The reproductive pattern of the *Gerbilliscus cf. leucogaster* (Rodentia: Muridae) from Namibia

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ABSTRACT

Very little is known about the reproductive biology of the *Gerbilliscus cf. leucogaster* (Peters, 1852), despite its wide distribution throughout the southern African sub-region. This study analyses body mass, reproductive–tract morphometrics and gonadal histology were studied over 12 months in wild caught *G. cf. leucogaster* from the central part of Namibia in an attempt to gain insights into the pattern of reproduction in this species. The number of Graafian follicles and corpora lutea in 93 females increased at the end dry period (September) and throughout the wet months of the year (October-May) relative to that of the dry season (Jun-Aug). Pregnant and lactating females were recorded during the wet months of the year, with a peak observed during February. Testicular mass relative to body mass, testicular volume and seminiferous tubule diameter in 64% of males increased significantly during the rainfall period (October-June). In addition, 8% of males exhibited little spermatogenesis and 28% showed no spermatogenesis or presence of sperm in the epididymis during the dry period (June-August). These findings suggest the *G. cf. leucogaster* breeds predominantly during the rainfall period in Namibia when the food resources are more abundant.

Key words: Reproduction, Namibian gerbil, seasonality, gonads, Namibia, *Gerbilliscus cf. leucogaster*

INTRODUCTION

Reproduction in many species of small mammal is timed to ensure that birth occurs at a period which maximises growth and survival of the offspring (Fitzgerald and McManus 2000). In temperate and polar latitudes, mammals show a strictly seasonal component to reproduction and avoid unfavourable conditions when the offspring are least likely to survive (Nelson et al. 1992; Nilsson 2001). However, there are situations in some species which possess short life spans, where reproduction may arise at any time of the year under favourable environmental conditions (Fitzgerald and McManus 2000; Prendergast et al. 2001).

Seasonal breeders successfully mate only during particular times of the year. This period allows for the birth of offspring at a time optimal for the survival of the young in terms of factors such as ambient temperature, food and water availability, and even changes in the predation behaviour of other species (Prendergast 2005). Female seasonal breeders may exhibit one or a series of oestrous cycles during the breeding season, and remain anoestrus during the unfavourable breeding period of the year. Male seasonal breeders may exhibit changes in testosterone levels, testes mass and spermatogenesis with a particular time of the year (Muteka et al. 2006*a*, 2006*b*).

The timing of reproduction in many mammalian species may be influenced by a number of environmental cues. The measurement of day length or photoperiod is a very prominent environmental trigger which controls the timing of reproduction in a large number of mammals, but particularly at higher latitudes, it appears to be less important in mammals inhabiting lower latitudes where the seasonal transition in day length is less defined (Reiter and Follett 1980; Tavolaro et al. 2015). The effect of changes in the length of the number of hours of daylight on reproductive processes has been studied extensively in the Siberian, *Phodopus* (Pallas 1773) and Syrian, *Mesocricetus* hamsters (Nehring 1894); (Prendergast et al. 2001) and many other small mammals. Studies on *Micaelamys namaquensis* (A. Smith 1803) and *Aethomys ineptus* (Thomas and Wroughton 1908) in Gauteng and the Mpumalanga Provinces of South Africa, repectively, were found to be responsive to photoperiodism (Muteka et al. 2006*c*). Photoperiod likely affects seasonal breeding through changes in melatonin secretion from the pineal gland which in turn alters gonadotropin-releasing hormone (GnRH) release from the hypothalamus and the secretion of luteinizing hormone (LH) and follicle-stimulating hormone (FSH) from the pituitary (Blank and Desjardins 1985; Tavolaro et al. 2015; Vasantha 2016).

