

Structure and allometry of genitalia in males and females of a social African ground squirrel with high polygynandry

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Abstract

The few studies that have looked at genital allometry in mammals have typically shown a positively allometric relationship with body size and high coefficients of variation. Cryptic female choice, sexual conflict or sperm competition are mechanisms underlying genital evolution and as these are not mutually exclusive, they are often difficult to disentangle. In addition, these mechanisms are affected by both male and female social structure and/or mating strategies and, as such, pre- and post-copulatory behaviours have been shown to alter selection on genitalia. We examined genital traits and allometry in a polygynandrous and social ground squirrel *Xerus inauris*. We found that male testes are positively allometric and account for 1.5% of their body weight, one of the highest percentages known for sciurids. The penis, at 42.4% of head/body length, was isometric while the female reproductive tract, 22.4% head/body length, demonstrated no such relationship. Based on the allometric relationships of both males and females presented here, in conjunction with high levels of competition for females and lack of male aggression and territoriality, we suggest that sperm competition is the most likely mechanism for the evolution of the extremely large genitalia in this species.

Introduction

Genitalia typically undergo rapid and divergent evolution across species if under sexual selection (Eberhard, 1985; Arnqvist, 1997, 1998; House & Simmons, 2003; Hosken & Stockley, 2004). Often selected traits are larger and more ornamental and such trends, while also seen in external fertilizers (e.g. plants, Andersson & Iwasa, 1996), are more pronounced in species with internal fertilization (Arnqvist, 1998). In polygynandrous systems, genitalia have greater levels of diversity, when compared to

monandrous systems, which is most likely attributed to variation in post-insemination paternity success (Arnqvist, 1998). Male genital morphology has been directly linked to fertilization success in both the water strider and the dung beetle (Arnqvist & Danielsson, 1999; House & Simmons, 2003) but the underlying mechanisms between genital morphology and fertilization success are difficult to disentangle. Furthermore, these mechanisms may not be mutually exclusive and can include female processes that affect male paternity success (cryptic female choice), the male–female antagonism over control of optimal fitness strategies (sexual conflict) and male gamete competition (sperm competition) (Arnqvist, 1998).

Levels of sperm competition (sperm from more than one male competing for the ova of one female) are expected to be greater in species with intense male–male competition and multiple partners in both sexes (Parker, 1970; Birkhead & Møller, 1998). The level of sperm competition can be determined based on the operational sex ratio (OSR), defined as the number of oestrous females to sexually active males (Emlen & Oring, 1977). Increased levels of competition result in males investing more heavily in sperm production and ejaculates (Kenagy & Trombulak, 1986; Møller, 1989; Møller & Birkhead, 1989). This increased investment requires a greater amount of gonadal tissue for sperm production and storage such that levels of sperm competition are often indicated by the occurrence of large testes (Kenagy & Trombulak, 1986; Dixson & Anderson, 2004; Ramm, Parker & Stockley, 2005). Because testis size has evolved in response to factors beyond the first-order influence of body size, the relative testes size (RTS; as calculated in Kenagy & Trombulak, 1986) is expected to increase with increased levels of sperm competition (Kenagy & Trombulak, 1986; Parker et al., 1997; Gage & Freckleton, 2003).

Male and female reproductive tracts are thought to co-evolve and copulatory behaviour, physiology and morphology all have the potential to influence selection on genital traits (Eberhard, 1985; Birkhead, 1995; Presgraves, Baker & Wilkinson, 1999; Hosken & Stockley, 2004; Cordoba-Aguilar, 2005; Minder, Hosken & Ward, 2005; Beese, Beier & Baur, 2006; Brennan et al., 2007). For example, female waterfowl have developed longer and more complex vaginal morphology in relation to male phallus length and frequency of extra-pair copulations (Brennan et al., 2007). Likewise, male stalk-eyed flies (Diopsidae) have co-evolved longer sperm or dimorphic sperm, in relation to female reproductive morphology and sperm storage site (Presgraves et al., 1999). Sexually selected traits are commonly driven by directional selection, resulting in both high levels of phenotypic variation (Pomiankowski & Møller, 1995; Hosken & Stockley, 2004) and positive allometry (where a trait is proportionately larger with increasing organismal size) (Green, 1992; Petrie, 1992). A study on mole rats (Bathyergidae) found positively allometric penises and vaginas relative to body size, suggesting that the penis may act as a 'good genes' indicator with which the vagina co-evolved (Kinahan et al., 2007). Similar studies on harp seals *Pagophilus groenlandicus* (Miller & Burton, 2001), bats *Nyctalus noctula* (Lüpold, McElligott & Hosken, 2004) and muskrats *Ondatra zibethicus* (Tasikas et al., 2007), also found positive allometry of reproductive traits, for example baculum or penis length, potentially due to directional sexual selection, as well as higher levels of phenotypic variation in these traits. Such allometric relationships have been attributed to mating strategies that prohibit females from assessing males before copulation and thus rely on cryptic, post-copulatory choice, with a reproductive advantage being incurred as a result of proportionally longer genitalia (Miller, Stewart

