Size variation in *Tachyoryctes splendens* (Mammalia, Spalacidae) and its implications for late Quaternary temperature change in equatorial East Africa

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Abstract

This study develops a new proxy for Quaternary temperature change in tropical Africa through analysis of size variation in East African mole-rat (*Tachyoryctes splendens*). In modern mole-rats, mandibular alveolar length is unrelated to annual precipitation, precipitation seasonality, temperature seasonality, or primary productivity. However, it is inversely correlated with mean annual temperature, in agreement with Bergmann's rule. This relationship is observed at temperatures below ~17.3°C, but not at higher temperatures. We apply these observations to late Quaternary mole-rats from Wakondo (~100 ka) and Kisaaka (~50 ka) in the Lake Victoria region and Enkapune ya Muto (EYM; ~7.2 to 3.2 ka) in Kenya's central rift. The Lake Victoria mole-rats are larger than expected for populations from warm climates typical of the area today, implying cooler temperatures in the past. The magnitude of temperature decline needed to drive the size shift is substantial (~4-6°C), similar in magnitude to the degree of change between the Last Glacial Maximum and Holocene, but is consistent with regional temperature records and with scenarios linking equatorial African temperature to northern hemisphere summer insolation. Size changes through time at EYM indicate that rising temperatures during the middle Holocene accompanied and potentially contributed to a decline in Lake Naivasha and expansion of grassland vegetation.

Keywords: Bergmann's Rule, Enkapune ya Muto, Karungu, Lake Naivasha, Lake Victoria, paleoclimate, paleoenvironment, Rusinga Island

1. Introduction

East African records of paleoclimate and paleoenvironment are central to understanding the mechanisms underlying Quaternary climate change in tropical Africa (e.g., DeMenocal, 1995; Trauth et al., 2003; Verschuren et al., 2009). It is clear that orbital forcing mechanisms translate to different responses at high latitudes versus the tropics (Clement et al., 2004), but a limited number of records from equatorial Africa prohibits the construction of regional climate histories and limits our understanding of the drivers of climate change in tropical Africa. Developing new climate proxies provides one opportunity to rectify this situation. Such work is not only important to understanding Quaternary climate dynamics, but is also relevant to human origins research (e.g., DeMenocal, 2004; Trauth et al., 2010; Blome et al., 2012). Paleoanthropologists have proposed links between changes in climate and human biology, behavior, and biogeography (Potts, 1998; Vrba et al., 1995; Blome et al., 2012; Potts and Faith, 2015), yet the details of these relationships are limited by few climate proxies that can be associated with archaeological and paleontological records (e.g., Blome et al., 2012) and by lack of a theoretically-grounded understanding of the relationships between climate, environment, and human populations (Behrensmeyer, 2006; Marean et al., 2015).

Our aim here is to develop a new proxy of Quaternary climate change through analysis of body size variation of modern and fossil specimens of East African mole-rat (*Tachyoryctes splendens*). Among contemporary vertebrates, size clines across environmental gradients are well-documented (e.g., Millien et al., 2006), potentially tracking changes in temperature, seasonality, and primary productivity, among other

variables (e.g., Rosenzweig, 1968; James, 1970; Boyce, 1978; Ashton et al., 2000; Gür, 2010). The best known of these relationships is Bergmann's Rule, which (broadly defined) proposes that populations living in cooler climates are larger than their conspecifics in warmer climates (Meiri and Dayan, 2003). Such relationships have long been studied by paleoecologists to reconstruct paleoclimate change in southern Africa from body size shifts of fossil carnivores and various small mammals (Avery, 1982, 2004; Klein, 1986, 1991; Klein and Cruz-Urbe, 1996). Parallel research in East Africa is lacking, although Marean et al. (1994) document potentially climate-mediated size shifts in the mandibular alveolar lengths of Holocene *T. splendens* from Enkapune ya Muto in Kenya's Central Rift Valley. At the time, the lack of modern data relating alveolar length to climate precluded a definitive interpretation of these patterns.

Tachyoryctes splendens is a solitary animal that is discontinuously distributed across portions of East Africa and Central Africa that receive >500 mm annual rainfall. It inhabits a wide range of environments, including tropical forests, open woodlands, and grasslands and occurs at altitudes up to ~4,000 m, preferring well-drained soils suitable for digging extensive burrows (Jarvis and Sale, 1971; Schlitter et al., 2008).

Tachyoryctes is well represented in the East African fossil record (Winkler et al., 2010) with the earliest records of the genus dating to the late Miocene in Ethiopia (Haile-Selassie et al., 2004; Wesselman et al., 2009) and extant *T. splendens* known from Late Pleistocene and Holocene sites in Kenya and Tanzania (Mehlman, 1989; Marean, 1992-b; Marean et al., 1994; Gifford-Gonzalez, 1998; Faith et al., 2015). Together, the occurrence of *T. splendens* in diverse habitats with varied climate regimes, its abundance in the fossil record, and previously documented size shifts make it an ideal

candidate to explore body size-climate relationships. We examine these relationships in modern *T. splendens* and apply our results to address paleoclimate change in Late Pleistocene samples from the Lake Victoria Basin (Tryon et al., 2014, In Press; Faith et al., 2015) and Holocene samples from Enkapune ya Muto (Marean et al., 1994) (Fig. 1).

