined as the propensity to be active and gather information in new environments or situations (Majelantle *et* *al.*, 2022). This capability allows animals to manipulate new objects or food sources, modify their environment (such as digging tunnels), and defend against threats. As a result, BF facilitates safer and more effective exploration in unfamiliar settings (Wroe *et al.*, 2005; Aguirre *et al.*, 2003). Furthermore, the exploratory behavior linked to BF enables active interaction with the environment, helping animals to find resources, assess potential risks, interact with other individuals, and adapt to changing conditions (Page *et al.*, 2018; Mehlhorn *et al.*, 2015; Crusio, 2021; Husak *et al.*, 2006).

African mole rats (Bathyergidae, Rodentia) consist of 16 species of underground rodents that inhabit complex tunnel systems (Kraus *et al.*, 2022; Desmet *et al.*, 2013; Burda, 1999). These species are predominantly social (Kraus *et al.*, 2022; Faulkes & Bennett, 2021; van Daele *et al.*, 2019; Bennett & Faulkes, 2000), engaging in cooperative tasks primarily associated with their exploratory behavior, such as tunnel excavation and foraging (van Daele *et al.*, 2019, Jarvis, 1981). In these subterranean species, the energetically demanding task of digging burrows (Lovegrove, 1989), has driven the evolution of a well-developed biting apparatus. This adaptation not only helps to overcome the mechanical resistance of the soil (Stein, 2000; Kubiak *et al.*, 2018) but also facilitate access to food resources like tubers and roots, which are often inaccessible to other rodents (Cox *et al.*, 2020; Sherman *et al.*, 1992). Consistent with the well-documented correlation between body mass and biting force across various taxa (Thomason *et al.*, 1990; Aguirre *et al.*, 2002; Dumont & Herrel, 2003; Thompson *et al.*, 2003; Wroe *et al.*, 2005; Freeman & Lemen, 2008a; Becerra *et al.*, 2014), previous studies have shown that physical characteristics like body mass seem to be reliable predictors of BF in African mole rats, as seen in *Fukomys* mole-rats (van Daele *et al.*, 2009; Kraus *et al.*, 2022), *Bathyergus* mole-rats (Kraus *et al.*, 2022) and in the naked mole-rat (Hite *et al.*, 2019; Kraus *et al.*, 2022). McIntosh & Cox (2016a) observed in the species *Fukomys mechowii* and *Batherygus suillus* that body mass varies with the hierarchical status of individuals. These results suggest a possible association between body mass and the biting force required to perform specific tasks, like burrowing, which may depend on the hierarchical status of individuals (McIntosh & Cox, 2016b; Anderson *et al.*, 2008; Sherman *et al.*, 1991). However, van Daele *et al.* (2019) found no significant correlation between the extent of work engagement and peak BF in their study on the mole rat *Fukomys micklemi*. This result casts doubt on the hypothesis that body mass and BF are linked to specific roles within the colony and, by extension, to exploratory behavior, suggesting that further investigation is needed to confirm any such relationship.

Figure 1. A naked mole rat (*Heterocephalus glaber*) isolated on blank background. Image provided by iStock/GlobalP.

The naked mole rat, *Heterocephalus glaber* (Fig. 1), provide an ideal model for studying the impact of BF and body mass on exploratory behavior in subterranean mammals. They are well-known for their complex social system, characterized by a well-defined division of labor within the colony (Jarvis, 1981; Bennett & Faulkes, 2000). A single female, the queen, and one to three males handle reproduction (Sherman *et al.*, 1992; Sherman *et al.*, 1991) while the rest of colony members, known as workers, are organized into different workgroups, each specialized in specific tasks, such as tunnel excavation, foraging, and burrow maintenance (Mooney *et al.*, 2015; Burda *et al.*, 2000). Workers use mainly their incisors for digging, clearing debris, defending the colony, feeding, and showing their dominance among their conspecifics (Brett, 1991). Thus, through their exploratory behavior and bite strength, workers facilitate the acquisition of essential resources for the colony while breeders ensure the perpetuation of the species.

The aim of this study was to examine the relationships (1) between BF and body mass; (2) between exploratory behavior and both body mass and BF, within a captive colony of naked mole rats, *Heterocephalus glaber*. To this end, we measured individual maximum BFs, body masses and exploratory behavior. Our results are discussed in the context of inter-individual variability and the species' social organization. In this framework, individuals that entered the tunnel on more experimental days and made more trips into the tunnel during each experiment are considered more active. Those that entered the tunnel more quickly and spent more time inside are considered as more exploratory. This classification aligns with the framework proposed by Blecher and Oosthuizen (2023) for the Damaraland mole-rats (*Fukomys damarensis*) and by Zablocki-Thomas *et al.* (2018) for the small primate *Microcebus murinus*.

We hypothesized that BF would correlate positively with body mass; and that that exploratory behavior would relate to these parameters, suggesting that the distribution into specialized workgroups is influenced by the individuals' age and/or morphological properties.

Material and Methods

Ethical note

This study received approval from the Comité Cuvier of the MNHN (Muséum national d’Histoire naturelle) as a scientifically justified project adhering to the 3Rs principles to ensure the ethical use of animals, as outlined by Russell and Burch (1959).

Studied Animals

All measurements and observations were conducted on a stable colony of 79 captive and captive-born individuals, consisting of 40 males, 35 females, and 4 unsexed individuals with an average age of 5.5 years (ranging from 1 to 14 years old). These animals were housed in transparent plastic containers interconnected by tubes with sawdust bedding, maintained at 28°C and 82% humidity in a dark room in the Ménagerie, zoo of the Jardin des Plantes in Paris. Their diet consisted of fresh vegetables provided *ad libitum*, including tubers at a rate of 6g per individual and vegetables mix at a rate of 3g per individual. All individuals were sexed, weighed and equipped with an individual subcutaneous RFID transponder during an inventory procedure conducted by veterinarians and caretakers of the Ménagerie. In addition, background music was continuously broadcast at a low volume to accustom animals to the sound of human speech.

Measurement of Bite Force and Body Mass

BFs were measured in vivo for each individual using a Kistler isometric force transducer (type 9203; range 0-5000 N, error 0.1 N; Kistler Inc., Switzerland) connected to a Kistler charge amplifier (type 5995, Kistler Inc.). For details on the experimental setup, see Herrel *et al.* (1999). The bite plates were covered with a thin layer of plaster to protect the incisors of the naked mole rats. All individuals were encouraged to bite between three and five times, and the maximum BF recorded was used to estimate their maximum biting performance (in Newtons). They were handled by the skin of the back with one hand and positioned by guiding the bite plates between their incisors. This method has been used to measure bite forces in multiple taxa, including birds (Herrel *et al.*, 2005a, b), turtles (Herrel & O'Reilly, 2006), lizards (Lappin & Husak, 2005), alligators (Erickson *et al.*, 2003), bats (Aguirre *et al.*, 2002; Dumont & Herrel, 2003), mice (Byron *et al.*, 2004) and rats (Ginot et al., 2019). Some naked mole rats did not bite the transducer during these tests. All individuals were weighed on a digital balance (precision

0.1g) and their ages were retrieved from the database Species360 Zoological Information Management System (ZIMS).

Observations of Exploratory Behavior

Exploratory behavior was assessed in a modified open field test, using a pipe to simulate a new tunnel, as described in Amari *et al.* (2024). The Plexiglas® pipe was closed at one end with an opaque cap, similar to the mouthpiece typically used where this new pipe was placed. Observations were conducted over 8 days, for 1 hour each morning, alternating the position of the pipe, upward with the inlet at ground level, and downward with the inlet at 52 cm above the ground (Fig. 2). Since olfaction is the primary mode of inter-individual recognition in this species (O'Riain & Jarvis, 1997), the pipe was cleaned with black soap between sessions to eliminate any odors left by the exploring individuals.

