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

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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 and 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 the 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 the 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- and vegetation type) which could impact mate searching, mating success and food resources.

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

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; Nakata 1984). In addition, sperm competition (Merilä and Sheldon 1998; Jolly and Phillips-Conroy 2001; Preston et al. 2002; Schulte-Hostedde and Millar 2004; Hettyey and Roberts 2006), scramble competition polygyny (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; Hettyey 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 1998; Hettyey 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*, *Heliophobius*, *Bathyergus*, *Georychus*, *Cryptomys* and *Fukomys* (Honeycutt et al. 1987; Janecek et al. 1992; Burda 2000; Faulkes et al. 2004; Ingram et al. 2004; Van Daele et al. 2007; Kock et al. 2009). 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 (Šumbera 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 inter-montane valleys of the Western Cape, south-western KwaZulu-Natal and in Mpumalanga (see Figure 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 and 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).

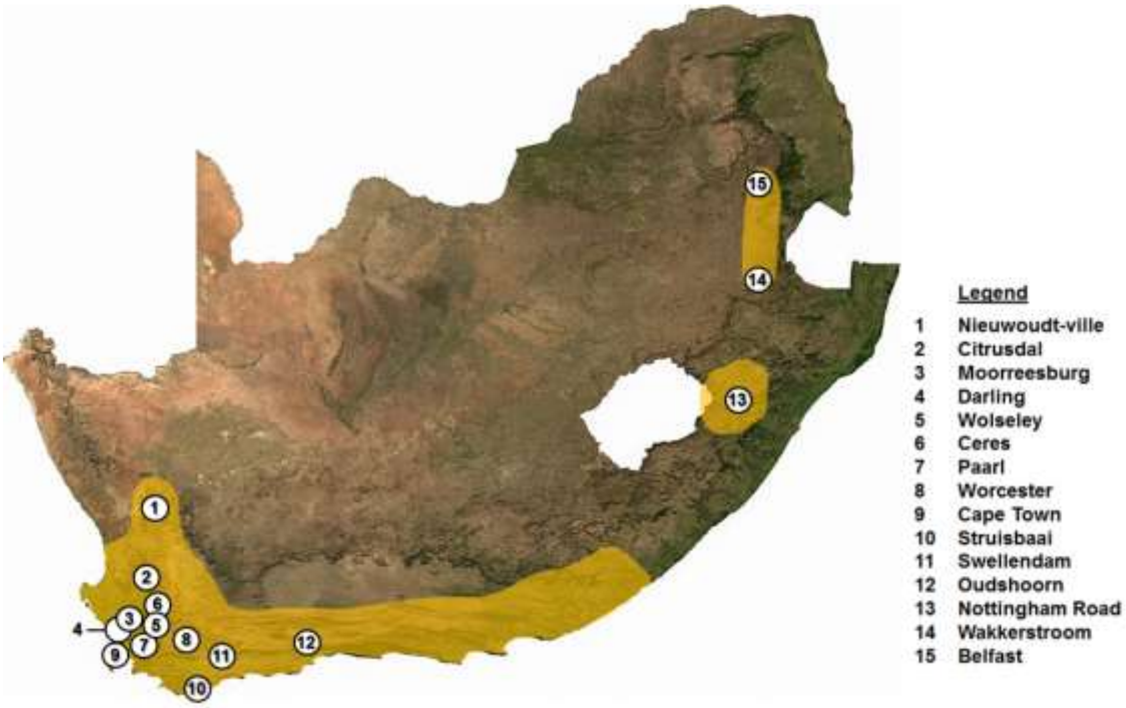

Figure 1 Map showing localities where *G. capensis* were sampled across South Africa. The distributional range (shaded) of the species is indicated (based on historical records).

Previous research on *G. capensis* has focused on its physiology (Oosthuizen et al. 2003, Oosthuizen and Bennett 2007; Oosthuizen et al. 2008; Oosthuizen and Bennett 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. 2004; 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 2012) 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 regional differences might be present.

Here, by including larger sample sizes for populations from across the entire South African range, we aim to 1) determine the current distribution of *G. capensis* and identify common ecological variables influencing the distribution of suitable habitat for this species, 2) investigate whether differences exist in body size across the range or between the sexes, 3) 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 4) 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 (IUCN) 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 *Georychus capensis* were collected from 15 distinct localities (Figure 1; see Table 2 for sample sizes and capture months) across their distributional range in the western Cape (CapeNature Permit Number: 0056-AAA041-00084), KwaZulu-Natal (EKZNW Permit Number: OP1716/2016) and Mpumalanga (MPTA Permit Number: 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* (200mm long and 400g in mass). This practice was approved by the Ethics Committee of the University of Johannesburg (Ethics number 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 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 and the embryos removed from gravid females while the testes of males were removed. 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, deposit age (from Keyser 1997), 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 Corporation 2011). The data for the sexes were analysed

Table 1 Information on the sampled *G. capensis* specimens showing the sampling locality, coordinates of the sampling locality, elevation above sea-level (in metres) 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), the age of the particular soil type and the vegetation type of the area (from Mucina and Rutherford 2006).

Locality	**Coordinates**	**Elevation**	**Mean rainfall**	**Sampling area**	**Soil type**	**Deposit age**	**Vegetation type**
Nieuwoudt-ville	S 31°22'; E 19°06'	720	285	Grazed area near vlei	Tillite; sandstone; shale	Palaeozoic	Nieuwoudt-ville Shale Renosterveld
Citrusdal	S 32°36'; E 19°01'	160	260	Grazed area near vlei and river	Shale; sandstone	Palaeozoic	Leipoldtville Sand Fynbos
Moorreesburg	S 33°17'; E 18°34'	90	425	Grazed area near vlei	Unconsolidated superficial deposits (limestone; sandstone)	Cainozoic	Swartland Silcrete Renosterveld
Darling	S 33°24'; E 18°24'	140	520	Grazed area near vlei	Unconsolidated superficial deposits (limestone; sandstone)	Cainozoic	Swartland Granite Renosterveld
Wolseley	S 33°24'; E 19°12'	280	480	Grazed area near vlei	Unconsolidated superficial deposits (limestone;	Cainozoic	Breede Alluvium Fynbos

					sandstone)		
Ceres	S 33°12'; E 19°14'	900	570	Grazed area near vlei and river	Shale; sandstone	Palaeozoic	Kouebokkeveld Shale Fynbos
Paarl	S 33°44'; E 18°58'	110	655	Rugby field near river	Quartzite; shale; tillite	Palaeozoic	Swartland Alluvium Fynbos
Worcester	S 33°40'; E 19°31'	240	265	Lawns near vlei and river	Unconsolidated superficial deposits (limestone; sandstone)	Cainozoic	Breede Alluvium Renosterveld
Cape Town	S 34°00'; E 18°31'	20	575	Lawn near vlei	Unconsolidated superficial deposits (limestone; sandstone)	Cainozoic	Cap Flats Sand Fynbos
Struisbaai	S 34°41'; E 20°00'	5	475	Grazed area near vlei	Unconsolidated superficial deposits (limestone; sandstone)	Cainozoic	Agulhas Sand Fynbos
Swellendam	S 34°03'; E 20°25'	90	520	Grazed area near river	Conglomerate; shale; sandstone; limestone	Mesozoic	Swellendam Silcrete Fynbos

Oudshoorn	S 33°51'; E 22°02'	600	785	Grazed area near vlei and river	Quartzite; shale; tillite	Palaeozoic	South Outeniqua Sandstone Fynbos
Nottingham Road	S 29°29'; E 29°52'	1800	890	Grazed area near vlei	Shale; mudstone; sandstone; grit; coal	Mesozoic	Drakensberg Foothill Moist Grassland
Wakkerstroom	S 27°18'; E 30°16'	2000	902	Grazed area near vlei	Shale; mudstone; sandstone; grit; coal	Mesozoic	Wakkerstroom Montane Grassland
Belfast	S 25°33'; E 30°04'	1940	858	Grazed area near vlei	Quartzite; shale; limestone; andesite; tuff; hornfels; conglomerates	Precambrian	Lydenburg Montane Grassland

together as well as separately. Non-parametric tests were used for analyses as 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 non-pregnant 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 less than 120 g were considered as juveniles and removed from the datasets 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 less than 120g an age of 15 months, which is well below the reproductive age.

Three different datasets were compiled for mass analyses: these were (i) all individuals irrespective of sex and age, (ii) only males and (iii) only females (for gravid females, the mass of embryos were subtracted from total mass). For consistency, these datasets were also analysed with juvenile animals (with a mass lower than 120g) 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. Body mass differences between males and females across

Table 2 Information on the sampled *G. capensis* specimens showing the sampling locality, number of sampled males, mass range (in grams) of sampled males, number of sampled females, mass range of sampled females (in grams), number of gravid sampled females, the number of embryos contained by these gravid females, the mass range of these gravid females (embryo mass subtracted) and the month of capture of the gravid individuals. The month of capture for populations containing no gravid individuals are indicated in brackets.

