Influence of breeding season and reproductive status on male reproductive characteristics in the common mole-rat, *Cryptomys hottentotus hottentotus*

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The effects of breeding season and reproductive status on male reproduction were investigated in the common mole-rat (*Cryptomys hottentotus hottentotus*), a co-operatively breeding rodent that exhibits seasonal reproduction and a reproductive division of labour. Testicular anatomical and histological morphometrics, and selected sperm parameters were studied in 50 males from 17 wild caught colonies. Males exhibited no apparent manifestation of season on testicular activity: spermatogenesis and sperm quality (motility and percentage normal morphology) were similar in the reproductively active and inactive periods. This maintenance of reproductive activity during the non-reproductive period is essential in *C. h. hottentotus* males, as this period coincides with the period of maximal dispersal opportunities. Such reproductive activation in dispersing males may aid intersexual recognition, and assist pair-bond formation or successful assimilation into foreign colonies, thereby facilitating later outbreeding. Consequently, outbreeding opportunities may be important determinants of reproductive activity in male common mole-rats, moderating seasonal effects. Reproductive and non-reproductive males revealed no differences in any of the testicular or sperm parameters studied. The absence of a physiologically well-defined suppression of reproduction in male common mole-rats is more typical of social suppression in male mammals.

Introduction

The common mole-rat, *Cryptomys hottentotus hottentotus*, is a social subterranean rodent, and lives in colonies of two to 14 individuals (Bennett, 1989). It is a widely distributed species occurring in both mesic and xeric areas of the southern African subregion (Skinner and Smithers, 1990). The common mole-rat is apparently unique among the social bathyergids in exhibiting seasonal reproduction (Bennett *et al.*, 1991; Jarvis and Bennett, 1991; N. C. Bennett and J. U. M. Jarvis, personal communication). Long-term mark-recapture studies revealed that birth of offspring in this species is restricted to the Southern Hemisphere summer period (late November to January), during which time a maximum of two litters may be reared (Skinner and Smithers 1990; Jarvis and Bennett, 1991; A. C. Spinks, N. C. Bennett and C. M. Rosenthal, unpublished). Gestation in common mole-rats lasts approximately 55–66 days (Bennett 1989), suggesting that most mating probably occurs between September and early November.

The reproductive periodicity evident in the common mole-rat is typical of both surface-dwelling and subterranean mammals inhabiting seasonal environments (see for example, Wehrenberg and Dyrenfurth, 1983; Gorman and Stone, 1990; Parreira and Cardoso, 1993; Kaplan and Mead, 1994; Page

et al., 1994). Annual alterations in environmental factors, modified by social factors, provide the proximate cues for such reproductive periodicity (Clarke, 1981; Ims, 1990; Bronson and Heideman, 1994; Turek and Van Cauter, 1994). In male mammals the non-reproductive period is typically characterized by testicular regression and the cessation of spermatogenesis (Clarke, 1981). In contrast, during the reproductive period, seasonal exteroceptive factors activate the testes through the anterior pituitary, resulting in sexual recrudescence (Clarke, 1981).

Interpretations of seasonal manifestations on common mole-rat male reproduction may be confounded by the reproductive division of labour prevalent in *C. h. hottentotus* colonies. Reproduction is typically restricted to the largest male and female in a colony, while the remaining colony members (both male and female) are reproductively quiescent (Bennett, 1989, 1992; Rosenthal *et al.*, 1992). Consequently, any manifestations of reproductive status on male reproductive characteristics are likely to obscure the effects of reproductive periodicity.

The common mole-rat provides a unique model to investigate the effects of both breeding season and reproductive status on the reproductive physiology of a co-operatively breeding rodent. The aims of this study were to investigate these effects on male reproduction, using data on testicular anatomical and histological morphometrics, and selected sperm parameters.

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Materials and Methods

A total of 50 male common mole-rats (16 reproductive males, 34 non-reproductive males) from 17 wild caught colonies, were used in this study. Animals were caught near Sir Lowry's Pass (18°55'E, 34°07'S) in the Western Cape, South Africa, using Hickman live-traps (Hickman, 1979).

The breeding season, defined as the period when both males and females are reproductively active, and when most mating is likely to occur, lasts from September to early November. During the non-breeding period males were caught in May–June. Animals caught during the breeding period were secured in September and early November (September and November groups were combined for subsequent analyses, as statistical analysis revealed no significant differences).