& Stenson, 1998; Miller & Burton, 2001; Lüpold et al., 2004; Kinahan et al., 2007; Tasikas et al., 2007). Predictions regarding intraspecific variation in genital size, form and allometry in male and female mammals are therefore difficult to make without some understanding of male and female social structure and mating strategies (Arnqvist, 1997; Miller & Burton, 2001; Kinahan et al., 2008).

Cape ground squirrels *Xerus inauris* exhibit a highly skewed OSR (11M:1F) due to year-round breeding and asynchronous, spontaneous ovulation (Waterman, 1998; Bouchie et al., 2006). *Xerus inauris* have a level of social organization unlike that described for any other ground squirrel where males and females form separate social groups that persist year round (Waterman, 1995). Males are not territorial or aggressive, but rather they compete for females through competitive searching (Waterman, 1998). Females are not forced into copulation and mate with an average of four males per oestrous (Waterman, 1994). While females may exert some level of mate choice by retreating underground with specific males, older, more dominant males typically obtain the first copulation of a female's oestrous (Waterman, 1998). The dominance hierarchy of males, however, is unrelated to external testes size or body size (Waterman, 1998): males have very obviously large external testes, about 20% of the head–body length (Waterman, 1998), and show no seasonality in external testicle size (Waterman, 1996).

The lack of direct male–male competition in *X. inauris* amid a high level of polygyny make this species an excellent subject for examining the association between mating strategies and genital allometry. Because mating often occurs above ground where female *X. inauris* are not coerced into mating and are able to assess males before copulation (Waterman, 1998), this study differs from mammals studied previously that may have less female choice due to the environments in which mating occurs (Miller & Burton, 2001; Lüpold et al., 2004; Kinahan et al., 2007; Tasikas et al., 2007). The objectives of this paper are to (1) describe male and female reproductive anatomy that have evolved in a competitive and polygynandrous mating system and (2) examine allometry of male and female genitalia. We predict that due to the level of polygyny, males will experience high sperm competition, resulting in investment in the testes and epididymes. However, due to the mating environment, we predict that *X. inauris* will not exhibit positive allometry in reproductive tract length because no reproductive advantage would ensue.

Materials and methods

We sampled 26 adult male and 21 adult female *X. inauris* from private farm lands throughout South Africa and Namibia, where animals were being removed for control measures. We included reproductive adults but excluded pregnant females; reproductive condition was assessed based on the size of testes for males and vaginal swelling and elongated nipples for females (Waterman, 1996). We trapped squirrels using Tomahawk[®] (Tomahawk Live Trap Co., Tomahawk, WI, USA) live traps baited with peanut butter and chicken feed and euthanized them on site with a halothane or a chloroform overdose. All handling was in accordance with the American Mammal Association guidelines (Gannon & Sikes, 2007) and was approved by the University of Central Florida IACUC committee.