Locality	**Number of males**	**Mass range (g) of males**	**Number of females**	**Mass range (g) of females**	**Number of gravid females**	**Number of embryos**	**Mass range (g) of gravid females**	**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 August
Darling	12	100 - 407	13	98 - 259	-	-	-	(1 July)
Wolseley	7	138 - 306	16	110 - 258	2	8	162 - 231	24 August
Ceres	11	68 - 264	12	52 - 280	1	8	280	5 September
Paarl	6	145 - 346	12	153 - 385	1	8	290	21 August
Worcester	4	138 - 241	10	147 - 339	9	51	147 - 339	15 August - 19 September
Cape Town	8	208 - 332	17	106 - 365	1	7	218	20 August
Struisbaai	3	61 - 193	17	99 - 208	1	5	160	15 July
Swellendam	3	143 - 290	15	124 - 248	10	38	131 - 248	13 August - 19 September

Oudshoorn	9	162 - 315	13	89 - 303	8	34	133 - 303	11 August
Nottingham Road	1	141	2	209 - 233	1	2	209	28 January
Wakkerstroom	6	91 - 243	13	91 - 291	2	2	214 - 230	16 January
Belfast	3	144 - 212	0	-	-	-	-	(14 January)
Total	122	-	261	-	67	336	-	-

the entire distributional range, as well as within each locality, were performed using a non-parametric 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 residuals 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 *G. capensis* mating season as evidenced by the presence of gravid females in all but four of 15 sampling locations (Table 2) and the large, round testes of trapped males (also see Šumbera 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 less than 120g were removed) from populations with sample sizes of more than 3 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 the 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 (mass/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 on Figure 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 datasets. Reproductive datasets included the relative testicular size in males, the mass-corrected litter size for females, the average litter size of a population (the average 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 61g and 407g, whereas female mass ranged between 52g and 396g (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 121g and 339g.

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 on Figure 1) or smaller (e.g., Struisbaai; locality 10 on Figure 1) in pairwise comparisons between populations (see Figure 2; Table 3; Supplementary Tables S1 and S2).

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 on Figure 1) were the largest, whereas those from the Darling and Struisbaai were the smallest (localities 7, 4 and 9 respectively on Figure 1; Figure 2C; Supplementary Tables S1 and S2). For males, specimens from Cape Town were the largest (locality 9 on Figure 1; Figure 2B; Supplementary Tables S1 and S2).

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 as the body condition of animals during this period should be similarly influenced across populations.

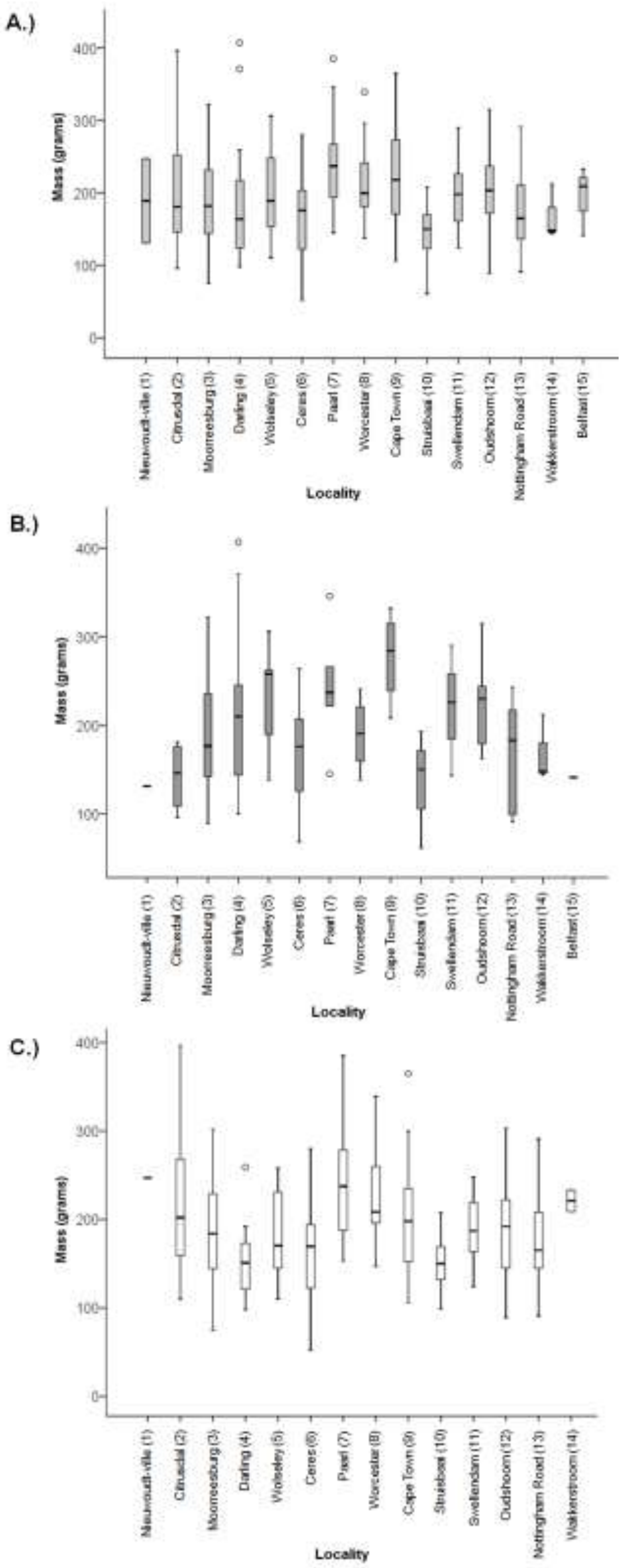

Figure 2 Graphs showing the differences in mass (mean and standard deviation) of *G. capensis* individuals between localities for A.) all individuals, B.) males and C.) females. Numbers in brackets correspond to localities in Figure 1.

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 *G. capensis* specimens. For each analysis, both the full dataset was used and a dataset of mature animals where all juvenile animals (<120g) were removed. The Chi-square statistic, degrees of freedom and *p*-value are given for each analysis.

Variables	**Chi-Square**	**df**	***p*-value**
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

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 *G. capensis* specimens. For each analysis, both the full dataset was used and a dataset of mature individuals only where all juvenile animals (<120g) were removed. The Mann-Whitney *U* statistic, number of females *N*(F), number of males *N*(M), *p*-value and the mean mass ± standard deviation (in grams) for females and males respectively are given for each analysis.

Variables	**Mann-Whitney *U***	***N*(F)**	***N*(M)**	***p*-value**	**Mean ± SD (F)**	**Mean ± SD (M)**
Male versus female mass between all localities	14653	261	122	0.209	188 ± 58	197 ± 67
Male versus female mass between all localities (juveniles removed)	11367.5	229	109	0.185	199 ± 52	210 ± 60
Population comparisons (All specimens)						
Population	**Mann-Whitney *U***	***N*(F)**	***N*(M)**	***p*-value**		
Citrusdal	13.000	17	4	0.065	221 ± 81	152 ± 40
Moorreesburg	2244.000	103	44	0.926	185 ± 53	186 ± 58
Darling	40.500	13	12	0.040	151 ± 44	217 ± 94
Wolseley	30.500	16	7	0.089	183 ± 52	229 ± 61
Ceres	63.500	12	11	0.880	163 ± 60	167 ± 57
Paarl	36.000	12	6	1.000	240 ± 66	242 ± 65
Worcester	14.000	10	4	0.454	224 ± 59	190 ± 43
Cape Town	22.000	17	8	0.006	200 ± 71	277 ± 45
Struisbaai	24.500	17	3	0.921	149 ± 29	135 ± 67
Swellendam	16.000	15	3	0.498	190 ± 39	220 ± 74
Oudshoorn	37.000	13	9	0.164	190 ± 55	223 ± 48
Nottingham Road	0.000	2	1	0.667	221 ± 17	141
Wakkerstroom	38.500	13	6	0.966	175 ± 53	169 ± 63
Population comparisons (Juveniles removed)						
Population	**Mann-Whitney *U***	***N*(F)**	***N*(M)**	***p*-value**		
Citrusdal	10.000	16	3	0.138	228 ± 78	158 ± 32
Moorreesburg	1693.500	89	39	0.828	197 ± 45	197 ± 52
Darling	28.500	10	11	0.061	165 ± 41	227 ± 90
Wolseley	30.500	14	7	0.172	193 ± 46	229 ± 61
Ceres	31.500	10	8	0.460	180 ± 47	194 ± 38
Paarl	36.000	12	6	1.000	240 ± 66	242 ± 65
Worcester	14.000	10	4	0.454	224 ± 59	190 ± 43
Cape Town	22.000	14	8	0.020	219 ± 63	277 ± 45
Struisbaai	9.500	13	2	0.571	162 ± 20	172 ± 30
Swellendam	16.000	15	3	0.498	190 ± 39	220 ± 74
Oudshoorn	37.000	12	9	0.247	198 ± 48	223 ± 48
Nottingham Road	0.000	2	1	0.667	221 ± 17	141
Wakkerstroom	14.000	11	4	0.343	188 ± 47	207 ± 33