Applying the criteria of Bennett (1989; 1992) and Rosenthal *et al.* (1992), reproductive male common mole-rats were identified on the basis of being the heaviest male in the colony. Bennett (1989; 1992) and Rosenthal *et al.* (1992) have shown conclusively that the reproductive male is the largest and most dominant colony member. No animals less than 50 g were used in this study, as they were assumed to be sexually immature.

Removal and preparation of reproductive tract tissue

Animals were killed by inhalation of halothane and the testes were removed. Testes are abdominally situated in the common mole-rat. Tissues used for anatomy and histology were immediately fixed in Bouin's solution, for a minimum of 7 days, and then transferred to 70% alcohol for storage. Tissues used for the assessment of sperm motility and morphology were placed in Ham's F10 culture medium, on a preheated microscope stage (34°C), and processed as described below.

Testicular anatomy

It was assumed that any size changes in the tissue examined, resulting from fixation, would be constant across all samples. Testes were blotted to remove excess fixative, and individually weighed to the nearest milligram. Maximum testes length and width were measured using a dissecting microscope fitted with a graduated graticule. Testicular volume was calculated using the formula for the volume (V) of an ellipsoid [$V = 4/3\pi ab^2$ where $a = \frac{1}{2}$ maximum length; $b = \frac{1}{2}$ maximum width (Woodall and Skinner, 1989)].

Testicular histology

Tissue samples were processed using standard histological techniques. Sections of 7 μm were cut from the equatorial region of each testis, and stained with haematoxylin and eosin. For each animal, mean seminiferous tubule diameter and seminiferous tubule epithelial thickness were determined from 15 circular seminiferous tubule cross-sections, from a single testis. All measurements were recorded using a compound microscope fitted with a graduated graticule.

Sperm motility

Epididymides were dissected away from the testes and cleared of surrounding adipose and connective tissue, and

blood vessels. Spermatozoa were extracted from a cleanly dissected portion of the cauda epididymis, into Ham's F10 culture medium. A 10 μl drop of sperm suspension was then placed in a 1 ml motility bath and examined on a preheated microscope stage (34°C), using negative phase-contrast optics at a magnification of $\times 160$. The base of the motility bath consisted of an optical coverslip, to allow for optimal microscopic conditions. The images were recorded onto videotape using a VHS recorder and a colour video camera. Sperm motility was analysed using a computerized image analysis system (Sperm Motility Quantifier, Wirson Scientific and Precision Equipment, Auckland Park, Johannesburg). This system has been used successfully on a range of mammalian and amphibian species (Kaskar *et al.*, 1993, 1994; Van der Horst *et al.*, 1995).

The recordings of sperm motion were captured with a frame skip of zero, at an analysis rate of 50 Hz. The average number of frames analysed was 21.16 ± 0.47 frames, with a minimum and a maximum of 10 and 32 frames, respectively, in the sperm trajectory. The following motility parameters were measured: curvilinear velocity; straightline velocity; average path velocity; linearity; amplitude of lateral head displacement; wobble; straightness; dance; radian; curvature; percentage motility and percentage progressive motility. A minimum of 200 spermatozoa, including at least 100 motile spermatozoa, were analysed for each animal.

Sperm morphology

Spermatozoa were aspirated from the cauda epididymis into Ham's F10 culture medium. A 10 μl sample of sperm suspension was incubated for 5 min at 34°C in 20 μl eosin–nigrosin stain, mounted on a glass slide, and examined under oil emersion at a magnification of $\times 1000$. A total of 200 spermatozoa were analysed per animal. Spermatozoa were categorized as normal or having one of the following structural defects: head defect (bicephalic, macrocephalic, microcephalic, other); tail/head-less; mitochondrial sheath defect, cytoplasmic droplet; bent midpiece; flagellar defect (bent primary piece, looped tail, coiled/knotted tail, biflagellate, circular tail).

Statistical analyses

Regression analysis revealed a strong correlation between testicular anatomical and histological morphometrics and body mass. Consequently, body mass was introduced as a covariant during subsequent analysis of these parameters. In contrast none of the sperm morphology or motility variables recorded correlated significantly with body mass. Accordingly these parameters were not standardized relative to body mass.

