A unified-models analysis of the development of sexual size dimorphism in Damaraland mole-rats, *Fukomys damarensis*

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Individual variation in growth rates often generates variation in fitness. However, the ability to draw meaningful inferences from growth data depends on the use of growth models that allow for direct comparisons of growth between the sexes, between populations, and between species. Unlike traditional sigmoid functions, a recently parameterized family of unified growth models provides a reliable basis for comparisons since each parameter affects a single curve characteristic and parameters are directly comparable across the unified family. Here, we use the unified-models approach to examine the development of sexual size dimorphism in Damaraland mole-rats (*Fukomys damarensis*), where breeding males are larger than breeding females. Using skeletal measurements, we show here that the larger size of male Damaraland mole-rats arises from an increased growth rate across the entire period of development, rather than through sex differences in the duration or timing of growth. Male-biased skeletal size dimorphism is not unusual among rodents, and our measures of sex differences in size in captive mole-rats are close to sexual size differences in the wild, where

size dimorphism = 1.04 (male/female). We hope our study will encourage the wide use of unified growth models by mammalogists.

Key words: Bathyergidae, cooperative breeder, growth interval equations, non-linear mixed effects models, ontogeny, sexual dimorphism, sociality

Sex differences in body size are a conspicuous feature of mammals and vary widely in magnitude and direction between species. For example, in southern elephant seals (*Mirounga leonina*), males can reach a body mass of 3,000 kg, some 5-6 times that of females (Wilson and Mittermeier 2014), while in other mammals, such as cliff chipmunks (*Tamias dorsalis*) and spotted hyenas (*Crocuta crocuta*), it is the females that are the larger sex (Ralls 1976; Schulte-Hostedde 2007; Swanson et al. 2013; Kilanowski and Koprowski 2017). The developmental processes that lead the sexes to differ in size can take various forms. While in some species sex differences in growth are apparent during gestation and then extend throughout the rest of the lifespan (Pedersen 1980; Clutton-Brock 1991; Korsten et al. 2009), in others they can be caused by differences in the duration of growth among adults (McNamara 1995), and in others still they are caused by a combination of these processes (Jarman 1983; Leigh and Shea 1996; O'Mara et al. 2012).

Identifying and comparing the processes responsible for sex differences in size is now a priority for studies of sexual dimorphism and sexual selection (Badyaev 2002; Blanckenhorn 2005; Lindenfors et al. 2007; Matějů and Kratochvíl 2013), but to do this, it will be necessary to compare growth rates at particular stages of the life history of individuals. There is now a bewildering array of modeling choices to aid in this pursuit, including non-linear mixed effects models (Cole et al. 2010; Sofaer et al. 2013; Aldredge 2016), spline curves (White et al. 1999; Meyer 2005), and finite mixture models (Shotwell et al. 2016), among others (Tonner et al. 2017). The merits of these different approaches vary

and the decision to choose one approach over another often depends on the focus of analysis, but they share a common requirement to explain growth accurately, without compromising generalizability.

To date, mammalogists have relied principally on the traditional three-parameter logistic, Gompertz, and von Bertalanffy functions to characterize growth (Zullinger et al. 1984), each of which varies in the placement of the inflection point relative to the upper asymptote (29.63%, 36.79%, and 50%, respectively). While it might be generally true that these three-parameter models successfully capture the shape of growth across a broad range of vertebrate taxa, it is also clear that in many cases they can return highly inaccurate parameter values. Sometimes this inaccuracy comes from the data itself: if very few individuals are sampled at the lower and upper ends of the growth curve, then three-parameter functions can struggle to recover biologically informed size estimates at these outer ranges of the size distribution, and researchers might need to fix specific parameters when this is the case (Austin et al. 2011; Tjørve and Tjørve 2017b). In other cases, it is the model itself that is inadequate: if the true inflection point lies away from that which is forced by the logistic, Gompertz, or von-Bertalanffy, or if an inflection point is absent in early life (as in monomolecular-like growth), then the three-parameter logistic models are unlikely to characterize growth accurately.

Fortunately, as the three-parameter models are part of the same sigmoid family, one can parameterize a generalized form of sigmoidal growth through the addition of a single shape parameter, '*d*':

$$S_t = \frac{A}{(1 + (d-1)e^{-k(t-T_i)})^{\frac{1}{(m-1)}}}$$

where S_t is the size at age t days, and A, k, T_i, and d are the upper asymptote, the maximum relative growth rate, the age at inflection point, and the shape parameter, respectively

(Richards 1959). The latter shape parameter affords this so-called Richards model its flexibility by allowing the timing of inflection to vary at some point along a continuum ranging from monotonic concave to monotonic convex (Leberg et al. 1989; Gaillard et al. 1997). The three-parameter functions then sit as specific cases of this generalized Richards function (also known as 'Chapman-Richards'). We carried out a literature search to quantify the cumulative use of the Richards function to model size-at-age data in mammals, in comparison to other two- or three-parameter growth functions. The details of this search are provided in Supplementary Data SD1, but in brief, we looked for all studies in four mammal-focused journals (*Journal of Mammalogy*, *Mammal Review*, *Mammal Study*, and *Marine Mammal Science*) that had fitted some form of sigmoid- or sigmoid-like function to size-at-age data since 1980. As Fig. 1 shows, the flexible Richards function is only fitted in a small proportion of total studies (20.8% as of the end of 2018), and in most cases, studies that did not fit a Richards function only fitted a single alternative function to the data (65.8%).

However, despite its flexibility, the Richards function in its traditional form still has two major drawbacks, as outlined by Tjørve and Tjørve (2010, 2017a; see also Zach et al. 1984; Davies and Ku 1977). Firstly, because model parameters influence multiple curve characteristics simultaneously, they become difficult to interpret. By extension, one cannot directly compare growth parameters between Richards models fitted to different datasets, as might be desirable, for example, if one wants to compare variation in the shape and pace of growth between populations, between species, or between the sexes. That parameters influence multiple curve characteristics also introduces a second unwanted feature, namely high correlations between model parameters (Davies and Ku 1977). These drawbacks are a major obstacle in attempts to understand how and why organisms vary so widely in size and structure.