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 on Figure 1) where males were larger than females. There was also a significant difference between male and female masses in the Darling locality (locality 4 on Figure 1) with non-significant 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 to smaller (and presumably younger) females (Supplementary Figure S4). In addition, significant variation (Chi-Square = 19.364, df = 10, $p = 0.036$) 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 removed, all animals belonging to smaller populations removed, mature animals with juveniles and small populations removed; Table 5). While there was a significant and strong correlation ($r^2 = 0.654$, $N = 97$, $p = 0.000$) between body mass and body length (Supplementary Figure S1), 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

Table 5 Summary of the statistical results for regression analyses investigating the relationship between testicular mass in male *G. capensis* and their body mass, as well as between relative testicular size and the percentage of females in the population where that male was sampled. Both the full dataset was used and a dataset of mature individuals only where all juvenile animals (<120g) were removed. In addition, populations where three or less animals were sampled were removed for further analyses. The results for the regression analyses using body condition index as a proxy for animal health are also shown. The r^2 values, number of samples (*N*) and the *p*-value are given for each analysis.

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

most of the variation in testicular mass, this relationship was used for subsequent analyses concerning relative testicular size.

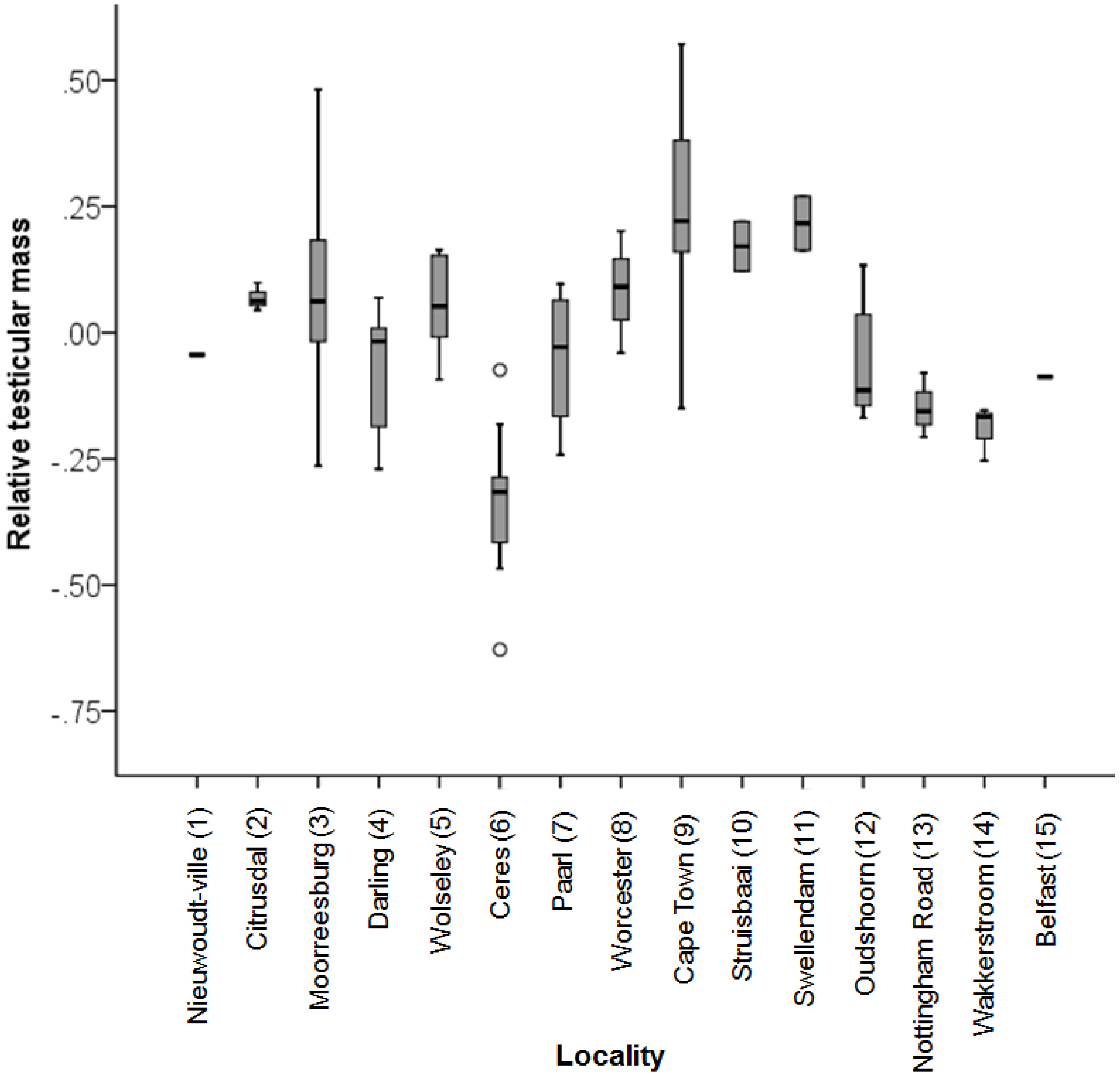

Figure 3 Graph showing the geographic variation between localities in relative testicular mass of mature *G. capensis* males. Numbers in brackets correspond to localities in Figure 1.

Relative testicular mass differed significantly among populations across the range (All males: Chi-Square = 48.932, df = 14, *p* = 0.000; Males with juveniles removed: Chi-Square = 43.566, df = 14, *p* = 0.000; Figure 3; Supplementary Table S3) and was consistently significantly correlated with the percentage of females within a population (all mature

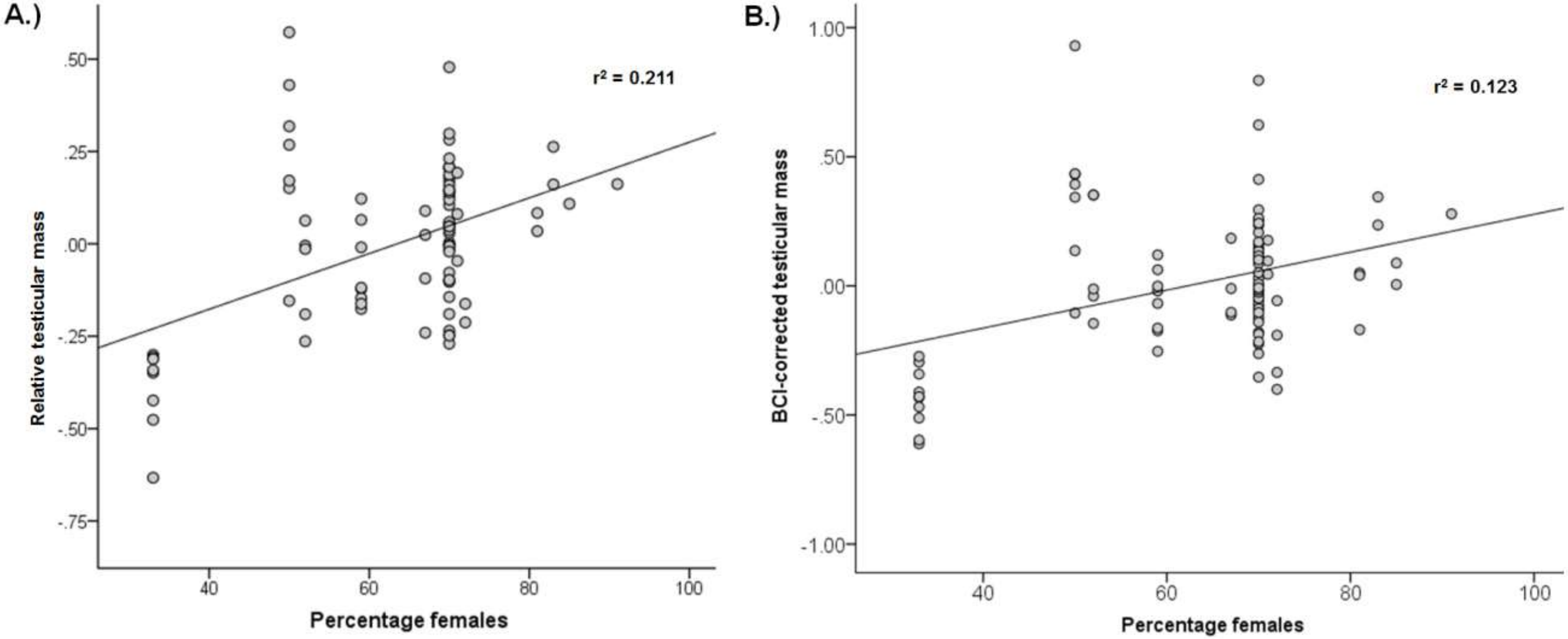

Figure 4 Regression showing the relationship between A.) relative testicular mass and B.) body condition index (BCI) corrected testicular mass of mature *G. capensis* males and the percentage of females in the population where the males were sampled.

animals with juveniles removed, all animals with small populations removed, mature animals with juveniles and small populations removed; Table 5; Figure 4) with populations containing fewer females displaying smaller relative testicular masses. No similar trends were evident when comparing relative testicular mass and the average number of embryos per gravid female or proportion of gravid females within each population (Supplementary Table S4).