2. Materials and Methods

2.1. The modern sample

Mandibular alveolar length, a proxy for body size (Hopkins, 2008), was obtained on modern *T. splendens* curated at the National Museum of Kenya (NMK) in Nairobi and at the National Museum of Natural History (NMNH) in Washington, D.C. We consider only those specimens where all molars are fully erupted and in active wear, in order to minimize effects of size differences as a function of ontogeny and potential variation in the age structure of the samples (e.g., because of collection methods or demographic variation across sampled populations). Because many specimens were collected decades to >100 years ago, and location notes are at times vague or place names have since changed, it was not always possible to determine geographic coordinates associated with any given specimen. However, we were able to determine the locations of 203 specimens from 23 localities in Kenya, Ethiopia, and the Democratic Republic of the Congo (Table 1, Fig. 1). For those specimens where collection dates are available (all NMNH specimens, $n = 176$), collection dates range from 1909 to 1994, with the majority ($n = 135$) obtained from 1909-1912. Climate data associated with each location, including mean annual temperature, temperature annual range, annual precipitation, and precipitation seasonality (coefficient of variation of monthly totals), were extracted

from the WorldClim global climate database (Hijmans, 2005). We use the intermediate resolution 5 arc-minute resolution climate layers, which average the climate signal from a broader area, to account for the lack of precise locality coordinates for some samples. In addition, we calculated annual net primary productivity (NPP), averaged from 2010-2014, from the MODIS MOD17 data (Zhao et al., 2005) over a 5 km radius around each locality.

Global climate change over the last ~100 years could contribute to a slight mismatch between mole-rat specimens, many collected in the early 1900s, and their associated climate data. However, the magnitude of such error is minor compared to magnitude of climatic variation between localities. For example, the IPCC (2015) reports an increase in average global temperature of ~0.85°C since 1880, two orders of magnitude lower than the range of mean annual temperatures across modern localities (13.6°C). While differences in climate between today and when the specimens were collected may contribute to a minor amount of analytical noise, this should be swamped out by the variation between localities.

The modern localities encompass substantial variation in annual precipitation (805 to 1943 mm/yr) and mean annual temperature (10.0 to 23.6°C). Temperature variation is related to elevation gradients (Table 1), as confirmed by a tight inverse correlation between mean annual temperature and elevation ($r = -0.982$, $p < 0.001$). Other studies of size clines in mammals typically explore variation across broad latitudinal gradients (e.g., Rosenzweig, 1968; Klein, 1986; Koch, 1986), over which temperature, seasonality, and primary productivity often co-vary, making it difficult to disentangle the factors driving size variation (see also Ashton et al., 2000; Gür, 2010).

Our sample is restricted to the tropics and is characterized by a limited latitudinal range (5.55°S to 11.25°N), with 16 of the 23 sample localities falling within 1.5° of the equator. There is a significant, but weak, correlation between the two variables related to seasonality (temperature annual range and precipitation seasonality: $r = 0.431$, $p = 0.040$), but otherwise there are no significant correlations between environmental variables considered here ($p > 0.15$ for all other pairwise comparisons).

2.2. Lake Victoria

The Late Pleistocene mole-rat samples were collected over successive field seasons from 2010 to 2015 at the Kisaaka locality at Karungu (Faith et al., 2015) and the Wakondo locality on Rusinga Island (Tryon et al., 2010), both situated near the shores of Lake Victoria in western Kenya (Fig. 1). These localities include exposures of the Late Pleistocene sedimentary sequence found throughout the region (~100 to 33 ka), which preserve abundant fossil fauna and Middle Stone Age (MSA) artifacts (Tryon et al., 2010, 2012, 2014, In Press; Faith et al., 2015). Stratigraphic control is provided by the presence of widespread volcanic ashes (Blegen et al., 2015). Samples from Kisaaka were collected from strata directly on top of and immediately below the Nyamita Tuff, which is exposed throughout the region and is bracketed by optically stimulated luminescence ages of 46 ± 4 ka and 50 ± 4 ka above and below the tuff respectively (Blegen et al., 2015). Because we cannot rule out the possibility that those specimens found below the tuff eroded from sediments above the tuff, we treat the Kisaaka mole-rat assemblage as a single aggregate dating to roughly 50 ka.

The Wakondo sample includes fossils collected from an outcrop known as Rat Hill (Fig. 2 in Blegen et al. 2015). At this locality, mole-rat remains are found over a small area (~5 x 5 meters) atop a ridge of Late Pleistocene sediment at a similar level to a nearby (~10 m) exposure of the Wakondo Tuff. The Wakondo Tuff is the basal tuff identified in the eastern Lake Victoria sequence and likely derives from a phonolitic eruption of Suswa or Longonot in the southern Kenyan Rift Valley dated to 100 ± 10 ka (Tryon et al. 2010; Blegen et al., 2015), an age estimate consistent with U-series dates of 94.0 ± 3.3 ka to 111.4 ± 4.2 ka obtained on a tufa deposit underlying the Wakondo Tuff at nearby Nyamita (Beverly et al., 2015-b). Because the Wakondo Tuff is not exposed in the immediate vicinity of the mole-rat collection area and all specimens were surface-collected, we refrain from assigning them to a precise position above or below the tuff. At present, our best estimate for the age of the Wakondo assemblage is ~100 ka, based on the age for the Wakondo Tuff.

