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Temporal changes in cranial size in South African vlei rats (*Otomys*): evidence for the ‘third universal response to warming’

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Using museum collections and recently collected specimens we studied geographical and temporal (from 1906 to 2013) changes in skull size of two sibling species of rodents, *Otomys auratus* and *O. angoniensis*, in northern South Africa occupying distinct temperate grassland (*O. auratus*) and subtropical savanna (*O. angoniensis*) biomes. We hypothesised that cranial size should vary in space and time within species according to Bergmann’s Rule, which predicts an inverse relationship between body size and temperature. We used the greatest length of the skull (GLS) as a robust indicator of body size. Cranial size of both *O. auratus* and *O. angoniensis* decreased significantly over the past 100 years, as expected given historical evidence of warming across northern South Africa since the 1950s. In terms of geographical patterns, GLS was inversely correlated with both latitude and longitude in *O. auratus* but these trends were correlated with annual rainfall rather than mean annual temperature. Conversely, cranial size of *O. angoniensis* was weakly positively correlated with longitude but with no climatic variables. Our results demonstrate rapid morphological changes in two herbivorous South African rodents over the past 100 years. Whilst the general decline in size with time in relation to increased temperature is consistent with Bergmann’s Rule, multiple drivers may underlie geographical trends in the two species.

Keywords: Bergmann’s Rule, body size, climate change, morphometric variation, Muridae, South Africa

Introduction

Global surface temperature has been reported to have increased by 0.08–0.14 °C per decade between 1950 and 2012 and it is predicted in many scenarios to rise by 2 °C by 2100 (IPCC 2014). In southern Africa over the last century, annual minimum and maximum temperatures have increased by an average of 0.057 °C and 0.046 °C, respectively, per decade (Davis 2011). Rising temperatures have also been reported in South Africa (Kruger and Shongwe 2004), particularly in Limpopo province (Tshiala et al. 2011).

Anthropogenic climate warming is one of the main threats to biodiversity today (Parmesan 2006). This warming affects phenology, distribution and morphology of species (Hughes 2000; Eastman et al. 2012). For instance, distribution margins of different montane species have been observed to be shifting towards the pole and upward in elevation where they are tracking favourable climatic conditions (Hughes 2000; Parmesan and Yohe 2003; Root et al. 2003; Mulungu et al. 2008). This kind of shift has also been reported for small mammals in Yosemite National Park (Moritz et al. 2008). Projected range shifts due to climate change in range-restricted species may result in high risk of extinction as reported for the Sokoke Scops Owl in Kenya and north-eastern Tanzania (Monadjem et al. 2012) and for the Perote ground squirrel in Mexico (García-Domínguez

et al. 2014). Similarly, high rates of local extinction due to climate change have been predicted for populations of montane vertebrates, particularly hydrophilous amphibians and vertebrates of montane regions of Latin America (McCain and Colwell 2011). Examples of phenological impacts include earlier arrival of Australian migratory birds (Beaumont et al. 2006) and earlier egg laying of 20 species of British birds (Crick et al. 1997).

Morphological changes due to global warming have been reported in a number of species on different continents and in both terrestrial and aquatic environments (Gardner et al. 2011). Studies have primarily used skull length as a measure or proxy for body size in both museum and modern specimens (e.g. Yom-Tov and Yom-Tov 2004; Pergams and Lawler 2009; Eastman et al. 2012; Tomassini et al. 2014). These morphological changes can sometimes be explained by Bergmann’s (1847) zoogeographical rule, which states that animal body size decreases with increasing temperature. Although this generalisation has been mostly tested with respect to variation in latitude and elevation (i.e. spatially), it should also apply temporally in the case of global warming associated with climate change. The debate over which factor(s) ultimately determine body size has not yet been settled (Yom-Tov and Geffen 2006).