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 (Figure 5A); males from regions with a lower annual rainfall had larger relative testicular masses compared to regions of higher rainfall (Figure 5B). Similarly, the mass-corrected litter sizes of females correlated with these two ecological variables, with a higher number of embryos found in females at lower elevations and in lower rainfall areas (Figure 5C and 5D). The average 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 (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 relative testicular masses: Palaeozoic, 0.010 ± 0.210 SD; Cainozoic, 1.701 ± 0.460 SD; Supplementary Figure S2A). A similar situation was evident in the mass-corrected litter sizes of females, where significantly more embryos were carried by

Table 6 Summary of the statistical results for analyses investigating the relationship between ecological variables including elevation above sea level (m), annual rainfall (mm) and the deposit age and vegetation type where *G. capensis* populations are found and the reproductive variables of these populations. Reproductive datasets 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), average litter size per population (the average 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 r^2 values, number of samples (N) and the p-values are given for the regression analyses, the Chi-Square values, degrees of freedom (df) an p-values for the comparisons between multiple different groups and the Mann-Whitney U values, number of samples (N) and the p-values for the comparison between two different groups.

Elevation

Reproductive Variable	r^2	N	**p-value**
Relative testicular mass in males	0.249	97	0.000
Residuals (Number of embryos vs. gravid female mass)	0.177	67	0.000
Number of embryos/Number of gravid females	0.428	11	0.029
Number of gravid females/Total number of females	0.000	11	0.975
Percentage of females in a population	0.059	13	0.424

Rainfall

Reproductive Variable	r^2	N	**p-value**
Relative testicular mass in males	0.098	97	0.002
Residuals (Number of embryos vs. gravid female mass)	0.109	67	0.006
Number of embryos/Number of gravid females	0.267	11	0.103
Number of gravid females/Total number of females	0.031	11	0.605
Percentage of females in a population	0.049	13	0.469

Deposit age

Reproductive Variable	**Chi-Square**	**df**	**p-value**
Relative testicular mass in males	24.007	3	0.000
Residuals (Number of embryos vs. gravid female mass)	8.801	3	0.032
Number of embryos/Number of gravid females	5.906	3	0.116
Number of gravid females/Total number of females	2.156	3	0.541
Percentage of females in a population	2.286	2	0.319

Vegetation type

Reproductive Variable	**Mann-Whitney U**	N	**p-value**
Relative testicular mass in males	152.000	97	0.007
Residuals (Number of embryos vs. gravid female mass)	7.000	67	0.001
Number of embryos/Number of gravid females	0.000	11	0.036
Number of gravid females/Total number of females	7.000	11	0.727
Percentage of females in a population	4.000	13	0.769

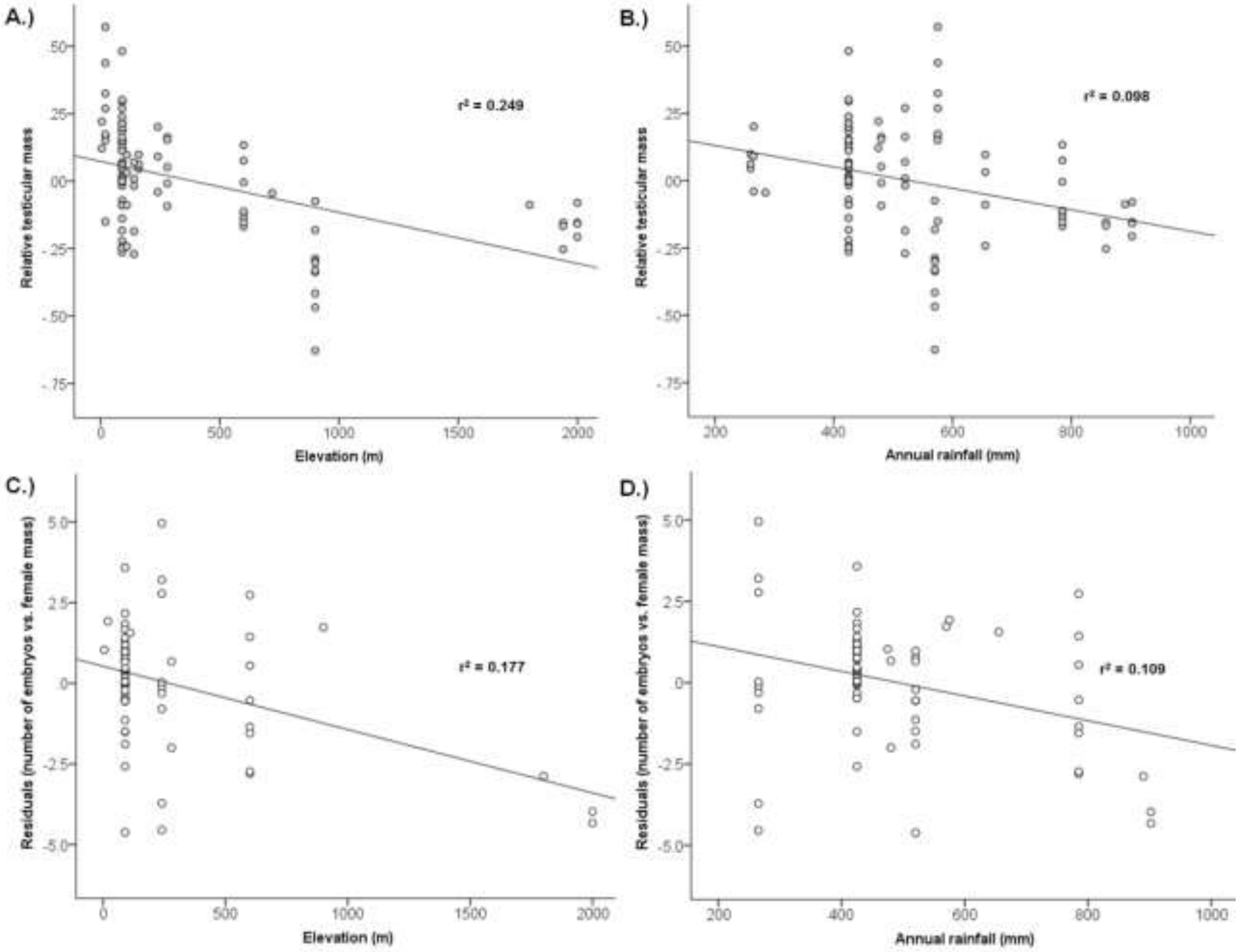

Figure 5 Regression showing the relationship between mating variables and ecological variables in sampled *G. capensis* populations with regards to A.) relative testicular mass in males and elevation above sea-level (m), B.) relative testicular mass in males and annual rainfall (mm), C.) female size-corrected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

females in the Palaeozoic and Cainozoic compared to the Precambrian deposits (mean mass-corrected litter sizes of females: Palaeozoic, 0.269 ± 1.379 SD; Cainozoic, 0.305 ± 2.970 SD; Precambrian, -3.728 ± 0.753 SD; Table 6; Supplementary Figure S2B). No similar trends were shared in any of the other female reproductive datasets.

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 to their Grassland counterparts (Supplementary Figure S2C and S2D). No similar trends were observed for any of the other female reproductive datasets.

