Laterality in the Cape mole-rat, *Georychus capensis*

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Highlights

- Solitary Cape mole-rats demonstrate a left-turning bias in both captive and wild populations.
- Individual left bias is more prominent in wild populations.
- The aggressive nature of Cape mole-rats could play a major role in behavioural asymmetry in turning biases.

Abstract

Behavioural lateralization, the differential use one side of the body, and/or the bilateral use of sensory organs or limbs, is common in many vertebrates. One way in which behavioural lateralization can be detected in animals is through turning biases, which is an inherent preference to either turn left or right. Mole-rats are a unique group of mammals that demonstrate a wide range of social organizations ranging from solitary to eusociality. Behavioural asymmetry has not previously been investigated in mole-rats. In this study, captive and wild solitary Cape-mole rats (*Georychus capensis*) were investigated for individual (relative laterality (L_R)) and population-level (absolute laterality (L_A)) laterality. Mole-rats in the captive group were in the laboratory for at least one year, whereas the wild group were captured and experimented on within 2 weeks of capture. Animals were placed in a Y-maze facing away from the centre of the maze, and the turn towards the centre of the maze was evaluated to determine individual turning biases. Lateralized individual turning biases were more apparent in wild (7/9), compared to captive (3/10) individuals. Both captive and wild populations demonstrated a left bias, which was higher in wild animals, but not significantly so. Cape mole-rats are extremely xenophobic and aggressive, and this aggressive behaviour may underlie the turning biases in these animals, as aggression is primarily a right hemisphere dominant process. The reduced lateralization observed in captive animals may be due to a reduced need for these behaviours as a result of different environments in captivity.

Keywords: Laterality; Behavioural asymmetry; Cape mole-rat; *Georychus capensis;* Wild; Captive

1. Introduction

Lateralization or laterality is the result of bilateral asymmetries in the brain resulting in biases in behaviour (Wiper, 2017). Ample evidence from several vertebrate, non-human animals has shown lateralization to be a universal feature of animal brains (Rogers et al., 2017; Petrazzini et al., 2020; Vallortigara and Rogers, 2005, 2020). Genetic and environmental factors such as light, hormones, rearing environment, pollution and stress have been determined to influence the development of the lateralized brain (Petrazzini et al., 2020). Laterality of an organism may likely be the result of the interaction between genetic and environmental drivers (Wiper, 2017; Cowell and Denenberg, 2002). Comparisons between wild and captive parrots foot preferences showed no significant differences in the direction or strength in laterality (Brown and Magat, 2011). However, it is uncertain whether this may apply to species other than birds, with studies lacking in non-primate mammals to detect whether wild and captive animals may differ in behavioural asymmetry.

Hemispheric asymmetries result in the differential use of cognitive function in the left versus the right hemisphere (Corballis, 2009; Walker, 1980), the left hemisphere specialises in the control of behaviour under familiar settings, whereas the right hemisphere specialises in responding to novel or unexpected stimuli (Leliveld et al., 2013; Rogers et al., 2013). An example includes the differential use of eyes (reviewed by Petrazzini et al. (2020)), where the right eye is used for feeding or prey catching in chicks (Mench and Andrew, 1986) and pigeons (Güntürkün and Kesch, 1987; Güntürkün et al., 2000), whereas the left eye used for escape response to predators in dunnarts (Lippolis et al., 2005), horses (Austin and Rogers, 2007), lizards (Bonati et al., 2013, 2010) and toads (Lippolis et al., 2002). It is, therefore, possible that a dominant hemisphere can dictate control of animal behaviour, since each hemisphere carries out different cognitive and emotional processes(Rogers, 2010; Rogers et al., 2013).