There have been disagreements between authors on the authenticity of Bergmann's rule (Scholander 1955; McNab 1971; Calder 1984 in Millien et al. 2006), and some studies conform to the rule while others do not. For example, Yom-Tov (2001) observed a body mass decline in four species of Israeli passerine birds (*Prinia gracilis*, *Passer domesticus*, *Pycnonotus xanthopygos* and *Sylvia melanocephala*) between the years 1950 and 1999. On the other hand, Yom-Tov et al. (2006) also reported a linear increase with time in body weight of four species of British passerine birds. The body size of ground squirrels *Spermophilus beecheyi* has been reported to have increased in northern California, where it is wetter and cooler than it was during the last glacial maximum (LGM) when it was much drier and colder, thus conforming to the expected pattern of Bergmann's rule, but this has been attributed to changes in precipitation not temperature (Blois et al. 2008). Yom-Tov and Yom-Tov (2004) showed a temporal increase in skull size of the Japanese rodent *Apodemus speciosus*. In the masked shrew *Sorex cinereus* of Alaska, Yom-Tov and Yom-Tov (2005) reported a decrease of body size associated with high latitudes and high January minimum temperatures, thus contradicting Bergmann's rule, and an identical pattern was found in five Eurasian species of shrews (*Sorex*) by Ochocińska and Taylor (2003). These changes in body size were attributed to scarcity of food in far northern climates selecting for small body size since smaller shrews require less food. Changes in temperature are therefore not the only factors that affect animal body size. There are other factors such as increased food availability (Yom-Tov 2003; Yom-Tov and Yom-Tov 2005; Eastman et al. 2012), predation (Yom-Tov et al. 2002) and anthropogenic effects such as increased urbanisation and human populations (Yom-Tov 2003; Pergams and Lawler 2009; Tomassini et al. 2014).

The murid tribe Otomyini is endemic to Africa (Taylor et al. 2004a). Most species of the genus *Otomys* are restricted to relict montane distributions, resulting in high levels of regional endemism and widespread disjunction (Clausnitzer and Kityo 2001; Taylor et al. 2009, 2011). The Angoni vlei rat *O. angoniensis* is widely distributed through central and southern Africa as well as East Africa (Bronner and Meester 1988; Taylor 2013a). It is mostly associated with typically lower-lying, mesic savanna habitats, which in South Africa correspond largely with the eastern mesic regions of the Savanna biome (Skinner and Chimimba 2005). The vlei rat *O. auratus* occurs in the north-eastern and central parts of South Africa as well as Lesotho, Swaziland and Zimbabwe (Engelbrecht et al. 2011; Taylor 2013b). In these areas it inhabits temperate grassland habitats associated with the Grassland biome in South Africa (Engelbrecht et al. 2011). In this study we examined the hypothesis that morphological characters of the two sibling species (*O. auratus* and *O. angoniensis*) occupying different biomes should vary both between species and in space and time within species according to the predictions of Bergmann's Rule. The more subtropical species occupying lower elevations (*O. angoniensis*) should be smaller sized than the temperate grassland species from higher altitudes (*O. auratus*). Within both species, size should decrease latitudinally towards the Equator as well as altitudinally.

Methods

Geographic scope and specimens sampled

A total of 254 skulls of *Otomys* were measured comprising 230 (111 *O. angoniensis* and 119 *O. auratus*) from the Ditsong National Museum (formerly Transvaal Museum: TM) from Gauteng, North West, Mpumalanga and Limpopo provinces (59 localities for *O. auratus* and 86 localities for *O. angoniensis*) and 24 (19 *O. angoniensis* and five *O. auratus*) newly collected specimens from Limpopo province (Soutpansberg and Waterberg ranges) and Gauteng province (Rietvlei Nature Reserve) (Figure 1). The recently collected specimens were all deposited in the mammal collection of the Durban Natural Science Museum. Standard small mammal live-trapping (with Sherman traps) and specimen preparation procedures were used to collect these specimens under collecting permits from the Limpopo Department of Environmental Affairs and Tourism (LEDET) (permit no. 001-CPM403-00010), and for Rietvlei Nature Reserve, with the permission of the Tshwane Municipality and Gauteng Department of Agriculture and Rural Development. Capture and handling followed the guidelines prescribed by the American Society of Mammalogists (Sikes et al. 2011).