At both Kisaaka and Wakondo, mole-rats were collected during general surface collection of fossil remains and through screening of the surface sediments through 1-mm mesh at areas where they are locally abundant (Rat Hill at Wakondo, Rodent Carbonate Site, Zebra Tooth Gulley, and Kisaaka Main at Kisaaka; see Faith et al., 2015). Preservation at both localities is remarkable, often including partial skeletons in articulation and cemented in carbonate, a taphonomic mode we interpret as likely reflecting burial of mole-rats in their burrows. The close association of the Wakondo mole-rats with the Wakondo Tuff, together with the absence of mole-rats found elsewhere at Wakondo despite several field seasons of survey, raises the possibility that this sample represents a catastrophic death assemblage related to the ash fall

event (e.g., suffocation). Thick (up to ~3.5 m) paleosols are exposed above and below the Wakondo and Nyamita Tuffs (Blegen et al., 2015; Beverly et al., 2015-a). These paleosols represent relatively stable land surfaces into which the mole-rats would have burrowed. Observation of modern mole-rats show that burrow depth is variable, with foraging burrows ranging from 10-60 cm below the surface, determined by the level of roots, tubers, or rhizomes on which they feed, nests ranging from 10-60 cm, and bolt-holes (blind tunnels into which the mole-rat hides when alarmed) up to ~180 cm (Jarvis and Sale, 1971). This burrowing behavior means that the mole-rat samples may be time-averaged over the lifespan of the paleosols (up to several kyr) and that some individuals may have burrowed lower in the section. However, the close association of the Kisaaka and Wakondo fossils with the Nyamita and Wakondo Tuffs, respectively, suggests that the two assemblages likely sample non-overlapping time intervals during the Late Pleistocene.

Several lines of paleoenvironmental evidence suggest that the Late Pleistocene deposits on Rusinga Island (Wakondo) and Karungu (Kisaaka) document conditions characterized by an expansion of C₄ grasslands and reduced precipitation compared to the present (~1400 mm/year today). The dominance of zebras (*Equus grevyi* and *Equus quagga*) and bovids belonging to the tribes Alcelaphini and Antilopini indicate widespread grasslands (Tryon et al., 2010, 2012; Faith et al., 2015), distinct from the evergreen bushlands, woodlands, and forests found in the area historically (White, 1983; van Breugel et al., 2012). Stable carbon isotope analysis of herbivore tooth enamel, including *T. splendens* from Karungu, indicates that C₄ grasslands were both locally and regionally widespread (Faith et al., 2015; Garrett et al., 2015). The presence

of arid-adapted species outside of their historic ranges, especially Grevy's zebra (*E. grevyi*) and oryx (*Oryx cf. beisa*), is consistent with a reduction in precipitation (Faith et al., 2013), as is the dominance of extinct species characterized by exceptional hypsodonty (Faith et al., 2011, 2012). Drier conditions are further suggested by the geochemical composition of the paleosols at Kisaaka, which provide precipitation estimates of ~760-960 mm/yr through the Late Pleistocene sequence (Beverly et al., 2015-a).

2.3. Enkapune ya Muto

Marean et al. (1994) recorded mandibular alveolar lengths for mole-rats from Enkapune ya Muto (EYM), which we re-examine here. EYM is a rockshelter located ~10 km west of Lake Naivasha on the eastern face of the Mau Escarpment (Fig. 1), preserving a rich archaeological and faunal sequence, including numerous micromammal remains, excavated by Ambrose in the 1980s (Marean, 1992a; Ambrose, 1998). The radiocarbon chronology for those stratigraphic units providing mole-rat remains is reported in Table 2, with dates calibrated in OxCal 4.2 (Bronk Ramsey, 2009, 2013) using the IntCal13 calibration curve (Reimer et al., 2013). The EYM assemblage spans the mid-Holocene from ~7,200 to 3,200 cal yrs BP. Gastric etching commonly observed on the micromammal remains indicates that owls likely deposited the mole-rats (Marean et al., 1994).

The Holocene mole-rat assemblage from EYM spans a phase of significant environmental and climatic change. Cores from Lake Naivasha as well as nearby lakes Nakuru and Elmenteita show a pronounced high-stand in the early Holocene (~12,000

to 5,500 cal yrs BP), followed by a rapid decline culminating in a phase of maximum aridity at ~3,000 cal yrs BP (Richardson and Richardson, 1972; Richardson and Dussinger, 1986). The pollen record from Lake Naivasha shows that the high-stand was associated with forest vegetation, with grasslands expanding as conditions became increasingly arid (Maitima, 1991; Street-Perrot and Perrott, 1993), a pattern also observed in the micromammal assemblage from EYM (Marean et al., 1994). The pollen data further suggest reduced mean annual temperatures during the early Holocene, perhaps due to increased cloudiness (Street-Perrot and Perrott, 1993). With respect to large mammals from EYM, measurements on third phalanges assigned to Reduncini show a decrease in body size that was interpreted to indicate a shift from the larger bohor reedbuck (*Redunca redunca*) to the smaller mountain reedbuck (*Redunca fulvorufula*), consistent with the lakeshore becoming increasingly distant from EYM as lake level declined (Marean, 1992a). Tragelaphini (e.g., bushbuck, *Tragelaphus scriptus*) show a similar pattern.

2.4 Analytical Methods

All statistical analyses are conducted using the Paleontological Statistics Package (PAST) (Hammer et al., 2001) and the R Statistical Package (R Core Team, 2014). Due to the uneven sample sizes across localities (Table 1), our analysis of size clines in modern *T. splendens* considers the mean alveolar length for a given locality, rather than all individual measurements. This is to prevent the handful of very well-sampled localities (e.g., Lake Naivasha, Mount Kenya) from disproportionately influencing the results. Because previous studies have demonstrated that size-climate relationships

can be linear (Klein, 1986) or quadratic (Klein and Cruz-Urbe, 1996), both least-squares linear and quadratic regressions are used here. For those size clines that are statistically significant, we conducted a breakpoint analysis using the maximum likelihood approach in the R package 'segmented' (see Muggeo, 2008) to identify possible changes in slope (i.e., breakpoints) indicative of environmental thresholds above or below which a size-cline is observed.