All comparative testing was done using either one-way analysis of variance (ANOVA) or multifactorial analysis of variance (MANOVA). In making statistical comparisons, the individual animal was considered to be the appropriate unit of replication and comparison. Consequently, when reporting averages for experimental groups (Table 1) and performing analyses of variance, computations were made using one value per animal (replicate measures made from a single animal were averaged to provide one value per animal).

Results

Breeding season effects

Seasonal effects on reproductive characteristics were revealed in the analysis of testicular anatomical and histological data. Males caught during the breeding period ($n = 35$) had testes of a significantly smaller mass and volume than those captured outside the breeding period ($n = 11$; Fig. 1a). Furthermore, the diameter and epithelial thickness of the seminiferous tubules of males caught during the breeding season ($n = 25$) were significantly smaller than those of males secured outside the breeding period ($n = 15$; Fig. 2a). Non-reproductive males caught during the breeding period exhibited significantly smaller testicular mass, testicular volume ($n = 24$), seminiferous tubule diameter and seminiferous tubule epithelial diameter ($n = 16$) than those caught outside the breeding period (testicular mass and volume, $n = 7$; seminiferous tubule diameter $n = 10$; seminiferous tubule epithelial diameter, $n = 9$; Figs 1c and 2c). Although a similar trend was evident in the reproductive males, differences in testicular measures were not statistically significant (in breeding: testicular mass and volume, $n = 11$; seminiferous tubule diameter and epithelial diameter, $n = 9$; out of breeding: testicular mass and volume, $n = 4$; seminiferous tubule diameter and epithelial diameter, $n = 5$; Figs 1b and 2b).

Seasonal differences in testicular anatomical and histological features did not, however, reflect changes in spermatogenic activity or sperm motility. The testes of all animals under investigation showed evidence of spermatogenesis. Moreover, all sperm motility parameters investigated were comparable for males caught during the breeding ($n = 8$) and non-breeding periods ($n = 8$; Table 1). However, although the percentage of spermatozoa with normal morphology did not differ significantly between animals caught during ($n = 6$) and after ($n = 8$; Table 1) the breeding period, there were significant differences in the distribution of sperm defects between these periods (Fig. 3). Males secured during the breeding period had significantly fewer spermatozoa with cytoplasmic droplets, and significantly more spermatozoa with flagellar defects, than did males caught outside the breeding period (Fig. 3).

Reproductive status effects

Differences in reproductive status were not reflected in any of the parameters measured. Testis mass and volume did not differ significantly between reproductive ($n = 15$) and non-reproductive males ($n = 31$; Fig. 4). Moreover, diameter and epithelial thickness of the seminiferous tubules were similar for reproductive ($n = 14$) and non-reproductive males ($n = 26$; Fig. 5).

Fig. 1. Mean ($\pm$ SEM) testicular mass ($\square$) and volume ($\blacksquare$) for *Cryptomys hottentotus hottentotus* males caught during the breeding (BP) and non-breeding (NBP) periods. (a) All males combined, x: MANOVA, $F(1,45) = 10.58$, $P = 0.002$; y: MANOVA, $F(1,45) = 7.41$, $P = 0.009$; (b) reproductive males and (c) non-reproductive males, x: ANOVA, $F(1,30) = 6.31$, $P = 0.02$; y: ANOVA, $F(1,30) = 5.33$, $P = 0.03$. Values are corrected for body mass by the extraction of residuals.

An analogous pattern was evident for the sperm parameters. As mentioned, spermatogenesis was observed in the testes of all animals in the study. There was no significant difference between the sperm motility parameters of reproductive ($n = 8$) and non-reproductive males ($n = 8$; Table 1). Reproductive ($n = 7$) and non-reproductive males ($n = 7$) had a comparable percentage of spermatozoa with normal morphology (Table 1). Furthermore, both groups showed an equivalent distribution of sperm defects (Fig. 3).

Discussion

In contrast to most subterranean mammals, which are exclusively solitary and highly xenophobic, the bathyergids display a range of sociality, from solitariness to eusociality (Jarvis, 1981; Bennett, 1989; Jarvis and Bennett, 1991, 1993). While all the solitary species examined exhibit strict reproductive periodicity, the majority of social mole-rats display no cyclicity in reproductive activity (Van der Horst, 1972; Bennett and Jarvis, 1988; Jarvis and Bennett, 1991). The common mole-rat, with its seasonal breeding system, is the exception to this general pattern.