Lateralized behaviour can be observed in many forms, but a common measure of behavioural lateralization is a bias in the direction an animal turns during orientation or navigation (ie. side bias) (Kight et al., 2008; Espmark and Kinderås, 2002). Biases in this way can vary both on an individual level and a population level (Frasnelli and Vallortigara, 2018; Byrne et al., 2004). At the population level, the majority of individuals may demonstrate a similar bias, whereas, at an individual level, an individual will have its own bias regardless of the bias of the general population (Wiper, 2017; Vallortigara and Rogers, 2005). These behavioural inclinations, at an individual level, have been associated with positive benefits such as avoiding the duplication of function in both hemispheres (Ghirlanda and Vallortigara, 2004; Vallortigara, 2006; Wiper, 2017), but also negative costs such as decreased interhemispheric communication (Dadda et al., 2009). (Wiper, 2017; Petrazzini et al., 2020). An example of interhemispheric communication can be observed in the teleost fish *Girardinus falcatus,* where highly lateralised individuals learned faster to catch live prey while simultaneously performing predator vigilance (Dadda and Bisazza, 2006). Highly lateralized individuals at least in fish, may more readily attend the feeding task with one eye and monitor for predators with the other eye (Dadda et al., 2009). Less lateralized individuals may not be able to utilise both hemispheres as efficiently as highly lateralized individuals, which may result increased vulnerability to predation or missed feeding opportunities. Despite these costs, laterality should provide an overall fitness benefit to the organism, but these costs do not explain population-level laterality(Vallortigara, 2006; Ghirlanda et al., 2009). Population-level asymmetries from antagonistic encounters are predictable and can be exploited by competitors (Ghirlanda et al., 2009; Ghirlanda and Vallortigara, 2004). Interestingly, models of lateralized individuals within a population predict that left and right type individuals can be evolutionary stable if in unequal numbers and has a frequency-dependent cost and benefit (Ghirlanda and Vallortigara, 2004; Raymond et al., 1996). An example of individual and population-level laterality was observed in sheep, where individuals had left and right biases in the direction of jaw movements during rumination or cud chewing, but in a different task had an overall right-side bias in the population avoiding an obstacle to rejoin conspecifics (Versace et al., 2007). Another example of turning biases was observed in fish, where they preferentially turned left to use their right eye to view a predator (Bisazza et al., 1997).

Behavioural laterality can have direct ecological consequences for survival by modulating the attributes of an individual such as a faster reaction time towards predators (Vallortigara, 2006) or turning when escaping a predator (Rogers and Andrew, 2002). Laterality can also influence reproduction through aggressiveness and courtship (Krakauer et al., 2016; Cantalupo et al., 1996). Aggressiveness can be used to maintain dominance, defend territories, and protect offspring (Ariyomo and Watt, 2013), where increased aggressiveness resulted in higher mating success in the greater sage-grouse, *Centrocercus urophasianus* (Krakauer et al., 2016). Other examples of fitness benefits to reproduction are depauperate, but behavioural laterality observations of aggression, stress and fear/anxiety (has been reviewed by Ocklenburg et al. (2016) and Leliveld et al. (2013)). Behavioural laterality has been investigated in terms of aggression in mammals are scarce, with research done in horses (Austin and Rogers, 2012), farrow deer *Dama dama* (Jennings, 2012), dogs (Siniscalchi et al., 2008, 2019), gelada baboons *Theropithecus gelada* (Casperd and Dunbar, 1996) and chimpanzees *Pan troglodytes* (Parr and Hopkins, 2000). The study in chimpanzees *Pan troglodytes* (Parr and Hopkins, 2000) demonstrated a right hemisphere dominance during negative emotional scenarios following scenes of play and aggression. Austin and Rogers (2012) found that feral horses have left-side biases of aggression, vigilance and reactivity responses to agonistic encounters. Dogs turn their head to the left side in response to thunderstorms (Siniscalchi et al., 2008). Aggressive behaviour of dogs towards sheep (gripping and the straight approach) occurred more frequently when dogs ran in a circle around the livestock in a counterclockwise direction (Siniscalchi et al., 2019). The visual analyses of the sheep were primarily observed through the left visual hemisphere which indicates a right hemisphere dominance (Siniscalchi et al., 2019). The majority of these studies have found a right hemisphere bias following agonistic encounters rather than aggressive responses. Agonistic encounters is likely to differ from aggressive encounters which intend to hurt another individual which may have resulted in the observed laterality differences (Jennings, 2012).

Only limited work has been done on subterranean mammals, owing to the inherent difficulties of observing and studying them, both in the laboratory and in the field (Burda et al., 1990; Kimchi and Terkel, 2001). Subterranean mammals that construct burrow systems, require a highly developed and efficient directional orientation sense to survive in a harsh underground environment (Hildebrand, 1985). The Cape mole-rat (*Georychus capensis,* Pallas, 1778) inhabit Southern Africa primarily in the eastern to western Cape provinces, with isolated populations in KwaZulu Natal near the Lesotho border and in the Mpumalanga Province (Bennett et al., 2006). These mole-rats are solitary, aggressive, xenophobic and highly territorial; this is also observed in captive individuals when another individual is placed within the same cage (Bennett et al., 2006). Cape mole-rats have a herbivorous diet consisting of geophytes with some vegetation that grows above ground (Bennett et al., 2006). These food items are found during excavating their tunnel systems, with their burrow system exceeding 130 m in length with a diameter of 100 mm (Bennett et al., 2006). They are generally considered to be nocturnal, with some activity occurring before dawn and after dusk (Oosthuizen et al., 2003).