To explore how size shifts at EYM relate to temporal trends in microfaunal species composition, we conduct a detrended correspondence analysis (DCA) on species abundances (data from Marean et al., 1994) across the sequence (see Greenacre and Vrba, 1984). This allows us to examine the association between different strata and different species; when plotted in two dimensions, stratigraphic units with similar species compositions plot together, as do species with similar temporal trends in abundance. We use the primary axis (Axis 1) scores for each stratum to broadly summarize its species composition, and examine how these values change through time (as in Faith, 2013). Marean et al. (1994) previously observed that the size decline in EYM mole-rats tracks an increase in its abundance; we exclude mole-rats from the DCA to render it independent of this taxon.

3. Results

*3.1 Size variation in modern *Tachyoryctes splendens**

There is substantial size variation across the modern mole-rat sample, with mandibular alveolar lengths ranging from 8.4 to 13.0 mm. Considering those localities with at least one specimen of each sex ($n = 11$), a two-way ANOVA reveals that alveolar lengths

differ significantly as a function of both locality ($F(11) = 62.54$, $p < 0.001$) and sex ($F(1) = 21.45$, $p < 0.001$). This analysis also reveals significant interaction between geography and sex ($F(11) = 3.295$, $p < 0.001$), indicating that the degree of dimorphism is variable across localities.

Figure 2 illustrates the relationship between alveolar length and the climatic and environmental variables. We observe no relationship between mean alveolar length and precipitation seasonality (linear: $r = 0.275$, $p = 0.205$; quadratic: $r = 0.291$, $p = 0.413$), annual precipitation (linear: $r = 0.348$, $p = 0.104$; quadratic: $r = 0.364$, $p = 0.242$), annual temperature range (linear: $r = -0.125$, $p = 0.571$; quadratic: $r = 0.217$, $p = 0.617$), or NPP (linear: $r = -0.156$, $p = 0.487$; quadratic: $r = 0.240$, $p = 0.569$). In contrast, there are strong correlations between mean alveolar length and mean annual temperature (linear: $r = -0.691$, $p < 0.001$; quadratic: $r = 0.891$, $p < 0.001$). These results are consistent with a multiple linear regression that considers all variables together (multiple $r = 0.768$, $p = 0.006$), in which only temperature has a significant influence on alveolar length (temperature: $p < 0.001$; annual temperature range: $p = 0.749$; annual precipitation: $p = 0.075$; precipitation seasonality: $p = 0.718$; NPP: $p = 0.956$).

The size-temperature relationship does not appear consistent across all temperature values, with an apparent levelling off at higher temperatures (above $\sim 17^\circ\text{C}$; Fig. 3). This is confirmed by the breakpoint analysis, which reveals a single linear model breakpoint at 17.3°C (95% CI: 16.2 to 18.4°C), with regression slopes before (-0.356 ; 95% CI: -0.437 to -0.274) and after (0.064 ; 95% CI: -0.048 to 0.176) the breakpoint exhibiting a significant difference ($p < 0.001$). Before the breakpoint (below 17.3°C) alveolar length declines as temperature increases ($r = -0.935$, $p < 0.001$; Spearman's

rho (r_s) = -0.832, $p < 0.001$), but there is no trend beyond the 17.3°C breakpoint ($r = 0.411$, $p = 0.209$; $r_s = 0.455$, $p = 0.160$).

3.2. Size variation in the Lake Victoria fossil sample

Mandibular alveolar lengths of the Kisaaka ($n = 17$) and Wakondo ($n = 20$) samples are plotted in Figure 3 at contemporary annual mean temperatures for the two sites (Kisaaka: 22.2°C; Wakondo: 22.6°C; from Hijmans et al., 2005). 95% confidence limits for the means are obtained by bootstrapping each sample with replacement 10,000 times. Confidence limits for both the Kisaaka (9.64 to 10.15 mm) and Wakondo (9.78 to 10.18 mm) fossil assemblages are significantly larger than those for all modern mole-rats from localities with mean annual temperature $>17.3^\circ\text{C}$ ($n = 74$; 9.30 to 9.52 mm). This difference is further supported by one-way ANOVA ($F(2,108) = 14.550$, $p < 0.001$).

3.3. Size variation in the Enkapune ya Muto fossil sample

Alveolar lengths of mole-rats across the EYM sequence are illustrated in Figure 4 alongside the modern sample from nearby Lake Naivasha ($n = 50$). One-way ANOVA reveals a significant difference in sample means across the EYM sequence ($F(4,64) = 3.495$, $p = 0.012$), which is characterized by a decline in mean alveolar length moving up the stratigraphic column ($r_s = -0.900$, $p = 0.037$; Fig. 4). Only in samples from higher in the sequence (RBL2.2 and RBL2.1) do the 95% confidence limits for the mean overlap those for the modern Naivasha sample, whereas those below are significantly larger (RBL2.3, DBS, and RBL3). These lower Holocene units also include large

specimens that fall well beyond the maximum observed size of the well-sampled modern assemblage from Lake Naivasha.