The museum sample included specimens collected between 1906 and 2003 for *O. angoniensis* and between 1907 and 1994 for *O. auratus*. Our recent collections (2010–2013) from the Soutpansberg and Rietvlei allowed comparisons with historical samples from the same localities collected in 1923 and 1970–1971, respectively. Sampling across time and space was random and fairly representative of all regions and time periods (Figure 1, Supplementary Tables S1 and S2; see also scatterplots in Results). We could not detect any biases due to sampling of particular

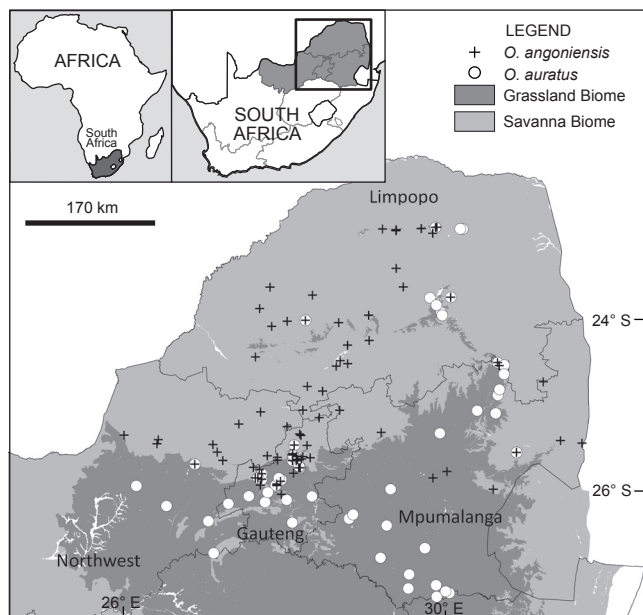


Figure 1: Map showing location of collecting localities of *Otomys* specimens in the four northern provinces of South Africa in relation to the boundaries of the Grassland and Savanna biomes

regions at particular times. For both species, year of collection was not significantly correlated with either latitude or longitude (results not shown but available from PJT).

Morphology

While preliminary analyses were conducted on six cranial and mandibular variables (Taylor and Kumirai 2001; Taylor et al. 2004b), trends were similar across all variables so final analyses were limited to just the greatest length of skull measured dorsally (GLS). Cranial measurements were taken by AN with the use of digital calipers to the nearest 0.01 mm. Locality data from these specimens were used to map species distributions for the study area (Figure 1). Skulls were assigned to one of five tooth-wear classes as described by Taylor and Kumirai (2001). All specimens in age category 1 and 2, most likely representing juveniles and subadults, were excluded from the analyses; thus, final multivariate analyses and sample statistics were based only on 261 'adult' (age class 3, 4 and 5) skulls, of which 130 were *O. angoniensis* and 129 were *O. auratus*. As previous studies have shown complete absence of sexual dimorphism in *Otomys* species (Taylor et al. 1993), we combined data for males and females.

Data analysis

For regression analyses of GLS, we used R version 3.0.3 (R Development Core Team, Vienna; available at <http://www.r-project.org>, downloaded 3 June 2014). Linear models (simple and multiple linear regression) were used to assess the relationship of GLS with seven predictor variables, including the relative age of specimens (tooth-wear class), year of collection, geographical (altitude, latitude and longitude) and environmental (mean annual temperature and annual rainfall) variables. Altitude, mean annual temperature and annual rainfall were obtained from the Worldclim database at 5 arc-minutes resolution (altitude) and 10 arc-minutes resolution (temperature and rainfall) (Hijmans et al. 2005; worldclim.org). ArcMap version 10.1 (<http://www.esri.com>) was used to extract altitude, temperature and rainfall data from the Worldclim coverages for each occurrence record using the 'Extract values to points' tool within the Spatial Analyst toolbox of ArcMap.

