

Distributional range, ecology, and mating system of the Cape mole-rat (*Georychus capensis*) family Bathyergidae

J.H. Visser, N.C. Bennett, and B. Jansen van Vuuren

Abstract: Interpopulation variation in life-history patterns are influenced by intrinsic and extrinsic factors. Life-history patterns have been intensely studied in the eusocial African bathyergid species, largely neglecting the solitary species. Of these solitary genera, the Cape mole-rat (*Georychus capensis* (Pallas, 1778)) is endemic to South Africa with a disjunct distribution across its range. Knowledge regarding this species is rudimentary; therefore, this study aimed to investigate the current distribution of the species with particular attention to common ecological variables, differences in body size between localities and sexes, as well as its reproduction and mating system. *Georychus* is a habitat specialist restricted to specific ecological areas. A lack of sexual size dimorphism and correlation between male testis size and number of females in the population, suggests a polygynous mating system, facilitated by the spatial distribution of the sexes. A positive relationship between male testes size and percentage of females in populations sampled suggests that larger sperm reserves (i.e., larger testes) are required in populations with a higher percentage of females. In addition, mating variables (testicular size and litter size) are linked to ecological factors (elevation, aridity, soil type, and vegetation type) that could impact mate searching, mating success, and food resources.

Key words: *Georychus capensis*, Cape mole-rat, mating system, seasonal breeding, male multiple mating.

Résumé : Les variations entre populations des types de cycles biologiques sont influencées par des facteurs intrinsèques et extrinsèques. Les types de cycles biologiques ont été abondamment étudiés chez les espèces eusociales de bathyergidés africains, les espèces solitaires ayant pour leur part fait l'objet de peu d'études. De ces genres solitaires, le rat-taube du Cap (*Georychus capensis* (Pallas, 1778)) est endémique à l'Afrique du Sud, sa distribution étant discontinue dans son aire de répartition. Les connaissances sur cette espèce étant rudimentaires, la présente étude visait à examiner la répartition actuelle de l'espèce en accordant une attention particulière aux variables écologiques communes, aux différences de taille du corps entre les sites et les sexes, ainsi qu'à la reproduction et au type d'accouplement de l'espèce. *Georychus* est un spécialiste en matière d'habitat, étant limité à certaines zones écologiques. L'absence de dimorphisme sexuel de la taille et une corrélation entre la taille des testicules des mâles et le nombre de femelles dans la population indiqueraient un type d'accouplement polygyne facilité par la répartition spatiale des sexes. Une relation positive entre la taille des testicules des mâles et le pourcentage de femelles dans les populations échantillonnées donne à penser que de plus grandes réserves de sperme (c.-à-d. des testicules plus grands) sont nécessaires dans les populations ayant un pourcentage de femelles plus important. En outre, des variables de l'accouplement (taille des testicules et taille des portées) sont reliées à des facteurs écologiques (altitude, aridité, type de sol et type de végétation) qui pourraient avoir une incidence sur la recherche de partenaires, le succès d'accouplement et les ressources alimentaires. [Traduit par la Rédaction]

Mots-clés : *Georychus capensis*, rat-taube du Cap, type de l'accouplement, reproduction saisonnière, accouplement multiple des mâles.

Introduction

Life-history variation is influenced by local adaptation to the environment (e.g., Berven 1982; Rohr 1997 and references therein; Lüddecke 2002; Laugen et al. 2003) and influences population dynamics and species' distributions (Rohr 1997). Measure of reproductive investment including male testes size, female litter size, and offspring sex ratio is influenced by a myriad of factors including breeding season, body mass, population density, social system, individual physiological and genetic factors, food availability, mortality, altitude, and latitude (Millar 1973 and references therein). In addition, sperm competition (Merilä and Sheldon 1999; Jolly and Phillips-Conroy 2003; Preston et al. 2003; Schulte-Hostedde and Millar 2004; Hetttyey and Roberts 2006), scramble competition po-

lygyny (Clutton-Brock 1989; Davies 1991), the temporal and spatial distribution of the sexes (Davies 1991; Reynolds 1996), and the operational sex ratio of a species (Greenwood 1980; Hetttyey and Roberts 2006) are also influential in determining intraspecific variation in reproductive biology. Such intraspecific geographic variation has been demonstrated in litter size (Hill 1972; Waltner 1991; Mathies and Andrews 1995; Rohr 1997; Lemos-Espinal et al. 1998) and testicular size (Merilä and Sheldon 1999; Hetttyey et al. 2005) due to various ecological and biological factors.

The family Bathyergidae is a monophyletic family of obligatory subterranean hystricognath rodents endemic to sub-Saharan Africa. Six genera are currently recognized, namely *Heterocephalus* Rüppell, 1842, *Heliophobius* Peters, 1846, *Bathyergus* Illiger, 1811, *Georychus* Illiger, 1811, *Cryptomys* Gray, 1864, and *Fukomys* Kock, Ingram, Frabotta,

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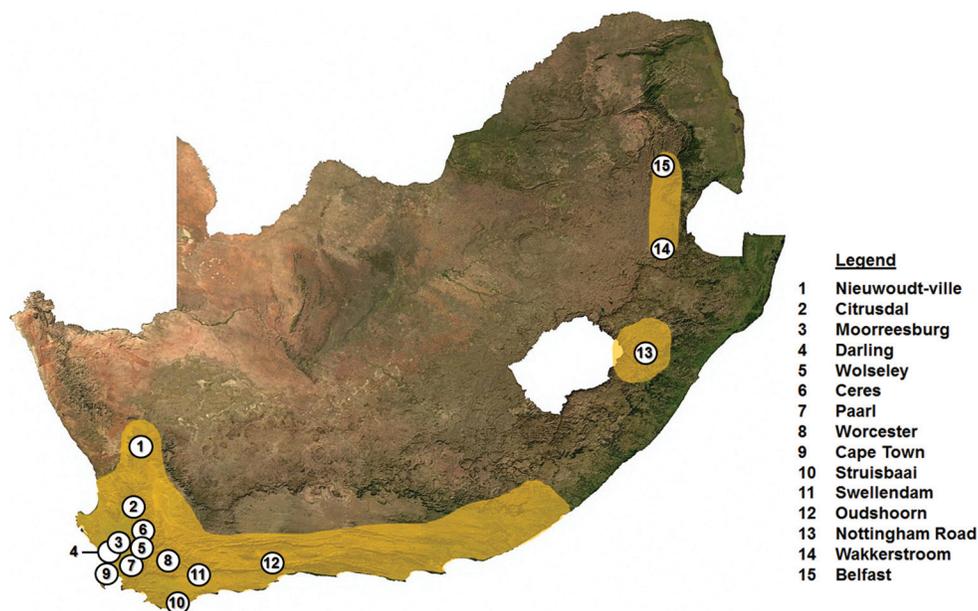
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Fig. 1. Map showing localities where Cape mole-rats (*Georychus capensis*) were sampled across South Africa. The distributional range (shaded) of the species is indicated (based on historical records).



Honeycutt, and Burda, 2006 (Honeycutt et al. 1987; Janecek et al. 1992; Faulkes et al. 1997; Burda 2000; Ingram et al. 2004; Kock et al. 2006; Van Daele et al. 2007). The social structures exhibited by these genera appear to be linked to ecological factors (Bennett 1988; but see Burda 2000). Two of the genera have received much attention in the reproductive biology literature due to their eusociality (*Heterocephalus* and *Cryptomys*; Bennett and Faulkes 2000). Captive breeding of animals for the past few decades have resulted in a considerable knowledge of their reproductive biology (Sumner et al. 2003 and references therein). The solitary genera (*Georychus*, *Bathyergus*, and *Heliophobius*) have received far less attention, with only minor aspects of their reproductive biology being investigated (Jarvis 1969; van der Horst 1972; Bennett and Jarvis 1988; Bennett et al. 1991).

Georychus, a monotypic genus, has a disjunct distribution across South Africa in the coastal dunes and sandy deposits along rivers and intermontane valleys of the Western Cape, southwestern KwaZulu-Natal, and in Mpumalanga (see Fig. 1; De Graaff 1981; Nanni 1988; Bronner 1990; Skinner and Chimimba 2005; Bennett et al. 2006). Fossil evidence suggests that *Georychus* once had a much wider distribution (Hendey 1969; Klein 1974; Avery 1998, 2000), which contracted during the Quaternary (Klein 1974; Avery 1991, 2000). Populations in Mpumalanga and KwaZulu-Natal provinces might therefore represent geographical relicts (Avery 1991).