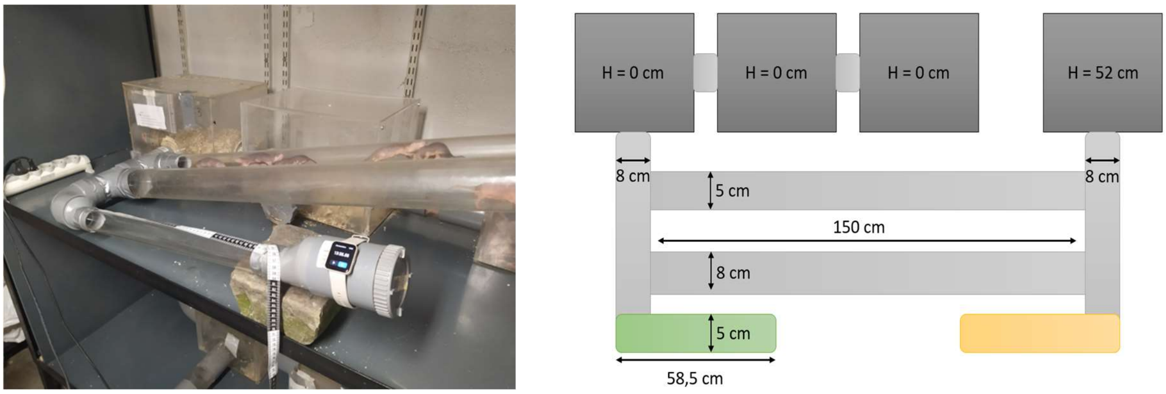

Figure 2. Photograph (left) and diagram (right) of the observation device. The diagram shows the dimensions of the pipes and the height of the boxes. The green pipe represents the new pipe installed from the bottom to the top, on observation days 1, 3, 5 and 7; while the yellow pipe represents the new pipe installed from the top to the bottom, on observation days 2, 4, 6 and 8. The photograph shows the observation setup on days 1, 3, 5 and 7.

During the hour of observation, the individuals were free to enter the pipe or not. An entry was counted when all four legs of the naked mole rat were inside the pipe, and then scanned with a microchip reader. Two measurements were taken: the timing of each entry and exit from the pipe. These data allowed us to determine, for each individual, the total number of entries, the latency of each entry, and the total time spent inside the pipe.

Replication Statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Colony	Species	8 observations, with 1 colony of 79 individuals

Statistical analysis

All statistical analyses were performed using R (version 4.2.3) (R Core Team, 2022). Two datasets were used: one summarizing individual-level data (one row per individual) and the other including all exploration-specific data (one row per exploration entry). Individuals were categorized as biters and non-biters based on whether they bit the transducer during BF measurements, and as explorers and non-explorers based on whether they engaged in exploration at least once during the entire experiment.

For the individual-level dataset, BF, mass, and age were scaled and centered. BF and total exploration time were normalized using the bestNormalize package (Peterson, 2021; Peterson & Cavanaugh, 2019) to ensure standardized distributions [bestNormalize]. Data and residuals normality were evaluated using QQ plots, histograms and Shapiro-Wilk tests [shapiro.test], and outliers in BF measurements were identified through boxplot analysis [boxplot.stats]. Generalized linear models [glm] were performed to assess the effects of mass, age, and sex on BF, biting behavior, and exploration parameters (including exploration initiation, number of entries, latency, total exploration time, and days spent exploring). Multicollinearity was assessed using variance inflation factor tests [vif]. BF was excluded from the exploration models due to excessive missing values (NAs) resulting from individual differences in biting behavior. Correlation analyses were performed to investigate the potential association between BF and each exploratory parameter, with Spearman [cor.test(*data*, method="spearman")] and Pearson [cor.test(*data*, method="pearson")] rank correlation tests.

For the exploration-specific dataset, BF, mass, and age were also scaled and mean-centered. Exploration time was normalized using the bestNormalize package [bestNormalize]. Normality was assessed using a QQ plot, histograms and a Shapiro-Wilk test [shapiro.test]. We investigated the effects of mass and age on exploration time per entry using a mixed-effects model [lmer] from the lme4 package (Bates *et al.*, 2015), with individual variation treated as a random effect. Multicollinearity was again evaluated using VIF tests [vif].

All visualizations were generated using the ggplot2 package (Wickham, 2016).

Results

Influence of body mass and age on bite force.

Table 1. Data for maximum bite forces (N), body masses (g) and ages (days) used in Spearman comparisons of means and correlation analyzes presented as mean values with 95% confidence intervals. These data were collected from all 79 individuals in the colony.

	Bite force (N)	**Mass (g)**	**Age (days)**
Mean	*13,4* [11,6–15,2]	*37,6* [25,5–39,7]	*2066* [1787–2345]
Minimum	1,0	25,0	388
Maximum	34,1	66,0	5044

The measurements of BF, body mass, and age are summarized in Table 1. We found that heavier individuals were significantly older ($p < 0.001$).

Of the 79 individuals in the colony, 48 were categorized as biters. These individuals were significantly heavier ($p = 0.027$) and younger ($p = 0.034$) (Fig. 3) but did not differ by sex (*p* =

0.15). If we consider only the biters, heavier and younger individuals were also stronger ($p_m < 0.001$; $p_a = 0.002$) (Fig. 4). Six BF outliers were identified: the 5 lowest measurements and the highest measurement (at 1.0 N; 1.4 N; 3.0 N; 4.5 N; 5.0 N and 34.1 N).

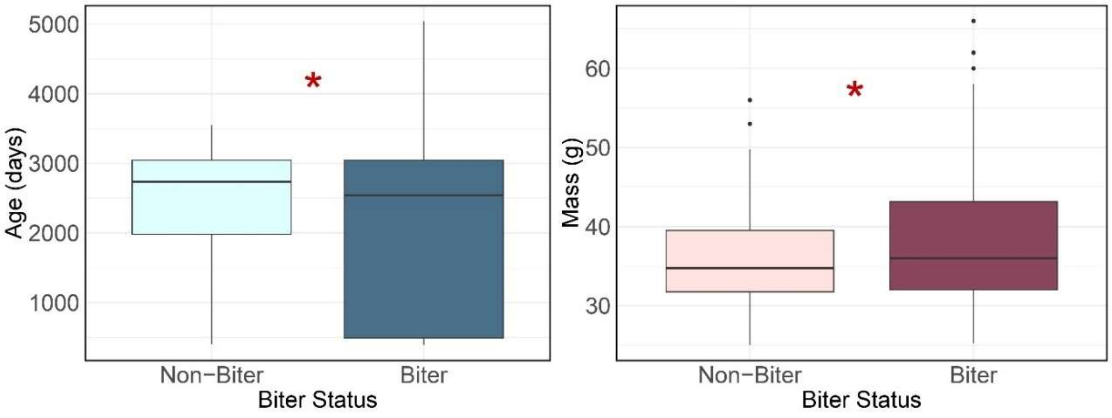

Figure 3. Means of body masses and ages for animals that bit the transducer versus those that did not. The line represents linear regression line. Standard deviations are represented by the bars surrounding the whisker boxes. Sample size are N = 48 for the "Biter" category and N = 31 for the "Non-Biter" category.