The synchronization of reproduction in small mammals usually coincides with favourable environmental conditions (ultimate factors) that promote rapid growth and maximal survival of offspring (Ims 1990). Seasonally breeding mammals may use the onset of rainfall, photoperiod, ambient temperature and social cues (proximate factors) to initiate reproductive events such as steroidogenesis, spermatogenesis, mating and conceiving to occur during the favourable time of the year that maximizes survival of offspring (Jameson 1988). Since the reproductive process requires significant amounts of energy, birth or breeding in many mammals, is found to peak during the time of the year when food and water is in sufficient quantities; and this is usually during the summer or rainy season in the southern hemisphere (Muteka et al. 2006*a*; Vasantha 2016). Food availability, including quantity and quality, is a major factor influencing the annual pattern of reproduction in mammals (Bronson 1985; Bronson and Heideman 1994; Htwe and Singleton 2014). Thus, reproduction may be deferred if food quantity and quality is insufficient during that period of the year.

Rainfall is an important zeitgeber in arid environments and triggers growth of numerous plant species; herbs, flowers, plant parts and insects that form the basic diet for many small mammals. Thus, in many mammals, breeding activities are often timed to coincide with periods of rainfall (Sisk and Bronson 1986). Interestingly, there is also a tendency for some animals to reproduce during anytime of the year whenever an opportunity arises (Prendergast et al. 2001). For example, the pouched mouse, *Saccostomus campestris* (Peters 1846) and the Tete veld rat, *Aethomys ineptus* are both considered opportunistic breeders, and are hence capable of breeding at any time of the year when environmental conditions permit (Tinney et al. 2001; Muteka et al. 2006*a*). Quality and quantity of basic nutrients plays a significant role in these situations of the reproductive process. An animal in a nutritionally-rich environment will be able to successfully reproduce since substantial amounts of energy is required for various physiological processes (Thompson and Nicoll 1986; Tavolaro et al. 2015; Vasantha 2016) and the energy is usually geared towards other processes such as metabolism and thermoregulatory costs. Although food availability plays a significant role in the process of reproduction, the ambient temperature, while not necessarily considered equally important, has a significant impact on the process of reproduction.

Mammalian reproduction may also be influenced by ambient temperature. Homeothermic animals need to maintain body temperature in order to survive. A decrease in body temperature increases thermoregulatory requirements of an animal and may subsequently reduce the amount of energy that is available for reproduction (Bronson and Pryor 1983; Bronson 1985; Sicard et al. 1993). High ambient temperature can have an adverse effect on testicular development and spermatogenesis in mammals. Research conducted on the desert pocket mouse, *Perognathus formosus* (Merriam 1889) has shown that the lining of seminiferous tubules becomes damaged at 33 °C but the same reproductive events are enhanced between 13 and 23 °C. Spermatozoa have been known to be sensitive to high temperatures. Seminiferous tubules are readily destroyed and spermatozoa production reduced if the testis is exposed to temperatures above body temperature over a long period of time (Bearden and Fuquay 1980; Setchell 2006).

The primary objective of this study was therefore, an attempt to gain an insight in the pattern of reproduction in *G. cf. leucogaster* within agriculturally-impacted areas, and gain an understanding of ecological and reproductive processes in small mammal communities within anthropogenically transformed landscapes in central part of Namibia. We hypothesize that the gerbil should be a seasonal breeder with reproduction confined predominantly to the summer months of the central region of Namibia. We predicted that with the onset of summer, males should show testicular recrudescence and females would show enhanced follicular development, preceding pregnancy. Whereas with a decline in ambient temperature and photoperiod, male and female gonadal regression would arise.

MATERIALS AND METHODS

Study Area

The study was conducted at Otjinakwi farm, in the Otjozondjupa region (-20^{o} 45'3.81" +17^{o}, 1' 21.80") 1440.24 m which is situated in the central part of Namibia. The study area is characterized by a semi-arid climate. Days are mostly warm with very hot days during the summer months, while nights are generally cool. The average annual temperature is 19.47 °C, considered to be relatively highly for a site located at such high altitude on the edge of the tropics (Namibia Meteorological Service, 2014; Goddard Institute, 1957–1987).