The Cape mole-rat (*Georychus capensis* (Pallas, 1778)) is a solitary and strongly territorial species (Bennett and Jarvis 1988; Narins et al. 1992) with an obligatory subterranean lifestyle (Taylor et al. 1985). Burrows are extended to obtain food and mates (Bennett 1988; Du Toit et al. 1985), and mate attraction is initiated by the males in the form of hind foot drumming (Bennett and Jarvis 1988; Narins et al. 1992; Bennett et al. 2006). The onset of this drumming breaks down territoriality between individuals; courtship is accompanied by increased testosterone levels (but see Oosthuizen and Bennett 2009) and enlargement of the testes and reproductive glands in males (Bennett 1988; Bennett et al. 2006).

Previous research on *G. capensis* has focused on its physiology (Oosthuizen et al. 2003; Oosthuizen and Bennett 2007, 2009), reproductive biology (Taylor et al. 1985; Bennett 1988; Bennett and Jarvis 1988; Kinahan et al. 2008), intergeneric relationships (Honeycutt et al. 1987; Nevo et al. 1987; Allard and Honeycutt 1992; Faulkes et al. 1997; Ingram et al. 2004), age determination (Taylor

et al. 1985), seismic communication (Narins et al. 1992), energetic cost of digging (Du Toit et al. 1985; Scantlebury et al. 2006), influence on plant communities (Hagenah and Bennett 2013), and burrowing dynamics (Romañach 2005; Thomas et al. 2012). Invariably, sample sizes in these studies were small and biased towards single regions within the distributional range, especially the Western Cape province. Consequently, little is known about the biology, ecology, and mating system of this species across its entire distributional range and whether or not regional differences might be present.

Here, by including larger sample sizes for populations from across the entire South African range, we aim to (i) determine the current distribution of *G. capensis* and identify common ecological variables influencing the distribution of suitable habitat for this species, (ii) investigate whether differences exist in body size across the range or between the sexes, (iii) investigate the reproductive biology of this species and compare testicular size and litter size across the distribution so as to infer possible mating strategies, and (iv) to identify ecological factors contributing to variation in reproductive parameters across the species range by exploring correlations between ecological factors and both testes size and litter size. A thorough understanding of the biology of species including distributions and ecological impacts may provide vital information for conservation and management. Documentation of variation in life-history parameters across a species range may provide insight into the adaptive basis and evolution of such variation and the evolution of life-history patterns in mole-rats in general. *Georychus capensis* is currently classified as least concern (International Union for Conservation of Nature) because of its relatively widespread distribution and absence of significant threats (Maree and Faulkes 2008). Novel information on this genus may therefore better inform its conservation status, especially given the fragmented nature of populations across the species range.

Materials and methods

Sampling and laboratory procedures

Specimens of *G. capensis* were collected from 15 distinct localities (Fig. 1; for sample sizes and capture months see Table 2) across their distributional range in the Western Cape (CapeNature permit No. 0056-AAA041-00084), KwaZulu-Natal (EKZMW permit No.

OP1716/2016), and Mpumalanga (MPTA permit No. 5524). In total, 383 *G. capensis* were captured across their range, comprising 122 males and 261 females. Specimens were captured by placing Gophinator traps baited with peanut butter inside the burrow systems. These traps are specifically designed to instantaneously and humanely kill rodents the size of *G. capensis* (200 mm long and 400 g in mass). This practice was approved by the Ethics Committee of the University of Johannesburg (Ethics No. 215086650-10/09/15). Traps were checked every hour and the killed animals were removed and immediately frozen at -10°C . To obtain body mass, specimens were weighed (in grams) on a RADWAG electronic scale that is accurate to two decimal places. Body length was measured (in millimetres) in a straight line from the tip of the nose to the base of the tail using a standard measuring tape. Animals were dissected to confirm sex; embryos were removed from gravid females, while the testes were removed from males. The embryos and testes were weighed (in grams) on a Sartorius research scale (Sarto Mass Services CC, Zeiss, West Germany) accurate to five decimal places. Both testes were weighed together to determine total mass; similarly, the embryos were also weighed together to determine total mass.

Ecological variables

Broad ecological variables were noted (i.e., landscape type and elevation) for each sampling area (Table 1). Further geographical and climatological information of these areas were gathered from the literature and databases; these included aspects of geology, soil type, and deposit age (from Keyser 1997), as well as rainfall and vegetation type (from Mucina and Rutherford 2006).

Statistical procedures

Statistical procedures were carried out using IBM SPSS Statistics version 20.0.0 (International Business Machines (IBM) Corporation 2011). The data for the sexes were analysed together, as well as separately. Nonparametric tests were used for analyses because the data were non-normally distributed.

For gravid females, the mass of the removed embryos was subtracted from their total body mass to obtain the true field mass of nonpregnant females. Because the smallest gravid female weighed 121 g (with embryos removed; Table 2), this mass was considered to be the minimum reproductive mass for *G. capensis*. Therefore, females weighing <120 g were considered juveniles and were removed from the data sets to obtain estimates of adult individuals only. In support of this, young *G. capensis* reach sexual maturity at approximately 1.5 years of age (Bennett and Faulkes 2000). Given a growth rate of 8.2 g/month for young mole-rats (Taylor et al. 1985), this gives individuals that weigh <120 g an age of 15 months, which is well below the reproductive age.

Three different data sets were compiled for mass analyses: (1) all individuals irrespective of sex and age, (2) only males, and (3) only females (for gravid females, the mass of embryos were subtracted from total mass). For consistency, these data sets were also analysed with juvenile animals (with a mass <120 g) removed to obtain estimates of mature animals only. All of these were used to investigate the differences in body mass between populations across the entire range, as well as differences in body mass between males and females. The body mass of males and females were also compared within each population to assess possible sexual size dimorphism.

Body mass differences among populations were investigated through a Kruskal–Wallis test in the IBM SPSS Statistics package. Differences in body mass between males and females across the entire distributional range, as well as within each locality, were performed using a nonparametric Mann–Whitney *U* test.

To account for any relationship between female size and litter size (allometry in litter size), the number of embryos in an individual gravid female was regressed (using a linear regression) against the body mass of the particular gravid female. The resid-

uals of this relationship were calculated to obtain estimates of female-mass-corrected litter sizes. Differences in mass-corrected litter sizes across the distributional range were compared using a Kruskal–Wallis test.

Males show enlargement of the testes and reproductive glands at the onset of the breeding season (Bennett 1988; Bennett et al. 2006). Our sampling period coincided with the mating season of *G. capensis* as evidenced by the presence of gravid females in all but 4 of 15 sampling locations (Table 2) and the large, round testes of trapped males (also see Sumbera et al. 2003). The synchronized sampling over this period would minimize any bias in testicular mass measurements due to breeding status.

Testicular mass was regressed against male body mass and the residuals of this relationship calculated to obtain relative testicular mass (a widely used measure of male reproductive investment; Hettyey et al. 2005) using a linear regression. This analysis was performed including only adult males (all males weighing <120 g were removed) from populations with sample sizes of more than three specimens (i.e., small populations were removed). Differences in relative testicular mass across the distributional range were compared using a Kruskal–Wallis test.

Relative testicular mass was then regressed against the percentage of females, mass-corrected litter sizes, and proportion of gravid females within each population (using a linear regression) to test for any relationship between male testes size and relative abundance of females in a given population, and possible reproductive variables linked to testis size. These analyses were also performed using a body condition index ($\text{mass}/\text{length}^2$) for males to account for any variability in the animals' condition between sampling localities. As only males were captured at Belfast (locality 15 in Fig. 1), this population was excluded from regression analyses concerning the proportion of females in populations.

The influence of ecological variables (Table 1) on reproductive parameters was analysed using several data sets. Reproductive data sets included the relative testicular size in males, the female-mass-corrected litter size, the mean litter size of a population (the mean number of embryos per gravid female), the proportion of gravid females to the total number of females sampled, and the percentage of females in a given population. The influence of the elevation above sea level and annual rainfall on reproductive variables was investigated using a linear regression. The impact of deposit age was analysed through a Kruskal–Wallis test using four deposit-age categories: Palaeozoic, Cainozoic, Mesozoic, and Precambrian. In addition, the effect of vegetation type was investigated using a Mann–Whitney *U* test; vegetation types were grouped into Fynbos–Renosterveld and Grassland — the former consisting of shrubland and heathland vegetation and the latter of grasses (see Mucina and Rutherford 2006). These two vegetation types constitute two strictly different biomes in the southern African subregion.

Results

The mass of males ranged between 61 and 407 g, whereas female mass ranged between 52 and 396 g (Table 2). Of the females, 67 were found to be gravid carrying 336 embryos in total (Table 2). Gravid female mass (with embryos removed) ranged between 121 and 339 g.