Discussion

Ecology and distribution

Georychus 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 Nieuwoudtville population; 720m above sea-level; locality 1 on Figure 1) to the highlands of Mpumalanga (Wakkerstroom and Belfast; 2000m and 1940m above sea-level respectively; localities 14 and 15 on Figure 1) and KwaZulu-Natal (Nottingham Road; 1800m above sea-level; locality 13 on Figure 1). The range reported here overlaps notably, but also extends that previously suggested by De Graaff (1981) (new records from Moorreesburg, Ceres and Oudshoorn: localities 3, 6 and 12 on Figure 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 which 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). *Georychus* likely spread from the north-eastern 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 Mya; Hendey 1969).

Georychus inhabits mesic regions across its distributional range - both in the winter rainfall zone of the western Cape (285 - 655mm p.a.; average 485mm; Mucina and Rutherford 2006) and the summer rainfall regions of KwaZulu-Natal (890mm p.a.) and Mpumalanga (858 - 902mm p.a.); an observation also made by Bennett et al. (2006). The higher annual rainfall allows burrowing for most of the year (Thomas et al. 2012) as it makes the soil workable (Scantlebury et al. 2006) and reduces the energetic cost of digging (Lovegrove 1989; Zelová et al. 2011; Okrouhlík 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 *Georychus*. All populations were associated with either vlei land areas or were close to rivers (Table 1). In addition, all populations were found in anthropogenically influenced (grazing of cattle or planted lawns) 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 2012). 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; Romañach 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/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 non-random search for these food items (Du Toit et al. 1985; Bennett and Faulkes 2000; Romañach 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 on Figure 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 as similar mesic habitat types are occupied across the range. Occurrence on planted grass lawns are the only ecological factor that set apart the Paarl and Cape Town populations (localities 7 and 9 respectively on Figure 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 2012; 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 360g is attained by *G. capensis*. In the current study, five animals (two males and three females) had body masses higher than 360g (between 365g and 407g). Given that young males grow at 7.4g/month (Taylor 1985) until they reach 60g (Bennett 1988) and at 5.8g/month thereafter, this would give the male weighing 407g 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 on Figure 1) population with males being significantly larger; a trend that was also weakly observed in Darling (locality 4 on Figure 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 (0.68 hectares) 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 intra-sexual competition between males for receptive females. Indeed, *Heliophobius argenteocinereus* (Peters 1846) exhibits a similar equal sex ratio and displays analogous size dimorphism between the sexes (Šumbera 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 of (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 Šumbera et al. 2003). A breeding season which 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, however, speculative whether the difference in breeding season between these areas represents a real adaptive shift.

A mean litter size of 5 (1-11) was found for the gravid females collected across the distributional range (30% of females contained 5 embryos). This is less than found in previous studies (mean litter size 6, range 3-10; Bennett 1988; Bennett et al. 2006), but is still significantly larger than reported for other mole-rat species (Bennett 1988; Šumbera et al. 2003). A larger litter size may be selected for in *Georychus* due to higher predation pressure as they move above-ground 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 which may accommodate a larger amount of embryos.

Similar allometry applied to testicular mass, which relied significantly on male body mass (also see Merilä and Sheldon 1998; Jolly and Phillips-Conroy 2001; Hettyey et al. 2005 for similar examples in other taxa). 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 non-gravid) are spatially clustered (between 1-30m; 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) which 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 which shift annually (likely due to mate searching) while females excavate circular burrow systems which 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) and burrow systems therefore need to be closely spaced (3-4m; 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 in *G. capensis* is biased towards females (also see the sampling of Oosthuizen et al. 2013 for a similar pattern) - a consequence of the mating system (Greenwood 1980) which 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 see Taylor et al. 1985 for a contrary finding) - a secondary sexual trait which may be related to competition over mates, as in *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 Green Finches and anurans; Merilä and Sheldon 1998 and Hettyey et al. 2005 respectively) and a linear increase in testicular size with body size (in common with other polygynous species -

Green Finches, *Cardeulis chloris*, L., 1758, Hamadryas baboons, *Papio hamadryas*, L., 1758, common frog, *Rana temporaria*, L., 1758; Merilä and Sheldon 1998; Jolly and Phillips-Conroy 2001; 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 Merilä and Sheldon 1998 for examples; Jolly and Phillips-Conroy 2001; see examples in Preston et al. 2002; Schulte-Hostedde and Millar 2004; Hettyey and Roberts 2006) with polygyny generally resulting in larger testes (Jolly and Phillips-Conroy 2001). 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 2001). The second instance involves scramble competition polygyny which arises when females and their ranges are not defendable (Clutton-Brock 1989; Davies 1991) and males range over a large area and attempt to mate with receptive females (Kappeler 1997). Male lemurs exhibit scramble competition linked to the temporal distribution of receptive females (Kappeler 1997) which favours larger testes (Harcourt et al. 1981) and weakly selects traits for competition (e.g., size dimorphism; see references in Kappeler 1997). As with *G. capensis*, lemurs (*Mirza coquereli*, Grandidier 1867) have no dimorphism, are solitary, polygynous, have a sex ratio biased towards females and display pronounced seasonal variation in testis size with an increase in the mating season (Kappeler 1997).

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 2001) and is associated with higher copulation rates (more females mated) and greater siring success as it allows for the storage and production of more sperm (Preston et al. 2002; 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 as fewer copulations are achieved. It is entirely possible that several males will not have access to a female during their lifetime and as such, 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 Figure S3). 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). It is therefore 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 which influences the energetic cost of digging and therefore mate searching (Lovegrove 1989; Zelová et al. 2011; Okrouhlík et al. 2015). In drier areas, mate searching may be more difficult and energetically expensive. Males in such areas therefore presumably invest in larger sperm reserves to maximize successful impregnation when a female is encountered.

Interestingly, the mass-corrected litter size in females 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 as a sampling bias exists (the Cape Peninsula; see Taylor et al. 1985) in the single study investigating breeding seasonality. It is therefore unclear whether a larger litter size in low elevation populations 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). 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 2009) 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) which were spatially more aggregated (<100m apart) than *G. capensis* populations in highland areas (<10 animals spaced >500m 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 the 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 as well as 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 2009). A higher availability of food (Hill 1972; Chapman et al. 1990; Rohr 1997) and also more nutritious foodstuffs (Hill 1972; Cameron 1973) results in larger litters as 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 demonstrated in the cottontail rabbit (*Sylvilagus floridarlus*, Bachman 1837) 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 the 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 life-time (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 which occurs only where particular ecological conditions prevail. This species is not nearly as cosmopolitan as *B. suillus* or *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/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 are, 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. 1986; Deuve et al. 2008); however genetic investigations suggest possible unique evolutionary units in KwaZulu-Natal (Honeycutt et al. 1987; Nevo et al. 1987; Honeycutt et al. 1991), 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 see Visser et al. 2014 for data on *B. suillus*). 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.

Acknowledgements

We are grateful to the land-owners who allowed collection of specimens on their properties. Funding for this project was provided by NRF grants to B. Jansen van Vuuren and N.C. Bennett.

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Supplementary Material

Supplementary Table S1 Summary of the statistically significant results for the pairwise comparisons between the masses of *G. capensis* for all individuals, only male individuals and only female individuals between the various sampling localities. The names of the two populations that were compared (Pop 1 and Pop2) are shown along with the Mann-Whitney *U* test statistic, number of samples in population 1 (*N*(Pop1)) and population 2 (*N*(Pop2)) and the *p*-value for the comparison.

Pairwise mass difference: All specimens					
Pop1	**Pop2**	**Mann-Whitney *U***	***N* (Pop1)**	***N* (Pop2)**	***p*-value**
Citrusdal	Paarl	-70.345	21	18	0.048
Moorreesburg	Paarl	-89.971	147	18	0.001
Darling	Paarl	-112.710	25	18	0.001
Wolseley	Paarl	-69.554	23	18	0.046
Worcester	Paarl	-125.359	23	18	0.000
Wakkerstroom	Paarl	113.566	19	18	0.002
Struisbaai	Paarl	165.500	20	18	0.000
Struisbaai	Citrusdal	95.155	20	21	0.006
Struisbaai	Moorreesburg	75.529	20	147	0.004
Struisbaai	Wolseley	95.946	20	23	0.005
Struisbaai	Worcester	124.929	20	14	0.001
Struisbaai	Cape Town	134.930	20	25	0.000
Struisbaai	Swellendam	-94.972	20	18	0.008
Struisbaai	Oudshoorn	-109.295	20	22	0.001
Worcester	Worcester	-84.787	23	14	0.024
Worcester	Oudshoorn	-69.154	23	22	0.036
Worcester	Cape Town	-94.789	23	25	0.003
Moorreesburg	Cape Town	-59.401	147	25	0.013