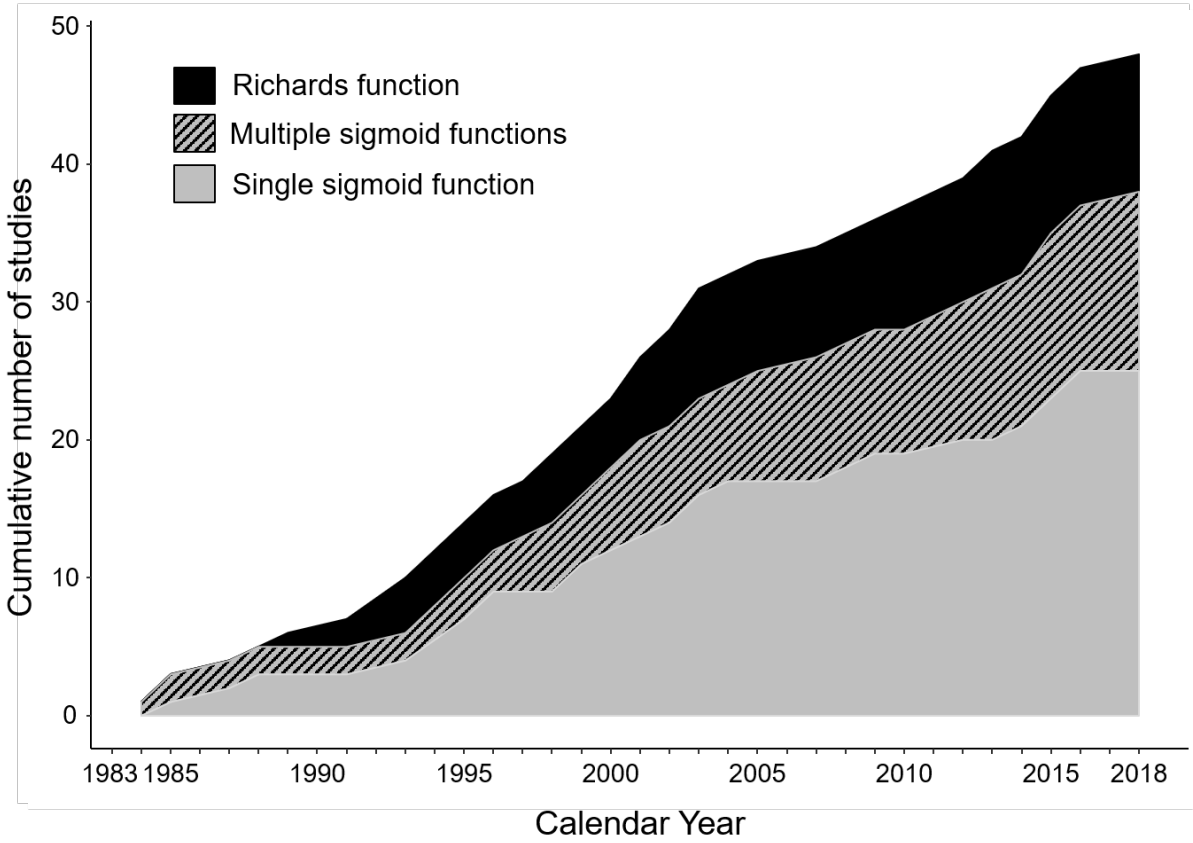

Fig. 1.— The cumulative use of sigmoid-like functions to model size-at-age data in the mammalian literature since 1980. Black fill refers to studies that have employed a Richards function (irrespective of whether other functions were also fitted alongside the Richards). Gray fill refers to studies that employed other two- or three-parameter growth functions (including Brody, logistic, monomolecular, Gompertz, von Bertalanffy, quadratic); when hatched, multiple comparisons were made between these different functions, and when solid, the study only tested a single growth function. See the main text Supplementary Data SD1 for details of literature searching.

In seeking to overcome the inherent limitations of the traditional sigmoid functions, Tjørve and Tjørve (2010) introduced a 'unified' Richards model whereby each parameter influences a single feature of the growth curve (Table 1). They were not the first to do so explicitly, for others had previously provided parameterizations of the Richards function where the growth rate constant was transformed into a coefficient which estimated maximum relative growth rate (Sugden et al. 1981). Even so, they were the first to develop and propose

a unified-models framework that incorporated the wider sigmoid family (Tjørve and Tjørve 2010, 2017a). In the intervening years this unified-models approach has been increasingly adopted in the avian literature (Tjørve and Tjørve 2017b; Svagelj et al. 2019; Vrána et al. 2019), no doubt stimulated by the relative ease with which growth data can be collected from birds, where individuals routinely reach adult mass in the 2-3 weeks that they are bound to the nest. In stark contrast, only a single study has used the approach in a mammal (García-Muñiz et al. 2019), in spite of its obvious benefits.

Table 1.— Parameterization of unified models of sigmoid growth. S_t is the size at age t days; A, k, T_i and the upper asymptote, the maximum relative growth rate, and the timing of inflection point, respectively; d shifts the inflection value vertically. W_i is the absolute value at maximum growth (i.e. size at inflection point), which can also be expressed as a percentage of the upper asymptote.

Model	Formula	Value at inflection point	
		W_i	as % of A
U-von Bertalanffy	$S_t = A.\left(1 - \frac{1}{3}.e^{-\frac{9}{4}k(t-T_i)}\right)^3$	$\frac{8}{27}.A$	29.6
U-Gompertz	$S_t = A.e^{-e^{-e.k.(t-T_i)}}$	$\frac{1}{e}.A$	36.8
U-Logistic	$S_t = \frac{A}{1 + e^{-4.k.(t-T_i)}}$	$\frac{1}{2}.A$	50.0
U4	$S_t = A.\left(1 + 3.e^{-4\frac{4}{3}.k.(t-T_i)}\right)^{-\frac{1}{3}}$	$4^{-\frac{1}{3}}.A$	63.0
U-Richards	$S_t = A.\left(1 + (d-1).e^{\left(\frac{-k.(t-T_i)}{d^{\frac{d}{1-d}}}\right)}\right)^{\frac{1}{1-d}}$	$d^{\frac{1}{1-d}}.A$	0 - 100

Here, we use the unified-family of models to explore the development of skeletal size dimorphism in the Damaraland mole-rat, *Fukomys damarensis*. Damaraland mole-rats are subterranean rodents that inhabit the red arenosols of the Kalahari Desert in cooperatively breeding groups. Groups are composed of 2-41 individuals, within which a single female is responsible for all reproductive output. Paternity is often shared between 1-3 unrelated males

that have immigrated into the group, the remaining individuals representing cohorts of offspring, who, having delayed dispersal, participate in burrow renovation, food acquisition and storage, group defense, and pup care (Bennett and Faulkes 2000). As in many other mammals, male Damaraland mole-rats are larger than females (Bennett and Faulkes 2000; Lindenfors et al. 2007; Young and Bennett 2013). While it has been stated that this dimorphism arises from an increased rate and a greater growth duration in males (Young and Bennett 2013), work on mole-rat growth has exclusively relied upon Gompertz and logistic equations; has often been fitted to small datasets with low temporal resolution; and has largely ignored individual variation in growth parameters (Bennett et al. 1991; Bennett and Navarro 1997; O'Riain and Jarvis 1998; Bennett and Faulkes 2000; Young and Bennett 2013; Zöttl et al. 2016). Consequently, a formal characterization of the shape of growth in male and female Damaraland mole-rats is currently missing.

The African mole-rats (family Bathyergidae) are a particularly interesting radiation in which to examine the processes leading to sex differences in size, for patterns of growth in this family are unusually variable both within and between species (Begall and Burda 1998; Scharff et al. 1999; Bennett and Faulkes 2000; Sumbera et al. 2003). Among the most social species, including the Damaraland mole-rats and naked mole-rats (*Heterocephalus glaber*), non-reproductive individuals can display a two-fold difference in their asymptotic mass (Bennett and Navarro 1997; O'Riain and Jarvis 1998; Zottl et al. 2016), and individuals have been shown to undergo periods of accelerated growth when reproductive opportunities present themselves (O'Riain and Jarvis 1998; Dengler-Crish and Catania 2007; Thorley et al. 2018). However, whereas Damaraland mole-rats display a male-biased size dimorphism irrespective of the female growth surge, in naked mole-rats, it is the reproductive individuals that are largest, and sexual size dimorphism (SSD) within reproductive individuals and within non-reproductive individuals is absent (Jarvis et al. 1991; Pinto et al. 2010). If we then take

two solitary species, the Namaqua dune mole-rat (*Bathyergus janetta*) and the Cape mole-rat (*Georychus capensis*), the former is size dimorphic in favor of males and the latter is monomorphic (Scantlebury et al. 2006). Explaining these patterns is not straightforward (Young and Bennett 2013), underscoring the need to better quantify the development of size in mole-rats.