Mass differences across the distribution

No consistent geographic trend was evident in body masses across the range of *G. capensis*. What was notable, however, was that individuals in some populations were, on average, consistently larger (e.g., Paarl and Cape Town; localities 7 and 9 in Fig. 1) or smaller (e.g., Struisbaai; locality 10 in Fig. 1) in pairwise comparisons

Table 1. Information on the sampled Cape mole-rat (*Georychus capensis*) specimens showing the sampling locality, coordinates of the sampling locality, elevation above sea level where animals were collected, mean rainfall of the locality (from Mucina and Rutherford 2006), type of area where animals were sampled, soil type of that area (from Keyser 1997), age of the particular soil type, and vegetation type of the area (from Mucina and Rutherford 2006).

Locality	Coordinates	Elevation (m)	Mean rainfall (mm)	Sampling area	Soil type	Deposit age	Vegetation type
Nieuwoudt-ville	31°22'S, 19°06'E	720	285	Grazed area near vlei	Tillite, sandstone, shale	Palaeozoic	Nieuwoudt-ville Shale Renosterveld
Citrusdal	32°36'S, 19°01'E	160	260	Grazed area near vlei and river	Shale, sandstone	Palaeozoic	Leipoldtville Sand Fynbos
Moorreesburg	33°17'S, 18°34'E	90	425	Grazed area near vlei	Unconsolidated superficial deposits (limestone, sandstone)	Cainozoic	Swartland Silcrete Renosterveld
Darling	33°24'S, 18°24'E	140	520	Grazed area near vlei	Unconsolidated superficial deposits (limestone, sandstone)	Cainozoic	Swartland Granite Renosterveld
Wolseley	33°24'S, 19°12'E	280	480	Grazed area near vlei	Unconsolidated superficial deposits (limestone, sandstone)	Cainozoic	Breede Alluvium Fynbos
Ceres	33°12'S, 19°14'E	900	570	Grazed area near vlei and river	Shale, sandstone	Palaeozoic	Kouebokkeveld Shale Fynbos
Paarl	33°44'S, 18°58'E	110	655	Rugby field near river	Quartzite, shale, tillite	Palaeozoic	Swartland Alluvium Fynbos
Worcester	33°40'S, 19°31'E	240	265	Lawns near vlei and river	Unconsolidated superficial deposits (limestone, sandstone)	Cainozoic	Breede Alluvium Renosterveld
Cape Town	34°00'S, 18°31'E	20	575	Lawn near vlei	Unconsolidated superficial deposits (limestone, sandstone)	Cainozoic	Cap Flats Sand Fynbos
Struisbaai	34°41'S, 20°00'E	5	475	Grazed area near vlei	Unconsolidated superficial deposits (limestone, sandstone)	Cainozoic	Agulhas Sand Fynbos
Swellendam	34°03'S, 20°25'E	90	520	Grazed area near river	Conglomerate, shale, sandstone, limestone	Mesozoic	Swellendam Silcrete Fynbos
Oudshoorn	33°51'S, 22°02'E	600	785	Grazed area near vlei and river	Quartzite, shale, tillite	Palaeozoic	South Outeniqua Sandstone Fynbos
Nottingham Road	29°29'S, 29°52'E	1800	890	Grazed area near vlei	Shale, mudstone, sandstone, grit, coal	Mesozoic	Drakensberg Foothill Moist Grassland
Wakkerstroom	27°18'S, 30°16'E	2000	902	Grazed area near vlei	Shale, mudstone, sandstone, grit, coal	Mesozoic	Wakkerstroom Montane Grassland
Belfast	25°33'S, 30°04'E	1940	858	Grazed area near vlei	Quartzite, shale, limestone, andesite, tuff, hornfels, conglomerates	Precambrian	Lydenburg Montane Grassland

Table 2. Information on the sampled Cape mole-rat (*Georchys capensis*) specimens showing the sampling locality, number of sampled males, mass range of sampled males, number of sampled females, mass range of sampled females, number of gravid sampled females, number of embryos contained by these gravid females, mass range of these gravid females (embryo mass subtracted), and month of capture of the gravid individuals.

Locality	No. of males	Mass range of males (g)	No. of females	Mass range of females (g)	No. of gravid females	No. of embryos	Mass range of gravid females (g)	Capture month
Nieuwoudt-ville	1	131	1	247	—	—	—	(5 July)
Citrusdal	4	96–181	17	110–396	—	—	—	(7 July)
Moorreesburg	44	89–322	103	75–302	31	173	121–302	3 July – 13 Aug.
Darling	12	100–407	13	98–259	—	—	—	(1 July)
Wolseley	7	138–306	16	110–258	2	8	162–231	24 Aug.
Ceres	11	68–264	12	52–280	1	8	280	5 Sept.
Paarl	6	145–346	12	153–385	1	8	290	21 Aug.
Worcester	4	138–241	10	147–339	9	51	147–339	15 Aug. – 19 Sept.
Cape Town	8	208–332	17	106–365	1	7	218	20 Aug.
Struisbaai	3	61–193	17	99–208	1	5	160	15 July
Swellendam	3	143–290	15	124–248	10	38	131–248	13 Aug. – 19 Sept.
Oudshoorn	9	162–315	13	89–303	8	34	133–303	11 Aug.
Nottingham Road	1	141	2	209–233	1	2	209	28 Jan.
Wakkerstroom	6	91–243	13	91–291	2	2	214–230	16 Jan.
Belfast	3	144–212	0	—	—	—	—	(14 Jan.)
Total	122	—	261	—	67	336	—	—

Note: The month of capture for populations containing no gravid individuals are indicated in parentheses.

between populations (see Figs. 2A–2C; Table 3; Supplementary Tables S1 and S2¹).

Similarly, no general trends were observed when the geographic differences in masses were compared within sexes. Some populations, however, again differed notably from most other populations. For females, specimens from, e.g., Paarl (locality 7 in Fig. 1) were the largest, whereas those from the Darling and Struisbaai were the smallest (localities 7, 4, and 9, respectively, in Fig. 1; Fig. 2C; Supplementary Tables S1 and S2¹). For males, specimens from Cape Town were the largest (locality 9 in Fig. 1; Fig. 2B; Supplementary Tables S1 and S2¹).

As sampling was carried out during the rainy season, seasonal variation in mass could not be evaluated. Sampling during the wetter periods coincided with the highest vegetation cover and therefore the highest possible availability of food resources. Little bias is therefore expected in the body-mass data because the body condition of animals during this period should be similarly influenced across populations.

Mass differences between the sexes

There was no statistically significant difference in the body masses between males and females across the range or within localities, even with juveniles removed (Table 4). The only consistent difference was the specimens from the Cape Town population (locality 9 in Fig. 1) where males were larger than females. There was also a significant difference between male and female masses in the Darling locality (locality 4 in Fig. 1), with nonsignificant trends towards differences when juveniles were removed.

Litter size

There was a significant relationship ($r^2 = 0.202$, $N = 67$, $p = 0.000$) between the mass of a particular female and the number of embryos carried by that female. Larger females carried larger litters compared with smaller (and presumably younger) females (Supplementary Fig. S4).¹ In addition, significant variation ($\chi^2_{[10]} = 19.364$, $p = 0.036$) in mass-corrected litter size was evident across the distributional range.

Testicular size differences across the distribution

Testicular mass was significantly and positively correlated with body mass in all instances (all mature animals with juveniles re-

moved, all animals belonging to smaller populations removed, mature animals with juveniles and small populations removed; Table 5). Although there was a significant and strong correlation ($r^2 = 0.654$, $N = 97$, $p = 0.000$) between body mass and body length (Supplementary Fig. S1),¹ the body condition index performed poorly at explaining testicular size relative to analyses using only body mass as a proxy for animal size (Table 5). Similarly, the relationship between relative (to body condition index) testicular size and the percentage of females in a given population was also weaker than when using only relative (to body mass) testicular size. Given the consideration that body mass explains most of the variation in testicular mass, this relationship was used for subsequent analyses concerning relative testicular size.