We recorded body mass (measured with a spring scale to ± 5.0 g), head–body length (from nasal bone to base of tail), tail length (base of the tail to the end of the caudal vertebra) and hind foot length (s.u.) for each animal as well as external testes length and width for all males. For internal genital measurements, we dissected the testes and penis of each male and recorded the length and mass of both testes separately, the mass of the surrounding epididymis (including the caput, corpus and cauda), the length of the entire penis in situ and the mass of the dissected penis. We also recorded the length of what we call the 'intromittent' portion of the penis of *X. inauris* as it has a well-defined flexure, or 'doubling-back', just beneath the foreskin. This flexure has been found in other sciurids, for example as illustrated in Prasad (1954), and we speculated that this may be the only part of the penis that enters the female, and hence measured it separately (hereafter 'intromittent' penis). We measured the depth of the female vaginal tract by inserting a probe into the vagina of the dissected female and measuring the distance from the point of insertion to the cervix at the point of uterine horn separation. All lengths and widths were recorded using Mitutoyo electronic calipers (Tokyo, Japan) to the nearest ± 0.1 cm for head/body and tail lengths and ± 0.1 mm for all other lengths and widths; mass was recorded on an AccuLab digital scale (Edgewood, NY, USA) to ± 0.01 g. To reduce the effect of sampling variability, all measurements were taken by the same person (M. M.).

Statistical analysis

Data were natural log transformed to meet the assumptions of normality. Males and females were compared for differences in body size and coefficients of variation (CV) were calculated using the standard method:

(Sokal & Rohlf, 1995). For allometry analyses, we used an ordinary least squares (OLS) model, that examines relationships between log–log regressions of trait size on body length. When OLS slopes showed a significant deviation ($\alpha < 0.1$) from zero, we determined deviations from isometry, where the slope is equal to one, using reduced major axis (RMA) regression (Lüpold et al., 2004; Kinahan et al., 2007). The latter method is more appropriate when variables are subject to measurement error and to overcome scale dependence (Sokal & Rohlf, 1995). Positively allometric traits result in $\beta > 1$, isometric traits $\beta = 1$ and negatively allometric traits $\beta < 1$. SAS 9.1 (SAS Institute Inc., Cary, NC, USA) was used for all statistical analyses.

Results

The structures of male and female genitalia are illustrated in Fig. 1a and b. Table 1a and b provide the mean and se for all traits measured for males and females, respectively. Relative to body length, males have an extremely long penis that is c. 42.4% of the head/body length and a mean 'intromittent' length that is 12.1% of the head/body length. Males have a mean relative testes size of 2.2 (as calculated for rodents in Kenagy & Trombulak, 1986), with testes mass accounting for 1.5% of the total body mass. Females have a mean vaginal depth of 5.4 cm, which is 22.4% of the head/body length.

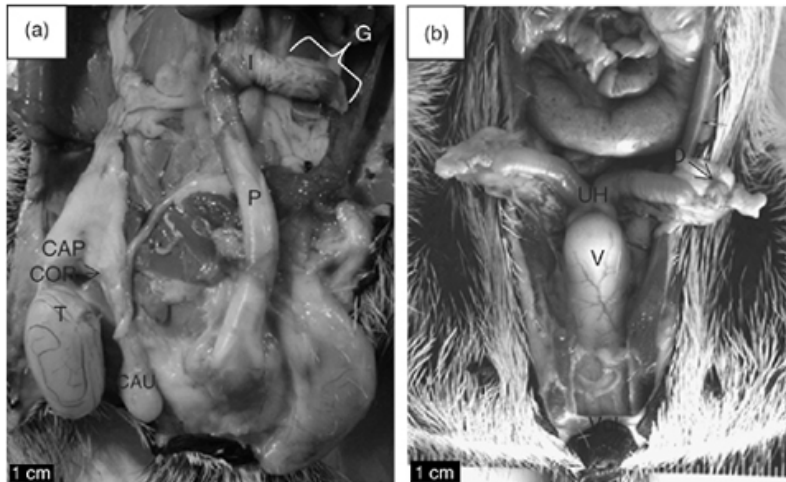


Figure 1 (a) In situ reproductive anatomy of an adult male *Xerus inauris*; T, testis; CAP, caput epididymis; COR, corpus epididymis; CAU, cauda epididymis; P, penis; I, intromittent; G, glans. (b) In situ reproductive anatomy of an adult female *Xerus inauris*; UH, uterine horns; O, ovary; V, vagina; Vul, vulva.