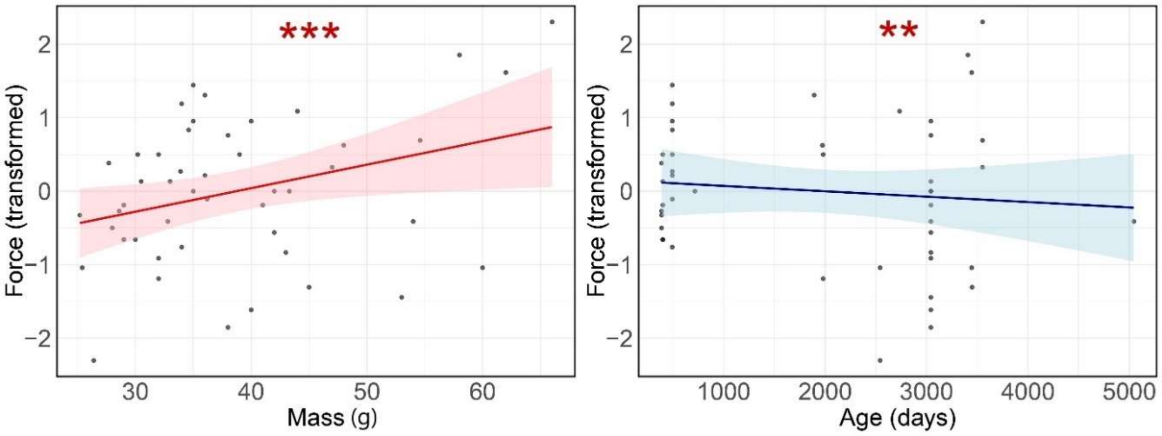

Figure 4. Scatter plots showing the relationship between body mass, age, and the maximum bite force (transformed with the bestNormalize package) measured in naked mole rats. The line represents linear regression line. Only individuals who bit during bite force measurements were included in the analysis. N = 48 individuals.

Influence of bite force, mass, and age on exploratory behavior.

Of the 79 individuals observed, only 54 engaged in exploratory behavior. These explorers were significantly weaker (*p* = 0.02), heavier (*p* = 0.012) and younger (*p* = 0.005) (Fig. 5), but did not differ by sex (*p* = 0.36).

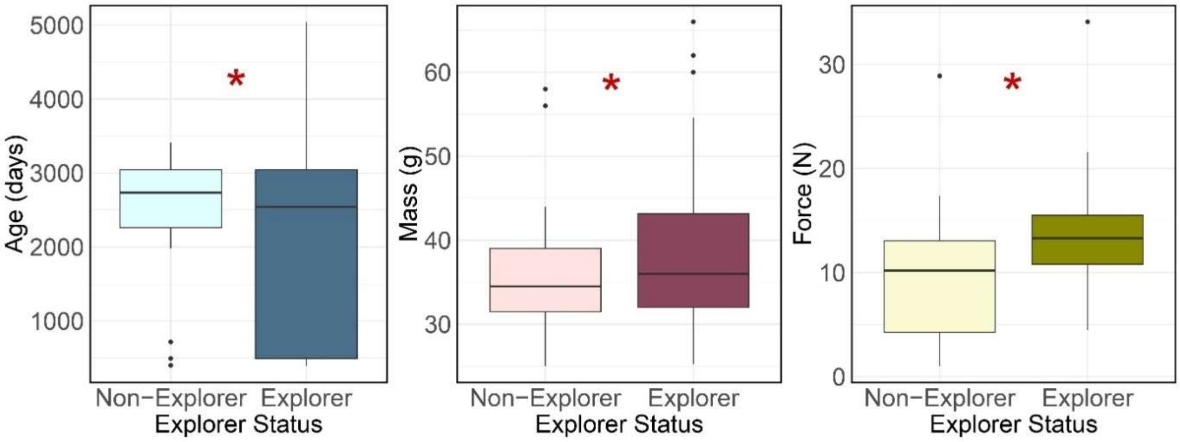

Figure 5. Means of bite forces (a), body masses (b), and ages (c) for animals that explored the pipe versus those that did not. Standard deviations are represented by the bars surrounding the whisker boxes. Sample size are N = 54 for the "Explorer" category and N = 25 for the "Non-Explorer" category.

If we consider only these explorers, younger (*p* = 0.006), heavier (*p* = 0.011) and stronger (*p* = 0.016) individuals entered more frequently compared to the others (Fig. 6).

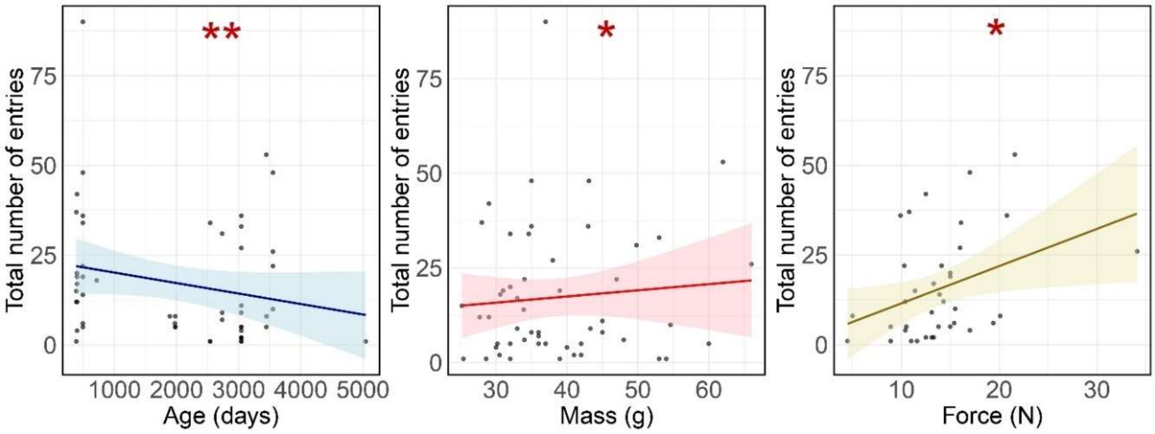

Figure 6. Total number of entries for each individual tested, as a function of age, body mass and bite force. The lines represent linear regression lines (age in blue, body mass in pink, and bite force in yellow). N = 79.

Younger (*p* = 0.024) and stronger (*p* = 0.02) individuals also spent more days in exploration than the rest of the group (Fig. 7), and younger individuals entered sooner (*p* = 0.041) (Fig. 8).

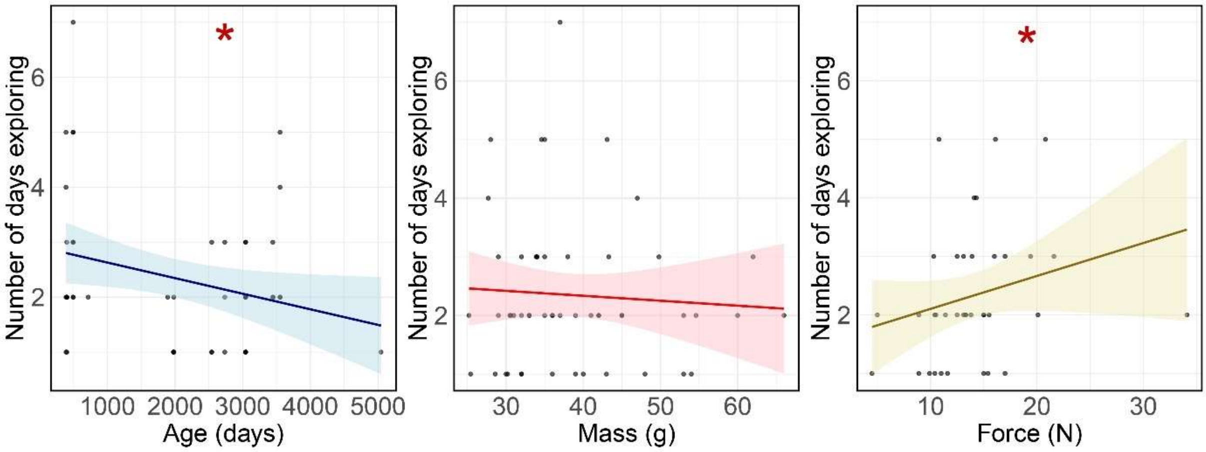

Figure 7. Number of exploration days for each individual tested, as a function of age, body mass and bite force. The lines represent linear regression lines (age in blue, body mass in pink, and bite force in yellow). N = 79.