Nine linear models were built for each species, seven involving individual predictor variables, a global model

combining all seven predictors, and the best model determined by ranking all subsets of variables according to their Akaike information criterion (AIC) values using the ' dredge' function in R. We used the AIC as 'this model selection criterion chooses a model that is a compromise between the amount of variance explained and the number of parameters included in the model' (Burnham and Anderson 2002). The model with the lowest AIC score was chosen as the most parsimonious model. We plotted residuals from all models to test for non-normality, non-constant error variance and independence (autocorrelation), and used the Shapiro–Wilk, Breusch–Pagan and Durbin–Watson tests, respectively, to test statistically for these assumptions. We used variance inflation factors computed from global models to test for collinearity between linear climatic, temporal and geographical variables with values exceeding 10 being considered for exclusion. In all models tested for both *O. auratus* and *O. angoniensis* we found no evidence for violation of any of the above model assumptions.

Since the model results showed significant effects of tooth-wear class, latitude and/or longitude on cranial variables, and to correct for these effects, we tested the effect of temporal changes (year of collection) on the residuals of GLS obtained after multivariate linear regression on tooth-wear class, latitude and longitude.

Results

Regression model results: geographical and temporal trends

Significant differences in cranial size (GLS) between tooth-wear (relative age) classes (TWCLS) were documented in *O. auratus* (explaining 29% of the variation) and *O. angoniensis* (explaining 20% of the variation) (Tables 1 and 2). As expected, in both species mean cranial size values increased significantly from younger (class 3) to older (class 5) individuals (Figure 2). No significant interaction was observed between TWCLS and the remaining predictor variables (results not shown).

In *O. auratus*, latitude, longitude and rainfall were all significantly inversely correlated with GLS explaining 9.4% (rainfall), 6.9% (latitude) and 6.3% (longitude) of the variance in cranial size, respectively; size therefore

Table 1: Akaike's information criterion (AIC) values, coefficients of determination (r^2) and degrees of freedom (df) for nine models fitted to explain changes in greatest length of the skull of *Otomys auratus*. The best model (with the lowest AIC value) is shown in bold

Model (variables)	r^2 (df)	AIC
1 Latitude	0.069 (1,122)**	597.8
2 Longitude	0.063 (1,122)**	598.6
3 Year	0.051 (1,122)	600.2
4 Mean annual temperature	0.010 (1,122)	605.6
5 Altitude	0.0001 (1,122)	606.8
6 Annual rainfall	0.094 (1,122)***	594.5
7 Tooth-wear class, TCLS (as factor)	0.290 (2,121)***	566.3
8 Latitude + Longitude + TWCLS + Year	0.452 (5,118)***	540.3
9 Global model	0.452 (8,115)***	546.2

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 2: Akaike's information criterion (AIC), coefficients of determination (r^2) and degrees of freedom (df) for nine models fitted to explain changes in skull length of *Otomys angoniensis*. The best model (with the lowest AIC value) is shown in bold

Model (variables)	r^2 (df)	AIC
1 Latitude	0.025 (1,128)	587.7
2 Longitude	0.037 (1,128)*	586.0
3 Year	0.019 (1,128)	588.4
4 Mean annual temperature	0.013 (1,128)	589.2
5 Altitude	0.026 (1,128)	587.5
6 Annual rainfall	0.008 (1,128)	590.0
7 Tooth-wear class, TWCLS (as factor)	0.204 (2,127)***	563.2
8 Latitude + TWCLS + Year	0.267 (4,125)***	556.6
9 Global model	0.287 (8,121)***	561.0