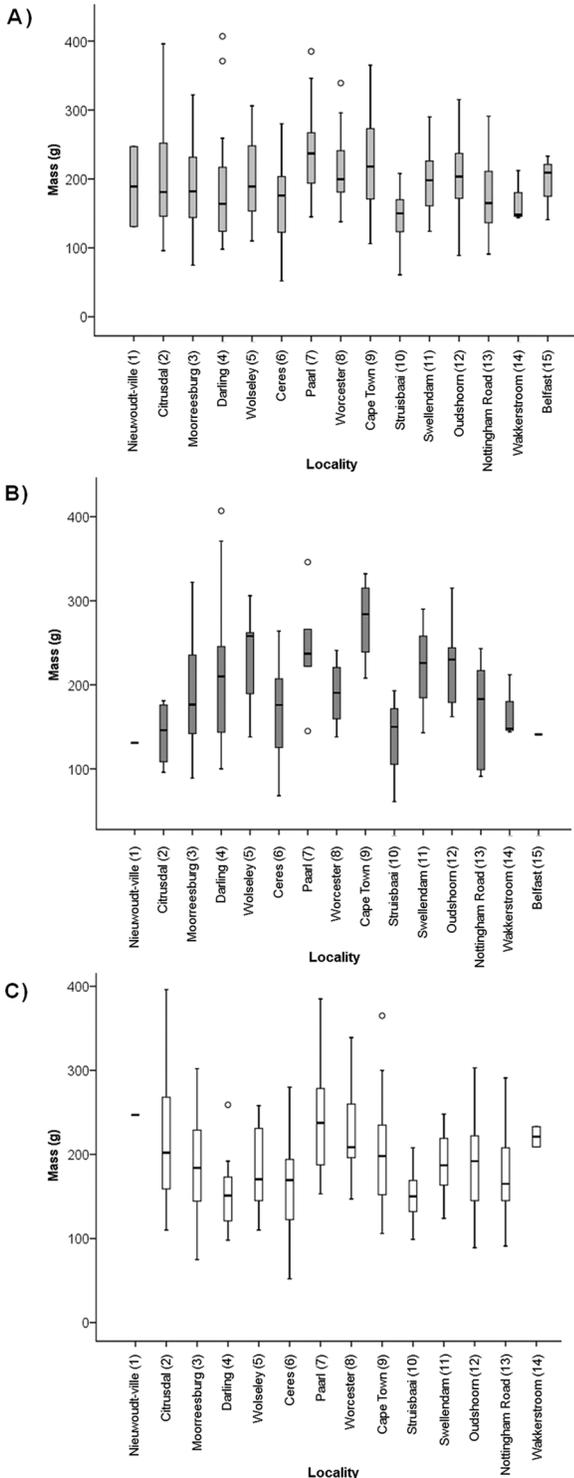
Relative testicular mass differed significantly among populations across the range (all males: $\chi^2_{[14]} = 48.932$, $p = 0.000$; males with juveniles removed: $\chi^2_{[14]} = 43.566$, $p = 0.000$; Fig. 3; Supplementary Table S3¹) and was consistently significantly correlated with the percentage of females within a population (all mature animals with juveniles removed, all animals with small populations removed, mature animals with juveniles and small populations removed; Table 5; Figs. 4A, 4B), with populations containing fewer females displaying smaller relative testicular masses. No similar trends were evident when comparing relative testicular mass and mean number of embryos per gravid female or proportion of gravid females within each population (Supplementary Table S4).¹

Reproduction and ecology

Relative testicular mass in males was significantly correlated with elevation and, to a lesser degree, with rainfall (Table 6). Populations at lower elevations displayed larger testicular masses than their highland counterparts (Fig. 5A); males from regions with a lower annual rainfall had larger relative testicular masses compared with regions of higher rainfall (Fig. 5B). Similarly, the female-mass-corrected litter sizes correlated with these two ecological variables, with a higher number of embryos found in females at lower elevations and in lower rainfall areas (Figs. 5C, 5D). The mean litter size of populations was also significantly and strongly correlated to elevation (Table 6) — females at lower elevations carried larger litters than those from higher elevations

¹Supplementary figures and tables are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2017-0016>.

Fig. 2. Graphs showing the differences in mass (mean and SD) of Cape mole-rat (*Georchys capensis*) individuals between localities for (A) all individuals, (B) males, and (C) females. Numbers in parentheses correspond to localities in Fig. 1.



(results not shown). No comparable trends were evident in the other female reproductive variables.

There was a significant difference in relative testicular mass between populations found in different deposit ages (Table 6). This was, however, largely influenced by a significant difference in relative testicular mass between populations in Palaeozoic and

Cainozoic deposits in which the former was significantly smaller than the latter (Mann–Whitney $U = 312.000$, $N = 87$, $p = 0.000$; mean (\pm SD) relative testicular masses: Palaeozoic, 0.010 ± 0.210 ; Cainozoic, 1.701 ± 0.460 ; Supplementary Fig. S2A¹). A similar situation was evident in the female-mass-corrected litter sizes where significantly more embryos were carried by females in the Palaeozoic and Cainozoic deposits compared with the Precambrian deposits (mean (\pm SD) female-mass-corrected litter sizes: Palaeozoic, 0.269 ± 1.379 ; Cainozoic, 0.305 ± 2.970 ; Precambrian, -3.728 ± 0.753 ; Table 6; Supplementary Fig. S2B¹). No similar trends were shared in any of the other female reproductive data sets.

Males from the Fynbos–Renosterveld vegetation types had significantly larger relative testicular masses than those in Grassland vegetation (Table 6); a similar pattern was observed in females where gravid females carried larger litters, both mass-corrected (individually) and, on average, in the Fynbos–Renosterveld vegetation compared with their Grassland counterparts (Supplementary Figs. S2C, S2D).¹ No similar trends were observed for any of the other female reproductive data sets.

Discussion

Ecology and distribution

Georchys capensis occurs over a wide range of elevations (Table 1) from the Western Cape lowland areas between the escarpment and the ocean (with the exception of the Nieuwoudt-ville population; 720 m above sea level; locality 1 in Fig. 1) to the highlands of Mpumalanga (Wakkerstroom and Belfast; 2000 and 1940 m above sea level, respectively; localities 14 and 15 in Fig. 1) and KwaZulu-Natal (Nottingham Road; 1800 m above sea level; locality 13 in Fig. 1). The range reported here overlaps notably, but also extends the range that was previously suggested by De Graaff (1981) (new records from Moorreesburg, Ceres, and Oudshoorn: localities 3, 6, and 12, respectively, in Fig. 1).

The most commonly preferred soil types are derived from sandstone, limestone, shale, and quartzite (Table 1), which together make up the sandy loam, clay, and alluvium soils that these mole-rats exclusively inhabit (also see De Graaff 1981; Skinner and Chimimba 2005). The substrates that *G. capensis* inhabit become more recent from the east towards the west (Precambrian to Cainozoic; see Keyser 1997; Table 1). *Georchys* likely spread from the northeastern parts of South Africa downward towards the south coast and subsequently to the west (also see the phylogeny of Honeycutt et al. (1987) where KwaZulu-Natal animals appear to be older). This is also supported by fossil evidence of *G. capensis* found at Elandsfontein in the Western Cape in layers that date back only to the late Pliocene (ca. 12 million years ago; Hendey 1969).

Georchys inhabits mesic regions across its distributional range — both in the winter rainfall zone of the Western Cape (285–655 mm/year; mean 485 mm; Mucina and Rutherford 2006) and the summer rainfall regions of KwaZulu-Natal (890 mm/year) and Mpumalanga (858–902 mm/year); an observation also made by Bennett et al. (2006). The higher annual rainfall allows burrowing for most of the year (Thomas et al. 2012) because it makes the soil workable (Scantlebury et al. 2006) and reduces the energetic cost of digging (Lovegrove 1989; Zelová et al. 2011; Okrouhlik et al. 2015). High rainfall also ensures reliable food resources for most of the year (Bennett 1988).

Although *G. capensis* is found in a diverse array of vegetation types (Table 1) including Fynbos, Renosterveld, and Grassland (also see Low and Rebelo 1998), it is limited by the presence of certain environmental conditions within these habitats such as alluvium and water (i.e., drainage systems). This is likely due to the preference for mesic soil conditions and the accompanying loamy and sandy soils formed by denudation in *Georchys*. All populations were associated with either vleiland areas or were close to rivers (Table 1). In addition, all populations were found in anthropogenically influenced (grazing of cattle or planted lawns)

Table 3. Summary of the statistical results for statistical analyses involving comparisons of mass between localities, between males of localities, and between females of localities for Cape mole-rat (*Georchus capensis*) specimens.

	χ^2	df	p
Mass difference between localities	38.749	14	0.000
Mass difference between localities (juveniles removed)	30.576	14	0.006
Male mass difference between localities	29.636	14	0.009
Male mass difference between localities (juveniles removed)	24.322	14	0.042
Female mass difference between localities	33.624	13	0.001
Female mass difference between localities (juveniles removed)	27.466	13	0.011

Note: For each analysis, both the full data set was used and a data set of mature animals where all juvenile animals (<120 g) were removed.

Table 4. Summary of the statistical results for statistical analyses involving comparisons of mass between males and females of all localities and within each locality, respectively, for Cape mole-rat (*Georchus capensis*) specimens.