Darling	Cape Town	-82.140	25	25	0.009
Wakkerstroom	Cape Town	82.996	19	25	0.014

Pairwise mass difference: Males

Pop1	**Pop2**	**Mann-Whitney *U***	***N* (Pop1)**	***N* (Pop2)**	***p*-value**
Nieuwoudt-ville	Cape Town	-82.875	1	8	0.027
Citrusdal	Cape Town	-71.875	4	8	0.001
Moorreesburg	Cape Town	-46.625	44	8	0.001
Darling	Cape Town	-37.500	12	8	0.020
Worcester	Cape Town	-56.193	11	8	0.001
Worcester	Cape Town	-44.625	4	8	0.039
Struisbaai	Cape Town	70.708	3	8	0.003
Nottingham Road	Cape Town	76.375	1	8	0.042
Wakkerstroom	Cape Town	54.792	6	8	0.004
Belfast	Cape Town	58.042	3	8	0.015
Worcester	Paarl	-38.485	11	6	0.032
Struisbaai	Paarl	53.000	3	6	0.034
Citrusdal	Paarl	-54.176	4	6	0.018
Citrusdal	Oudshoorn	-46.111	4	9	0.030
Citrusdal	Wolseley	-49.000	4	7	0.027
Struisbaai	Wolseley	47.833	3	7	0.050

Pairwise mass difference: Females

Pop1	**Pop2**	**Mann-Whitney *U***	***N* (Pop1)**	***N* (Pop2)**	***p*-value**
Moorreesburg	Paarl	-60.113	103	12	0.009
Wolseley	Paarl	-63.885	16	12	0.027
Worcester	Paarl	-88.250	12	12	0.004
Wakkerstroom	Paarl	76.474	13	12	0.011
Struisbaai	Paarl	113.673	17	12	0.000
Struisbaai	Citrusdal	83.000	17	17	0.001
Struisbaai	Moorreesburg	53.759	17	103	0.007
Struisbaai	Worcester	98.806	17	10	0.001

Struisbaai	Cape Town	66.235	17	17	0.012
Struisbaai	Swellendam	-62.806	17	15	0.019
Struisbaai	Oudshoorn	-60.224	17	13	0.030
Struisbaai	Nottingham Road	-111.206	17	2	0.049
Darling	Citrusdal	79.102	13	17	0.004
Darling	Moorreesburg	49.861	13	103	0.025
Darling	Paarl	-109.974	13	12	0.000
Darling	Worcester	-94.908	13	10	0.003
Darling	Cape Town	-61.337	13	17	0.027
Darling	Swellendam	-58.908	13	15	0.039
Worcester	Citrusdal	57.377	12	17	0.044
Worcester	Worcester	-73.183	12	10	0.024

Supplementary Table S2 Summary of the statistically significant results for the pairwise comparisons between the masses of mature *G. capensis* (individuals with a mass <120g removed) for all individuals, only male individuals and only female individuals between the various sampling localities. The names of the two populations that were compared (Pop 1 and Pop2) are shown along with the Mann-Whitney *U* test statistic, number of samples in population 1 (*N*(Pop1)) and population 2 (*N*(Pop2)) and the *p*-value for the comparison.

Pairwise mass difference: All specimens (Juveniles removed)					
Pop1	**Pop2**	**Mann-Whitney *U***	***N* (Pop1)**	***N* (Pop2)**	***p*-value**
Struisbaai	Citrusdal	85.553	15	19	0.011
Struisbaai	Moorreesburg	69.655	15	128	0.009
Struisbaai	Wolseley	-92.550	15	21	0.006
Struisbaai	Worcester	96.179	15	14	0.008
Struisbaai	Cape Town	134.955	15	22	0.000
Struisbaai	Oudshoorn	-90.543	15	21	0.006
Struisbaai	Paarl	136.75	15	18	0.000
Moorreesburg	Paarl	-67.095	128	18	0.006
Darling	Paarl	-86.107	21	18	0.006
Worcester	Paarl	-88.111	18	18	0.007
Swellendam	Paarl	70.528	18	18	0.030
Wakkerstroom	Paarl	75.550	15	18	0.027
Belfast	Paarl	126.583	3	18	0.035
Belfast	Cape Town	126.788	3	22	0.035
Moorreesburg	Cape Town	-65.300	128	22	0.004
Darling	Cape Town	-84.312	21	22	0.005
Worcester	Cape Town	-86.316	18	22	0.005
Swellendam	Cape Town	68.732	18	22	0.027
Wakkerstroom	Cape Town	73.755	15	22	0.024
Pairwise mass difference: Males (Juveniles removed)					

Pop1	**Pop2**	**Mann-Whitney *U***	***N* (Pop1)**	***N* (Pop2)**	***p*-value**
Nieuwoudt-ville	Cape Town	-82.875	1	8	0.013
Citrusdal	Cape Town	-63.708	3	8	0.003
Moorreesburg	Cape Town	-40.375	39	8	0.001
Darling	Cape Town	-32.375	11	8	0.027
Worcester	Cape Town	-41.812	8	8	0.008
Worcester	Cape Town	-44.625	4	8	0.021
Struisbaai	Cape Town	55.125	2	8	0.027
Nottingham Road	Cape Town	76.375	1	8	0.023
Belfast	Cape Town	58.042	3	8	0.007
Citrusdal	Paarl	-46.000	3	6	0.040

Pairwise mass difference: Females (Juveniles removed)

Pop1	**Pop2**	**Mann-Whitney *U***	***N* (Pop1)**	***N* (Pop2)**	***p*-value**
Struisbaai	Citrusdal	73.668	13	16	0.003
Struisbaai	Moorreesburg	52.486	13	89	0.008
Struisbaai	Wolseley	55.538	13	14	0.033
Struisbaai	Worcester	80.831	13	10	0.004
Struisbaai	Cape Town	73.016	13	14	0.004
Struisbaai	Oudshoorn	-53.272	13	12	0.045
Struisbaai	Paarl	95.897	13	12	0.000
Moorreesburg	Paarl	-43.411	89	12	0.033
Worcester	Paarl	-68.967	10	12	0.015
Swellendam	Paarl	51.067	15	12	0.047
Wakkerstroom	Paarl	58.985	11	12	0.033
Darling	Paarl	-90.367	10	12	0.001
Darling	Citrusdal	68.138	10	16	0.011
Darling	Worcester	-75.300	10	10	0.011
Darling	Cape Town	-67.486	10	14	0.014

Supplementary Table S3 Summary of the statistically significant results for the pairwise comparisons between the relative testicular masses of *G. capensis* for all males and only mature males (individuals with a mass <120g removed) between the various sampling localities. The names of the two populations that were compared (Pop 1 and Pop2) are shown along with the Mann-Whitney *U* test statistic, number of samples in population 1 (*N*(Pop1)) and population 2 (*N*(Pop2)) and the *p*-value for the comparison.

Pairwise relative testicular mass difference: All specimens					
Pop1	**Pop2**	**Mann-Whitney *U***	***N* (Pop1)**	***N* (Pop2)**	***p*-value**
Worcester	Citrusdal	49.800	10	3	0.007
Worcester	Moorreesburg	48.247	10	38	0.000
Worcester	Wolseley	47.400	10	5	0.002
Worcester	Worcester	-53.133	10	3	0.004
Worcester	Struisbaai	-68.800	10	2	0.002
Worcester	Swellendam	-74.800	10	2	0.001
Worcester	Oudshoorn	-29.300	10	8	0.028
Worcester	Cape Town	-70.050	10	7	0.000
Moorreesburg	Cape Town	-21.803	38	7	0.046
Darling	Cape Town	-44.050	5	7	0.006
Paarl	Cape Town	-38.750	4	7	0.025
Oudshoorn	Cape Town	40.750	8	7	0.004
Wakkerstroom	Cape Town	54.875	4	7	0.001
Belfast	Cape Town	60.750	3	7	0.001
Darling	Swellendam	-48.800	5	2	0.038
Oudshoorn	Swellendam	45.500	8	2	0.041
Wakkerstroom	Swellendam	59.625	4	2	0.011
Belfast	Swellendam	65.500	3	2	0.011
Belfast	Struisbaai	59.500	3	2	0.021
Wakkerstroom	Struisbaai	53.625	4	2	0.028