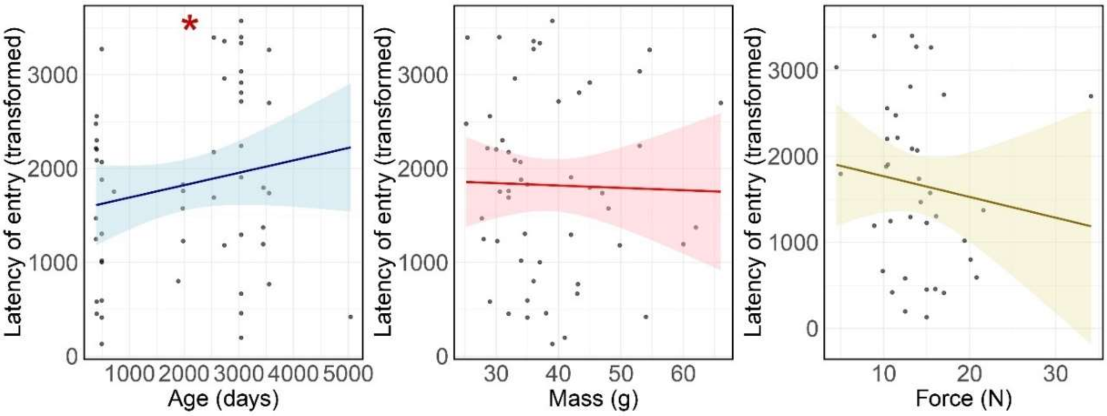

Figure 8. Mean latency of first entry for each individual tested, as a function of age, body mass and bite force. The lines represent linear regression lines (age in blue, body mass in pink, and bite force in yellow). N = 79.

Total exploration time showed no significant association with either age (*p* = 0.13), body mass (*p* = 0.9) or bite force (*p* = 0.24). However, lighter individuals spent significantly more time in the tunnel at each entry compared to the rest of the group (*p* = 0.012) (Fig. 9). Sex was not linked to any exploratory factor.

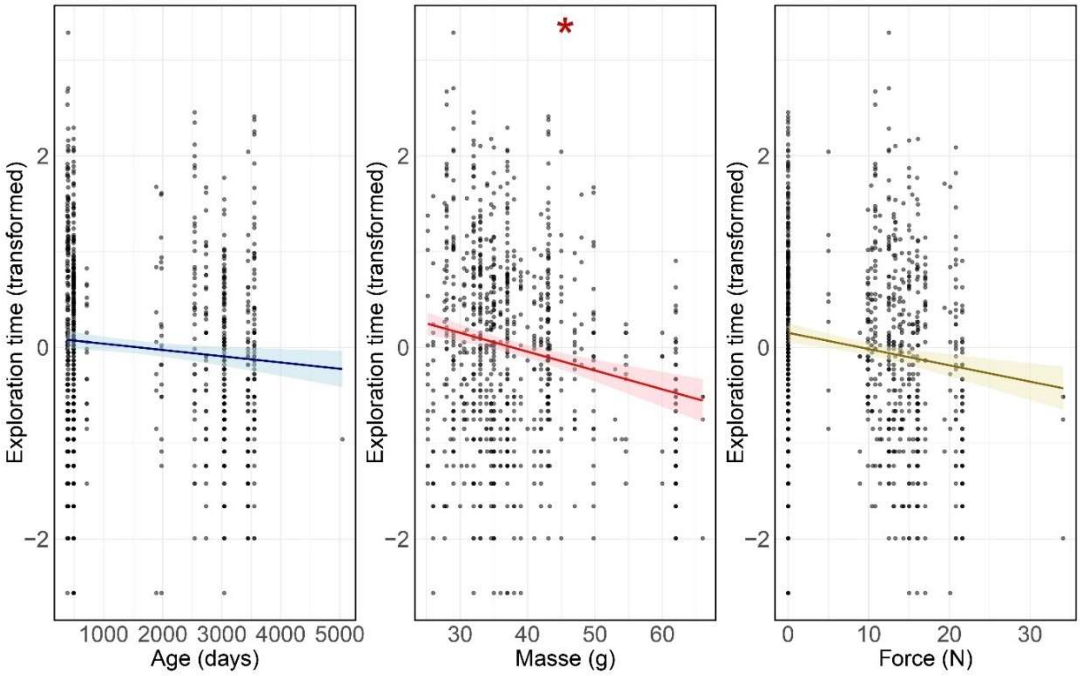

Figure 9. Exploration time for each entry (transformed with the bestNormalize package) as a function of the age, body mass and bite force of the naked mole rats tested. The lines represent linear regression lines (age in blue, body mass in pink, and bite force in yellow). N = 841.

Biters entered the pipe significantly earlier than non-biters, with an average entry time of 31 minutes compared to 34.8 minutes for non-biters ($p < 0.001$). Additionally, biters spent less time exploring the new pipe (averaging 43.1 seconds) than non-biters (averaging 50.3 seconds) ($p = 0.037$).

Discussion

Younger individuals are stronger and lighter.

Given that naked mole-rats reach adulthood around one year of age and can live for over 30 years, the individuals in our colony represent relatively young adults (Jarvis *et al.*, 1994; Buffenstein & Craft, 2021). Our findings are particularly valuable because we know the exact birth dates and ages of the animals tested, unlike earlier studies that relied on wild-caught naked mole-rats (Jarvis, 1981; Lacey & Sherman, 1991; Jarvis *et al.*, 1991). We observed a significant relationship between age and body mass, with older animals being heavier, which is consistent with previous findings in this species (Hite *et al.*, 2019). Additionally, we found that body mass was correlated with BF, with heavier animals generally exhibiting higher BF, which goes along with our initial hypothesis. This finding also aligns with previous research on the naked mole-rat (Hite *et al.*, 2019), as well as on the Micklem's mole-rats (*Fukomys micklemi*) (van Daele *et al.*, 2019), other rodents (Becerra *et al.*, 2014; Freeman & Lemen, 2008a), or else bats (Aguirre *et al.*, 2002; Dumont & Herrel, 2003), opossums (Thomason *et al.*, 1990; Thompson *et al.*, 2003), and mammalian predators (Wroe *et al.*, 2005).

Interestingly, we also found a significant correlation between age and BF, with younger individuals demonstrating stronger bite force. This result is unexpected and contrasts with findings in other taxa, where strength typically increases with age, as observed in mammals (Binder & van Valkenburg, 2000; Thompson *et al.*, 2003), lizards (Herrel *et al.*, 1999; Meyers *et al.*, 2002), alligators (Erickson *et al.*, 2003), turtles (Herrel & O'Reilly, 2006), birds (Herrel *et al.*, 2005b), and fish (Hernandez & Motta, 1997). Furthermore, while Herrel & Gibb (2006) discuss compensatory mechanisms in juveniles for locomotor performance, they note that such compensation is rare for feeding traits like bite force. Therefore, the enhanced bite strength observed in younger naked mole-rats may reflect a unique adaptation, potentially allowing them to compensate for their smaller size and limited experience, and access harder or more challenging food resources.