The winter months (June-September), usually experience little or no rain and minimum temperatures range between −5 °C and 18 °C. Nights are usually cool and very cold before dawn. The summer months (October-May) are usually characterised by warm to hot temperatures, ranging from a maximum of 20-31°C with mean annual rainfall around 360 mm. The natural vegetation of the area is scrub and steppe (savannah woodland) (Namibia Meteorological Service, 2014, Goddard Institute 1957-1987).

Sampling and handling of animals

A total of 158 adult specimens of *Gerbilliscus cf. leucogaster* were sampled on a monthly basis between September 2007 and September 2008. A mixture of peanut butter, syrup, oatmeal and fish was used as bait. A total of 150 Sherman live traps were placed in a configuration of 5 x 30 placed at 10 m apart. The traps were baited during the afternoon and checked at 07h00 in the morning over a period of 5 nights per trapping session. Once in the laboratory, the animals were kept in polyurethane cages with wood shavings provided as bedding for a minimum period of three days. Oats and water were provided *ad libitum* during the time prior to processing. The animals were kept in the laboratory for a maximum period of three days so as to avoid acclimatization.

Determination of reproductive status and processing of specimens

Females were assessed for reproductive status by determining features such as prominent teats, perforated vagina, and once euthanized, for the presence or absence of embryos to assess the reproductive status of females. Anoestrous females were imperforate and showed thin uterine horns lacking placental scars. The gonads were dissected out and ovarian and testicular weights recorded. In addition to the follicular count, the presence of placental scars and foetuses were recorded during the processing of samples in the laboratory. Each animal was sacrificed using halothane and the body mass was obtained using a digital balance. The gonads were weighed to the nearest 0.0001g using a high precision scale (Ohaus Corp. Pine Brook, N.Y. USA). Digital callipers (Sylvac Opto RS 232, Ultra Praezision Messzeuge GmbH, Germany) were used to determine the length and the width of the testes to the nearest 0.01mm. Testicular volume was calculated using the following formula for the volume of an ellipsoid as described by Woodall and Skinner (1989):

$$V = 4/3\pi ab^2$$

a = 1/2 maximum length and b = 1/2 maximum breadth.

The ovaries and the testes were then fixed in Bouin's fluid for a minimum of 24 hours prior to being rinsed and stored in 70% ethanol.

Histology of gonads

The histology of the paired ovaries of 93 adult females and the testes of 65 adult males were prepared following Ross et al. (1995) and Leeson et al. (1985). Ovaries were dehydrated and embedded in paraffin wax, serially sectioned at 7.0 μm and mounted onto microscopic slides. The slides were then stained in Ehrlich's haematoxylin and counter-stained in eosin and examined using a light microscope at the following magnifications: 100x, 200x and 400x. Ovarian follicles were counted and categorised according to Ross et al. (1995). Diameters of seminiferous tubules were determined. All male specimens were examined for signs of spermatogenesis, spermatozoa and stages of testicular development during the 12-months of the year.

Analysis of data

General Linear Modelling (Cohen et al. 2003; McCullagh and Nelda 1989) was used to test for differences in seminiferous diameters, testicular mass, testicular volumes and differences in follicular development between months. Observations were tested for differences using the Tukey's Honestly Significant Difference (HSD) test set at $P > 0.05$. The data were analysed using Microsoft Excel version 14 (McDonald 2014a) and Statistical Application Software (SAS) version 9.1 (McDonald 2014b). Differences with a probability value of 0.05 or less were considered significant and all results are expressed as mean ± 1 standard error (S.E.).

RESULTS

The male Namibian gerbils were significantly heavier than females (Males = 70.48 ± 18.47; Females = 56.15 ± 9.79.42; $F_{(1, 157)} = 6.31$; $P = 0.001$) (Fig.1). The mean mass of the captured animals was greater from October to June ($F_{(1, 73)} = 3.53$; $P = 0.007$). The seasonal (wet/dry) changes in mass were not statistically different within and between the sexes $F_{(2, 73)} = 3.41$, $P = 0.29$.