Table 1 Summary data of morphological measurements for male (a) and female (b) *Xerus inauris*

	<i>n</i>	Mean \pm SE	Range	% CV
<i>(a) Male traits</i>				
Body mass	26	678.0 \pm 15.0	515–805	11.97
Head/body length	26	258.3 \pm 3.8	232.6–310.0	7.51
L hind foot	26	62.1 \pm 0.4	58.3–66.2	3.60
Penis length	26	108.9 \pm 1.9	93.3–130.6	9.05
Intromittent length	12	29.2 \pm 0.7	24.9–34.1	8.40
Testes mass	25	10.3 \pm 0.5	4.9–15.3	23.68
Epididymis mass	25	5.6 \pm 0.3	2.4–9.8	27.58
	<i>n</i> *	Mean \pm SE	Range	CV
<i>(b) Female traits</i>				
Body mass	21	603.0 \pm 10.0	545–750	8.02
Head/body length	20	244.5 \pm 3.3	213.1–277.0	5.95
L hind foot	21	60.2 \pm 0.4	54.8–63.3	3.33
Vaginal depth	18	54.1 \pm 1.9	40.4–67.4	14.77
Vaginal mass	12	6.1 \pm 1.2	1.6–14.0	67.61

Masses are recorded in grams and lengths are in millimetres. % CV=percentage coefficient of variation.

* Excluding pregnant females.

OLS regressions on the reproductive traits of males showed a significant relationship between body length and penis length, and body length and epididymal mass (Table 2). Females demonstrated no relationship between body length and reproductive tract depth or mass (Table 2). RMA regressions show that total penis length is isometric

(i.e. increases in direct proportion) with respect to body size while epididymal mass and testes mass are positively allometric in relation to body size (Table 2). The male traits exhibiting positive allometry also had higher phenotypic CVs than isometric traits.

Table 2 Results of linear ordinary least squares (OLS) and reduced major axis (RMA) regressions for male and female *Xerus inauris* morphological traits (y-axis) regressed against body length (x-axis)

	<i>n</i>	<i>r</i>	OLS			RMA			Allometry
			Slope ± se	<i>t</i> value	<i>P</i>	Slope ± se	<i>t</i> value	<i>P</i>	
Penis length	26	0.57	0.68 ± 0.18	3.39	<0.01	1.19 ± 0.20	0.95	0.35	Isometric
'Intromittent' length	12	0.27	0.48 ± 0.54	0.90	0.39				
Testis mass	25	0.36	1.25 ± 0.67	1.85	0.08	3.47 ± 0.67	3.67	<0.01	Positive
Epididymal mass	25	0.67	2.65 ± 0.61	4.34	<0.01	3.95 ± 0.61	4.84	<0.01	Positive
Vaginal depth	18	0.19	0.07 ± 0.09	0.77	0.45				
Vaginal mass	12	0.30	0.03 ± 0.03	0.98	0.35				

Discussion

The Cape ground squirrel has a relative testes size of 2.2 (sensu Kenagy & Trombulak, 1986), which, to the best of our knowledge, is one of the greatest proportional testes sizes recorded for any squirrel species (Kenagy & Trombulak, 1986). Levels of competition, as indicated by the OSR, can be high in other squirrel species, such as *Spermophilus beecheyi* (14:1) and *Sciurus carolinensis* (10.6:1), (Koprowski, 1993; Boellstorff et al., 1994; Waterman, 1998) but *X. inauris* has a larger relative testes size than either of these species (2.03 and 1.63, respectively) (Kenagy & Trombulak, 1986). The large relative testes size could be a product of the male grouping system and year-round breeding, which does not occur in *S. beecheyi* or *S. carolinensis*, such that sperm competition risk is ever present and intensity is often high. Testes size is directly related to sperm competition intensity and has been shown to increase in polygynandrous mating systems (Parker et al., 1997; Hosken & Ward, 2001; Pitnick et al., 2001; Ramm et al., 2005). Given that female Cape ground squirrels mate with multiple males (Waterman, 1998), a large relative testes size is expected, as males should invest more in testicular tissue to increase the number of sperm per ejaculate. However, unlike other rodents where larger testes are also correlated with multiply sired litters (Ramm et al., 2005), Cape ground squirrels, with an average litter size of 1.6, are less likely to have multiply sired litters (Waterman, 1996). A small litter size does not, however, preclude a high level of sperm competition; in fact, it may encourage greater investment in competitive ejaculates due to the low paternity returns expected from each female.