Individuals exhibit different behaviors based on their age and body mass.

During the BF measurements, animals displayed varying behaviors: some barely bit the transducer, resulting in particularly low bite forces, while others did not engage with it at all. This inter-individual variability in biting behavior could be influenced by several factors, including stress from handling or differences in temperaments.

Social isolation during handling, which is known to increase stress in mice (Guo *et al.*, 2004; Bibancos *et al.*, 2007), may have raised the stress levels of the individuals, potentially exacerbating or reducing aggressive behaviors, which might explain variations in biting responses (Grippo et al., 2008). However, the stress response to social isolation has not been fully explored in naked mole rats. Additionally, Blecher *et al.* (2020) found that social isolation increases stress-related cortisol levels in female but not male naked mole-rats, suggesting a sex-based stress response, and our results show no clear correlation between biting behavior and sex.

Conversely, these behavioral differences were correlated with body mass and age, with animals that bit the transducer being both heavier and younger. Similarly, the decision to explore the new area was also correlated with body mass and age, with explorers being both heavier and younger. The inter-individual variability in these behaviors may therefore reflect influences beyond stress alone, such as temperament. The term temperament refers to consistent behavioral differences, between or within individuals, in similar contexts (Sih *et al.*, 2004; Réale *et al.*, 2007). The consistent differences between individuals, associated with body mass and age, may therefore be attributed to variations in temperament, with heavier and younger individuals tending to exhibit more risk-taking behavior. This is further supported by our observation that biters tend to enter the new area sooner than non-biters, suggesting greater risk-taking (as seen in the Damaraland mole-rats; Blecher & Oosthuizen, 2023), or increased boldness (as observed in mouse lemurs; Zablocki-Thomas *et al.*, 2018).

Stronger, heavier and younger individuals are more active.

Our findings indicate that the decision to explore is also linked to BF, with stronger individuals being more likely to engage in exploration. Among those that did explore, stronger individuals were more active, making more trips each session and consistently returning each day to explore further. More active animals were also significantly heavier and younger.

Exploratory behavior is known to help animals familiarize themselves with new environments, as shown by Russell *et al.* (2010) in the brown rat (*Rattus norvegicus*) under natural conditions. In naked mole-rats, Majelantle *et al.* (2022) identified a behavioral syndrome where the most exploratory individuals are also the most daring, exhibiting a greater propensity for risk-taking. In light of this study, our results may suggest that boldness in naked mole-rats is associated with strength, mass, and age, with stronger, heavier, and younger individuals potentially exhibiting greater boldness. This pattern aligns with observations in other social animals, such as dogs, where boldness correlates with body mass and, to a greater extent, strength (Svartberg, 2002). However, van Oers *et al.* (2005) noted in the great tit (*Parus major*) that the relationship between exploratory behavior and risk-taking can heavily depend on social context. Wilson *et al.* already noted in 1994 that such behavioral traits often vary depending on ecological and social contexts, emphasizing the role of environment in shaping the interplay between exploratory behavior and boldness. Additionally, Majelantle *et al.* (2022) noted that boldness and exploration in naked mole-rats can vary between individuals but remain stable over time, suggesting distinct temperamental traits. Furthermore, our study involved a colony born and raised in captivity, where the animals were not required to leave their tunnels and were protected from predation. As suggested by Desmet *et al.* (2013) in *Fukomys micklemi*, another social mole-rat species, this controlled environment may have affected the role of boldness in our study.

Exploration may reflect a performance-, age-, or size-based polyethism.

We observed that heavier individuals spent less time exploring the tunnel for each entry, while younger and weaker individuals initiated exploration sooner, suggesting that these traits may be linked to higher exploratory tendencies. Additionally, individuals who did not exhibit biting behavior during BF measurements generally entered the new area later. We believe that these findings may reflect how exploration behavior and temperament vary according to the workgroup individuals belong to, with variation influenced by factors such as age, body mass, and performance.

In African mole-rats, both age- and size-based polyethism have been observed to influence task distribution within colonies, as seen in the Ansell's mole-rat (*Fukomys anselli*) (Sklíba *et al.*, 2016), the Damaraland mole-rat (Zöttl *et al.*, 2016; Thorley *et al.*, 2018) and the naked mole-rat (Lacey & Sherman, 1991; Jarvis *et al.*, 1991; Gilbert *et al.*, 2020; Siegmann *et al.*, 2021). Younger and lighter individuals typically belong to subordinate groups, engaging in tasks like digging and tunnel maintenance (Jarvis, 1981**;** Hite *et al.*, 2019**;** Gilbert *et al.*, 2020), whereas heavier and older individuals tend to be dominant or breeders, primarily involved in nest maintenance and juvenile care (Jarvis, 1981; Hite *et al.*, 2019**;** Burda *et al.*, 2000). Previous research also highlights latency of emergence as an indicator of workgroup differences in African mole-rats (Hite *et al.*, 2019; Blecher & Oosthuizen, 2023). In naked mole rats, Hite *et al.* (2019) observed that subordinates exhibit faster exploratory latencies compared to dominants. Similarly, Blecher and Oosthuizen (2023) reported that in Damaraland mole-rats, workers—typically lighter and weaker—initiate exploration sooner and spent more time exploring, potentially reflecting their subordinate status or anxiety-like behavior. They also reported no significant difference in the total duration of tunnel exploration between workers and breeders, a finding corroborated by our data. Furthermore, previous studies have suggested that the division of individuals into the different workgroups was not influenced by sex (Hite *et al.*, 2019), which is also supported by our observations. These ideas partially align with our data, as well as with findings on the Damaraland mole-rat, a genetically close relative of the naked mole-rat, which showed that subordinate individuals enter new spaces more quickly and explore new areas more thoroughly than breeders (Hite *et al.*, 2019).

Together, these studies highlight how individual traits such as performance, body mass, and age may shape task allocation and exploration behavior in mole-rats' colonies, with subordinate typically being lighter and younger, and often exhibiting delayed yet more prolonged exploration compared to their dominant counterparts. While these patterns are generally consistent, the relationship between tasks and individual traits may vary across colonies (Gilbert *et al.*, 2020), and task allocation systems might be more complex than previously thought (Gilbert *et al.*, 2020; Siegmann *et al.*, 2021; Yamakawa *et al.*, 2024). Further research is needed to clarify the relationship between individual traits and specific colony tasks, such as digging, transporting, and breeding. This could provide deeper insights into how individual characteristics shape activity levels and social organization within colonies.

Conclusions

In our study, we found that age, body mass and performance in BF correlate with activity levels, boldness, and exploration in naked mole rats. Notably, we observed enhanced bite strength in younger individuals, which may represent a unique type of adaptation. Our observations suggest distinct behavioral patterns based on individual traits: younger, heavier, and stronger animals were more likely to display high activity levels and engage in risk-taking behaviors, whereas younger, lighter, and weaker individuals exhibited greater exploratory tendencies. We suggest that individual temperament may explain the observed behavioral differences during the biting and exploration experiments, and that the connection between exploration, activity, and performance may be influenced by the specific tasks assigned to individuals within their workgroups. Further research should incorporate assessments of individual temperament alongside social factors such as isolation and task allocation to refine these hypotheses. This approach could deepen our understanding of workgroup dynamics in naked mole-rat colonies, clarify how individuals are distributed within these groups, and reveal how this distribution influences their overall performance.