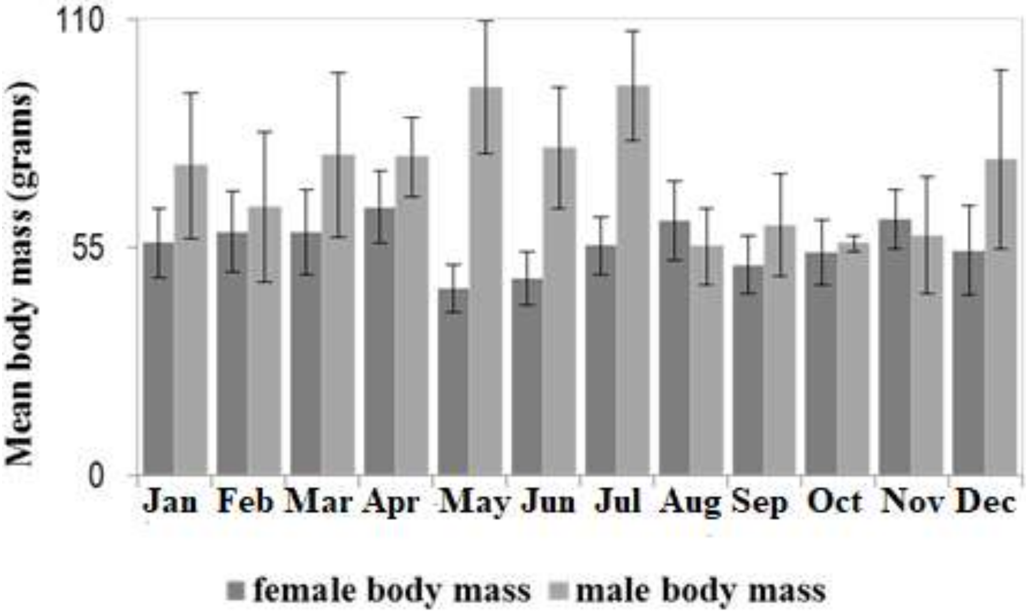

Fig. 1: Body mass for female (*n* = 93) and male (*n* = 65), *Gerbilliscus cf. leucogaster* from central Namibia.

Primordial follicles were found throughout the year. Except during the January month, no significant difference was found in the number of primordial follicles in the ovaries between the months ($F_{(1, 573)} = 4.47$; $P = 0.07$; (Table. 1). Similarly, primary follicles were found throughout the entire sampling period. No significant differences were found between months ($F_{(1, 353)} = 6.21$; $P = 0.08$) and no patterns were found in the distribution of primary follicles during the entire sampling period (Table 1). Secondary follicles were found throughout the year and again no significant differences were found between the months ($F_{(1, 176)} = 5.81$; $P = 0.09$). No patterns were observed in the distribution of secondary follicles during the 12-month period (Table 1). The number of atretic follicles was significantly higher between September and May ($F_{(1, 148)}$ = 5.33; P = 0.0038) (Table 1).

Table 1. The number (mean ± 1 SE) of primordial, primary, secondary and atretic follicles in the Namibian gerbil, *Gerbilliscus cf. leucogaster* from central Namibia.

	N	**Primordial**	**Primary**	**Secondary**	**Atretic**
Jan	8	109.9(±9.6)	107.6(±10.9)	21.0 (±2.1)o	35.1(±9.6)
Feb	8	21.8(±13)	19.3(±2.6)	11.5(±6.4)	9.3(±2.19)
Mar	9	54.6(±16.6)	26.8 (±12.2)	15.3(±3.3)	13.9(±7.2)
April	12	14.4(±5.6)	11.0 (±3.6)	13.4(±2.5)	8.5(±2.4)
May	9	28.3 (±6.1)	14.8(±10.9)	10.4(±2.1)	6.7(±2.1)
Jun	6	29.7(±21.8)	19.0(±8.8)	14.2(±4.6)	6.1(±3.1)
Jul	7	23.3(±13.5)	19.4(±4.72)	11.7(±1.9)	6.7(±2.3)
Aug	7	6.1(±3.7)	19.6(±12.0)	15.9 (±6.2)	11.0(±5.6)
Sept	6	66.3(±8.1)	44.8 (±12.6)	21.3(±7.4)	19.0(±7.1)
Oct	7	77.8 (±14.1)	31.2 (±23.0)	12.8(±7.1)	15.4(±3.6)
Nov	7	14.5(±5.6)	18.0(±12.1)	13.25(±3.9)	22.0(±5.9)
Dec	7	16.4(±4.5)	22.3(±11.5)	15.7(±3.1)	17.1(±4.9)