	Mann–Whitney U	N_{female}	N_{male}	p	Mass (g; mean \pm SD)	
					Female	Male
Male vs. female mass between all localities	14 653	261	122	0.209	188 \pm 58	197 \pm 67
Male vs. female mass between all localities (juveniles removed)	11 367.5	229	109	0.185	199 \pm 52	210 \pm 60
Population comparisons: all specimens						
Citrusdal	13.0	17	4	0.065	221 \pm 81	152 \pm 40
Moorreesburg	2 244.0	103	44	0.926	185 \pm 53	186 \pm 58
Darling	40.5	13	12	0.040	151 \pm 44	217 \pm 94
Wolseley	30.5	16	7	0.089	183 \pm 52	229 \pm 61
Ceres	63.5	12	11	0.880	163 \pm 60	167 \pm 57
Paarl	36.0	12	6	1.000	240 \pm 66	242 \pm 65
Worcester	14.0	10	4	0.454	224 \pm 59	190 \pm 43
Cape Town	22.0	17	8	0.006	200 \pm 71	277 \pm 45
Struisbaai	24.5	17	3	0.921	149 \pm 29	135 \pm 67
Swellendam	16.0	15	3	0.498	190 \pm 39	220 \pm 74
Oudshoorn	37.0	13	9	0.164	190 \pm 55	223 \pm 48
Nottingham Road	0.0	2	1	0.667	221 \pm 17	141
Wakkerstroom	38.5	13	6	0.966	175 \pm 53	169 \pm 63
Population comparisons: juveniles removed						
Citrusdal	10.0	16	3	0.138	228 \pm 78	158 \pm 32
Moorreesburg	1 693.5	89	39	0.828	197 \pm 45	197 \pm 52
Darling	28.5	10	11	0.061	165 \pm 41	227 \pm 90
Wolseley	30.5	14	7	0.172	193 \pm 46	229 \pm 61
Ceres	31.5	10	8	0.460	180 \pm 47	194 \pm 38
Paarl	36.0	12	6	1.000	240 \pm 66	242 \pm 65
Worcester	14.0	10	4	0.454	224 \pm 59	190 \pm 43
Cape Town	22.0	14	8	0.020	219 \pm 63	277 \pm 45
Struisbaai	9.5	13	2	0.571	162 \pm 20	172 \pm 30
Swellendam	16.0	15	3	0.498	190 \pm 39	220 \pm 74
Oudshoorn	37.0	12	9	0.247	198 \pm 48	223 \pm 48
Nottingham Road	0.0	2	1	0.667	221 \pm 17	141
Wakkerstroom	14.0	11	4	0.343	188 \pm 47	207 \pm 33

Note: For each analysis, both the full data set was used and a data set of mature individuals only where all juvenile animals (<120 g) were removed.

landscapes (also see Bennett 1988) with no individuals present in pristine natural habitats. Conversely, it has also been shown that the presence of *G. capensis* may increase the abundance of grass through disruption of other vegetation types by selective feeding (Hagenah and Bennett 2013). Whether mole-rats prefer grasslands, or whether their presence facilitates grassland formation, remains unknown and requires additional study.

The distribution, composition, and abundance of geophytes are also a determining factor in the distribution of suitable habitat for *G. capensis* (Bennett 1988; Románach 2005). Mole-rat diet consists mainly of geophytes (bulbs, tubers, and corms; Du Toit et al. 1985; Lovegrove and Jarvis 1986), but also contains a certain amount (6.9%; Broll 1981) of grass or aerial plant material (Davies and Jarvis 1986; Bennett 1988; Bennett et al. 2006). In the mesic regions, geophytes (high digestibility) show a clumped, albeit patchy, distribution (Du Toit et al. 1985). Notwithstanding, geophytes are relatively easy to find and this food source may therefore ensure the maintenance of their energy budget (Bennett 1988). Indeed,

they extend burrows and perform a nonrandom search for these food items (Du Toit et al. 1985; Bennett and Faulkes 2000; Románach 2005). Mole-rats also maintain food stores during the drier parts of the year when food is more scarce or difficult to find (Du Toit et al. 1985; Bennett 1988; Bennett et al. 2006; Thomas et al. 2012). Indeed, food stores were observed in the Belfast and Morreesburg localities (localities 3 and 15 in Fig. 1) where burrow systems were excavated (in the rainy seasons of January and July–August, respectively). Burrow systems were not excavated during the drier months of the year, thereby leaving the potential for food storage in *G. capensis* during these periods as speculative.

Size differences across the distribution

There was no clear geographic trend in animal body mass from different populations across the distribution; however, some populations differed significantly from others. The factors driving the size differences in single areas are not immediately obvious because similar mesic habitat types are occupied across the range.

Table 5. Summary of the statistical results for regression analyses investigating the relationship between testicular mass in male Cape mole-rat (*Georychus capensis*) and their body mass, as well as between relative testicular size and percentage of females in the population where that male was sampled.

	r^2	N	p
All specimens			
Testicular mass vs. body mass	0.513	97	0.000
Residuals vs. percentage of females	0.211	94	0.000
Juveniles removed			
Testicular mass vs. body mass	0.416	83	0.000
Residuals vs. percentage of females	0.192	83	0.000
Small populations removed			
All specimens			
Testicular mass vs. body mass	0.503	92	0.000
Residuals vs. percentage of females	0.211	92	0.000
Juveniles removed			
Testicular mass vs. body mass	0.412	82	0.000
Residuals vs. percentage of females	0.210	82	0.000
Body condition index			
All specimens			
Testicular mass vs. body condition index	0.157	92	0.000
Residuals vs. percentage of females	0.123	92	0.000
Juveniles removed			
Testicular mass vs. body condition index	0.056	82	0.019
Residuals vs. percentage of females	0.112	82	0.001

Note: Both the full data set was used and a data set of mature individuals only where all juvenile animals (<120 g) were removed. In addition, populations where three or less animals were sampled were removed from further analyses. The results for the regression analyses using body condition index as a proxy for animal health are also shown.

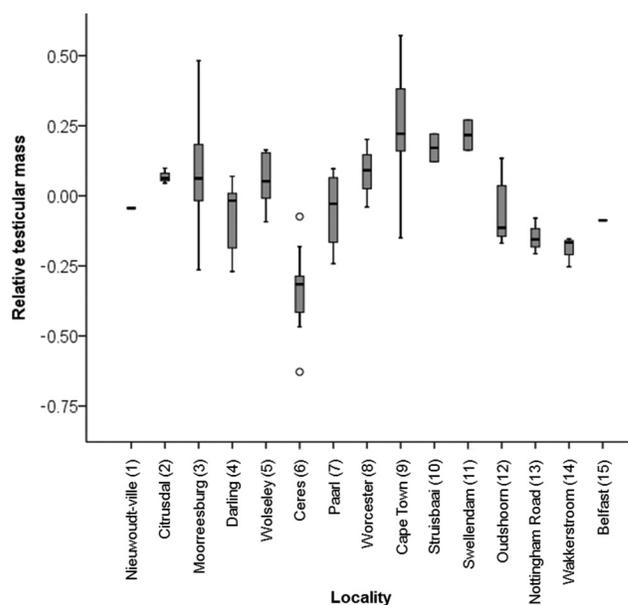
Occurrence on planted grass lawns are the only ecological factor that set apart the Paarl and Cape Town populations (localities 7 and 9, respectively, in Fig. 1) where animals are consistently larger. The availability of grass as a food source year-round may increase growth (see Taylor et al. 1985).

Body masses for all animals, as well as males and females separately, fall within the range reported by previous authors (e.g., Du Toit et al. 1985; Taylor et al. 1985; Bennett et al. 2006; Hagenah and Bennett 2013; Oosthuizen et al. 2013). Body mass is significantly correlated with age ($r = 0.76$) and growth continues after maturity (Taylor et al. 1985). According to Smithers (1983), a maximum body mass of 360 g is attained by *G. capensis*. In the current study, five animals (two males and three females) had body masses higher than 360 g (between 365 and 407 g). Given that young males grow at 7.4 g/month (Taylor et al. 1985) until they reach 60 g (Bennett 1988) and at 5.8 g/month thereafter, this would give the male weighing 407 g an age of 5.7 years, which is in line (albeit slightly higher) with a lifespan of 5 years proposed by Bennett and Faulkes (2000).