Our paper includes two analyses. In the first, we used unified sigmoid models to investigate sex-specific skeletal growth trajectories in a captive population of Damaraland mole-rats, focusing on body length and incisor width (as a reliable proxy of skull size). We chose to use skeletal estimates of size rather than body mass as body mass is more prone to changes in resource acquisition in captivity (e.g., Klimentidis et al. 2011; Morfeld et al. 2016). In a second analysis, to further reduce the possibility that our interpretations of mole-rat growth might have been influenced by captivity and associated feeding and husbandry practices, we modeled skeletal growth in wild Damaraland mole-rats. As individuals captured in the wild are of unknown age, we fitted interval equations to skeletal data acquired across repeated captures of individuals (Schoener and Schoener 1978). Modeling was implemented throughout using non-linear mixed-effects models that are implicitly well equipped to deal with the hierarchical clustering that is inherent in growth data (Sofaer et al. 2013).

MATERIALS AND METHODS

Morphological data were collected from captive and wild Damaraland mole-rats between October 2013 and January 2019. Our study population was located around the Kuruman River Reserve in the Northern Cape of South Africa (S26.98706° E21.81229°), where group sizes range from 2–26 individuals (mean = 9.47 ± 5.44 *SD*, median = 8). A captive population was founded at the reserve in February 2013 using animals sourced from the local population, and these founding individuals were either maintained in their original group or

selected to create new groups, achieved through the pairing of a reproductively naïve female with an unrelated male. All individuals were part of groups housed in artificial tunnel systems made of polyvinyl-chloride (PVC) pipes. The pipes were modified to have transparent plastic 'windows' through which behavior can be observed, and within each tunnel system, pipes connect various compartments that serve as a nest box, a toilet, a food store, and a large waste box. Depending on group size, one to three vertical pipes were incorporated into the tunnel design through which clean sand from the surrounding area can be added. Animals then replicate their natural behavior by clearing the sand from the vertical pipes and moving it through the tunnel system to the peripheral waste box, thereby gaining access to food placed behind the previously sand-filled tunnel. Animals were provisioned twice daily (ad libitum) on a diet of sweet potatoes and cucumbers. Pieces of tissue paper were also introduced into the tunnel system periodically and were readily used as nesting material. Tunnel systems were cleaned briefly every day and more thoroughly once per week.

All captive individuals used in this study were of known-age, being born into existing groups in captivity. Throughout their development, individuals were sampled for morphometrics while under isoflurane anesthesia. Efforts were made to repeatedly sample individuals at landmark ages, but sampling often also coincided with the collection of blood samples or X-rays as part of ongoing cross-sectional studies in the lab. Here, we use two morphometric measures of skeletal body size: incisor width and total body length. Incisor width, a highly repeatable measure of skull size (Young and Bennett 2010), was measured at the widest point using digital calipers (± 0.1 mm), and body length was measured dorsally from the tip of the nose to the base of the tail using a tape measure (± 0.1 mm). All morphometric samples were taken in duplicate by two observers, and we took the mean of the two measures for every sampling event. In total, the dataset on captive mole-rats comprised 3,471 teeth-width measures (n = 287 females, mean/female = 6.14, SD = 5.14 measures; n =

269 males, mean/male = 6.35, *SD* = 4.57) and 3,335 body-length measures (*n* = 278 females, mean/female = 6.08, *SD* = 4.91; *n* = 265 males, mean/male = 6.21, *SD* = 4.29).

Incisor-width and body-length data from wild mole-rats were taken as part of an ongoing capture-mark-recapture study. Groups were trapped periodically (3- to 12-month intervals) using modified Hickman traps that were baited with sweet potato and positioned into tunnel systems by digging. On capture, animals were placed into a closed, sand-filled box with other group members, and provided food and shelter, before being transported back to the laboratory where they were measured under anesthesia. Unlike the lab animals, the age of wild individuals was unknown. As such, our modeling approach relied on the parameterization of 'interval' growth equations that estimate the change in size trait across successive capture events (see below). The wild dataset comprised 447 'repeat-capture' events where incisor width was measured (*n* = 124 females, mean/female = 1.78, *SD* = 1.06; *n* = 128 males, mean/male = 1.77, *SD* = 1.04), and 448 similar measures for body length (*n* = 287 females, mean/female = 1.78, *SD* = 1.06; *n* = 269 males, mean/male = 1.76, *SD* = 1.04).

For females, we only included morphometrics taken when individuals were reproductively naïve (i.e., not a dominant, reproductively active female), as skeletal growth curves of reproductive females are known to change around the acquisition of a breeding position (Young and Bennett 2010; Thorley et al. 2018). Reproductive females can be readily identified by their perforate vagina and prominent teats. As similar status-related changes in skeletal traits have not been reported in males, a similar exclusion was not made for males.

Growth in captivity: the unified sigmoid family.— We fitted five forms of unified growth function to incisor width and body length data: U-logistic, U-Gompertz, U-von Bertalanffy, U4, and U-Richards (Table1, see Tjørve and Tjørve 2017a for full details). The U4 simply represents a three-parameter model where the inflection point falls to 63% of the upper asymptote, an arbitrary position not covered by the other three-parameter models. This

serves to illustrate that one can parameterize any three-parameter model from the U-Richards model according to the proportion of the asymptote at which the inflection points falls ($S_i = d^{1/(1-d)}$); $S_i = 0.63$ when $d = 4$. One might wish to do so with small datasets, where the fitting of the four-parameter U-Richards might struggle to converge. Each of these forms of unified growth represents the so-called T_i-form, with T_i estimating the timing of inflection. The functions can equally well be presented in a W_0-form, which would estimate the weight at birth. These forms differ only in the specification of their location parameters, T_i and W_0, which shift the growth curve horizontally. One needn't fit both equations, as one form can easily be estimated from the other (Appendix A in Tjørve and Tjørve 2017a).

Each unified growth function was specified as a non-linear mixed effect model (NLMM). Separate models were fitted to the datasets for males and females for each skeletal trait, and for each unified function, random effects of A, k and T_i were first specified at the level of the individual, so that variation in growth parameters between individuals was estimated. Random effects were assumed to be independent of one another. As other studies have found that some growth parameters vary little between individuals (Sofaer et al. 2013), we also refitted each function with different combinations of random effects (e.g., only random effects at the level of the individual for A and k), judging the best-fitting model by Akaike's information criterion (AIC) and likelihood ratio tests; this model was taken to represent the best unified function for a given trait in each case. The best-fitting of the five functions were likewise compared by AIC (Burnham and Anderson 2002).