Due to the rate of spermatogenesis in species with high levels of sperm competition, the role of the epididymis in the storage of mammalian ejaculates is more important than its role in maturation of sperm (Jones, 1999). Mammalian testes typically provide sperm for 0.5–2.0 ejaculates day⁻¹ but the storage capacity of the epididymis allows for continuous spermatogenesis and for controlled delivery of spermatozoa during each mating (Jones, 1999). Investing in proportionally larger epididymes may confer a reproductive advantage to those males by enabling a greater capacity for the

accumulation and storage of spermatozoa, resulting in the observed positively allometric relationship.

In *X. inauris*, the frequency of repeated copulations per male increases as females encounter and mate with subsequent males (Waterman, 1998). For males, the presence of another male or their knowledge of whether a female has already mated indicates the 'risk' of sperm competition, which may induce males to produce more sperm. Increasing numbers of rival males result in diminishing returns for increased sperm production and indicate 'intensity' of sperm competition, where males may be predicted to invest fewer sperm per mating or forego mating entirely (Wedell, Gage & Parker, 2002). For *X. inauris*, the mating system and social structure (Waterman, 1998) generate both a high risk and a high intensity of sperm competition (Parker & Ball, 2005). This high level of intensity and risk can lead to an increase in testis size as well as sperm expenditure (Parker & Ball, 2005), although the latter will require further study.

Optimal ejaculate expenditure is affected by the social or dominance status that influences the order of mating and/or access to females (Parker, 1990). Male *X. inauris* have a dominance hierarchy based on age, not external testes size, and older males are typically able to find oestrous females earlier and obtain the first copulation (Waterman, 1998). However, females copulate with younger males throughout the oestrous (Waterman, 1998), suggesting that all males may have access to the female and should theoretically optimize ejaculate expenditure depending on perceived risk and intensity of sperm competition.

Female *X. inauris* have deep, thick-walled vaginas that demonstrate no allometric relationship with body length. In mating systems where pre-copulatory choice is not possible, females may gain greater control of conception by selecting for increased reproductive tract length (Birkhead, 1995), resulting in a positive allometric relationship with body size. Because male and female genitalia are thought to co-evolve (Arnqvist, 1997), males may respond by developing a proportionally longer penis (Kinahan et al., 2007) so that sperm can be placed closer to the oviducts, thus increasing chances of fertilization (Birkhead, 1995). However, female *X. inauris* assess males before copulation (Waterman, 1998). In addition, polyandrous species not only have significantly longer oviducts, but they are also more convoluted than in monogamous species (Anderson, Dixson & Dixson, 2006). The additional complexity and length within the female reproductive tract further challenges the sperm of competing males such that females may be able to select sperm of males with the greatest reproductive potential (Anderson et al., 2006). Hence, no reproductive advantage is gained by either sex investing in proportionally longer genitalia. However, the penis in male *X. inauris* is long relative to body length. Greater levels of sperm competition increase genital length in rodents (Ramm, 2007) and the penis length and its potential relationship with sperm competition in the Cape ground squirrel merits further empirical study.

Despite the lack of positive allometry in females, we did see a high coefficient of variation in both vaginal depth and mass. Because *X. inauris* are aseasonal breeders, reproductive females within a population are in various stages of their oestrous cycles at any one time. A considerable loss of collagen is associated with the changes in uterine size during an oestrous cycle (Van Veen & Peereboom-Stegeman, 1987). We

were unable to distinguish where females were in their cycle and we suspect that these collagen changes are the cause of the high variability in our data. Seasonally breeding Cape dune mole-rats *Bathyergus suillus* have a positively allometric relationship only during the breeding season, suggesting that physiological changes may modify female reproductive anatomy (Kinahan et al., 2007).

This study shows strong support that in the highly competitive, highly polygynandrous *X. inauris*, the predominant mechanism underlying the genital evolution and competition for paternity is sperm competition. This is evident by the large testes size, long penis and positively allometric epididymis. As sperm competition risk and intensity models predict, genitalia are affected by both the level of competition as well as the mating rate (Parker & Ball, 2005), both of which are correlated with mating systems. The unique male social structure of the Cape ground squirrel sets this species apart from other mammals studied previously and further supports the hypothesis that positively allometric genitalia should not be considered to be the rule with regard to mammals but rather a reflection of their mating strategies (Kinahan et al., 2008).

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