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

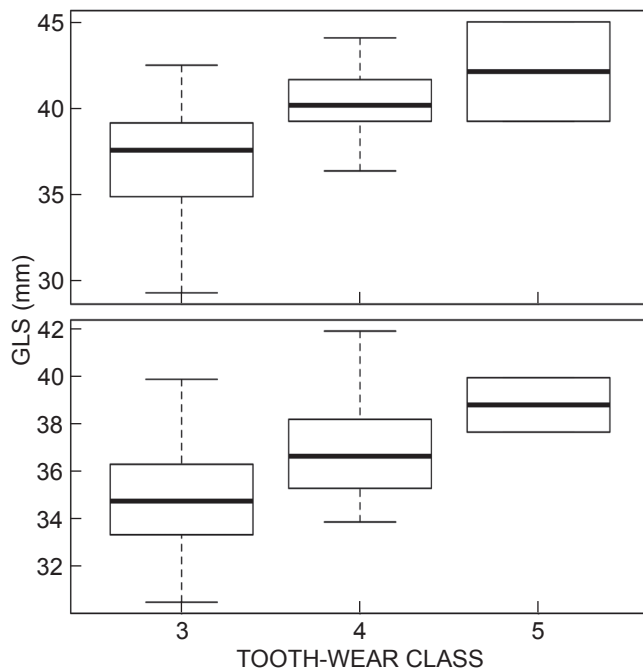


Figure 2: Box-and-whisker plots describing differences in greatest length of the skull (GLS) between tooth-wear classes of *Otomys auratus* (top) and *O. angoniensis* (bottom). The thick horizontal line indicates the median value, the lower and upper limits of the box represent the lower and upper quartiles, and the lower and upper horizontal 'whiskers' represent the minimum and maximum values

decreased along a northerly and easterly moisture gradient in the study area (Table 1, Figure 3). However, in *O. angoniensis*, of the geographical and climatic variables, only longitude was significantly positively correlated with GLS, explaining 3.7% of variation ($p < 0.05$). For both species, the best model having the lowest AIC value (determined using the 'dredge' function in R) involved the same four predictor variables (latitude, longitude, TWCLS and year of collection) or a subset thereof (Tables 1 and 2). In both cases the best model considerably out-performed the global model containing all seven predictor variables.

In *O. auratus*, after correcting for tooth-wear (age) class, latitude and longitude, year of collection was significantly negatively correlated with GLS ($r^2 = 0.090$, $p < 0.001$) (Figure 4). In *O. angoniensis*, after correcting for tooth-wear (age) class, latitude and longitude, year of collection was marginally significantly negatively correlated with GLS ($r^2 = 0.043$, $p = 0.018$) (Figure 5).

Discussion

As clarified by Blackburn et al. (1999), Bergmann's Rule was originally applied to closely related species, but as noted by James (1970) it was later adapted to apply to 'races of a species' (see Mayr 1956). Blackburn et al. (1999) proposed restricting the definition of Bergmann's Rule to cases of interspecific patterns and using the term 'James's Rule' to apply to cases of intraspecific variation.

At the intraspecific level (James's Rule *sensu* Blackburn et al. 1999), the latitudinal pattern in GLS in *O. auratus*,