To minimize heteroscedasticity, a power variance function was also consistently applied as per English et al. (2012), and significantly improved the fit of models. Specifically, nlme's *varPower* function was set so that observations were assumed to vary normally about a mean given the expected size of an individual (μ), with a standard deviation parametrized according to Υ and ρ:

$$S_t \sim \mathrm{N}(\mu = \mathrm{E}(S_t), \sigma = \Upsilon \cdot \mu^{\rho})$$

Because of the nature of growth data, we also identified strong temporal autocorrelation within individuals. We therefore also included an AR-1 auto-correlation structure, which models the residual at age *t* (ε_t) as a function of the residual at age *t*-1 ($\varphi\varepsilon_{t-1}$), along with a noise term (η_t) as:

$$\varepsilon_t = \varphi\varepsilon_{t-1} + \eta_t$$

Here, φ represents the correlation between residuals one unit apart in time and must be estimated from the data. In our study, φ varied from 0.39 – 0.54 when considering the best-fitting models of each trait.

In addition to the unified functions, we also fitted a general additive mixed model (GAMM) with a smoother term for age to each of the morphological datasets. As GAMMs allow for a flexible trajectory of size with age, we compared the fit of the GAMMs to the NLMMs to check whether certain features of the raw data were being poorly estimated by the unified models. In each GAMM, we specified individual identity as a random effect, and the age smoother was set with 6 knots.

Growth in the wild.— To investigate the extent to which our results in captivity could be considered representative of growth under natural conditions, we then modeled growth of wild mole-rats. However, mole-rats captured in the wild were of unknown age, and we had no information that could be used to infer age with any confidence (e.g., tooth wear, Hart et al. 2007). This being the case, we could not use conventional age-dependent models of growth for wild mole-rats, and instead chose to use the 'interval equations' set out by Schoener and Schoener (1978; see also Fabens 1965). These interval equations have as their dependent variable the size of the animal at the end of a time interval (here, the recapture of previously caught mole-rats), with the size at the beginning of the interval, and the length of the interval, forming the two independent variables. Each such model then estimates two

growth parameters, the population-level asymptotic mass and the population-level growth rate constant (excepting any random terms that might be included in a mixed-effects framework).

We fitted two forms of interval equation to skeletal data from wild mole-rats, a von Bertalanffy parameterization and a logistic parameterization (Schoener and Schoener 1978). For the von Bertalanffy, the size of an individual on recapture was modelled as:

$$S_2 = A - (A - S_1)e^{-k.D},$$

and for the logistic as:

$$S_2 = A.S_1/(S_1 + (A - S_1).e^{-k.D}),$$

where S_1 and S_2 are size at capture 1 and 2 (recapture) respectively, D is the time interval between capture events, and A and k are the growth parameters to be estimated. As above, models for males and females were fitted separately for both incisor width and body length, and AIC comparisons were used to determine relative fit. In all cases, models also specified random terms at the level of the individual for both A and k. Also note that k here is not directly comparable to k in the unified-growth models employed for captive mole-rats; it is nonetheless instructive for making comparisons between the sexes.

All NLMMs were fitted in the *nlme* package in R v. 3.5.2 (R Core Team, 2018). GAMMs were fitted in *mgcv*. We provide example code for the fitting of NLMMs in the Supplementary Data. We provide the mean ± 1 *SEM* for all estimates unless otherwise stated.

The research carried out in this study was approved by the University of Pretoria animal ethics committee (permit numbers EC089-12 and SOP-004-13) and align with ASM guidelines (Sikes et al. 2016). The data used in the manuscript are deposited in the University of Cambridge repository, doi: 10.17863/CAM.37910.

RESULTS

The various forms of unified model differed widely in their ability to capture variation in mole-rat skeletal growth in captivity (Table 2). As expected, there was a general tendency for the unified Richards function to outperform the three-parameter functions for male incisor width, female body length, and male body length, the exception being shown by female incisor width, which was best explained by a U-von Bertalanffy function. When directly compared, the best-fitting models for males and females indicated that the greater asymptotic mass of males in captivity (Table 3) arose principally from an increased growth of males across development (Table 3, g_{max}; Fig. 2 a, b). In contrast, there was no clear trend for males to prolong the duration of their growth beyond that of females. For incisor width, females were predicted to reach 90% of their asymptotic mass by 1.44 years of age, as compared to 1.50 years for males, whereas for body length, 90% asymptotic mass was reached at 1.13 and 1.09 years of age for females and males, respectively. Fitting age-related smoothers to morphological data using GAMMs confirmed that the growth rates of males and females had converged by the time individuals were approximately one and a half years of age (Fig. 2c).

Estimates of growth parameters showed substantial variation among models according to sex and skeletal trait (Table 3, Supplementary Data SD2 and SD3). Variation was particularly pronounced for the inflection point, T_i, with a standard deviation among models consistently above 65 days (female incisor width, *SD* = 77.11; male incisor width, *SD* = 74.35; female body length, *SD* = 82.08; male body length, *SD* = 67.28; we could not use the coefficient of variation as some inflection points were negative). For incisor width, the best-fitting models suggested that for females the inflection point occurred at 4 days of age, by which point females were 29.6% of their estimated upper asymptotic size (d = 0.6667), whereas for males for males, inflection occurred at 112 days of age, 43.8% of their asymptotic size (d =1.45). Marked contrasts in T_i and d were also shown in the best-fitting models for body length

(Table 3). One might expect these differences in parameter estimates to translate into sex-specific differences in the shape of growth, but with the very low relative growth rates in mole-rats (*k*), which reduces the magnitude of changes either side of the inflection point, this is not the case (Fig. 2). On the contrary, aside from the higher absolute growth rate of males, the plotting of predicted curves highlighted that male and female size trajectories are extremely similar, and any inflection values estimated by growth models only generated minor deviations in growth rate. These patterns were corroborated by GAMMs, which indicated that in mole-rats postnatal growth rate is fastest at birth and declines thereafter: mole-rat skeletal growth does not display a strong inflection.

Table 2.— Model comparisons of skeletal growth in Damaraland mole-rats (*Fukomys damarensis*). Female incisor width $d = 0.82$, male incisor width $d = 1.45$, female body length $d = 0.50$, male body length $d = 2.87$.

	Females			Males		
Model	k	ΔAIC	Weights	k	ΔAIC	Weights
Incisor width						
U-von Bertalanffy	8	0.00	0.65	9	29.37	0
U-Gompertz	8	2.90	0.16	9	7.78	0.02
U-Logistic	9	23.94	0	9	8.91	0.01
U4	9	121.66	0	9	138.97	0
U-Richards	9	2.62	0.18	10	0	0.97
Body length						
U-von Bertalanffy	8	5.64	0.06	8	29.58	0
U-Gompertz	8	10.16	0	8	21.37	0
U-Logistic	9	23.45	0	8	2.89	0.15
U4	9	48.80	0	8	1.97	0.23
U-Richards	9	0.00	0.94	9	0	0.62

Table 3.— Growth parameter estimates from models fitted to skeletal traits on captive Damaraland mole-rats (Fukomys damarensis). A is the upper asymptote, k the relative maximum growth rate, Ti the time of inflection, and d the shape parameter that controls the inflection value. The size at birth, W0, and the absolute maximum growth rate, gmax, are estimated from model outputs. SSD is calculated from equivalent models. Random effects variation can be found in Table SD2.