Although Graafian follicles were found year-round, the numbers were significantly higher during end of winter and throughout the summer months ($F_{(1, 133)}$ = 2.6; P =0.004 and lower during the dry, winter months (Fig. 2*a*). The mean number of pregnant and cyclic corpora lutea was significantly higher between October and May (Pregnant CL= 3.3 ± 1.17; $F_{(1, 39)}$ = 2.5; P = 0.002; and Cyclic CL = 3.7 ± 1.39; $F_{(1, 43)}$ = 3.5; P = 0.004; (Fig. 2*b*) respectively and

31.3% of females with Corpus haemorrhagicum were observed during October and between January to March (Fig. 2*c*). Pregnant females were observed between October and May (with the exception of two months; November and January), with a mean number of three (3 ± 1.4) embryos per female (Fig. 2*d*). This was supported by the presences of corpora lutea of pregnancy; no pregnant female was observed between June and September (Table 2).

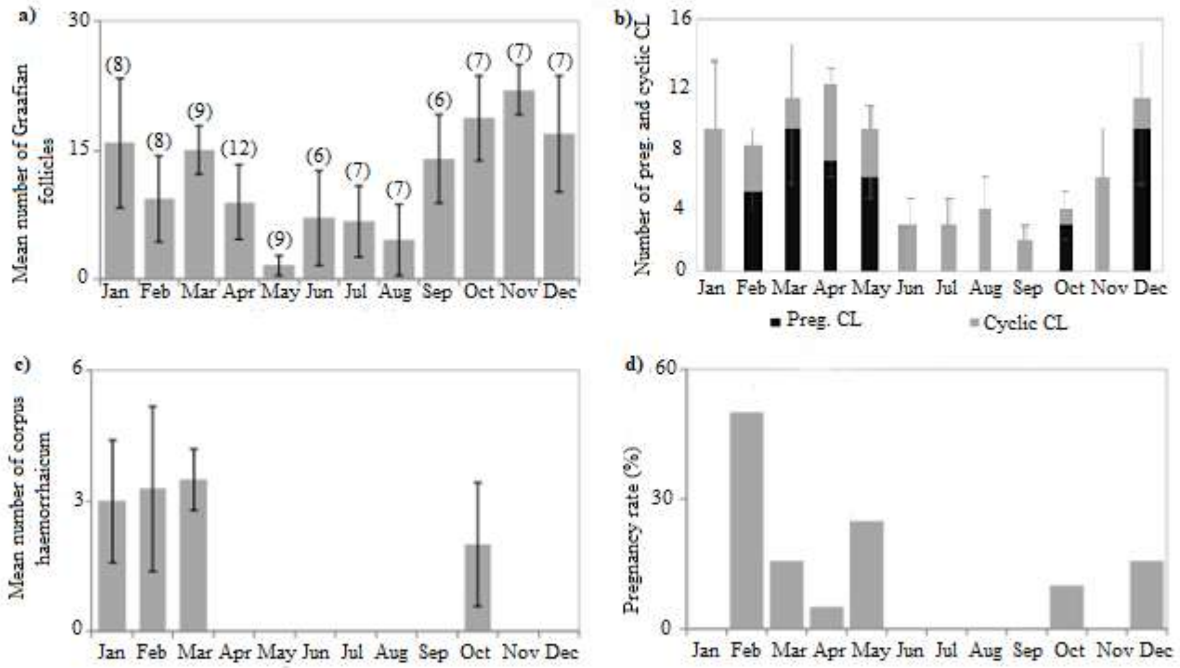

Fig. 2: Female *Gerbilliscus* cf. *leucogaster* from central Namibia (n = 93) showing (*a*) number of Graafian follicles, with monthly sample sizes in parentheses; (*b*) pregnant and cyclic numbers of corpora lutea (CL); (*c*) number of corpus haemorrhagicum; and (*d*) frequency of pregnancies. Values in panels *a*–*c* are mean ± 1 SE..

Table 2. Number of females, females with embryos, number of embryos, and percentage of lactating females of the *Gerbilliscus* cf. *leucogaster* from central Namibia..

	Jan	Feb	Mar	Apr	Mar	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Total females sampled	8	8	9	12	9	6	7	7	6	7	7	7
Females with embryos	0	4	4	2	3	0	0	0	0	3	0	3
Mean number of embryos	0.0	3.3	3.0	3.5	3.0	0.0	0.0	0.0	0.0	2.7	0.0	3.0
% lactating females	0.0	50.0	44.4	16.7	33.3	0.0	0.0	0.0	0.0	42.9	0.0	42.9

Specific testicular weight and seminiferous tubule diameters were significantly higher from September to June ($F_{(1,10)}$ = 2.13; P = 0.02, Fig. 3*a*; and ($F_{(1,10)}$ = 3.61; *P* = 0.003, Fig. 3*c*, respectively. Testicular volume was significantly higher from September to May ($F_{(1,10)}$ = 3.31; *P* = 0.01 (Fig.3*b*). Between September and May 64% of males had spermatozoa in the seminiferous tubules as well as in the epididymis, and very little spermatogenic activity in the seminiferous tubules were observed in 8% of the males sampled between June and August (Fig. 3*d*).