Reproductive cyclicity in the common mole-rat is presumably a result of it having invaded a seasonal habitat. The western Cape population used in this study inhabits a winter rainfall region, with an annual precipitation of about 640 mm and most rain falling between May and August. It is well established that periodicity in environmental cues provides the proximate stimulus for seasonality in mammalian reproduction (Clarke, 1981; Ims, 1990; Bronson and Heideman, 1994; Turek and Van Cauter, 1994). Furthermore, Jarvis and Bennett (1991) recognized that seasonality in temperature and rainfall were important determinants of seasonal breeding in the solitary bathyergids.

The observed pattern of reproductive cyclicity in common mole-rats was not reflected in male gonadal function. Males exhibited no apparent manifestation of season on testicular activity, spermatogenesis and sperm quality (motility and percentage normal morphology) were similar in the reproductively active and inactive periods. This maintenance of reproductive activity outside of the breeding season is uncommon amongst seasonal breeding mammals. The solitary, seasonal breeding Cape dune mole-rat (*Bathyergus suillus*) and Cape mole-rat (*Georchus capensis*) both exhibit distinctive cyclicity in male reproductive characteristics (Van der Horst, 1972; Bennett and Jarvis, 1988). In both species a cessation of spermatogenesis and testicular regression occur during the non-active period. With the onset of the breeding season, testicular

Fig. 2. Mean (± SEM) seminiferous tubule diameter (□) and seminiferous tubule epithelial diameter (■) for *Cryptomys hottentotus hottentotus* males caught during the breeding (BP) and non-breeding (NBP) periods. (a) All males combined, x: MANOVA, $F(1,39) = 23.16$, $P < 0.00001$; y: MANOVA, $F(1,38) = 33.28$, $P < 0.00001$; (b) reproductive males and (c) non-reproductive males, x: ANOVA, $F(1,25) = 30.13$, $P < 0.00001$; y: ANOVA, $F(1,24) = 28.10$, $P < 0.00001$. Values are corrected for body mass by the extraction of residuals.

Table 1. Comparative sperm motility and sperm morphology characteristics for common mole-rat males (i) of differing reproductive status, and (ii) caught during the breeding and non-breeding periods

Variable	Breeding season			Reproduction status				
	BP	NBP	F-ratio	P	RM	NRM	F-ratio	P
Sperm motility								
VCL ($\mu\text{m s}^{-1}$)	148.25 $\pm$ 4.46 (8)	149.60 $\pm$ 4.03 (8)	0.05	0.8	148.36 $\pm$ 4.39 (8)	149.54 $\pm$ 4.10 (8)	0.04	0.9
VSL ($\mu\text{m s}^{-1}$)	120.29 $\pm$ 6.12 (8)	119.41 $\pm$ 4.75 (8)	0.01	0.9	120.84 $\pm$ 5.89 (8)	118.86 $\pm$ 5.00 (8)	0.06	0.8
VAP ($\mu\text{m s}^{-1}$)	131.79 $\pm$ 5.69 (8)	130.22 $\pm$ 4.71 (8)	0.04	0.8	131.64 $\pm$ 5.95 (8)	130.36 $\pm$ 4.39 (8)	0.03	0.9
Linearity (%)	76.48 $\pm$ 2.37 (8)	75.05 $\pm$ 1.51 (8)	0.24	0.6	76.37 $\pm$ 2.07 (8)	75.16 $\pm$ 1.92 (8)	0.18	0.7
ALH (μm)	4.69 $\pm$ 0.13 (8)	4.32 $\pm$ 0.12 (8)	4.55	0.053	4.40 $\pm$ 0.17 (8)	4.62 $\pm$ 0.09 (8)	1.65	0.2
Wobble	0.86 $\pm$ 0.02 (8)	0.84 $\pm$ 0.01 (8)	1.01	0.3	0.85 $\pm$ 0.02 (8)	0.85 $\pm$ 0.01 (8)	0.15	0.7
STR	0.87 $\pm$ 0.02 (8)	0.88 $\pm$ 0.01 (8)	0.21	0.7	0.87 $\pm$ 0.01 (8)	0.87 $\pm$ 0.02 (8)	0.06	0.8
Dance ($\mu\text{m}^2 \text{ s}^{-1}$)	430.32 $\pm$ 38.62 (8)	479.37 $\pm$ 39.17 (8)	0.98	0.4	403.79 $\pm$ 39.59 (8)	505.90 $\pm$ 29.76 (8)	4.25	0.06
Radian (μm)	1.42 $\pm$ 0.07 (8)	1.43 $\pm$ 0.06 (8)	0.03	0.9	1.42 $\pm$ 0.05 (8)	1.43 $\pm$ 0.07 (8)	0.002	1.0
Curvature	0.42 $\pm$ 0.03 (8)	0.39 $\pm$ 0.02 (8)	1.33	0.3	0.41 $\pm$ 0.01 (8)	0.40 $\pm$ 0.03 (8)	0.01	0.9
% motile	62.11 $\pm$ 5.50 (8)	61.73 $\pm$ 3.15 (8)	0.003	1.0	62.57 $\pm$ 4.10 (8)	61.27 $\pm$ 4.82 (8)	0.04	0.9
% prog. motile	57.24 $\pm$ 5.53 (8)	55.14 $\pm$ 3.42 (8)	0.10	0.8	56.82 $\pm$ 4.08 (8)	55.56 $\pm$ 5.08 (8)	0.04	0.9
Sperm morphology								
Normal morphology (%)	25.00 $\pm$ 2.41 (6)	28.50 $\pm$ 1.23 (8)	2.13	0.2	28.71 $\pm$ 1.71 (7)	25.29 $\pm$ 1.80 (7)	2.08	0.2