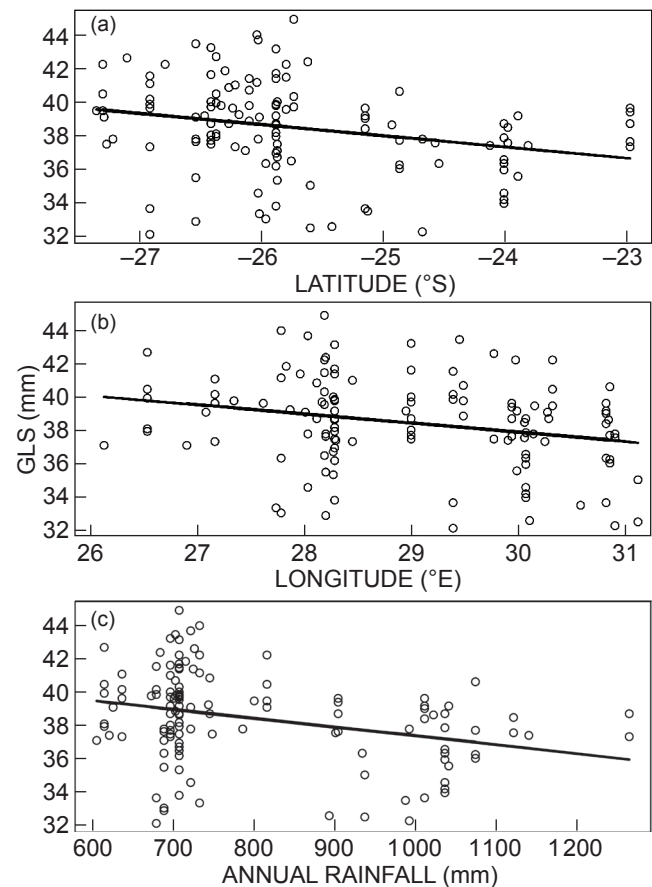


Figure 3: Scatterplots and corresponding regression lines between greatest length of the skull (GLS) and latitude (a), longitude (b) and total annual rainfall (c) in *Otomys auratus*. Cranial size decreased with increasing latitude (northwards), increasing longitude (eastwards) and increasing rainfall. Regression lines were described by the following equations and coefficients of determination: $GLS = -0.664 (\text{Latitude}) + 21.426$, $r^2 = 0.069$, $p = 0.003$ (a); $GLS = -0.550 (\text{Longitude}) + 54.437$, $r^2 = 0.063$, $p = 0.005$ (b); $GLS = -0.005 (\text{Rainfall}) + 42.676$, $p < 0.001$ (c)

and the temporal patterns observed in both species are consistent with the predictions of Bergmann's Rule, reflecting a decrease in size towards the Equator and with time over the past century (between 1906 and 2013). The linear model for GLS against year of collection in *O. auratus* predicted a 6% decline in skull length between 1900 (predicted GLS mean of 39.9 mm) and 2000 (predicted GLS mean of 37.4 mm). In *O. angoniensis*, skull length declined by 3.1% between 1900 (predicted mean 36.2 mm) and 2000 (predicted mean 35.1 mm).

Unequivocal demonstration of Bergmann's Rule would require confirmation that temperature is the causal factor in these observed geographical and temporal patterns. Historical analyses of climate data in South Africa confirm a general increase in minimum, mean and maximum temperatures since the 1950s in many areas, reaching 0.1 °C per decade for example in parts of northern Limpopo, but this varies considerably spatially (Kruger and Shongwe 2004; Tshiala et al. 2011). If the temporal changes in skull size in *O. auratus* and *O. angoniensis* were due to

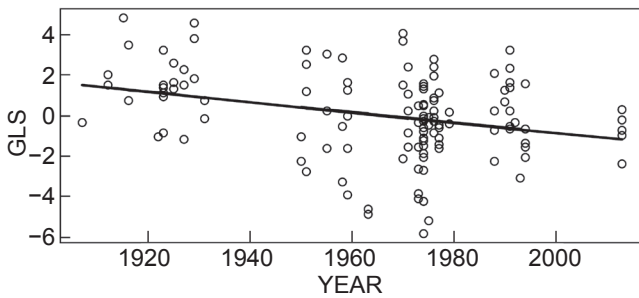


Figure 4: Temporal changes in cranial size in *Otomys auratus*. Scatterplot and corresponding regression line represent the relationships between year of collection and residuals (corrected for tooth-wear class, latitude and longitude) of greatest length of the skull (GLS). Regression equations and coefficients of determination are as follows: $GLS(\text{residuals}) = -0.026(\text{Year}) + 50.14$, $n = 124$, $r^2 = 0.090$, $p < 0.001$

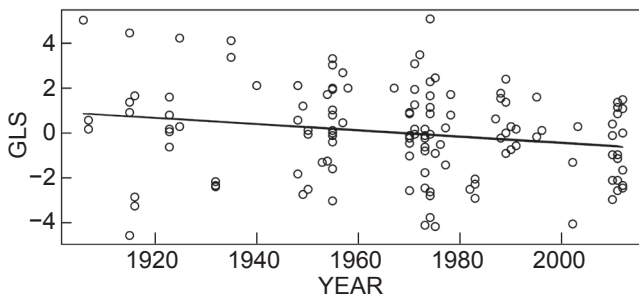


Figure 5: Temporal changes in cranial size in *Otomys angoniensis*. Scatterplots and corresponding regression lines represent the relationships between year of collection and residuals (corrected for toothwear class, latitude and longitude) of greatest length of the skull (GLS). Regression equation and coefficient of determination are as follows: $GLS(\text{residuals}) = -0.003(\text{Year}) + 5.825$, $n = 130$, $r^2 = 0.043$, $p = 0.018$