		A (*SE*)	*k* (*SE*)	T_i (*SE*)	W_0	*d*	Time to reach 90% Asymptotic Mass, years	g_{max}, mm/day	m:f SSD
Females									
Incisor width	U-von Bertalanffy	6.59 (0.04)	0.00194 (0.00004)	3.65 (2.85)	1.91	-	1.44	0.013	-
	U-Gompertz	6.57 (0.02)	0.00172 (0.00004)	32.04 (2.51)	2.06	-	1.41	0.011	-
	U-Logistic	6.48 (0.03)	0.00147 (0.00003)	101.79 (2.34)	2.30	-	1.31	0.010	-
	U4	6.45 (0.03)	0.00121 (0.00003)	189.08 (2.56)	2.69	-	1.28	0.008	-
	U-Richards	6.58 (0.04)	0.00183 (0.00003)	17.47 (2.67)	2.17	0.82	1.42	0.012	-
Males									
Incisor width	U-von Bertalanffy	7.65 (0.04)	0.00180 (0.00004)	39.07 (2.15)	1.73	-	1.64	0.014	1.16
	U-Gompertz	7.58 (0.04)	0.00167 (0.00003)	74.00 (2.00)	1.86	-	1.57	0.013	1.15
	U-Logistic	7.42 (0.04)	0.00146 (0.00003)	147.59 (2.09)	2.20	-	1.44	0.011	1.15
	U4	7.26 (0.04)	0.00132 (0.00002)	232.22 (2.50)	2.59	-	1.32	0.012	1.13
	U-Richards	7.50 (0.04)	0.00154 (0.00003)	111.60 (1.99)	3.39	1.45	1.50	0.012	1.14
Females									
Body length	U-von Bertalanffy	18.49 (0.08)	0.00194 (0.00005)	-119.13 (6.40)	9.53	-	1.10	0.036	-
	U-Gompertz	18.46 (0.08)	0.00167 (0.00004)	-97.88 (5.90)	9.72	-	1.63	0.031	-
	U-Logistic	18.36 (0.08)	0.00130 (0.00003)	-38.5 (4.71)	10.09	-	1.27	0.029	-
	U4	18.42 (0.07)	0.00097 (0.00003)	46.08 (3.75)	10.76	-	1.06	0.018	-
	U-Richards	18.56 (0.08)	0.00399 (0.00010)	-167.11 (7.66)	9.02	0.00	1.13	0.074	-
Males									
Body length	U-von Bertalanffy	19.82 (0.08)	0.00204 (0.00005)	-77.36 (5.01)	8.92	-	1.15	0.040	1.07
	U-Gompertz	19.79 (0.08)	0.00177 (0.00004)	-55.03 (4.55)	9.19	-	1.13	0.035	1.07
	U-Logistic	19.71 (0.08)	0.00137 (0.00003)	1.66 (3.58)	9.82	-	1.10	0.027	1.07
	U4	19.61 (0.07)	0.00109 (0.00003)	85.93 (2.83)	10.53	-	1.07	0.021	1.06
	U-Richards	19.68 (0.07)	0.00120 (0.00003)	41.32 (3.08)	11.22	2.87	1.09	0.024	1.06

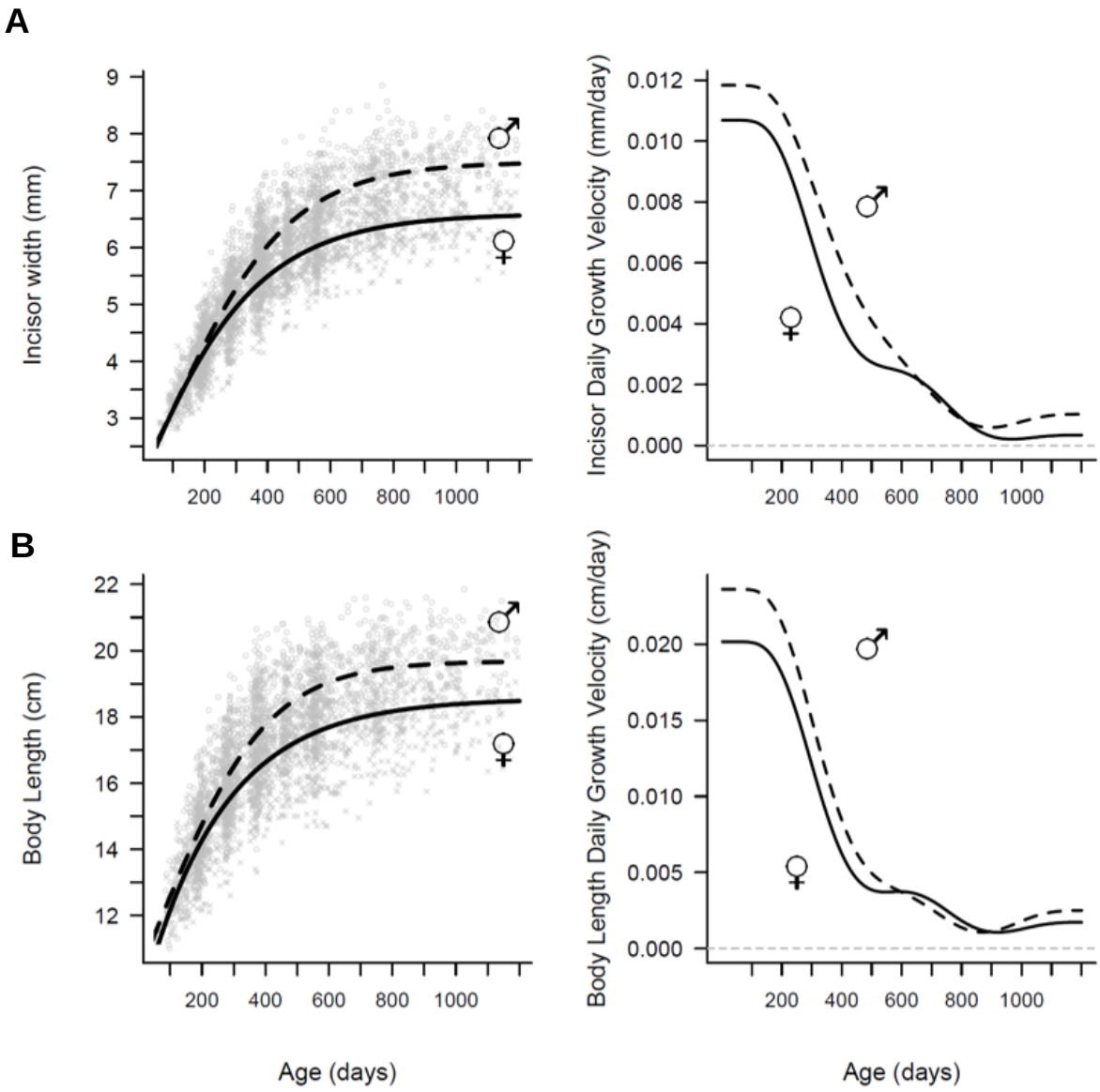

Fig. 2.— Sex-specific patterns of skeletal growth in captive Damaraland mole-rats (*Fukomys damarensis*): A) incisor width, B) body length. Left-hand plots display the predicted growth curves from the best fitting unified growth model for each trait (females– solid line, males– dashed line), with the points showing the raw data (females– crossed, males– circles). Right-hand plots show the instantaneous growth rate (growth velocity) of each trait, here taken as the first derivative (gradient) of general additive mixed models fitted to morphological datasets with a smoother for age (females– solid, males– dashed).