Size differences between the sexes

No sexual dimorphism exists across the distributional range of *G. capensis*, which is in agreement with previous investigations (Smithers 1983; Taylor et al. 1985; Bennett 1988; Bennett and Faulkes 2000; Bennett et al. 2006; Scantlebury et al. 2006; Thomas et al. 2012). The lack of sexual dimorphism across the distributional range points to an absence of competition for resources such as mates (i.e., due to the mating system) and (or) ecological constraints (also see Pochron and Wright 2002); their specialized habitat selects for a certain size optimum in both sexes. Sexual dimorphism was, however, evident in the Cape Town (locality 8 in Fig. 1) population with males being significantly larger; a trend that was also weakly observed in Darling (locality 4 in Fig. 1). The factors influencing this dimorphism are not immediately obvious; however, the sex ratio in the Cape Town population is 1:1 (also observed in the Darling population), the area occupied is small

Fig. 3. Graph showing the geographic variation between localities in relative testicular mass of mature Cape mole-rat (*Georychus capensis*) males. Numbers in parentheses correspond to localities in Fig. 1.



(0.68 ha), and burrow systems are closely spaced. As previously noted, sex ratio in subterranean mammals is affected by population density and competition (Malizia and Busch 1997; Nevo 1999; Zenuto et al. 1999; Busch et al. 2000). The mating system in this small area may therefore involve intrasexual competition between males for receptive females. Indeed, silvery mole-rat (*Heliophobius argenteocinereus* Peters, 1846) exhibits a similar equal sex ratio and displays analogous size dimorphism between the sexes (Sumner et al. 2003).

Reproduction

Reproduction in *Georychus* is influenced by various factors, both intrinsically and extrinsically. Intrinsic factors include female allometry in litter size, male allometry in testicular size, and a mating strategy linked to the sex ratio and distribution of receptive females. On the other hand, extrinsic factors comprise ecological aspects such as elevation, rainfall, soil type, and vegetation.

Litters

Georychus is a seasonal breeder (Bennett and Jarvis 1988) with the potential of producing two litters per breeding season (Taylor et al. 1985). Gravid females were collected during July to September in the Western Cape province and during late January in the KwaZulu-Natal and Mpumalanga areas (Table 2). The gravid period for the Western Cape is in agreement with other studies (Taylor et al. 1985; Bennett and Jarvis 1988; Bennett et al. 2006), which found that young were born in August to December. The later date of capture for the gravid individuals from the KwaZulu-Natal and Mpumalanga areas may indicate a shift in the breeding season; young will likely be born in February to March. The link between mating season and rainfall seasonality (winter rainfall in the Western Cape and summer rainfall in the east of South Africa) may give young animals the opportunity to disperse from their natal burrows and establish their own territories (Bennett 1988), which would require moist soil (also see Sumner et al. 2003). A breeding season that coincides with the wetter months would therefore prove advantageous. As sampling did not cover a full year in the Western Cape, KwaZulu-Natal, and Mpumalanga, it is speculative whether the difference in breeding season between these areas represents a real adaptive shift.

Fig. 4. Regression showing the relationship between (A) relative testicular mass and (B) body condition index (BCI) corrected testicular mass of mature Cape mole-rat (*Georychus capensis*) males and the percentage of females in the population where the males were sampled.

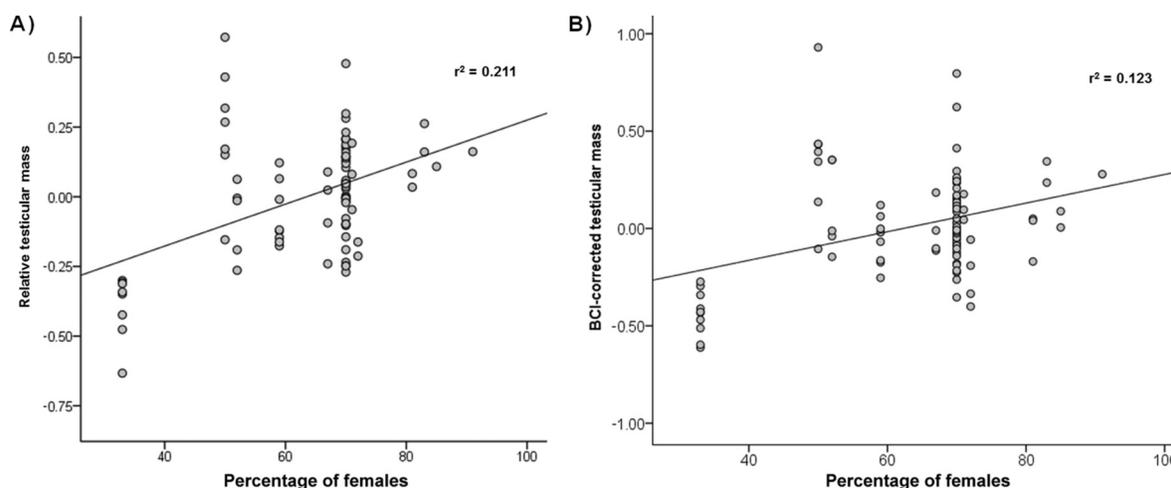


Table 6. Summary of the statistical results for analyses investigating the relationship between the ecological variables elevation above sea level, annual rainfall, deposit age, and vegetation type where Cape mole-rat (*Georychus capensis*) populations are found and the reproductive variables of these populations.

	Elevation (m)			Annual rainfall (mm)			Deposit age			Vegetation type		
	<i>r</i> ²	<i>N</i>	<i>p</i>	<i>r</i> ²	<i>N</i>	<i>p</i>	χ^2	df	<i>p</i>	Mann–Whitney <i>U</i>	<i>N</i>	<i>p</i>
Relative testicular mass in males	0.249	97	0.000	0.098	97	0.002	24.007	3	0.000	152.0	97	0.007
Residuals (no. of embryos vs. gravid female mass)	0.177	67	0.000	0.109	67	0.006	8.801	3	0.032	7.0	67	0.001
No. of embryos/no. of gravid females	0.428	11	0.029	0.267	11	0.103	5.906	3	0.116	0.0	11	0.036
No. of gravid females/total no. of females	0.000	11	0.975	0.031	11	0.605	2.156	3	0.541	7.0	11	0.727
Percentage of females in a population	0.059	13	0.424	0.049	13	0.469	2.286	2	0.319	4.0	13	0.769

Note: Reproductive data sets included the relative testicular size in males, the size-corrected number of embryos per particular gravid female (residuals of the regression of the number of embryos versus the mass of the particular gravid female), mean litter size per population (the mean number of embryos per gravid female), the proportion of gravid females to the total number of females sampled, and the percentage of females in a given population.

A mean litter size of 5 (1–11) was found for the gravid females collected across the distributional range (30% of females contained five embryos). This is less than what was found in previous studies (mean litter size 6, range 3–10; Bennett 1988; Bennett et al. 2006), but is still significantly larger than what was reported for other mole-rat species (Bennett 1988; Sumbera et al. 2003). A larger litter size may be selected for in *Georychus* because of higher predation pressure as they move aboveground more frequently than other members of the bathyergids and are consequently preyed upon by birds of prey, small carnivores, and domestic pets (J.H. Visser, personal observation).

Allometry in sexual traits

Female size has a significant effect on litter size in *G. capensis* — this allometry in litter size has been noted in various other taxa (Burkholder and Walker 1973; Western 1979; Eisenberg 1981; Clutton-Brock and Harvey 1983; Peters 1983; Fitch 1985; Harvey and Clutton-Brock 1985; Harvey et al. 1986; Vitt and Breitenbach 1993; Wapstra and Swain 2001; Rocha et al. 2002). Larger females can presumably invest more resources into reproduction or have a larger reproductive tract that may accommodate a larger amount of embryos.

Similar allometry applied to testicular mass, which relied significantly on male body mass (for similar examples in other taxa see Merilä and Sheldon 1999; Jolly and Phillips-Conroy 2003; Hettzey et al. 2005). In addition, the body condition index of males also has a slight effect on testicular mass; however it seems that testicular growth is, to a larger extent, an allometric function of an individual’s size than of its body condition. As similar conditions prevailed across the sampled distribution and sampling