The Cape mole-rat is an ideal model to investigate laterality in a subterranean mammal due to its temperamental nature (xenophobic and aggressive), as well as requiring energy efficiency due to being a burrow dwelling animal (Bennett et al., 2006; Lovegrove, 1989). Aggressiveness is well documented to be a consistently a right hemisphere process (Bisazza and de Santi, 2003; Vallortigara and Rogers, 2005), and would make it likely that the Cape mole-rat may demonstrate behavioural asymmetry through a predominantly right hemisphere process (i.e. left-turning biases). These qualities can facilitate behavioural asymmetry research to understand whether specific behavioural attributes (e.g. aggression) or energetically expensive processes (e.g. digging) may predominate other lateralized environmental processes (e.g. predator responses and foraging) in a subterranean mammal. Cape-mole rats are exposed to predation from snakes, jackals, birds and mongooses during mound formation, dispersing or from burrows being flooded from heavy rain (Bennett et al., 2006). When the relative importance of a response to a predator is removed (e.g. a captive population versus a wild population), it is possible that behavioural asymmetries may change. In support of this, a range of species demonstrate left hemisphere control during non-stressful situations and right hemisphere responses to unexpected and or emergency stimuli (Rogers, 2010, 2008). One example includes the chronic stress of rats resulted in physiological changes in the neurons in the cortex of the right hemisphere but not the left hemisphere (Perez-Cruz et al., 2009).

There may, however, be circumstances (especially in the wild) where a right hemisphere bias may be preferable, which assists in predator responses. However, the well-being of animals in captivity should favour left hemisphere dominance, particularly situations that are likely to be stressful (Rogers, 2010). A left hemisphere response will result in an attenuated stress response, for example, a reduced adverse response to light and sound (Morgan and Tromborg, 2007). This also emphasizes the benefit of hemispheric dominance in specific situations, allowing each hemisphere to process different sensory inputs and carry out different functions, resulting in overall increased brain efficiency that may increase fitness (Vallortigara and Rogers, 2020). Lastly, since each hemisphere controls the opposite side of the body (Bisazza et al., 1998), these contexts can bias the direction of a turn and emphasise the importance of behavioural lateralization to animal ecology (Vallortigara and Rogers, 2005; Ghirlanda et al., 2009; Ghirlanda and Vallortigara, 2004).

2. Material and methods

Experimental animals were collected near Darling, Western Cape, South Africa (33˚22′S, 15˚25′E) using Hickman live traps (Hickman 1979). Female Cape mole-rats were captured and transported to the University of Pretoria where experiments were conducted. We tested two groups of animals. The laboratory group comprised of 10 animals (body mass 166 ± 42 g) that were maintained in captivity for at least one year prior to the commencement of experiments. The wild group was comprised of 9 mole-rats (body mass 137 ± 31 g), these animals were subjected to experimental testing upon arrival in the laboratory (within two weeks of capture). All animals were housed individually in plastic crates lined with wood shavings and tissue paper was provided as nesting material. Animals were fed *ad libitum* on chopped sweet potato, apple, gem squash and carrot. A trapping permit was obtained from the Western Cape Nature conservation authority (AAA004-000412-0035).

2.1. Experimental design

Data for this experiment originate from the analysis of recorded videos from another project in which we looked at memory and learning of the animals (Oosthuizen et al., 2013), therefore the experimental design was dictated by that experiment. Animals were tested in a Perspex Y-maze, with each arm measuring 50 × 10 × 20 cm. The bottom of the Y-maze was filled with about 1 cm of water (at room temperature) to motivate animals to move. On the distal end of one arm was an escape hole connected to a Perspex tunnel and a dry nest box. Blocked tunnels were also placed at 'false exits' so that all arms looked identical from the centre. The goal was for the animals to find a dry nest box connected to one of the arms within one minute. Animals were released into the start arm facing away from the centre of the maze. Animals then would require to turn to face the center of the maze and move towards the center of the maze. This turn to face the maze was used for turning biases. Once at the center of the maze, animals had a choice to turn left or right, with a right turn leading to the escape hole (which was required for the learning and memory experiment and not used in the current study) (Oosthuizen et al., 2013). Animals were subjected to the Y-maze for four consecutive days with 10 trials per day. For each individual, the time between trials varied between 45 and 60 min. We were interested in the initial turn after the animals were inserted into the maze.