All results are expressed as means $\pm$ SEM (*n*).

RM = reproductive males; NRM = non-reproductive males; BP = breeding period; NBP = non-breeding period; VCL = curvilinear velocity; VSL = straightline velocity; VAP = average path velocity; ALH = amplitude of lateral head displacement; STR = straightness; prog. = progressively.

Fig. 3. The distribution of sperm defects in (a) *Cryptomys hottentotus hottentotus* males caught during the breeding (BP) and non-breeding (NBP) periods, x: MANOVA, $F(1,13) = 20.76$, $P = 0.0008$; y: MANOVA, $F(1,13) = 6.27$, $P = 0.03$, and (b) reproductive (RM) and non-reproductive (NRM) *C. h. hottentotus* males. ■, head defect; ▨, tail/head-less; □, mitochondrial sheath defect; ▤, cytoplasmic droplet; ▩, bent midpiece; ■, flagellar defect.

recrudescence and a resumption of spermatogenic activity occur.

The atypical pattern of male reproductive activity prevalent in common mole-rats, may reflect an interaction between social status and mating strategy. Long-term demographic studies appear to indicate that the common mole-rat is an obligate outbreeder (A. C. Spinks, N. C. Bennett and C. M. Rosenthal, unpublished), and consequently must disperse to find a mate. Mole-rats are forced to restrict burrowing, and hence dispersal, to periods after rainfall, when the reduced soil compaction and increased soil cohesion are energetically optimal for digging (Jarvis and Bennett 1991). In the seasonal habitat occupied by the common mole-rat, with precipitation predictably restricted to winter, dispersal opportunities are maximal outside the breeding period. This would necessitate the maintenance of reproductive activity throughout the year, particularly during the non-breeding period. Such reproductive activation in dispersing males may aid intersexual recognition, and facilitate pair-bond formation. The solitary mole-rats, like most subterranean rodents, are typically extremely aggressive, except when they are ready to breed (Bennett and Jarvis, 1988; Jarvis

and Bennett, 1990, 1991). Sexual recrudescence reduces intersexual aggression, enabling pairing and copulation (Bennett and Jarvis, 1988; Jarvis and Bennett, 1990, 1991). Consequently, the continuous reproductive activity in the common mole-rat may afford dispersing animals a greater chance of successful assimilation into foreign colonies, facilitating outbreeding.