References

Aguirre L., Herrel A., van Damme R. & E. Matthysen, 2002. Ecomorphological analysis of trophic niche partitioning in a tropical savannah bat community. *Proc. Roy. Soc. B: Biol. Sc.* **269**(1497):1271–1278. DOI: 10.1098/rspb.2002.2011.

Aguirre L., Herrel A., van Damme R. & E. Matthysen, 2003. The implications of food hardness for diet in bats. *Funct. Ecol.* **17**:201–212. DOI: 10.1046/j.1365-2435.2003.00721.x.

Amari M., Mary A., Zablocki-Thomas P., Bourgeois A. & E. Pouydebat, 2024. Positive effect of a diggable substrate on the behaviour of a captive naked mole rat colony. *Sci. Rep.* **14**:20138. DOI: 10.1038/s41598-024-64146-w.

Anderson R., Mcbrayer L. & A. Herrel, 2008. Bite force in vertebrates: Opportunities and caveats for use of a nonpareil whole animal performance measure. *Biol. J. Linn. Soc.* **93**:709–720. DOI: 10.1111/j.1095-8312.2007.00905.x.

Arnold S., 1983. Morphology, performance and fitness. *Am. Zool.* **23**:347–361. DOI: 10.1093/icb/23.2.347.

Bates D., Maechler M., Bolker B. & S. Walker, 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*. **67**(1):1-48. DOI: 10.18637/jss.v067.i01.

Becerra F., Echeverría A., Casinos A. & A. Vassallo, 2014. Another one bites the dust: Bite force and ecology in three caviomorph rodents (Rodentia, Hystricognathi). *J. Exp. Zoo*, *Part A, Ecol. Genet. Physio*. **321**(4):220-232. DOI: 10.1002/jez.1853.

Bennett N. & C. Faulkes, 2000. African mole-rats: Ecology and eusociality. *Cambridge University Press*. ISBN: 9780521771993

Bibancos T., Jardim D., Aneas I. & S. Chiavegatto, 2007. Social isolation and expression of serotonergic neurotransmission-related genes in several brain areas of male mice. *Genes Brain Behav.* **6**:529–539. DOI: 10.1111/j.1601-183X.2006.00280.x

Binder W. & B. Van Valkenburgh, 2000. Development of bite strength and feeding behaviour in juvenile spotted hyenas (*Crocuta crocuta*). *J. Zool. (Lond.)*. **252**:273–283. DOI: 10.1111/j.1469-7998.2000.tb00622.x

Blecher A., Bennett N., Medger K., Hagenah N., Ganswindt A., & M. Oosthuizen, 2020. Effect of colony disruption and social isolation on naked mole-rat endocrine correlates. *Gen. Comp. Endocrinol*. **295**:113520. DOI: 10.1016/j.ygcen.2020.113520.

Blecher A. & M. Oosthuizen, 2023. Social Isolation Does Not Alter Exploratory Behaviour, Spatial Learning and Memory in Captive Damaraland Mole-Rats (*Fukomys damarensis*). *Animals*. **13**(3):543. DOI: 10.3390/ani13030543.

Boag P. & P. Grant, 1981. Intense natural selection in a population of Darwin's Finches (Geospizinae) in the Galapagos. *Science*. **214**(80):82–85. DOI: 10.1126/science.214.4516.82.

Brett R., 1991. The ecology of naked mole-rat colonies: burrowing, food and limiting factors. In P. Sherman, J. Jarvis & Alexander R. (*Eds*.). The Biology of the Naked Mole-Rat (pp. 137–184). New Jersey, NJ: *Princeton University Press*. DOI: 10.1515/9781400887132-008.

Buffenstein, R. & W. Craft, 2021. The idiosyncratic physiological traits of the naked mole-rat; a resilient animal model of aging, longevity, and healthspan. In: Buffenstein R., Park T., & Holmes M. (*Eds*.). *The Extraordinary Biology of the Naked Mole-Rat* (pp. 221–254). Cham, Switzerland: *Springer*. DOI: 10.1007/978-3-030-65943-1_8.

Burda H., 1999. Syndrome of eusociality in African subterranean mole-rats (Bathyergidae, Rodentia), its diagnosis and aetiology. In: Wasser S. (*Eds*.). *Evolutionary Theory and Processes: Modern Perspectives* (pp. 385–418). Dordrecht: *Springer Netherlands*.

Burda H., Honeycutt R., Begall S., Grütjen O. & A. Scharff, 2000. Are naked and common mole-rats eusocial and if so, why? *Behav. Ecol. Sociobiol*. **47**:293–303. DOI: 10.1007/s002650050669.

Byron C., Borke J., Yu J., Pashley D., Wingard C. & M. Hamrick, 2004. Effects of increased muscle mass on mouse sagittal suture morphology and mechanics. *Anatomical Record*. **279**: 676–684. DOI: 10.1002/ar.a.20055.

Christiansen P. & S. Wroe, 2007. Bite forces and evolutionary adaptations to feeding ecology in carnivores. *Ecology*. **88**:347–358. DOI: 10.1890/0012-9658(2007)88[347:bfaeat]2.0.co;2

Clarke F. & C. Faulkes, 2001. Intracolony Aggression in the Eusocial Naked Mole-Rat, *Heterocephalus glaber*. *Anim. Behav*. **61**:311–324. DOI: 10.1006/anbe.2000.1573.

Cornette R., Tresset A., Houssin C., Pascal M. & A. Herrel, 2015. Does bite force provide a competitive advantage in shrews? The case of the greater white-toothed shrew. *Biol. J. Linn. Soc*. **114**(4):795-807. DOI: 10.1111/bij.12423.

Cox P., Faulkes C. & N. Bennett, 2020. Masticatory musculature of the African mole-rats (Rodentia: Bathyergidae). *PeerJ*. **8**:e8847. DOI: 10.7717/peerj.8847.

Crusio W., 2021. Genetic dissection of mouse exploratory behaviour. *Behav Brain Res*. **125**(1-2):127-32. DOI: 10.1016/s0166-4328(01)00280-7.

van Daele P., Herrel A., & D. Adriaens, 2009. Biting performance in teeth digging African mole-rats (*Fukomys*, Bathyergidae, Rodentia). *Phys. Bioch. Zool*. **82**(1):40–50. DOI: 10.1086/594379.

van Daele P., Desmet N., Šumbera, R. & D. Adriaens, 2019. Work behaviour and biting performance in the cooperative breeding Micklem's mole-rat *Fukomys micklemi* (Bathyergidae, Rodentia). *Mammal. Biol*. **95**:69–76. DOI: 10.1016/j.mambio.2019.02.002.

Desmet N., van Daele P. & D. Adriaens, 2013. A methodological analysis of behavioural observation in social African mole rats (Bathyergidae, Rodentia). *Mammalia*. **77**(1):59-69. DOI: 10.1515/mammalia-2012-0021.

Dumont E. & A. Herrel, 2003. The effects of gape angle and bite point on bite force in bats. *J. Exp. Biol.* **206**:2117– 2123. DOI: 10.1242/jeb.00375.

Erickson G., Lappin A. & K. Vliet, 2003. The ontogeny of bite-force performance in American alligator (*Alligator mississippiensis*). *J. Zool.* **260**:317–327. DOI: 10.1017/S0952836903003819.

Faulkes C. & N. Bennett, 2021. Social evolution in African mole-rats–a comparative overview. *The Extraordinary Biology of the Naked Mole-Rat*. 1-33. DOI: 10.1007/978-3-030-65943-1_1.

Freeman P. & C. Lemen, 2008a. A simple morphological predictor of bite force in rodents. *J. Zool*. **275**(4):418–422. DOI: 10.1111/j.1469-7998.2008.00459.x.