2.2. Data acquisition and statistics

All experiments were recorded with an overhead video recorder and data was captured manually after the completion of the experiments. The relative lateralization (L_R) was determined of each mole by computing the total number of left turns across all trials. This was determined according to the following formula: absolute value of [(number of left-turn - number of right-turn)/(total number of turns (40 in this case) x 100]. Absolute laterality (L_A) is the absolute value of the L_R, and represents the strength of the laterality irrespective of their preferences to turn left or right. The L_A index ranges from 0 (an individual that turned in equal proportion to the right and to the left—no bias) to 100 (an individual that turned in the same direction in all 40 trials). Each individual mole was tested for laterality regarding their turning biases by comparing the number of left turns to right turns in a non-parametric two-tailed binomial test (Table 1). To determine whether the population as a whole showed a non-random turning bias, we compared the L_R score of all the moles using a one-tailed *t*-test. We completed the same analysis for the captive and wild group separately. To compare L_A, we tested the effect of captivity (fixed factor) in a one-way ANOVA. Statistical analyses were performed with SPSS (version 25) (IBM Corp. Armonk, NY). For all analyses, data met the assumptions of normality and heteroscedasticity.

Table 1. Wild and captive individual level turning biases in the Cape mole-rat. For each individual, the total number of left and right turns are given with the total number of trials, together with the two-tailed binomial significance (p or ns for not significant) for individual laterality.

Mole #	Wild/captive	Left turn	Right turn	Total trials	Binomial probability
1	Wild	17	21	38	Ns
2	Wild	16	15	31	Ns
3	Wild	39	0	39	p<0.01
4	Wild	27	12	39	p=0.024
5	Wild	35	3	38	p<0.01
6	Wild	37	2	39	p<0.01
7	Wild	47	32	39	p<0.01
8	Wild	10	30	40	p<0.01
9	Wild	36	2	38	p<0.01
10	Captive	21	14	35	ns
11	Captive	33	4	37	p<0.01
12	Captive	24	16	40	ns
13	Captive	21	17	38	ns
14	Captive	38	2	40	p<0.01
15	Captive	21	9	30	ns
16	Captive	39	0	39	p<0.01
17	Captive	13	23	36	ns
18	Captive	23	16	39	ns
19	Captive	10	23	33	ns

3. Results

We determined the individual and population laterality of the Cape mole-rat. Lateralized turning biases were more consistent in wild individuals (7 out of 9) than in captive individuals (3 out of 10) (Table 1). Due to the small sample sizes, the power to detect a difference was minimal when comparing individual laterality between wild and captive individuals.

At the population level, when all mole-rats were considered together, a significant left-turning bias was detected (one-sample *t*-test, $t_{19} = 2.5$, $p = 0.02$). However, considered separately, the captive (one-sample *t*-test, $t_{10} = 1.55$, $p = 0.18$) and wild (one-sample *t*-test, $t_9 = 2.1$, $p = 0.07$) populations did not significantly differ in turning biases (Fig. 1).