With the modest inflection in growth, estimates of relative maximum growth rate, *k*, which are estimated at the point of inflection, should be interpreted with caution. We can gain some insights from the estimates of *k* in the incisor width models, as the inflection point is

positive in all models, and thus *k* is estimated within the range of the data. Doing so, we see that the relative growth rate of males is lower than females, but only modestly so. In contrast, body length models frequently returned negative inflection values, and it is therefore not intuitive to use estimates of *k*. Consequently, we chose to use GAMMs and model predictions to make inferences about sex differences in the pace of growth, which as noted above, are minor. For other species with a stronger inflection in growth during development, *k* will provide a more useful metric.

Unlike the other parameters, variation among models in the upper asymptote (*A*) was small. This was reflected by low coefficients of variation across models: *CV* was always less than 2.02 in A (female incisor width, *CV* = 0.98; male incisor width, *CV* = 2.02; female body length, *CV* = 0.41; male body length, *CV* = 0.43). Using the population-level estimates for *A*, we estimated a male-biased skeletal size dimorphism of 1.14 for incisor width, and 1.06 for body length. There was also considerable between individual variation in *A*, which was always retained as a random effect, as was *k* (Supplementary Data SD4, SD5).

The modeling of growth in the wild supported our interpretations of mole-rat growth in captivity (Supplementary Data SD6; Fig. 3 and Fig. 4). Firstly, we found that the von-Bertalanffy interval equations provided a better fit to the data than the logistic curve, in keeping with the general monotonic concave shape of mole-rat growth. Secondly, we identified a greater absolute rate of growth in males versus females for body length (female $k = 0.0034 \pm 0.0002$); male $k = 0.0044 \pm 0.0002$), and these differences contributed to a male-biased body length dimorphism of 1.04 (female $A = 18.83 \pm 0.15$; male $A = 19.60 \pm 0.10$). Differences in growth rate were not detected for incisor width (female $k = 0.0040 \pm 0.0002$; male $k = 0.0039 \pm 0.0002$), but asymptotic incisor width was similarly male biased (female $A = 6.05 \pm 0.06$; male $A = 6.79 \pm 0.06$), equating to an SSD (male/female) in incisor width of

1.12. As a result, mole-rats in the wild are skeletally similar in size to the mole-rats in captivity, and SSD is invariant with respect to location.

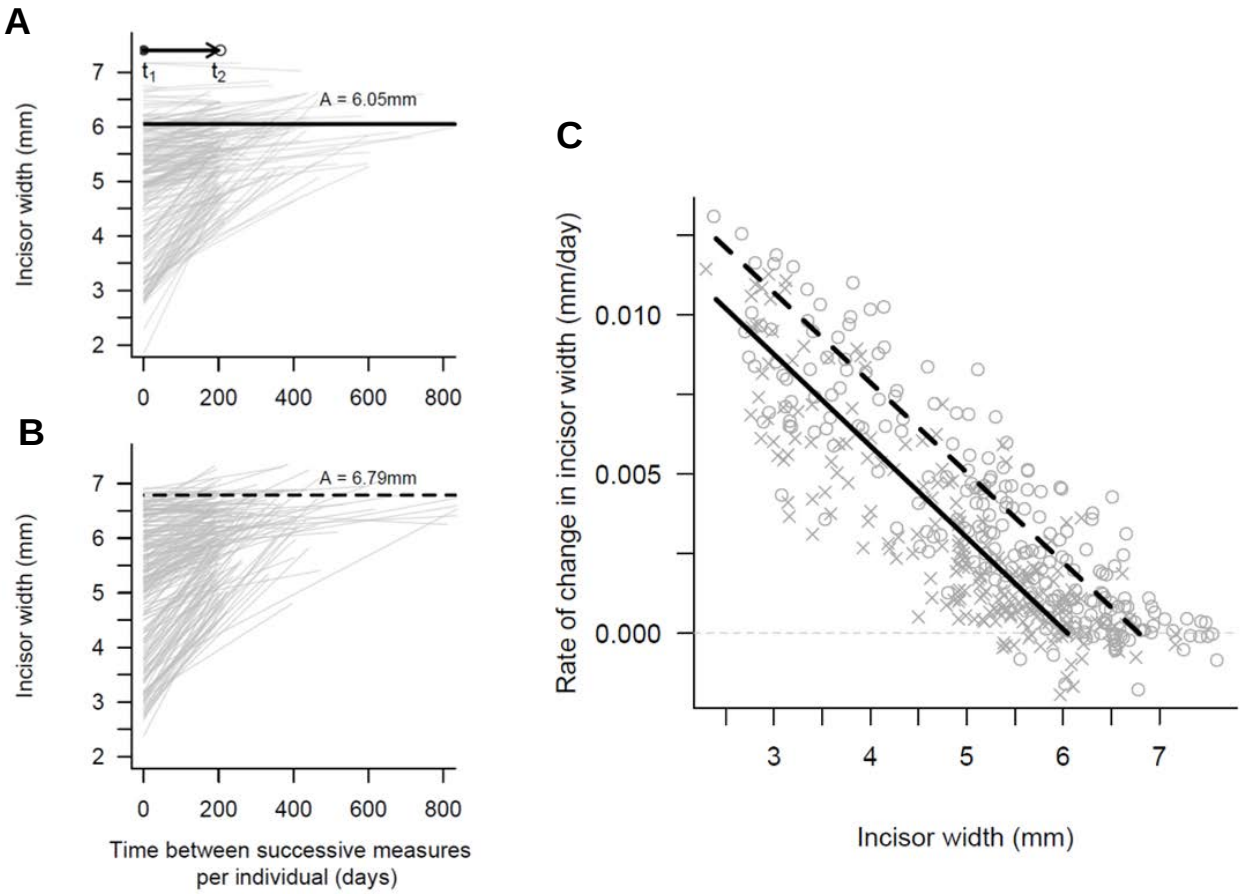

Fig. 3.— Skull growth (incisor width) of wild Damaraland mole-rats (*Fukomys damarensis*). As individuals are of unknown age, asymptotic mass and growth rate were estimated from a von Bertalanffy growth curve reparametrized as an interval equation (Schoener and Schoener 1978). The equation models the change in size across repeated capture events as a function of the time difference between capture events and initial size. Figures A) and B) display the raw data for repeated captures on females and males, respectively; each slope displays the change in incisor width across a single recapture event: i.e., from t_1 to t_2. Note that with increasing initial incisor width, the slope of the change in incisor width converges on the estimated population-level asymptote, highlighted by the horizontal black line. C) Fitted growth rates for females (solid line) and males (dashed line) with changing initial incisor width; each point represents a single slope from A and B.