Freeman P. & C. Lemen, 2008b. Measuring bite force in small mammals with a piezo-resistive sensor. *J. Mamm*. **89**(2):513–517. DOI: 10.1644/07-mamm-a-101r.1.

Gilbert J., Rossiter S. & C. Faulkes, 2020. The relationship between individual phenotype and the division of labour in naked mole-rats: it's complicated. *PeerJ*. **8**:e9891. DOI: 10.7717/peerj.9891.

Ginot S., Herrel A., Claude J. & L. Hautier, 2019. Morphometric models for estimating bite force in *Mus* and *Rattus*: mandible shape and size perform better than lever-arm ratios. *J Exp Biol*. **222**(12): jeb204867. DOI: 10.1242/jeb.204867.

Grippo A., Wu K., Hassan I. & C. Carter, 2008. Social Isolation in Prairie Voles Induces Behaviors Relevant to Negative Affect: Toward the Development of a Rodent Model Focused on Co-Occurring Depression and Anxiety. *Depress. Anxiety*. **25**:17–26. DOI: 10.1002/da.20375.

Guo M., Wu C., Liu W., Yang J. & D. Chen, 2004. Sex difference in psychological behavior changes induced by long-term social isolation in mice. *Prog. Neuro-Psychopharmacol. Biol. Psych.* **28**:115–121. DOI: 10.1016/j.pnpbp.2003.09.027.

Hernandez L. & P. Motta, 1997. Trophic consequences of differential performance: ontogeny of oral jaw crushing performance in the sheepshead, *Archosargus probatocephalus* (Teleostei: Sparidae). *J. Zool. (Lond.)*. **243**:737–756. DOI: 10.1111/j.1469-7998.1997.tb01973.x.

Herrel A., Spithoven L., van Damme R. & F. De Vree, 1999. Sexual dimorphism of head size in *Gallotia galloti*; testing the niche divergence hypothesis by functional analyses. *Fun. Ecol*. **13**: 289–297. DOI: 10.1046/j.1365-2435.1999.00305.x.

Herrel A., Podos J., Huber S. & A. Hendry, 2005a. Evolution of bite force in Darwin's finches: a key role for head width. *J. Evol. Biol*. **18**:669–675. DOI: 10.1111/j.1420-9101.2004.00857.x.

Herrel A., Podos J., Huber S. & A. Hendry, 2005b. Bite performance and morphology in a population of Darwin's finches: implications for the evolution of beak shape. *Funct. Ecol*. **19**:43–48. DOI: 10.1111/j.0269-8463.2005.00923.x.

Herrel A. & A. Gibb, 2006. Ontogeny of performance in vertebrates. *Phys. Bioch. Zool.* **79**:1–6. DOI: 10.1086/498196.

Herrel A. & J. O'Reilly, 2006. Ontogenetic scaling of bite force in lizards and turtles. *Physiol. Biochem. Zool.* **79**:31–42. DOI: 10.1086/498193.

Herrel A., de Smet A., Aguirre L. & P. Aerts, 2008. Morphological and mechanical determinants of bite force in bats: Do muscles matter? *J. Exp. Biol.* **211**(1):86–91. DOI: 10.1242/jeb.012211.

Herrel A., Petrochic S. & M. Draud, 2017. Sexual dimorphism, bite force and diet in the diamondback terrapin. *J. Zool.* **304**(3):217–224. DOI: 10.1111/jzo.12520.

Hite N., Germain C., Cain B., Sheldon M., Perala S. & D. Sarko, 2019. 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. DOI: 10.3389/fnint.2019.00070.

Husak J., Lappin A., Fox S. & J. Lemos-Espinal, 2006. Bite-force performance predicts dominance in male venerable collared lizards (*Crotaphytus antiquus*). *Copeia*, **2**:301–306. DOI: 10.1643/0045-8511(2006)6[301:BPPDIM]2.0.CO;2.

Husak J., Lappin A. & R. van Den Bussche, 2009. The fitness advantage of a high-performance weapon. *Biol. J. Linn. Soc.* **96**:840–845. DOI: 10.1111/j.1095-8312.2008.01176.x.

Jarvis J., 1981. Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. *Science*, **212**(4494):571–573. DOI: 10.1126/science.7209555.

Jarvis J., O'Riain M. & E. McDaid, 1991. Growth and factors affecting body size in naked mole-rats. In: Sherman P., Jarvis J., Alexander R. (*Eds*.). The Biology of the Naked Mole-Rat (pp. 358–383). Princeton, NJ: *Princeton University Press*. DOI: 10.1515/9781400887132-015.

Jarvis J., O'Riain M., Bennett N. & P. Sherman, 1994. Mammalian eusociality: a family affair. *Trends Ecol. Evol.* **9**:47–51. DOI: 10.1016/0169-5347(94)90267-4.

Kraus A., Lövy M., Mikula O., Okrouhlík J., Bennett N., Herrel A. & R. Šumbera, 2022. 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**(9): 2344-2355. DOI: 10.1111/1365-2435.14132.

Kubiak B., Maestri R., de Almeida T., Borges L., Galiano D., Fornel R., & T. de Freitas, 2018. Evolution in action: Soil hardness influences morphology in a subterranean rodent (Rodentia: Ctenomyidae). *Biol J. Linn. Soc.* **125**(4):766–776. DOI: 10.1093/biolinnean/bly144.

Lacey E. & P. Sherman, 1991. Social organization of naked mole-rat colonies: evidence for divisions of labor. In: Sherman P., Jarvis J., Alexander R. (*Eds*.). The Biology of the Naked Mole-Rat (pp. 275–336). Princeton, NJ: *Princeton University Press*. DOI: 10.1515/9781400887132-013.

Lappin A. & J. Husak, 2005. Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *Am. Nat.* **166**:426–436. DOI: 10.1086/432564.

Law C., Young C. & R. Mehta, 2016. Ontogenetic scaling of theoretical bite force in Southern Sea Otters (*Enhydra lutris nereis*). *Physiol. Biochem. Zool.* **89**:347–363. DOI: 10.1086/688313.

Lovegrove B., 1989. The cost of burrowing by the social mole rats (Bathyergidae) *Cryptomys damarensis* and *Heterocephalus glaber*: The role of soil moisture. *Phys. Zool.*, **62**(2):449–469. DOI: 10.1086/physzool.62.2.30156179.

McIntosh A. & P. Cox, 2016a. The impact of gape on the performance of the skull in chisel-tooth digging and scratch digging mole-rats (Rodentia: Bathyergidae). *Roy. Soc. Op. Sci.* **3**(10):1–10. DOI: 10.1098/rsos.160568.

McIntosh A. & P. Cox, 2016b. Functional implications of craniomandibular morphology in African mole-rats (Rodentia: Bathyergidae). *Biol. J. Linn. Soc.* **117**:447–462. DOI: 10.1111/bij.12691.

Magalhães A., Damasceno E., & D. Astúa, 2020. Bite force sexual dimorphism in Canidae (Mammalia: Carnivora): Relations between diet, sociality and bite force intersexual differences. *Hystrix*. **31**(2):1–6. DOI: 10.4404/hystrix-00332-2020.

Majelantle T., Ganswindt A., Pirk C., Bennett N. & D. Hart, 2022. Aggression, Boldness, and Exploration Personality Traits in the Subterranean Naked Mole-Rat (*Heterocephalus glaber*) Disperser Morphs. *Animals (Basel)*. **12**(22):3083. DOI: 10.3390/ani12223083.