Results of the DCA are illustrated in Figure 5. The Axis 1 scores for each stratigraphic unit decline through time, with a slight uptick in RBL2.1. These values are perfectly correlated with the change in mole-rat average tooth-row length ($r_s = 1$, $p = 0.017$), suggesting that changes in mole-rat size are paralleling other – presumably environmentally-driven – changes in micromammal community composition. As indicated in Figure 5, DCA Axis 1 values capture a contrast between unstriped grass rat (*Arvicanthis niloticus*), a species that prefers fire climax grasses, and zebra mouse (*Lemniscomys* sp.), though the latter is represented only by a single specimen in RBL3 and could belong to one of several species with diverse habitat preferences. The percent abundance of unstriped grass rat, which increases through the sequence, is significantly correlated with DCA Axis 1 scores ($r_s = -0.900$, $p = 0.037$). It follows that, excluding changes in mole-rats, the principal change in micromammal community composition at EYM is a temporal increase in unstriped grass rat.

4. Discussion

4.1. Size variation in modern *Tachyoryctes splendens*

To the extent that alveolar length is a reasonable proxy for body size (see Hopkins, 2008), size variation in modern *T. splendens* broadly conforms to Bergmann's rule, whereby populations inhabiting cooler climates are larger than those from warmer climates. This is consistent with variation in cranial size across populations examined by Beolchini and Corti (2004). While there is broad support for Bergmann's rule among

mammals (Ashton et al., 2000; Meiri and Dayan, 2003; Millien et al., 2006), there is debate about the underlying mechanisms (e.g., Rosenzweig, 1968; James, 1970; Boyce, 1978; Ashton et al., 2000; Gür, 2010). Bergmann (1847) proposed that large size is optimal in cooler climates because of a decrease in the surface area to mass ratio, thereby limiting heat dissipation per unit of mass. Others suggest that size clines observed across broad latitudinal gradients may instead be driven by seasonality and its effects on resource availability (Boyce, 1978, 1979; Lindstedt and Boyce, 1985), which could favor larger individuals due to their enhanced fasting endurance (i.e., ability to survive through periods of forage scarcity) (Millar and Hickling, 1990), or differences in primary productivity (Rosenzweig, 1968; Geist, 1987). Our observations are inconsistent with either scenario, as body size in *T. splendens* is unrelated to seasonality or primary productivity (Fig. 2).

The size-temperature relationship is not observed across the entire range of mean annual temperatures in the sample. Rather, size is unrelated to temperature above ~17.3°C, but increases as temperature declines below this threshold (Fig. 3). This pattern has implications for the potential mechanisms underlying the Bergmann's rule pattern; while Bergmann's rule is typically framed in terms of heat conservation, others have emphasized the importance of heat dissipation (James, 1971, 1991), with smaller body size facilitating heat loss, especially under elevated humidity. At least for *T. splendens*, our observations suggest that heat conservation is more important than heat dissipation; if the latter were driving size variability, we would expect to see size changes at the high end of the temperature spectrum, rather than only at temperatures below ~17.3°C. Assuming that size changes in mole-rats reflect heat conservation, it is

possible that at higher temperatures (above 17.3°C) any requirements for conservation of body heat are met by increased insulation through changes in hair density or hair length (Wasserman and Nash, 1979), while at lower temperatures (below 17.3°C) heat is conserved through an increase in body mass. Whatever the explanation, this threshold remains an important feature when exploring size variation in fossil samples.

In addition to temperature, it is conceivable that mole-rat alveolar length could be influenced by diet or burrowing substrate (they dig with their incisors), which in turn may vary across environmental gradients. Although we lack diet or substrate data for the modern sample, the morphometric analysis of mole-rat crania provided by Beolchini and Corti (2004) provides important insights. They show that cranial *size* is related only to temperature and altitude (variables that co-vary in our dataset), whereas cranial *shape* varies in relation to numerous climatic and geographical variables. The shape differences are related to those portions of the skull associated with insertion of the masseter and temporal muscles, which are essential to mastication and burrowing. This provides reason to believe that potential differences in diet (e.g., food type) or substrate (e.g., soil moisture), likely influenced by a combination of environmental variables, are reflected by shape differences, whereas size variation is underpinned primarily by temperature (Beolchini and Corti, 2004).

Differential access to high-quality forage may play an additional role in driving variability in mole-rat body size. This could include, for example, access to domestic crops, as East African mole-rats frequently forage in agricultural lands (Fielder, 1994). Because forage quality is related to body mass in some species (Case, 1979; Lindsay, 1986), higher-quality foods could translate to larger body sizes. Although we lack dietary

observations, we can provide an indirect assessment of whether forage quality mediates mole-rat body size. In contemporary East African ecosystems, plant nitrogen content, an index of plant quality to herbivores, declines substantially as precipitation increases (Olf et al., 2002). The modern mole-rat localities examined here are characterized by substantial variation in annual precipitation (805 to 1943 mm/yr), over which plant nitrogen content should also vary considerably. If forage quality plays an important role in determining the size of *T. splendens*, there should be a relationship between body size and precipitation. However, our analysis fails to document any such relationship (Fig. 2); precipitation – and by extension, forage quality – are not responsible for size variation in modern mole-rats. It follows that differential access to high-quality foods is probably not a major factor in the body size of modern *T. splendens*. In the absence of viable alternatives, temperature seems to be the most important factor.