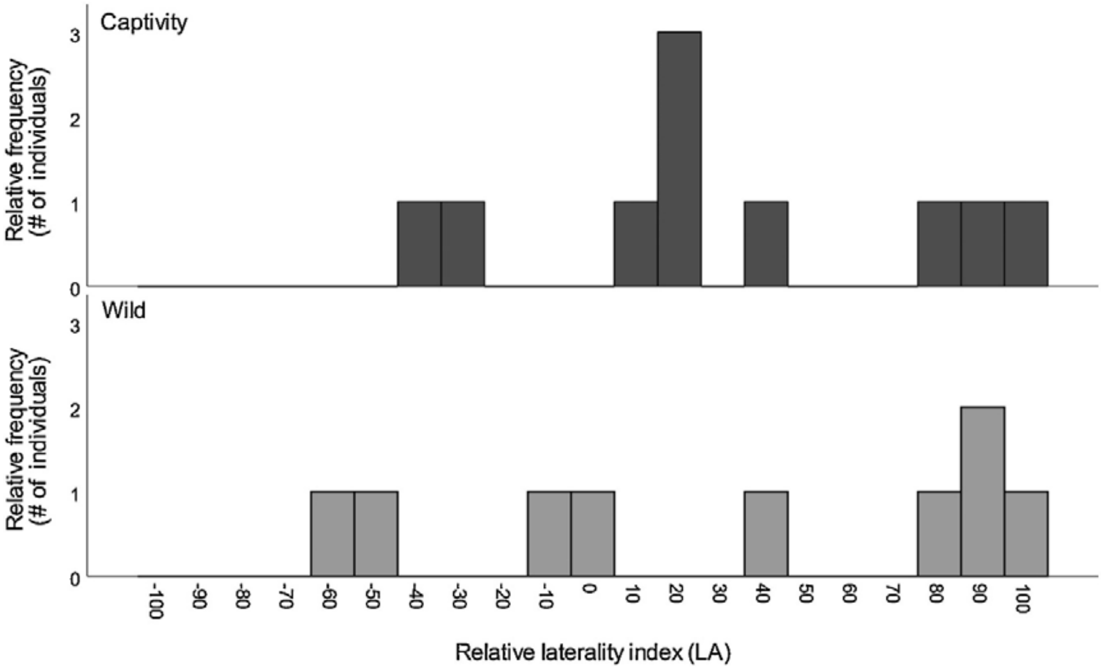

Fig. 1. The relative frequency of captive and wild Cape mole-rats along a relative laterality index. The X-axis scale from the left represents right turning with increased turning to the left as the index increased from -100 to 100. Relative laterality of 0 means an individual turned left and right in equal amounts demonstrating no behavioural asymmetry in turning biases.

The one-way ANOVA to test for the effect of captivity on LA showed no significant difference ($F_{1,17} = 0.85$, $p = 0.37$). Both groups demonstrated a similar strength in their left-turning bias, the wild group demonstrated a 59 % L_A and the captive group a 43 % L_A (Fig. 2).

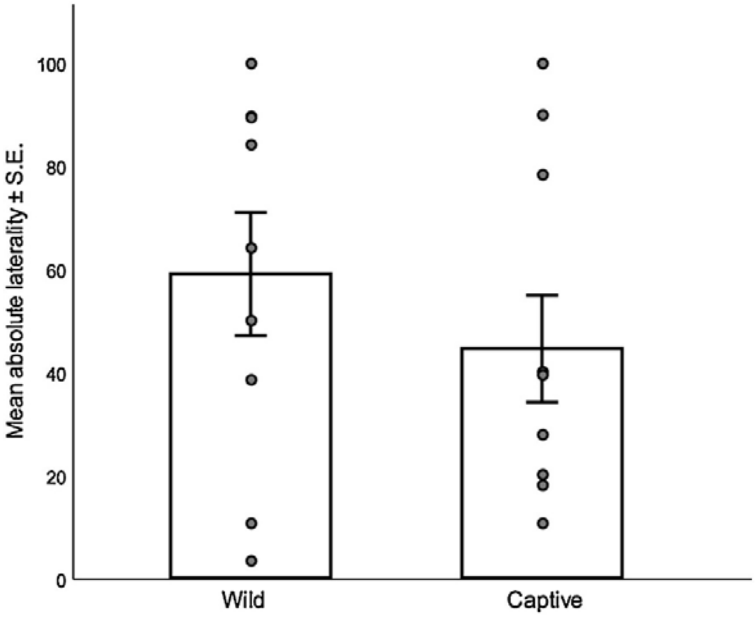

Fig. 2. The mean absolute laterality of wild and captive Cape mole-rats.

4. Discussion

Our study is the first to investigate the individual and population-level laterality of a solitary mole-rat species through the use of turning biases. At the individual level, our results demonstrate clear lateralized turning biases in most wild individuals, which was only apparent in a few captive individuals. All individuals together demonstrated a significant left-turning population bias, which was not apparent when captive and wild individuals were analysed separately. Furthermore, the strength (mean absolute laterality of a group) of the lateralized turning biases was higher in individuals from the wild group as compared to the group of individuals maintained in captivity.

Learning is important in side preference tasks, as dopamine may modify an inherent turning bias (Glick and Ross, 1981). This is due to the different sides of the brain containing different amounts of dopamine, which directly influences spatial preferences through the effects of learning (Glick and Ross, 1981). Due to the design of the experiment, the initial turn had minimal influence on the success of the learning part of the experiment, and therefore initial turning preferences should remain unaffected by the effects of learning.