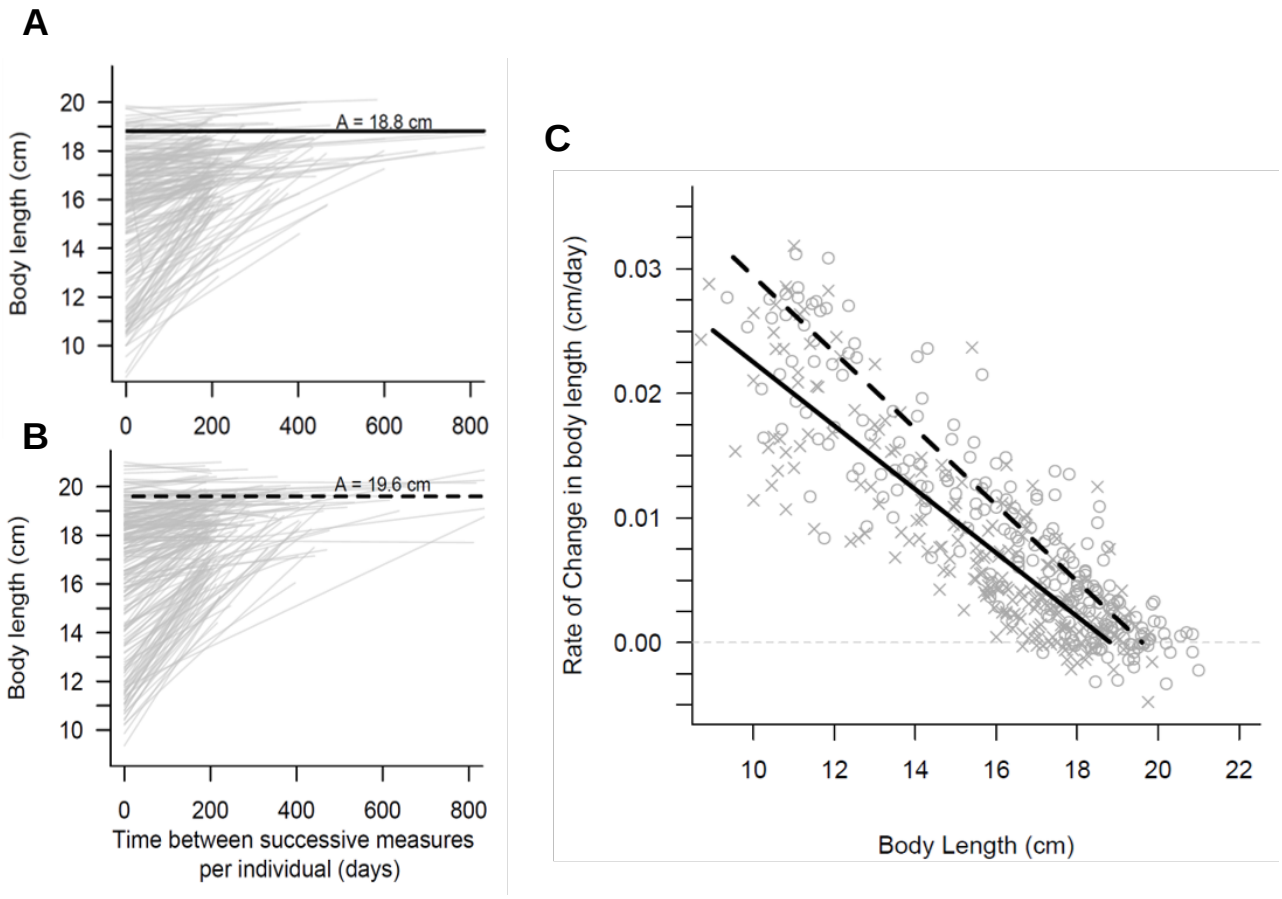

Fig. 4.— Body-length growth of wild Damaraland mole-rats (*Fukomys damarensis*). A) and B) display the raw data for repeated captures on females and males, respectively, with the thicker black line showing the population-level asymptote estimate from the best-fitting models. C) Fitted body-length growth rates for females (solid line) and males (dashed line) with changing initial body length width; each point represents a single slope from A and B.

If we compare SSD in body length of mole-rats (in the wild) to other rodents using information compiled by Schulte-Hostedde (2007), we see that mole-rats lie at the 75th percentile of the distribution (Fig. 5), where 1 represents a 1:1 male to female ratio. The mean sexual size dimorphism in rodents is 1.011 ± 0.004, though some families contribute more heavily to this distribution than others.

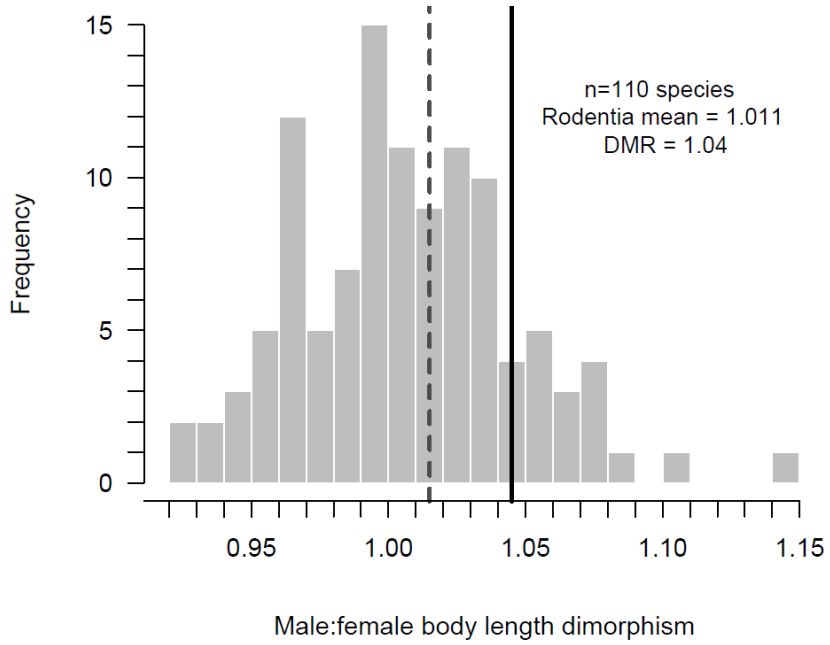

Fig. 5.— Male:female body length dimorphism in Rodentia. Data provided for 110 species across eight rodent families (Bathyergidae– 2, Chinchillidae– 1, Ctenomyidae– 1, Geomyidae– 4, Heteromyidae– 50, Muridae– 29, Sciuridae– 22, Zapodidae– 2), taken from Schulte-Hostedde (2007). Mean across rodents = 1.04 (dashed line; *SD* = 0.004). Value for wild Damaraland mole-rats (*Fukomys damarensis*), as predicted by models, shown by the solid vertical line: 1.04.

DISCUSSION

Our study provides an in-depth examination of sex differences in Damaraland mole-rat growth. Focusing on skeletal traits, we show that the greater size of males of this species is caused principally by their higher absolute growth rate and that contrasts in the duration of growth between males and females were minimal (as for incisor width), or absent (as for body length). Our modeling approach relied upon a unified framework of sigmoid equations that has seldom been applied to mammals despite several attractive features: unified parameters are directly comparable across members of the family; each parameter affects a single curve characteristic; and correlations between parameters are reduced. By incorporating these unified equations into non-linear mixed effects models, we could also quantify the considerable individual variation in growth that has been documented in African mole-rats (Jarvis et al. 1991; O'Riain and Jarvis 1998; Bennett and Faulkes 2000; Zottl et al.

2016). Although our use of these equations was restricted to known-age individuals sampled in captivity under ad libitum feeding conditions, a broader examination of mole-rat growth in the wild suggested that patterns of growth in captivity were largely consistent with those operating in natural populations.