4.2. Size variation in the Lake Victoria fossil sample

The Lake Victoria samples from Kisaaka and Wakondo are from areas that are today characterized by high mean annual temperatures (Kisaaka: 22.2°C; Wakondo: 22.6°C), well above the 17.3°C threshold below which we expect body size to change as a function of temperature. Both the Kisaaka and Wakondo specimens are larger than expected for mole-rats in environments warmer than ~17.3°C. Based on the modern relationship between size and temperature (Fig. 3) and taking into account the 95% confidence limits for the 17.3°C breakpoint (16.3 to 18.4°C), a temperature drop of ~4-6°C is required to drive these size increases. This is comparable to the magnitude of temperature change between the Last Glacial Maximum (LGM) and Holocene (~3.5 to

5°C) observed in cores at Lake Challa on the slopes of Mount Kilimanjaro (Sinninghe Damsté et al., 2012), Lake Tanganyika (Tierney et al., 2008), and Lake Malawi (Powers et al., 2005; Woltering et al., 2011). While such declines at ~50 ka and ~100 ka are substantial, pre-LGM temperature variations of similar magnitude are evident in the records from Lake Tanganyika (Tierney et al., 2008) and Lake Malawi (Woltering et al., 2011). In particular, cool conditions are observed in both lakes during portions of Marine Isotope Stage (MIS) 3 corresponding to the age of the Nyamita Tuff (between 46 ± 4 ka and 50 ± 4 ka) and the likely age of the Kisaaka mole-rats, although these records do not extend to the likely age of the Wakondo mole-rats.

Tierney et al. (2008) propose that tropical African temperatures are controlled in part by northern hemisphere summer insolation (see also Clement et al., 2004; Woltering et al., 2011). There is a moderate low in northern hemisphere summer insolation at ~46-47 ka, corresponding to the probable age of the Kisaaka specimens, and a more prominent low in northern hemisphere summer insolation at ~94-95 ka (Berger and Loutre, 1991), which falls within the likely age range of the Wakondo Tuff (Fig. 6). We presently lack the tight chronological control required to confidently link the Lake Victoria specimens to these insolation minima, but the potential for substantially cooler temperatures in equatorial East Africa associated with northern hemisphere insolation minima during MIS 3 and 5 remains an intriguing possibility.

Aside from cooler temperatures, alternative explanations for the large size of the Lake Victoria mole-rats include (1) taphonomic bias towards large-bodied males, and (2) enhanced forage quality due to reduced atmospheric CO₂ concentrations. The former seems unlikely, as it is unable to account for the presence of extremely large

specimens outside the range of modern mole-rats from localities with mean annual temperatures above 17.3°C (Fig. 3). With respect to the latter, physiological models and experimental observations indicate that lower CO₂ concentrations are associated with higher plant nutrient content, especially nitrogen, and fewer secondary compounds (Fajer et al., 1989; Kinney et al., 1997; Cotrufo et al., 1998; Tissue et al., 1999; Luo et al., 2004; Bigras and Bertrand, 2006). Given that forage quality can influence body mass (Case, 1979; Lindsay, 1986), it is possible that the Kisaaka and Wakondo mole-rats are large because lower CO₂ during the Late Pleistocene (Petit et al., 1999) contributed to more nutritious and digestible forage (see Gingerich, 2003 for a similar argument). As discussed above, however, the lack of any relationship between mole-rat size and precipitation, which in turn should mediate plant nutrient content (Olff et al., 2002), suggests that reduced CO₂ and enhanced forage quality do not explain the large body size. Instead, cooler temperatures remain the more plausible mechanism underpinning the large size of the Lake Victoria mole-rats.

4.3. Size variation in the Enkapune ya Muto fossil sample

EYM lies in an area today characterized by mean annual temperatures of ~16.3°C (Hijmans, 2005). The mole-rats from RBL2.2 (~6,000 cal yrs BP) and RBL2.1 (~3,200 to 5,600 cal yrs BP) correspond closely to modern mole-rats from nearby Lake Naivasha, but those from earlier in the sequence (RBL3, DBS, and RBL2.3), dated from ~7,200 to 6,100 cal yrs BP, are significantly larger. Marean et al. (1994) proposed four potential explanations for this decrease in size: (1) a warming climate, (2) a decline in rainfall, (3) a decline in tuber size and density because naked mole-rat (*Heterocephalus glaber*)

body mass is known to correlate with both (Jarvis et al., 1991), and (4) a taphonomic scenario.

Our analysis shows that mole-rats do not vary as a function of rainfall (Fig. 2), so we can exclude explanation 2. As noted above, the Reduncini and Tragelaphini show similar body size changes as the mole-rats (Marean, 1992a). Since neither eats the same diet as *T. splendens*, explanation 3 seems unlikely. The taphonomic explanation derives from the fact that mole-rats are most susceptible to predation by raptors when they leave their burrows, typically in the case of large adult males in search of mates. When mole-rat densities are low, juveniles forced from their mother's burrow often branch off to a separate section of the burrow complex and seal it off. However, when mole-rat densities are high, the young must leave the mother's burrow and move above-ground to establish a new burrow complex, rendering them vulnerable to predation (Jarvis, 1973). Because mole-rats increase in abundance through the EYM sequence (Marean et al., 1994), which likely indicates an increase in mole-rat densities, the temporal size decline could reflect increased access to juveniles by the owl accumulators. We can now rule out this hypothesis. The samples from RBL2.3, DBS, and RBL3 include specimens well above the maximum size of mole-rats from the Naivasha area today. While changes in owl access to adults and juveniles could contribute to changes in mean size, it cannot account for the presence of oversized mole-rats. Sample size effects, in which greater sampling effort will lead to greater maximum values, are also unlikely, given that the modern Naivasha sample is substantially larger than any of the fossil samples. It follows that temperature change is a more suitable explanation.