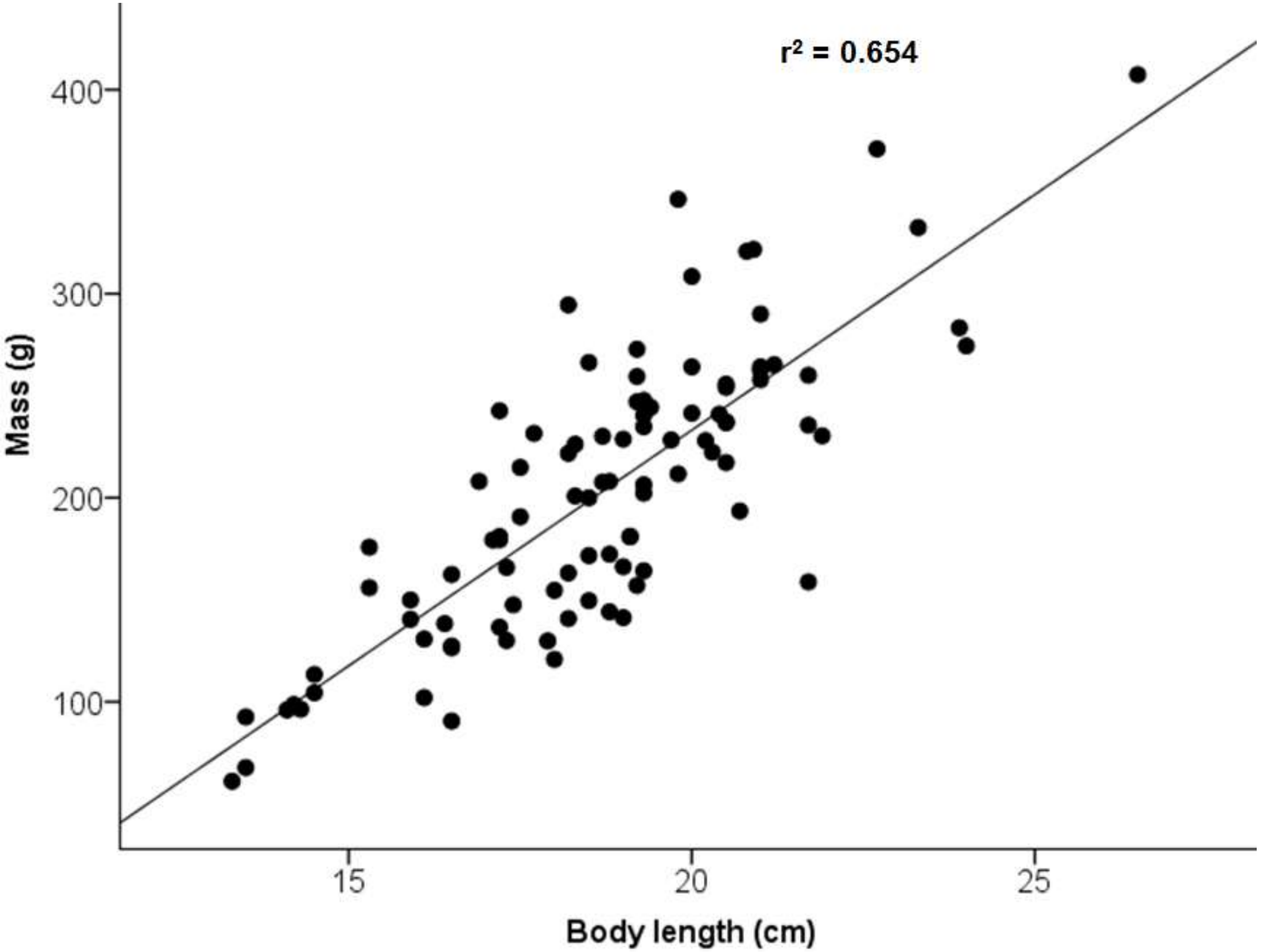
Wakkerstroom	Moorreesburg	33.072	4	38	0.025
Belfast	Moorreesburg	38.947	3	38	0.021

Pairwise relative testicular mass difference: Juveniles removed

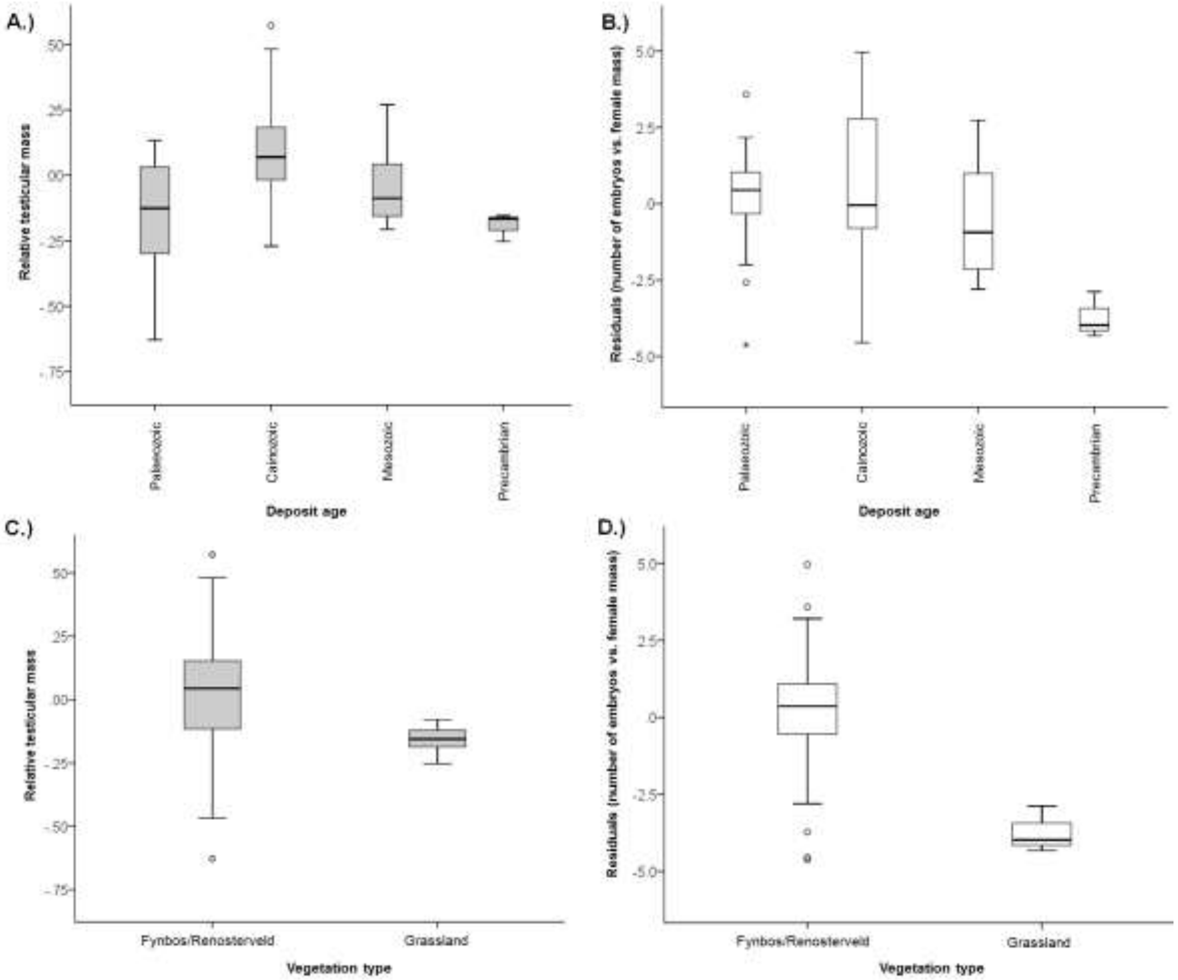
Pop1	**Pop2**	**Mann-Whitney *U***	***N* (Pop1)**	***N* (Pop2)**	***p*-value**
Worcester	Citrusdal	47.500	7	2	0.018
Worcester	Moorreesburg	46.265	7	34	0.000
Worcester	Wolseley	45.200	7	5	0.002
Worcester	Paarl	-32.750	7	4	0.036
Worcester	Worcester	-50.667	7	3	0.003
Worcester	Struisbaai	-55.000	7	1	0.039
Worcester	Swellendam	-69.500	7	2	0.001
Worcester	Oudshoorn	-30.000	7	8	0.020
Worcester	Cape Town	-66.125	7	7	0.000
Moorreesburg	Cape Town	-19.860	34	7	0.043
Darling	Cape Town	-38.925	5	7	0.006
Paarl	Cape Town	-33.375	4	7	0.029
Oudshoorn	Cape Town	36.125	8	7	0.004
Wakkerstroom	Cape Town	52.125	2	7	0.008
Belfast	Cape Town	53.792	3	7	0.001
Belfast	Swellendam	57.167	3	2	0.012
Darling	Swellendam	-42.300	5	2	0.043
Oudshoorn	Swellendam	39.500	8	2	0.045
Wakkerstroom	Swellendam	55.500	2	2	0.026
Belfast	Moorreesburg	33.931	3	34	0.024

Supplementary Table S4 Summary of the statistical results for regression analyses investigating the relationship between relative testicular mass in male *G. capensis* and reproductive variables such as the average number of embryos in a population and the proportion of gravid females in a population. Both the full dataset was used and a dataset of mature individuals only where all juvenile animals (<120g) were removed. The r^2 value, number of samples (N) and the p-value are given for each analysis.