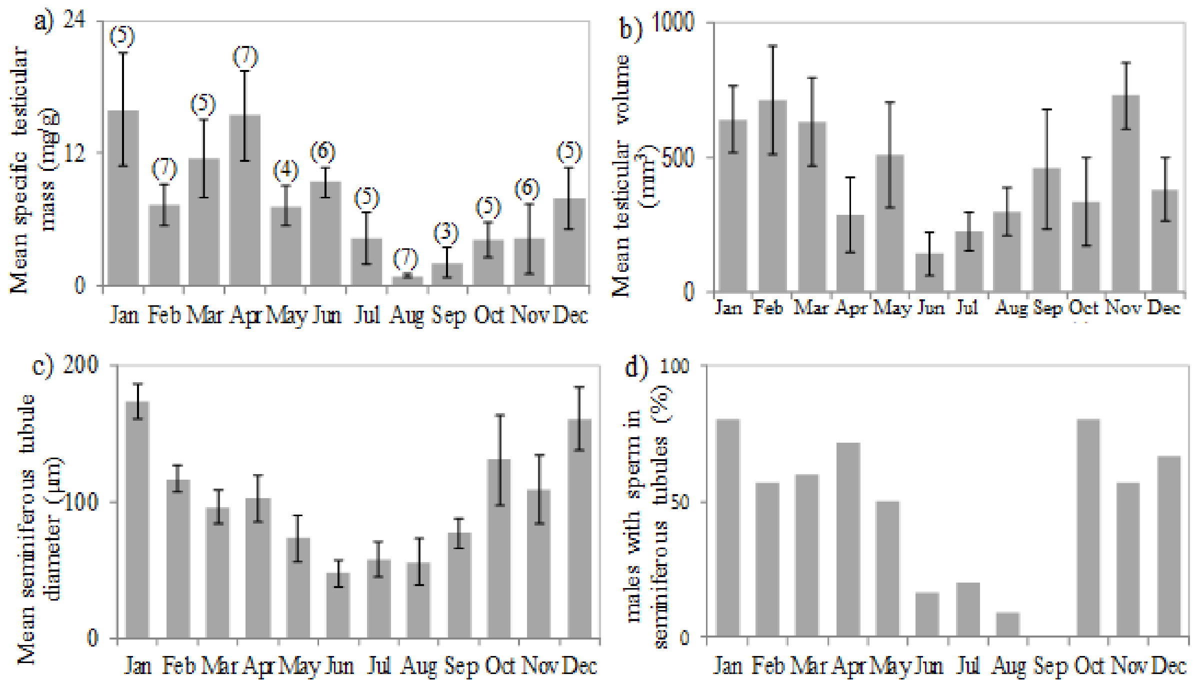

Fig. 3: Male *Gerbilliscus* cf. *leucogaster* from the Otjozondjupa Region of Namibia (*n* = 65) showing (*a*) specific testicular mass (mg/g), with monthly sample sizes in parentheses; (*b*) testicular volume (mm^3); (*c*) seminiferous tubule diameter (µm) and (*d*) percentage of males with sperm in seminiferous tubules (%). Values in panels *a–c* are mean ± 1 SE.

DISCUSSION

Reproduction is an energetically demanding process requiring adequate resources for both the recrudescence of gonads as well as the nourishment of developing foetuses (Thompson and

Nicoll 1986; Flowerdew 1987; Khokhlova 2000). Food availability, both quantity and quality, is a major factor determining the annual pattern of reproduction in mammals (Bronson 1985; Bronson and Heideman 1994, Vasantha 2016). In environments in which food availability varies with season, reproduction is highly seasonal and generally coincides with the abundance of high quality food (Merson and Kirkpatrick 1983; Cameron and Eshelman 1996; Dooley and Prendergast 2012). The habitat in which the *Gerbilliscus cf. leucogaster* occurs in central Namibia shows significant climatic seasonal variation (Namibian Meteorological Services 2014) influencing the reproductive variation within small mammals in the wild.

The onset of reproduction starts with anatomical changes within the reproductive system in both male and female (Tavolaro et al. 2015; Vasantha 2016). In the *Gerbilliscus cf. leucogaster*, relative testicular mass gradually increased from October through to April. This depicts the breeding period in *Gerbilliscus cf. leucogaster* in the Otjozondjupa and Khomas regions of central Namibia. Although testicular mass regressed during June through to August, males appear to be capable of reproductive activity since the seminiferous tubules reveal minimal spermatozoa production during the winter.