The large size of mole-rats from units RBL3, DBS, and RBL2.3 is best explained by cooler temperatures compared to the present during the Lake Naivasha high-stand (Richardson and Dussinger, 1986), consistent with interpretations of the Lake Naivasha pollen record (Street-Perrot and Perrott, 1993). The reduction in size in RBL2.2 and RBL2.1 suggests an increase in temperatures at ~6,000 cal yrs BP that parallels declining lake levels (Richardson and Dussinger, 1986), expansion of grasslands (Maitima, 1991), large mammal evidence for drier conditions (Marean, 1992a), and changes in micromammal community composition (Fig. 5), namely increasing abundances of *Arvicanthis niloticus* (Marean et al., 1994), a species that prefers fire climax grasses. While such changes are typically linked to orbitally-controlled precipitation dynamics, rising temperatures could have played a complementary role. Rising temperatures translate to elevated evaporation rates, contributing to the decline of Lake Naivasha (Bergner et al., 2003; Dühnforth et al., 2006). Warmer temperatures also serve to increase the flammability of plant matter through its effects on evapotranspiration, which – especially coupled with drier conditions – will increase the frequency and severity of wildfire (e.g., Westerling et al., 2006), and in turn drive an expansion of grassland vegetation (Norton-Griffiths, 1979).

Mid-Holocene warming is also evident in records from Lake Turkana (Berke et al., 2012b), Lake Malawi (Powers et al., 2005; Woltering et al., 2011) and Lake Tanganyika (Tierney et al., 2008), although it is not seen in records from Lake Challa (Sinninghe Damsté et al., 2012) or Lake Victoria (Berke et al., 2012-a), attesting to regional variability. Although temperature shifts over orbital time-scales are in part related to maxima in northern hemisphere summer insolation, the mid-Holocene

temperature increase takes place in the context of declining northern hemisphere summer insolation (Fig. 6), indicating an alternate mechanism. Peak local insolation from September to November at ~5 ka has been proposed as one possibility (Tierney et al., 2010; Berke et al., 2012b), but it is unclear why the three equatorial records (Lake Challa, Lake Victoria, and EYM) show contrasting signals. Identifying the mechanisms driving Holocene temperature variability, both locally and regionally, will require longer-term and more finely resolved records than those provided here.

5. Conclusion

Our analysis of East African mole-rats shows that alveolar length, and by extension body size (Hopkins, 2008), is inversely related to mean annual temperature, consistent with Bergmann's rule. This relationship is observed at temperatures below 17.3°C, but there is no trend at higher temperatures. We observe no significant influence of annual precipitation, seasonality of temperature or precipitation, or primary productivity on mole-rat size, in contrast to some explanations for the Bergmann's rule pattern (Rosenzweig, 1968; Boyce, 1978, 1979; Lindstedt and Boyce, 1985). Our results suggest that size changes in fossil *T. splendens* can be used to track paleotemperature change in Quaternary fossil assemblages.

Late Pleistocene mole-rats from Kisaaka (~50 ka) and Wakondo (~100 ka) in the Lake Victoria region are larger than mole-rats from warm climates (>17.3°C), indicating a substantial decline in temperature relative to the present (~4-6°C). Such change can be accommodated by scenarios linking African temperature dynamics to northern hemisphere summer insolation (Tierney et al., 2008) and raise the possibility for very

cool conditions during parts of MIS 3 and MIS 5. Temporal shifts in mole-rat size at EYM show that rising temperatures through the middle Holocene accompanied – and likely contributed to – a decline in Lake Naivasha and expansion of grassland vegetation. While precipitation dynamics remain a focus of research on tropical African paleoenvironments, our results raise the possibility that the effects of temperature change play a role in modulating the effects of rainfall on ecosystem change.

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832

Figure Captions

Figure 1. Location of modern *T. splendens* samples and (inset) fossil assemblages from Kisaaka, Wakondo, and Enkapune ya Muto. Key to sites: 1. Kahungu; 2. Lwiro; 3. Rutchuru; 4. Ngong, Karen, Muguga, and Nairobi; 5. Kijabe; 6. Lake Naivasha; 7. Aberdare Mountains and Aberdare National Park; 8. Laikipia; 9. Mount Kenya; 10. Njoro; 11. Subukia; 12. Kakumega Forest; 13. Cherangani; 14. Mount Elgon; 15. Gogeb; 16. Agaro; 17. Nazareth; 18. Fatam; 19. Dangila.

Figure 2. Mandibular alveolar length plotted against climatic and environmental variables. Linear (solid line) and quadratic regressions (dotted line) are calculated using mean alveolar lengths for each of the 23 sample localities.

Figure 3. (A) Mandibular alveolar lengths plotted against annual mean temperature for modern mole-rats (diamonds) and fossils from Kisaaka and Wakondo (circles). The Kisaaka and Wakondo samples are plotted at modern temperatures for these localities. Vertical line indicates the 17.3°C breakpoint, with the grey bar indicating its 95% confidence intervals. (B) Box plots illustrating mandibular alveolar lengths of the modern mole-rat samples from areas with mean annual temperatures >17.3°C, and for fossil mole-rats from Kisaaka and Wakondo. Horizontal line is the range, open horizontal bar indicates the 25th and 75th quartile, vertical line is the mean, dark grey horizontal bar indicates 95% confidence limits for the mean, and the light grey vertical bar indicates 95% confidence limits for the mean of the modern sample. Sample size in parentheses.

Figure 4. Box plots illustrating mandibular alveolar lengths of the modern mole-rat sample from Lake Naivasha compared to the Holocene assemblages from EYM. Horizontal line is the range, open horizontal bar indicates the 25th and 75th quartile, vertical line is the mean, dark grey horizontal bar indicates 95% confidence limits for the mean, and the light grey vertical bar indicates 95% confidence limits for the mean of the modern Lake Naivasha sample. Sample size in parentheses.