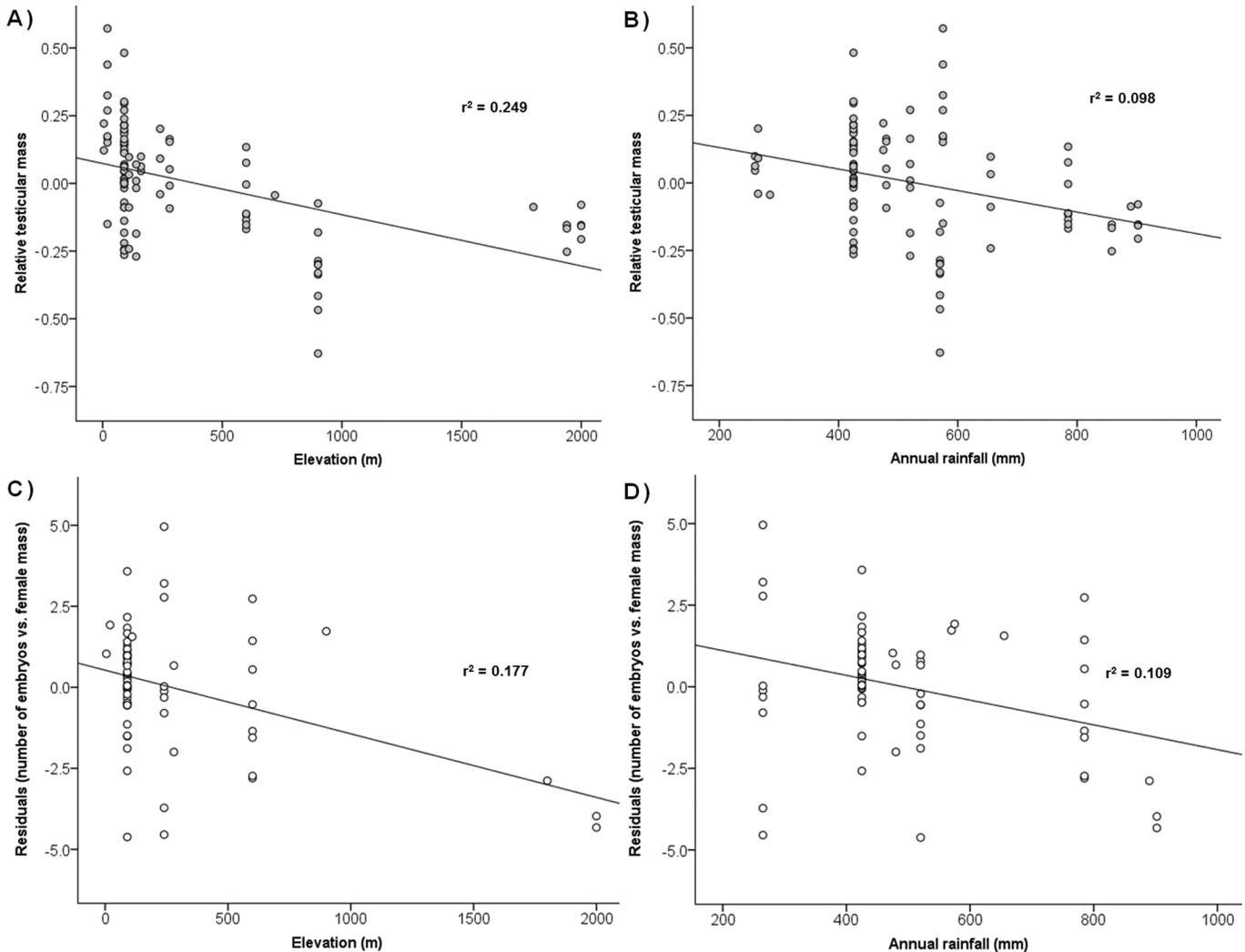
covered only a single breeding season, body condition was presumably similarly influenced in all populations. The effect of animals’ body condition on testicular size must therefore be investigated across a longer time span and between different seasons before a robust conclusion may be drawn.

Mating system

The mating system of a species is determined by the temporal and spatial distribution of males and receptive females (Davies 1991; Reynolds 1996). In *Georychus*, females (gravid and nongravid) are spatially clustered (between 1 and 30 m; spatial networks not shown) around male burrow systems. This proximity (also see Bennett 1988; Bennett et al. 2006) is likely due to two factors. First, the subterranean lifestyle imposes certain constraints on the ability of individuals to find receptive mates due to low vagility. The solitary, strongly territorial nature of this species (Bennett 1988; Narins et al. 1992) also leads to permanent territories (single burrow systems) that are occupied for life (Bennett and Faulkes 2000; Herbst et al. 2004). To obtain mates in such a system, males of *G. capensis* excavate linear tunnel systems that shift annually (likely due to mate searching), whereas females excavate circular burrow systems that are nearly permanently maintained (Bennett and Faulkes 2000; Herbst et al. 2004). Secondly, *Georychus* communicates with conspecifics (advertising sex and reproductive status) using seismic signalling in the form of foot drumming with its hind legs (Bennett and Jarvis 1988; Narins et al. 1992; Bennett et al. 2006); therefore, burrow systems need to be closely spaced (3–4 m; Narins et al. 1992) for such communication to be effective.

In *G. capensis*, the males may be the driver that determines females’ spatial location (also see Thomas et al. 2012). The sex ratio

Fig. 5. Regression showing the relationship between mating variables and ecological variables in sampled Cape mole-rat (*Georychus capensis*) populations with regards to (A) relative testicular mass in males and elevation above sea level (m), (B) relative testicular mass in males and annual rainfall (mm), (C) female-size-corrected litter size and elevation above sea level (m), and (D) female-size-corrected litter size and annual rainfall (mm).



in *G. capensis* is biased towards females (for a similar pattern see the sampling of Oosthuizen et al. 2013) — a consequence of the mating system (Greenwood 1980) that may influence male reproductive variables through differences in the amount of polyandrous matings (Hettyey and Roberts 2006). Together with this, there is no size dimorphism between the sexes and male animals do not have fat padding around the neck as observed in the two *Bathyergus* species, suggesting less competition for female acquisition (Scantlebury et al. 2006). Females, however, have a significantly larger zygomatic arch width (Thomas et al. 2012; but for a contrary finding see Taylor et al. 1985) — a secondary sexual trait that may be related to competition over mates, as in the Cape Dune mole-rat (*Bathyergus suillus* (Schreber, 1782)) (Thomas et al. 2009).

Given these life-history traits, *G. capensis* likely exhibits a polygynous mating system. This consideration is supported by the larger relative testis size (size-dependent variation in testis size) in *G. capensis* populations with more females, geographic structuring of relative testis size (also noted in geographically and genetically discrete populations of polygynous Greenfinches (*Carduelis chloris* (L., 1758)) (Merilä and Sheldon 1999) and anurans (Hettyey et al. 2005)), and a linear increase in testicular size with body size (in

common with other polygynous species such as Greenfinches (Merilä and Sheldon 1999), Hamadryas baboons (*Papio hamadryas* (L., 1758)) (Jolly and Phillips-Conroy 2003), and Common Frogs (*Rana temporaria* L., 1758) (Hettyey et al. 2005).

In polygynous social systems, two scenarios may explain increased testis size. In the first instance, relative testis size is strongly and phylogenetically independently related to sperm competition in most taxa (see examples in Merilä and Sheldon 1999; Jolly and Phillips-Conroy 2003; Preston et al. 2003; Schulte-Hostedde and Millar 2004; Hettyey and Roberts 2006) with polygyny generally resulting in larger testes (Jolly and Phillips-Conroy 2003). Sperm competition arises when females mate with more than one male, and male gametes have to compete within the reproductive tract (as seen in polyandrous species; Jolly and Phillips-Conroy 2003). The second instance involves scramble competition polygyny that arises when females and their ranges are not defensible (Clutton-Brock 1989; Davies 1991) and males range over a large area and attempt to mate with receptive females (Kappeler 1997a, 1997b). Male lemurs exhibit scramble competition linked to the temporal distribution of receptive females (Kappeler 1997a, 1997b), which favours larger testes (Harcourt et al. 1981) and weakly selects traits for competition (e.g., size dimorphism; see references in Kappeler 1997a,

1997b). As with *G. capensis*, giant mouse lemurs (*Mirza coquereli* (A. Grandidier, 1867)) have no dimorphism, are solitary, polygynous, have a sex ratio that is biased towards females, and display pronounced seasonal variation in testis size with an increase in the mating season (Kappeler 1997a, 1997b).

In *G. capensis*, relative testicular size in relation to female availability exhibits the opposite trend than predicted for sperm competition or scramble competition. A likely explanation may involve the number of females in close proximity to a male dictating the ejaculate volume and stored sperm volume required for successful mating. Larger testes are favoured when a male has the opportunity to mate with a number of females in a limited space of time (negates potential sperm depletion; Jolly and Phillips-Conroy 2003) and is associated with higher copulation rates (more females mated) and greater siring success because it allows for the storage and production of more sperm (Preston et al. 2003; Schulte-Hostedde and Millar 2004). Indeed, in *G. capensis*, mating takes place multiple times, consisting of a series of brief copulations (Bennett 1988; Bennett et al. 2006). The possibility therefore exists that larger testes in this species would facilitate multiple ejaculations and sufficient sperm reserves to negate sperm depletion. In areas with few females and given that animals are not able to move over large distances, males invest in smaller testes because fewer copulations are achieved. It is entirely possible that several males will not have access to a female during their lifetime, thus there is no need to invest in larger testes.