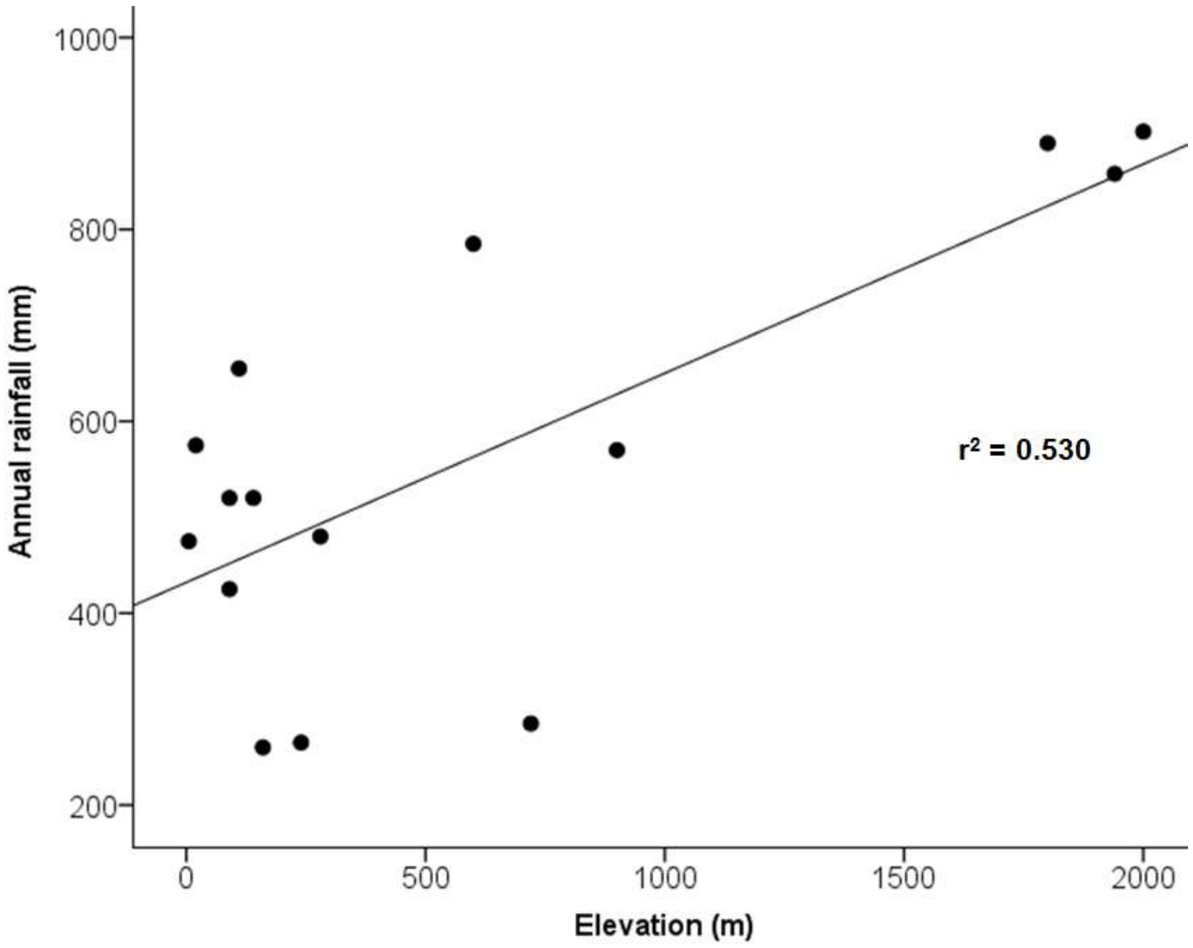
Average number of embryos			
All specimens	r^2	N	p**-value**
Relative testicular mass vs. average number of embryos in a population	0.013	85	0.219
Juveniles removed	r^2	N	p**-value**
Relative testicular mass vs. average number of embryos in a population	0.016	75	0.281
Proportion of gravid females			
All specimens	r^2	N	p**-value**
Relative testicular mass vs. proportion of gravid females in a population	0.012	85	0.322
Juveniles removed	r^2	N	p**-value**
Relative testicular mass vs. proportion of gravid females in a population	0.007	75	0.474



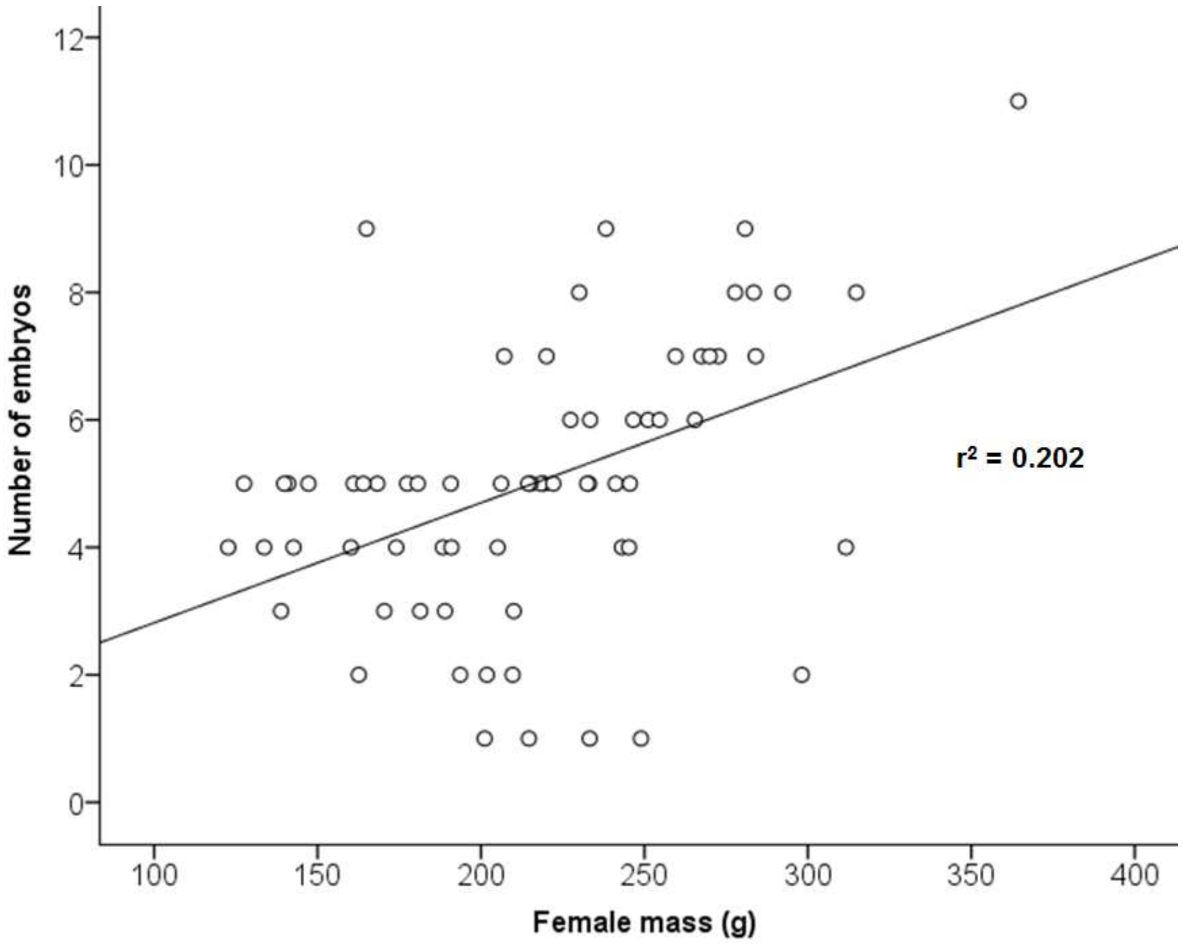
Supplementary Figure S1 Regression showing the relationship between body mass (g) and body length (mm) in male *G. capensis*.



Supplementary Figure S2 Graphs (mean and standard deviation) showing the differences in *G. capensis* A.) relative testicular mass (males) and B.) female size-corrected litter size in soils of different ages. In addition, the differences C.) relative testicular mass (males) and D.) female size-corrected litter size in different vegetation types are shown.



Supplementary Figure S3 Regression showing the relationship between annual rainfall (mm) and elevation above sea-level (m) across the populations where *G. capensis* was sampled.



Supplementary Figure S4 Regression showing the relationship between the number of embryos in a gravid female *G. capensis* and the mass (g) of that particular female.