Figure 5. DCA of micromammal species abundances at EYM. (A) Axis 1 versus Axis 2. Species indicated by open diamonds and stratigraphic units by filled diamonds. 1 = *Arvicanthis niloticus*; 2 = *Otomys irroratus*; 3 = *Elephantulus brachyrhynchus*; 4 = *Thamnomys* sp.; 5 = *Oenomys hypoxanthus*; 6 = *Crocidura* sp. and *Dendromus* sp.; 7 = *Praomys* sp.; 8 = *Lophuromys* sp.; 9 = *Dasymys incomius*; 10 = *Molymys dybowski*; 11 = *Lemniscomys* sp. (B) Axis 1 scores moving up the stratigraphic column.

Figure 6. Approximate ages of the fossil mole-rat assemblages compared to northern hemisphere (30°N) summer insolation (insolation values from Berger and Loutre, 1991).

Table 1. Summary of the modern mole-rat samples. Net primary productivity (NPP - g carbon/m²) is log-transformed. Standard deviation (SD) of alveolar length reported in parentheses.

Locality	N	Elevation (m)	Latitude	Longitude	Mean (SD) Alveolar length (mm)	NPP	Temperature (°C)		Precipitation (mm)	
							Mean	Annual range	Annual	Seasonality (CV)
Kahungu, DRC	4	731	-5.55	19.35	9.6 (0.14)	2.80	23.6	13.1	1650	56.5
Lwiro, DRC	3	1986	-2.23	28.8	9.7 (0.5)	3.16	16.5	11.6	1694	43.6
Ngong, Kenya	1	1843	-1.36	36.67	9.09	2.99	17.6	15.9	890	80.4
Karen, Kenya	1	1877	-1.31	36.7	8.9	3.39	17.4	15.9	972	80.7
Nairobi, Kenya	24	1733	-1.29	36.82	9.14 (0.49)	3.77	18.4	16.2	935	79.4
Muguga, Kenya	1	1973	-1.26	36.66	8.71	3.03	16.9	15.9	913	79.7
Rutchuru, DRC	2	1292	-1.18	29.45	9.75 (0.07)	3.18	21.2	13.3	1250	31.8
Kijabe, Kenya	9	1910	-0.95	36.59	9.62 (0.43)	2.94	17.1	17.8	896	75.4
Lake Naivasha, Kenya	50	2047	-0.72	36.44	9.93 (0.48)	3.18	16.2	18.5	808	55.1
Aberdare Mountains, Kenya	16	2730	-0.65	36.65	10.78 (0.51)	3.08	11.6	16.6	1433	50.4
Aberdare National Park, Kenya	1	3031	-0.48	36.73	11.8	3.04	10	15.8	1748	52.9
Njoro, Kenya	8	2196	-0.34	35.94	10.2 (0.67)	2.96	15.8	18.3	941	43.4
Laikipia, Kenya	3	1918	-0.2	36.95	9.57 (0.50)	2.83	16.5	19.2	888	57.8
Mount Kenya, Kenya	31	2965	-0.16	37.2	12.07 (0.51)	2.99	10.9	15.9	1464	61.7
Subukia, Kenya	1	1929	0	36.23	9.4	2.99	16.9	19.0	1031	51.3
Kakumega Forest, Kenya	26	1703	0.13	34.84	9.5 (0.49)	3.06	19.5	18.4	1943	36.6
Cherangani, Kenya	6	1869	0.98	35.22	9.72 (0.19)	2.94	18.2	19.1	1044	54.2
Mount Elgon, Kenya	3	2138	1.04	34.8	9.23 (0.46)	3.02	16.9	17.1	1251	49.7
Gogeb, Ethiopia	6	1383	7.42	36.37	9.53 (0.32)	2.98	20.9	19.4	1536	54.3
Agaro, Ethiopia	1	1755	7.85	36.58	9.7	3.10	19.4	20.0	1817	67.7
Nazareth, Ethiopia	2	1614	8.54	39.27	9.85 (0.78)	3.57	20.6	19.9	805	103.2
Fatam, Ethiopia	1	1147	10.29	37.01	9.2	2.89	22.7	21.1	1265	109.2
Dangila, Ethiopia	2	2084	11.25	36.84	9.55 (0.07)	2.90	17.0	20.2	1527	106.0

Table 2. Radiocarbon chronology of the mole-rat samples from Enkapune ya Muto (after Ambrose, 1998)

Stratum	Lab no.	14C yrs BP	Cal yrs BP
RBL2.1	ISGS-1946	3,110 $\pm$ 70	3,310 $\pm$ 87
	ISGS-2040	3,030 $\pm$ 70	3,217 $\pm$ 98
	ISGS-2308	3,990 $\pm$ 70	4,468 $\pm$ 122
	GX-9942	4,475 $\pm$ 210	5,119 $\pm$ 271
	GX-9943	4,535 $\pm$ 170	5,191 $\pm$ 220
	ISGS-1742	4,860 $\pm$ 70	5,592 $\pm$ 90
RBL2.2	GX-9944	5,265 $\pm$ 220	6,041 $\pm$ 237
RBL2.3	GX-9399	5,365 $\pm$ 235	6,147 $\pm$ 258
DBS	ISGS-1732	5,220 $\pm$ 70	6,009 $\pm$ 100
	GX-9945	5,470 $\pm$ 215	6,260 $\pm$ 242
	GX-9946	5,785 $\pm$ 200	6,636 $\pm$ 278
RBL3	ISGS-1750	6,350 $\pm$ 150	7,241 $\pm$ 162
	GX-9947	5,860 $\pm$ 200	6,699 $\pm$ 195

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6