Relative testicular mass and total testicular volume, were significantly higher from September through to June, but was significantly lower during winter (July-August). These changes were reflected in changes in the diameter of the seminiferous tubules and the ovarian activity. The low testicular mass and volume suggests that reproduction in the *Gerbilliscus cf. leucogaster* may be retarded during winter months (June-August) perhaps due to the insufficient food resource base (Blank and Desjadins 1985; Vasantha 2016) and low ambient temperature that is usual in the Namibian highveld during this time of the year.

Food deprivation has been found to retard reproduction in a number of small mammals for example, the water vole, *Arvicola terrestris* (Linnaeus 1758), (Hamilton and Bronson 1985) but, food supplementation enhanced the reproductive activity in the rock mouse, *Peromyscus* *difficilis* (J.A. Allen, 1891), (Galindo-Leal and Krebs 1998). Thus, reproduction during winter is minimized due to the lower availability of food and reduced environmental temperatures. Neal (1991) showed that for two populations of bushveld gerbils (*Gerbilliscus leucogaster*) from different habitats, one population started breeding three months earlier than the other, and that the difference in duration of breeding in the two areas was related to food availability. Contrary, in Burkina Faso, characterised by abundant food available all year round, reproduction in the form of activated gonads and the production of young is found to be continuous throughout the year in Hubert's Multimammate mouse, *Mastomys huberti* (Wroughton 1909), (Khokhlova et al. 2000).