In the present study, an unusual pattern of increased testis mass, testis volume, seminiferous tubule diameter and seminiferous tubule epithelial diameter was prevalent in males during the non-reproductive period. In seasonally breeding mammals, in which cyclicity in male reproductive characteristics has been demonstrated, testicular regression and an associated reduction in testicular morphometrics typically occurs during the non-reproductive period (Clarke, 1981; Keverne, 1987; Kaplan and Mead, 1994; Page *et al.*, 1994). In a review of seasonal aspects of testis function, Lincoln (1981) indicated that a reduction in testes size to less than 80% of the seasonal maximum is necessary before there is a reduction in spermatogenic activity. Consequently, these changes in *C. h. hottentotus* males may not be of adaptive significance. This contention is supported by the

Fig. 4. Mean ($\pm$ SEM) testicular mass ($\square$) and volume ($\blacksquare$) for reproductive (RM) and non-reproductive (NRM) *Cryptomys hottentotus hottentotus* males. Values are corrected for body mass by the extraction of residuals.

Fig. 5. Mean ($\pm$ SEM) seminiferous tubule diameter ($\square$) and seminiferous tubule epithelial diameter ($\blacksquare$) for reproductive (RM) and non-reproductive (NRM) *Cryptomys hottentotus hottentotus* males. Values are corrected for body mass by the extraction of residuals.

fact that seasonal differences in testicular anatomical and histological features did not reflect changes in spermatogenesis, sperm motility or the percentage of spermatozoa with normal morphology.

Results from the present study indicate that common mole-rat males display a similar status-related reproductive capacity to that of the Damaraland mole-rat (Bennett *et al.*, 1993; Faulkes *et al.*, 1994). Reproductive quiescence does not translate into repressed testicular activity. This absence of a physiologically well-defined suppression of reproduction in male common and Damaraland mole-rats is more typical of social suppression in male mammals (for example, Creel *et al.*, 1992; Faulkes *et al.*, 1994). It is possible that physiological suppression of one sex (females) may functionally suppress the other sex (males) by limiting reproductive opportunity (Creel *et al.*, 1992), although this remains to be investigated.

In contrast to the cryptomids, naked mole-rats exhibit physiological manifestations of suppression in subordinates of both sexes (Faulkes and Abbott, 1991; Faulkes *et al.*, 1990, 1991). In non-reproductive males, social cues are physiologi-

cally translated into diminished spermatogenic activity and sperm quality (Faulkes *et al.*, 1991, 1994; Faulkes and Abbott, 1991). Faulkes *et al.* (1991, 1994) observed that such an acute block to reproduction is rare, and possibly without precedent, in socially suppressed male mammals.

These interspecific differences in the extent of reproductive suppression within the social Bathyergidae probably reflect the effects of a number of evolutionary factors. The phylogenetic hypothesis proposed by Allard and Honeycutt (1992) and Faulkes (C. G. Faulkes, personal communication) suggests that the naked mole-rat and the social cryptomids represent divergent groups with relatively independent evolutionary trajectories. This hypothesis has led Jarvis and Bennett (1993) and Faulkes *et al.* (1994) to postulate that social behaviour and reproductive suppression have evolved separately but in parallel in the Bathyergidae, and have given rise to different physiological mechanisms of suppression in the two taxa. However, variation in mating strategies and dispersal may provide a more parsimonious explanation for this infrafamilial divergence in the mechanisms of reproductive control (Faulkes *et al.*, 1994). Whereas naked mole-rats appear to be facultative inbreeders (Honeycutt *et al.*, 1991; O'Riain *et al.*, 1996), laboratory and field studies suggest incest avoidance and concomitant outbreeding in the Damaraland and common mole-rats (Bennett, 1994; Jarvis *et al.*, 1994; A. C. Spinks, N. C. Bennett and C. M. Rosenthal, unpublished). In both cryptomid species, all colony members are the offspring of the reproductive pair and do not reproduce until conditions (both social and ecological) favour dispersal and outbreeding (Jarvis *et al.*, 1994; A. C. Spinks and C. M. Rosenthal, unpublished). Furthermore, recent evidence (Bennett, 1994; Burda, 1995; Rickard and Bennett, in press) suggests that reproductive quiescence in non-reproductive cryptomids may reflect an interaction between reproductive suppression by parental manipulation and incest avoidance. Incest taboos among subordinate colony members in the social cryptomids may negate the need for a rigorous suppression of reproduction. By contrast, in inbred naked mole-rats, the absence of incest avoidance necessitates the evolution of stringent reproductive control and hence the heightened degree of suppression in this species.

In conclusion, dispersal and subsequent outbreeding opportunities appear to be important determinants of reproductive function in common mole-rat males, moderating both season and status-related effects on reproductive activity.

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