A study on the blind mole-rat *Spalax ehrenbergi* (Nehring, 1898) did not demonstrate any significant laterality when presented with a symmetrical open ditch trial to solve (Kimchi and Terkel, 2001). Despite also being a solitary, burrowing rodent, similar to the Cape mole-rat, this species did not demonstrate laterality, unlike the Cape mole-rat. Glick and Ross (1981) stated that left and right individual laterality is environmentally determined and the strength of the laterality is genetically determined. It may be that the population where the blind mole rats originated from did not demonstrate any left or right lateral preferences, suggesting no preferences of left brain over right brain processes (e.g. approach vs avoidance). This was not the case in laboratory rats (Sprague Dawley and Wistar); rats demonstrated right-sided biases (Glick and Ross, 1981; Andrade et al., 2001; Santin et al., 1996), which is in contrast to the current study where the majority of individuals demonstrated left sides biases. This may be attributed to differences in early life experience (Maier and Crowne, 1993; Denenberg, 1981) and reduced stress from being in captivity due to being laboratory-bred (Santin et al., 1996). Stress has been shown to influence lateralized processes, resulting in more prominent right hemisphere dominant processes (Rogers, 2010; Da Costa et al., 2004; Perez-Cruz et al., 2009; Sullivan, 2004), to reduce the stress response from novel stimuli (Morgan and Tromborg, 2007). Few studies have directly compared captive and wild animals and how laterality may influence them (Hopkins et al., 2007), however, similar to wild and captive birds (Brown and Magat, 2011), wild and captive Cape mole-rats did not show any significant differences in population-level laterality.

The Cape mole-rat is highly territorial, xenophobic and aggressive (Bennett et al., 2006). Several studies have found that aggressive behaviour is a right hemisphere dominant process (Rohlfs and Ramírez, 2006; Hews et al., 2004). Therefore, the aggressive and xenophobic nature of the Cape mole-rat may to some extent underlie the left-turning biases in this species. Furthermore, the handling of the animals shortly before measuring the turning bias may have resulted in an aggressive response, causing the animals to turn left. A previous study on Cape mole-rats demonstrated that captive individuals were less active and had less variability in behaviour compared to wild animals (Oosthuizen et al., 2013). Captive animals were also found to be more stressed and aggressive (Oosthuizen et al., 2013). Thus, it was expected that captive individuals should show a stronger left-turning bias as compared to their wild counterparts, be it either from increased stress or aggression resulting in higher right hemisphere dominance in behaviour (Rogers, 2010; Hews et al., 2004). The costs and benefits of being lateralized may vary following differences in environmental conditions and ecological circumstances from predator-prey and/or cooperation-antagonistic interactions (Chivers et al., 2016; Vallortigara, 2006; Ghirlanda and Vallortigara, 2004; Ghirlanda et al., 2009). Thus, captive and wild conditions could not explain why individuals demonstrated a high percentage of right hemisphere individuals, despite the negative costs of being highly lateralized in a population (Ghirlanda et al., 2009; Ghirlanda and Vallortigara, 2004). Other important ecological circumstances or behaviour may likely explain the behavioural asymmetry in this species (e.g. digging behaviour).

In conclusion, aggressive behaviour derived from interactions with other conspecifics (e.g. territoriality), along with environmental circumstances (captivity vs wild) may be very important to determine lateralized behaviour in animals. The influence of captivity (changes to the animals' immediate environment) may result in less extreme lateralized behaviour in captive animals, but not enough to detect significant differences, however, this may have been due to the small sample size in our study. Changes to the direction of laterality have been observed as a heritable trait in fishes (Bisazza et al., 2000, 2001) and primates (Hopkins et al., 2009; Gómez-Robles et al., 2016), where the direction is dependent on individual experience (Bisazza and Brown, 2011), and could also have modulated the difference between wild and captive individual laterality and requires further investigation. Other environmental factors may also contribute to the behavioural asymmetry observed in these animals (e.g. energy efficiency in digging). This may differ in other mole-rat species, which may be less aggressive. Furthermore, other communication behaviour may underlie lateralized behaviour in more social mole-rat species, and therefore other mole-rat species should be investigated in future studies to broaden our understanding of laterality in these animals.

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CRediT authorship contribution statement

Paul. J. Jacobs: Conceptualization, Methodology, Formal analysis, Writing - original draft.
M.K. Oosthuizen: Methodology, Investigation, Resources, Writing - original draft, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors report no declarations of interest.

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