temperature change, and assuming that the underlying mechanism is due to Bergmann's Rule, we might expect that the observed latitudinal trends should also be correlated with temperature. However, our models for *O. auratus* and *O. angoniensis* showed that temperature was uncorrelated with cranial size (GLS).

Instead, rainfall was significantly correlated with GLS in *O. auratus* and appeared to explain both the latitudinal and longitudinal trends found in this species. Rainfall can be regarded as a proxy for productivity, which might be expected to be positively correlated with food availability, improved nutrition and body size in mammals (as shown by Yom-Tov and Geffen 2006). However, our data show a significant negative rather than positive correlation between GLS and rainfall, refuting this hypothesis. Food availability resulting from increased human densities (and therefore food supplementation) has also been invoked to explain temporal increases in body and cranial size over the past 100 years in commensal carnivores (Yom-Tov and Yom-Tov 2004) and rodents (Gardner et al. 2011). Although human population densities and urbanisation have increased considerably in northern South Africa over the past few decades, given the general decrease rather

than increase over time in cranial variables reported by this study, this does not appear to be a factor in the case of *O. angoniensis* and *O. auratus*. On the other hand, in *O. angoniensis*, GLS showed a marginally significant ($p < 0.05$) decrease in size with longitude (in an easterly direction) rather than a latitudinal trend.

This study provided evidence that rapid morphological change has occurred in two South African herbivorous rodents over the past century, corroborating similar findings for rodents worldwide (Pergams and Lawler 2009). We found a general decrease in cranial size with time in both *O. auratus* and *O. angoniensis*, supporting the idea that decreased body size is the 'third universal ecological response to global warming' besides changes in distributional shifts of species to higher altitudes and latitudes and seasonal changes in life-cycle events (Daufresne et al. 2009; Gardner et al. 2011). Although global warming might be surmised to explain these temporal trends, estimated mean annual temperature was not a significant determinant of geographical variation in either species. In *O. angoniensis* no significant geographic variation was detected in GLS, whereas in *O. auratus* significant latitudinal and longitudinal trends were detected. In addition, annual rainfall, but not altitude or mean annual temperature, was significantly correlated with GLS. Multiple factors rather than temperature alone have been shown to contribute to Bergmann's Rule (Jones et al. 2005).

The rate of morphological adaptation can vary according to life history and biogeographical factors, e.g. in rodents it is higher in species occupying islands (Pergams and Lawler 2009), and this would also be expected to apply to species occupying more fragmented habitat-islands. Given that *O. auratus* occurs in higher-altitude temperate grasslands that have a highly patchy distribution, particularly in Limpopo province (Figure 1), compared with *O. angoniensis* occupying more continuous savanna habitats, we might have expected a greater rate of morphological change in *O. auratus* in space and time compared with *O. angoniensis*. Although our results are not clear-cut, greater model-predicted size decreases from 1900 to 2000 in *O. auratus* (6%) compared with *O. angoniensis* (3%), as well as the significant geographical trends observed in *O. auratus* but not in *O. angoniensis*, are suggestive of more pronounced changes in the former species.

Museum collections involving long time series constitute an invaluable resource to discover temporal changes in morphology. While cranial variables have smaller errors of measurement than external measurements (such as head and body length, tail length, ear length and hind foot length), the latter are also widely available from labels on museum specimens. Given the availability of such collections in South Africa, future studies should aim to investigate historical patterns and environmental correlates of cranial and body size of a range of rodents (and other homeotherms) of different life histories and evolutionary and biogeographical histories and to conclusively test the generality of the 'third universal response to warming'.

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