Marshall C., Guzman A., Narazaki T., Sato K., Kane E. & B. SterbaBoatwright, 2012. The ontogenetic scaling of bite force and head size in loggerhead sea turtles (*Caretta caretta*): implications for durophagy in neritic, benthic habitats. *J. Exp. Biol*. **215**:4166–4174. DOI: 10.1242/jeb.074385.

Mehlhorn K., Newell B., Todd P., Lee M., Morgan K., Braithwaite V., Hausmann D., Fiedler K. & C. Gonzalez, 2015. Unpacking the exploration-exploitation tradeoff: a synthesis of human and animal literatures. *Decision*. **2**(3):191-215. DOI: 10.1037/dec0000033.

van der Meij M. & R. Bout, 2004. Scaling of jaw muscle size and maximal bite force in finches. *J. Exp. Biol*. **207**:2745–2753. DOI: 10.1242/jeb.01091.

Meyers J., Herrel A. & J. Birch, 2002. Scaling of morphology, bite force and feeding kinematics in an iguanian and a scleroglossan lizard. In: P. Aerts, K. D'Aout, A. Herrel, & R. Van Damme (*Eds*.) Topics in Functional and Ecological Vertebrate Morphology (pp. 47–62). Maastricht, Netherlands, *Shaker*.

Mooney S., Filice D., Douglas N. & M. Holmes, 2015. Task specialization and task switching in eusocial mammals. *Anim. Behav*. **109**:227-233. DOI: 10.1016/j.anbehav.2015.08.019.

Nogueira M., Peracchi A. & L. Monteiro, 2009. Morphological correlates of bite force and diet in the skull and mandible of phyllostomid bats. *Funct. Ecol*. **23**(4):715–723. DOI: 10.1111/j.1365-2435.2009.01549.x.

O'Riain M. & J. Jarvis, 1997. Colony Member Recognition and Xenophobia in the Naked Mole-Rat. *Anim. Behav*. **53**:487–498. DOI: 10.1006/anbe.1996.0299.

van Oers K., Klunder M. & P. Drent, 2005. Context dependence of personalities: risk-taking behavior in a social and a nonsocial situation. *Behav Ecol*. **16**(4):716–723. DOI: 10.1093/beheco/ari045.

Page H., Sweeney A., Pilko A. & N. Pinter-Wollman, 2018. Underlying mechanisms and ecological context of variation in exploratory behaviour of the Argentine ant, *Linepithema humile*. *J. Exp. Biol*. **221**:jeb188722. DOI: 10.1242/jeb.188722.

Peterson R. & J. Cavanaugh, 2019. Ordered quantile normalization: a semiparametric transformation built for the cross-validation era. *Journal of Applied Statistics*. **47**:13-15, 2312-2327. DOI: 10.1080/02664763.2019.1630372.

Peterson R., 2021. Finding Optimal Normalizing Transformations via bestNormalize. *The R Journal*. **13**:1, 310-329. DOI: 10.32614/RJ-2021-041.

R Core Team, 2022. R: A language and environment for statistical computing. Vienna, Austria: *R Foundation for Statistical Computing.*

Réale D., Reader S., Sol D., McDougall P. & N. Dingemanse, 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews*, **82**(2):291–318. DOI: 10.1111/j.1469-185X.2007.00010.x.

Russell J., McMorland A. & J. MacKay, 2010. Exploratory behaviour of colonizing rats in novel environments. *Anim. Behav*. **79**(1), 159–164. DOI: 10.1016/j.anbehav.2009.10.020.

Sakamoto M., Lloyd G. & M. Benton, 2010. Phylogenetically structured variance in felid bite force: the role of phylogeny in the evolution of biting performance. *J. Evol. Biol*. **23**:463–478. DOI: 10.1111/j.1420-9101.2009.01922.x.

Santana S., Dumont E. & J.L. Davis, 2010. Mechanics of bite force production and its relationship to diet in bats. *Funct. Ecol*. **24**:776–784. DOI: 10.1111/j.1365-2435.2010.01703.x.

Sherman P., Jarvis J. & R. Alexander, 1991. The Biology of the Naked Mole-Rat. Princeton, NJ: *Princeton University Press*.

Sherman P., Jarvis J. & S. Braude, 1992. Naked mole-rats. *Sci. Amer*. **267**:72-78. DOI: 10.1038/scientificamerican0892-72.

Siegmann S., Feitsch R., Hart D., Bennett N., Penn D. & M. Zöttl, 2021. Naked mole-rats (*Heterocephalus glaber*) do not specialise in cooperative tasks. *Ethology*. **127**(10):850–864. DOI: 10.1111/eth.13160.

Sih A., Bell A., Johnson J. & R. Ziemba, 2004. Behavioral syndromes: an intergrative overiew. *Q Rev Biol*. **79**(3):241-77. DOI: 10.1086/422893.

Sklíba J., Lövy M., Burda H. & R. Šumbera, 2016. 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. DOI: 10.1038/srep37497.

Stein B., 2000. Morphology of subterranean rodents. In Lacey E., Patton J. & Cameron G. (*Eds.*). Life underground: The biology of subterranean rodents (pp. 19–61). *University of Chicago* Press.

Svartberg K., 2002. Shyness–boldness predicts performance in working dogs. *App. Ani. Behav. Sci*. **79**(2):157–174. DOI: 10.1016/s0168-1591(02)00120-x.

Thomason J., Russell A. & M. Morgeli, 1990. Forces of biting, body size, and masticatory muscle tension in the opossum *Didelphis virginiana*. *Can. J. Zool.* **68**(2):318–324. DOI: 10.1139/z90-047.

Thomason J., 1991. Cranial strength in relation to estimated biting forces in some mammals. *J. Zool.* **69**(9):2326–2333. DOI: 10.1139/z91-327.

Thompson E., Biknevicius A., & R. German, 2003. Ontogeny of feeding function in the gray short-tailed opossum *Monodelphis domestica*: empirical support for the constrained model of jaw biomechanics. *J. Exp. Biol.* **206**(5):923– 932. DOI: 10.1242/jeb.00181.

Thorley J., Mendonça R., Vullioud P., Torrents-Ticó M., Zöttl M., Gaynor D. & T. Clutton-Brock, 2018. No task specialization among helpers in Damaraland mole-rats. *Anim. Behav.* **143**:9–24. DOI: 10.1016/j.anbehav.2018.07.004.

Wickham H., 2016. ggplot2: Elegant Graphics for Data Analysis. *Springer-Verlag New York.*

Wilson D., Clark A., Coleman K. & T. Dearstyne, 1994. Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*. **9**(11):442–446. DOI: 10.1016/0169-5347(94)90134-1.

Wroe S., McHenry C. & J. Thomason, 2005. 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. DOI: 10.1098/rspb.2004.2986.

Yamakawa M., Miura K. & N. Kutsukake, 2024. Helping syndrome is partially confirmed in the eusocial naked mole-rat. *Animal Behaviour*. **210**:289-301. DOI: 10.1016/j.anbehav.2024.01.005.

Zablocki-Thomas P., Herrel A., Hardy I., Rabardel L., Perret M., Aujard F. & E. Pouydebat, 2018. Personality and performance are affected by age and early life parameters in a small primate. *Ecol. and Evol.* **8**(9):4598–4605. DOI: 10.1002/ece3.3833.

Zöttl M., Vullioud P., Mendonça R., Ticó M., Gaynor D., Mitchell A. & T. Clutton-Brock, 2016. Differences in cooperative behavior among Damaraland mole rats are consequences of an age-related polyethism. *Proc. Natl. Acad. Sci.* **113**(37):10382–10387. DOI: 10.1073/pnas.1607885113.