In the *Gerbilliscus cf. leucogaster* the breeding season occurs from October to April. This period coincides with the rainfall period in the Khomas region of Namibia during which the environment would have sufficient food in the form of grass seeds to sustain reproduction in the form of recrudescence and activation of the gonads and the production of young. Bronson (1985), Bronson (1989) and Muteka et al. (2006*a*, 2006*b*) showed that the increased diameters of the seminiferous tubules in male rodents coincides with the onset of follicular growth and the rise of both oestradiol and progesterone concentrations in conspecific females. Similarly, seminiferous tubule diameters are significantly larger during September through to May and decrease gradually during winter months (June - August). The presence of spermatozoa in only a few male epididymides and some spermatogenic activity during winter months (June to August) further indicates the opportunity for an opportunistic breeding strategy, which may be triggered by availability of nutrients and also potentially other environmental cues such as temperature (Meredith et al. 1986; Sisk and Bronson 1986; Bronson 1989; Muteka et al. 2006*a*, 2006*b*). The highveld gerbil may thus could potentially use several environmental cues (e.g., photoperiod, food and ambient temperature) to initiate reproductive events during periods when environmental conditions become favourable (Bernard and Hall 1995, Vasantha 2016).

Graafian follicles were present during all months of the year in our study. According to Clark (1981), the regression of Graafian follicles should occur in small mammals which exhibit a clear-cut seasonal reproductive strategy. The presence of corpora lutea, but absence of embryos during winter months of sampling indicates that this species may be capable of breeding throughout the year, but optimizes breeding during favourable rainy months. However, corpora hemorrhagicum were only found during October and from January to April, and this was coupled with the observation of pregnant females from October to April, suggesting that the Namibian gerbil may be an opportunistic breeder. This opportunistic breeding strategy is typical for short-lived mammals such as rodents, where environmental conditions are often unpredictable as they seldom live for a year and maximum reproductive success can only be achieved by breeding at every appropriate opportunity (Bronson and Perrigo 1987; Khokhlova et al. 2000). These variations in the reproductive performance determined by local or microclimate conditions are observed between species and also between populations and within populations (Neal 1991; Prendergast et al. 2001). In South Africa, the four-striped field mouse *Rhabdomys pumilio* (Thomas 1916) breeds opportunistically. In areas experiencing mild winters in its geographic distribution, the field mouse breeds throughout the year, whereas in harsh environments, females cease breeding when conditions are unfavourable, although males remain reproductively active year-round (Gray 2000). Jackson and Bernard (2001) reported a similar reproductive strategy in the pouched mouse, *Saccostomus campestris,* in which reproduction during winter was inhibited as a result of a reduction in both food quantity or quality and due to a decrease in ambient temperature. Furthermore, the Tete veld rat, *Aethomys ineptus,* employs a relatively similar reproductive strategy whereby a major part of its breeding is confined to the summer, rainy months in the Gauteng Province of South Africa; histological analyses of the gonads revealed that the testes and ovaries were active during the other months of the year (Muteka et al. 2006*a*). Thus, the

Namibian gerbil, *Gerbilliscus cf. leucogaster* may be an opportunistic breeder which uses food availability and temperature changes to control reproductive events (Bronson 1989; Prendergast et al. 2001).

CONCLUSION

Both male and female histology of gonads exhibit seasonal patterns of reproduction in *G. cf. leucogaster*. The presence of testicular and ovarian activities in a few individuals of this species during the dry period in central Namibia, is indicative of a possible opportunistic breeding strategy. The opportunistic breeding option may be controlled by the availability of feed resource base and conducive environmental conditions. Thus, the Namibian gerbil may be an opportunistic breeder which uses food availability and temperature changes to control reproductive events (Bronson 1989; Prendergast et al. 2001).

ACKNOWLEDGEMENTS

The study was funded by the University of Namibia to SPM and by the Univeristy of Pretoria and the South African National Research Foundation to NCB and CTC. We thank the Government of Namibia through the Ministry of Environment and Tourism for granting permits to trap the gerbils for this project. The research was authorised by the Animal Ethics Committee (EC066-17), University of Pretoria.

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