Reproduction and ecology

A significant relationship ($r^2 = 0.530$, $N = 15$, $p = 0.002$) exists between elevation and annual rainfall at sampling localities across the distribution of *G. capensis* (Supplementary Fig. S3).¹ In this regard, areas of lower elevation also have a lower annual rainfall and vice versa. Altitudinal effects on reproductive parameters through a difference in climatic conditions are common in reptiles (Fitch 1985; Vitt and Breitenbach 1993). Therefore, it is also notable that testicular size in male *G. capensis* correlates with both elevation and annual rainfall. The larger relative testicular masses in this species are restricted to lower elevations and in lower rainfall (arid) areas. As such, variation in this reproductive trait may be linked to moisture — a factor that influences the energetic cost of digging and therefore mate searching (Lovegrove 1989; Zelová et al. 2011; Okrouhlik et al. 2015). In drier areas, mate searching may be more difficult and energetically expensive. Therefore, males in such areas presumably invest in larger sperm reserves to maximize successful impregnation when a female is encountered.

Interestingly, the female-mass-corrected litter size followed a similar pattern to relative testicular mass in males — females carry larger litters in arid, lowland habitats than their highland counterparts where more mesic conditions prevail. In many lizard species, a harsher climate makes activity more difficult and shortens the breeding season; therefore, litter size is increased to compensate for only a single breeding episode (Rocha et al. 2002 and references therein). Even though *Georychus* has the potential of producing two litters per breeding season, it is unclear whether this is a cosmopolitan phenomenon across populations because a sampling bias exists (the Cape Peninsula; see Taylor et al. 1985) in the single study investigating breeding seasonality. Therefore, it is unclear whether a larger litter size in populations at low elevation may be the result of a single reproductive bout.

Assuming a similar pattern in breeding seasonality across all *G. capensis* populations (two litters per year), two potential scenarios are likely: either the impregnation rate by males is maximized through the larger sperm reserves in arid areas, or larger litter sizes may ensure demographic stability. The former scenario is unlikely given that there is no significant relationship between relative testicular mass in males and female reproductive variables (Supplementary Table S4).¹ In the latter scenario, larger litters would ensure survival of at least a few young, should the

mortality rate be linked to aridity, physiological stress on females, or predation. Indeed, larger litters suffer an increased mortality rate (Cameron 1973; Millar 1973 and references therein; Johnson et al. 1999; Madsen and Shine 1999) due to nutritional stress (lower quantity and quality of milk; Cameron 1973; Millar 1973), predation in the nest before and during dispersal, and maternal mortality (Cameron 1973). No data were collected, however, on the mortality rate of young in the present study, thereby leaving these considerations as speculative. Conversely, larger litters may also result in higher population densities, a situation which would aid mate searching in arid areas. Population densities were not estimated in this study; however, it was observed that populations at lower elevations contained a higher number of individuals (>50 animals) that were spatially more aggregated (<100 m apart) than *G. capensis* populations in highland areas (<10 animals spaced >500 m apart; J.H. Visser, personal observation).

Smaller litters in *Georychus* populations at higher altitudes may also result from other extrinsic factors. Similar patterns of smaller size-specific litters at higher altitudes relative to their lowland counterparts have been reported for populations of various lizard species (Waltner 1991; Mathies and Andrews 1995; Rohr 1997; Lemos-Espinal et al. 1998). This phenomenon has been attributed to environmental conditions such as lower resource availability (Rohr 1997).

Indeed, environmental conditions relating to soil type and vegetation differ among the sampling areas in this study. The older deposits form the higher parts of South Africa with the low-lying areas being of a more recent origin (Cowling et al. 2009). Along with this variation in geomorphology, the west-to-east rainfall gradient across the country has also influenced the evolution and establishment of Fynbos and Renosterbos in the western parts with the Grassland biome remaining in the interior and highlands (Patridge and Maud 2000; Chase and Meadows 2007). Given this link between geomorphology and vegetation type with the ecological variables of elevation and rainfall, it is not surprising that relative testicular mass and the mass-corrected litter size in *Georychus* populations were similarly influenced by the age of deposits and the vegetation type.

Annual rainfall patterns influence life-history patterns through soil moisture and food availability, even at fine spatial scales, in the dusky rat (*Rattus colletti* (Thomas, 1904)) (Madsen and Shine 1999). A higher availability of food (Hill 1972; Chapman et al. 1990; Rohr 1997) and also more nutritious foodstuffs (Hill 1972; Cameron 1973) result in larger litters because more energy may be allocated to reproduction (Millar 1973 and references therein; McNab 1980, 1986). As such, soil type may also influence litter size — larger litters have been demonstrated in the cottontail rabbit (*Sylvilagus floridanus* (J.A. Allen, 1890)) in more fertile soils (Hill 1972). The fertility of the soil influences the vegetation type found in such soil, and hence, the quality and quantity of food available (Hill 1972). Given the dependence of *Georychus* on the geophyte richness of an area (Du Toit et al. 1985; Lovegrove and Jarvis 1986; Bennett 1988; Romañach 2005), it is possible that the geophyte richness of the Grassland areas (older soil types) may be lower than for the Fynbos–Renosterbos regions (younger soil types). Correspondingly, this would result in smaller litter sizes in the lower nutrition areas. The effects of soil type and vegetation type on relative testicular mass in males is not as easily explained and may result from a link between climate, geology, and vegetation. The influence of food availability on the reproduction of *G. capensis* remains, however, speculative without any data on the soil fertility and geophyte richness of sampled areas.

In addition, the results of the difference in reproductive variables (especially embryo counts) across the distribution must be viewed with caution. Sample sizes in the Mpumalanga and KwaZulu-Natal areas were comparatively lower than in the Western Cape. Litter size may also vary between breeding seasons due

to variation in female physiology and female size over a lifetime (Krohne 1981). Indeed, sampling only spanned a single breeding season. These sampling effects therefore preclude robust conclusions about the influence of ecology on the mating system of *Georychus* and the geographic differences in mating variables reported in this study need further investigation to confirm possible adaptive differences among populations.

Conclusion

Georychus capensis is a habitat specialist that occurs only where particular ecological conditions prevail. This species is not nearly as cosmopolitan as *B. suillus* or the Southern African mole-rat (*Cryptomys hottentotus* (Lesson, 1826)) and is dependent on mesic conditions and areas associated with vleis or that are close to rivers. In addition, the breeding cycle of *G. capensis* appears to depend on rainfall and its seasonality, which may have selected for different breeding seasons in animals from the Western Cape and KwaZulu-Natal or Mpumalanga areas, respectively.

No size dimorphism exists between males and females and this, together with a female-biased sex ratio and testicular size dependent on the sex ratio in a population, points to a complex mating system. Due to the low vagility of these subterranean animals, females are spatially distributed around males to facilitate breeding. As a result of the higher number of females in some populations, males have the opportunity to copulate with several females and, therefore, need larger sperm reserves to negate sperm depletion. The mating system is therefore one where females only mate with a few or single males during a breeding season, but males are polygynous; indeed, it is possible that males possess harems. Parentage analysis would be beneficial to determine whether the young of gravid females and juveniles close to such females are indeed fathered by the local resident male.

In addition, reproduction in *Georychus* is also influenced by various ecological factors such as elevation, rainfall, soil type, and vegetation. Areas of lower elevation and a more arid climate are correlated with increased male testicular size and female litter size relative to highland, mesic areas. Presumably, a more arid environment makes mate searching a more arduous task. To maximize fertilization, males therefore display larger sperm reserves in such areas, presumably to maximize fertilization success should a female be encountered. In turn, larger litter sizes in such areas could be the result of a higher fertilization rate, although demographic effects and fine-scale distributional effects are more likely — a more aggregated and larger population would facilitate locating receptive mates in a fossorial system. Lastly, the mating system of *G. capensis* also appears linked to soil and vegetation type (both of which are in turn linked to elevation and rainfall). The influence of these ecological factors is presumably linked to the distribution of adequate food resources; however, this is speculative.

Georychus is currently monotypic due to a lack of karyotypic or morphological variation (Nevo et al. 1987; Deuve et al. 2008); however, genetic investigations suggest possible unique evolutionary units in KwaZulu-Natal (Honeycutt et al. 1987, 1991; Nevo et al. 1987), Mpumalanga (Ingram et al. 2004), and the Western Cape. Animals from these areas may therefore represent putative species, and given the fragmented and isolated distribution of populations, occupation of different soil and vegetation types together with the geographic variation in traits such as testicular size, litter size, and breeding season, the genus may represent a species complex (for example, for data on *B. suillus* see Visser et al. 2014). Incorporation of the genetic material from all sampled individuals in a phylogeographic study will shed light on intraspecific and even interspecific relationships within *Georychus* and will inform conservation management approaches.

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