While previous studies have assumed growth of Damaraland mole-rats to follow a logistic or Gompertz trajectory (Bennett and Navarro 1997; Young and Bennett 2013; Zöttl et al. 2016), we show that for skeletal traits, growth of mole-rats is more monomolecular-like in form (see also Thorley 2019 for an examination of body mass), lacking a strong inflection point across development. Strictly speaking, most of the unified equations did identify an inflection point in early life, but when plotted, it became apparent that any such inflections were modest. Likewise, an age-related smoother fitted to the raw data did not yield an inflection point, implying that postnatal growth of mole-rats is fastest at or around birth and declines thereafter. It is not unlikely that many other mammal populations display a similar monotonic concave growth trajectory, but with only a handful of studies formally comparing multiple growth functions on any given taxa in the published literature, it is difficult to know the extent to which this is the case. There are examples we can draw upon, nonetheless. Meerkats (*Suricata suricatta*), roe deer (*Capreolus capreolus*), and spotted hyenas have all been shown to display monomolecular growth in body mass and skeletal traits (Duncan et al. 2000; English et al. 2012; Swanson et al. 2013), and Gaillard et al. (1997) documented various other examples in a comparative analysis. In our own study, the U-logistic or the U-Gompertz curves did not unduly affect estimates of asymptotic mass, but this is certainly not true for other mammalian datasets where it can sometimes deviate substantially from the empirically determined asymptote (e.g., Leberg et al. 1989; Neuenhoff et al. 2011; Teleken et al. 2017).

With such diversity in growth patterns apparent across mammals, the continued overreliance on the traditional three-parameter functions is unwise when a flexible alternative is readily apparent in the form of the Richards function. Previously, a caveat of the Richards functions was the interdependence of estimated parameters, which rendered the interpretation of growth patterns challenging. Parameterized in its unified form, this no longer holds, and as a result we suggest that the U-Richards models should form the default sigmoid-like growth curve for mammals where no a priori knowledge of the shape of growth is available, as has already been proposed for birds (Tjørve and Tjørve 2010, 2017).

In this study, we used the unified Richards equation to compare sex differences in growth parameters of male and female mole-rats. One of our initial intentions in doing so was to directly compare sex differences in *k*, which represents the relative maximum growth at the time of inflection. Our analysis of incisor width found a slightly higher *k* in females, but in our analysis of female body length the inflection point was negative and therefore represents some arbitrary timepoint before parturition. In this context, knowledge of *k* carries no relevant information. This presents a caveat in using the unified approach when growth it not clearly sigmoidal, and where this the case we recommend that researchers instead make use of model predictions and additional growth estimates that can be readily extracted from the model output, such as the time to 90% asymptotic mass (see also France et al. 1996).

In rodents, as in mammals generally, it is typically males that are the larger sex (Lindenfors et al. 2007; Schulte-Hostedde 2007). In some cases, the SSD of adults is produced primarily by contrasts in the duration of growth, as for many terrestrial herbivores (McNamara 1995), but in most mammalian species, it seems that both a prolonged growth duration and an increased growth rate contribute to SSD (Badyaev 2002). Our results suggest that Damaraland mole-rats are somewhere intermediate, because although we clearly

demonstrate the increased growth rate of males, the evidence for a prolonged growth duration is weak, and if apparent, its influence on sexual size dimorphism is minimal.

Although the magnitude of male-biased size dimorphism in Damaraland mole-rats (m:f SSD of 1.04 for body length in wild animals) is not unusual among rodents, it is unexpected in a cooperative breeder where reproductive skew is greater in females than males (Bennett and Faulkes 2000). Conventional sexual selection theory would predict that females should be larger than males, with associated masculinized traits (Hauber and Lacey 2005; Clutton-Brock et al. 2006). However, just as in mole-rats, other cooperatively breeding vertebrates with greater female reproductive skew also fail to display reversed size dimorphism (Young and Bennett 2013), and so it seems that unlike in polygynous societies where males are large and heavily armed, skew cannot account for sexual size dimorphism in cooperative breeders. One possible explanation for the absence of any association between skew and size in cooperative breeders is that females are trading off investment in growth against investment in reproduction (or future reproduction, i.e., fecundity selection versus sexual selection), but empirical tests of this assertion are currently absent. Comparisons with growth in the wider bathyergid family could prove particularly useful in helping to understand the ecological pressures shaping size dimorphism in Damaraland mole-rats, for with such large variation in SSD spread across species differing in their mating systems (Begall and Burda 1998; Scharff et al. 1999; Bennett and Faulkes 2000; Sumbera et al. 2003), it seems plausible that SSD reflects selective pressures operating in contemporary populations, rather than an evolutionary relic of selection in evolutionary time, or as Blankenhorn (2005) puts it, a ‘ghost of SSD evolution past’ (i.e., the phylogenetic signal in SSD is weak).

Growth rate is one the most important aspects of a species’ ecology, and the accuracy of its estimation has been a focus of interest for decades (Parks 1982; Starck and Ricklefs

1998). Studies of domesticated mammals have been particularly influential in driving this body of work, but surprisingly few studies of mammals have gone beyond the characterization of growth to ask ecologically informed questions. In one of the few exceptions, Gaillard et al. (1997) used a formulation of the Richards model to investigate the relationship between precocity and the form of growth across 69 mammal species. Their results suggested that peak relative growth rate is relatively earlier in precocial than altricial species, but this pattern only held at the higher taxonomic level of Order. Other examples are conspicuously rare. We suggest that in the era of open data, the unified family of equations that we present in this study can serve as a powerful tool to better investigate mammalian growth in a comparative setting, and we encourage its widespread adoption by mammalogists.

ACKNOWLEDGEMENTS

We are grateful to the Kalahari Research Trust and the Kalahari Meerkat Project for access to facilities in the Kuruman River Reserve, South Africa, and to M. Manser, who helps to maintain the field site with grants from the University of Zurich and the Swiss National Science Foundation. During the period of this study project, the research on Damaraland mole-rats has been supported by a European Research Council Advanced Grant (Nos 294494 and 742808) to T. Clutton-Brock. J. Thorley was funded by a Natural Environment Research Council (UK) Doctoral Training program during the inception of the work. We would like to thank the Northern Cape Department of Environment and Nature Conservation for permission to conduct the research (FAUNA 1020/2016), and P. Vullioud, M. Zöttl, D. Gaynor, T. Vink, and numerous other research assistants, for their historic and continued work with the mole-rats in the Kalahari.

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SUPPLEMENTARY DATA

Supplementary Data SD1.— Methods for the literature search of the use of different sigmoid growth formulations in the mammal literature.

Supplementary Data SD2.— Instantaneous growth rate equations for unified models of sigmoid growth.

Supplementary Data SD3.— Instantaneous growth rates (growth velocity) for the unified growth models applied to female incisor width (a), male incisor width (b), female body length (c), and male body length (d). Instantaneous growth rates represent the first derivative of the best-fitting non-linear mixed effects model in each case. Points on each curve highlight the estimated point of maximum growth in either model. All models were fitted to data on known-age, captive individuals.

Supplementary Data SD4.— The best-fitting random effects structure for each form of unified growth model fitted to skeletal traits.

Supplementary Data SD5.— Estimates for random effects, temporal autocorrelation, and power of variance covariate in models of skeletal growth on captive Damaraland mole-rats.

Supplementary Data SD6.— Parameter estimates and model comparison for ‘interval equation’ models of growth in wild Damaraland mole-rats.

Supplementary Data SD7.— Example R code to fit unified models to mole-rat skeletal data.