

The pattern of reproduction in the Libyan jird (*Meriones libycus*; Rodentia: Muridae) from central Saudi Arabia in the absence of rainfall

D.W. Hart, A.A. Alghamdi, N.C. Bennett, O.B. Mohammed, N.M. Amor, and A.N. Alagaili

Abstract: The reproductive pattern of the Libyan jird (*Meriones libycus* Lichtenstein, 1823) from central Saudi Arabia was investigated in the absence of rainfall. In this study, body mass, morphometry of the reproductive tract, the histology of the reproductive organs, and the hormone concentrations of males and females were studied over 12 consecutive months in a wild population of the Libyan jird from central Saudi Arabia. Previous studies have found the breeding season of the Libyan jird from the Sahara desert of Algeria to occur during the wet months of spring. In the absence of rainfall, temperature and photoperiod were found to be important activators of reproductive activity. The cooler temperatures and shorter days of winter triggered the onset of ovulation in females and increased testes size and seminiferous tubule diameter in males. Only two pregnancies were found during the sampling period, which occurred during the cooler winter and early spring and coincided with a rise in plasma progesterone concentration in females. The Libyan jird was found to shift its breeding to the cooler months of winter in the absence of rainfall. This study strengthens the findings that changes in rainfall and temperature in dry deserts are critical cues for the onset of reproduction in small mammals.

Key words: Libyan jird, *Meriones libycus*, absence of rainfall, reproduction, temperature, seasonality, histology.

Résumé : Les habitudes de reproduction de la mérione de Libye (*Meriones libycus* Lichtenstein, 1823) dans le centre de l'Arabie saoudite ont été examinées en l'absence de pluie. La masse corporelle, la morphométrie de l'appareil reproducteur, l'histologie des organes reproducteurs et les concentrations d'hormones des mâles et des femelles ont été étudiées sur 12 mois consécutifs dans une population sauvage de mériones de Libye du centre de l'Arabie saoudite. Des études précédentes ont constaté que la saison de reproduction des mériones de Libye dans le désert du Sahara en Algérie était pendant les mois pluvieux du printemps. En l'absence de pluie, la température et la photopériode s'avèrent être d'importants déclencheurs de l'activité reproductrice. Les températures plus fraîches et les jours plus courts de l'hiver provoquaient le début de l'ovulation chez les femelles et l'augmentation de la taille des testicules et du diamètre des canalicules séminifères chez les mâles. Seulement deux grossesses ont été observées durant la période d'échantillonnage, durant la période plus froide de l'hiver et du début du printemps, coïncidant avec une augmentation de la concentration de progestérone plasmatique chez les femelles. Nous avons constaté que les mériones de Libye se reproduisent durant les mois plus frais de l'hiver en l'absence de pluie. L'étude corrobore les observations à l'effet que des variations de la pluviométrie et de la température dans les déserts secs constituent des signaux déclencheurs clés du début de la reproduction chez les petits mammifères. [Traduit par la Rédaction]

Mots-clés : mérione de Libye, *Meriones libycus*, absence de pluie, reproduction, température, saisonnalité, histologie.

Introduction

Deserts, such as those of Saudi Arabia, are harsh environments where daily and seasonal temperatures are extreme and rainfall is scant or non-existent. Solar radiation is intense and there is little primary productivity in the form of vegetation (Degen 1997). The climate of the Arabian Peninsula is characteristically harsh with rainfall being sporadic and unpredictable and temperatures climbing often well above 40 °C (Schmidt-Nielsen 1964). Under such conditions food resources and water are scarce, yet many small mammals are able to survive and reproduce (Petter et al. 1984; Sicard 1992; Ouali and Bensalem 1996; Bozinovic et al. 2003; Shanas and Haim 2004; Belhocine et al. 2007; Alagaili et al. 2017).

Reproduction in mammals requires a large investment from both energy and resource perspectives. Arid-adapted small mammals breed when the climatic and resource conditions are favourable for the raising of offspring and require access to adequate food and water to increase their chances of survival. When conditions become unfavourable, many small-mammal species cease all reproductive activity and channel their energy towards vital and more immediate processes to survive (Khokhlova et al. 2000; Belhocine et al. 2007). Reproduction in small mammals usually occurs at a time that maximises the growth and survival of the offspring (Fitzgerald and McManus 2000).

The majority of small mammals occurring in desert regions breed seasonally to optimise the chance of survival for their off-

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spring (El-Bakry et al. 1998; Belhocine et al. 2007; Alagaili et al. 2017). This pattern of breeding is characterised by seasonal variation in body mass, gonadal mass and volume, and plasma reproductive hormones. In the Ethiopian hedgehog (*Paraechinus aethiopicus* (Ehrenberg, 1832)) (Alagaili et al. 2017), sand rat (*Psammodromus obesus* Cretzschmar, 1828) (Khammar and Brudieux 1987), Sundevall's jird (*Meriones crassus* Sundevall, 1842) (Boufermes 1997), Shaw's jird (*Meriones shawi* (Duvernoy, 1842)) (Zaime et al. 1992), Baluchistan gerbil (*Gerbillus nanus* Blanford, 1875) (Sarli et al. 2015), and Arabian spiny mouse (*Acomys dimidiatus* (Cretzschmar, 1826)) (Sarli et al. 2016), the non-breeding season is typically characterised by a reduction in the size of the gonads and reduced plasma reproductive hormone, in particular testosterone and progesterone in males and females, respectively. Contrastingly, some small-mammal species in these desert regions breed continuously through the year, e.g., the Indian jird (*Meriones hurrianae* Jordon, 1867) has been observed to breed throughout the year in the semi-arid region of Rajasthan (India) (Kaul and Ramaswami 1969).

Other factors that play a role in controlling reproduction in arid regions are to a lesser extent photoperiod, temperature, and dietary salinity (Bronson and Heideman 1994; Wube et al. 2009; Sarli et al. 2015, 2016; Alagaili et al. 2017). In the absence of rainfall, temperature in Saudi Arabia may play an important role for the timing of reproduction, as has been seen in the Baluchistan gerbil (Sarli et al. 2015), Arabian spiny mouse (Sarli et al. 2016), and the Ethiopian hedgehog (Alagaili et al. 2017).

The Libyan jird (*Meriones libycus* Lichtenstein, 1823) occurs in the Arabian Peninsula, North Africa, and parts of western and central Asia. Its range extends from Mauritania and Morocco through to Saudi Arabia, Kazakhstan, and western China (Aulagnier et al. 2008; Alagaili et al. 2013). The typical habitat for the Libyan jird is deserts and semi-deserts, river floodplains, wadis, and areas with stable sand dunes (Aulagnier et al. 2008; Alagaili et al. 2013). The Libyan jird occurs in burrows with multiple entrances usually constructed under shrubs (Lewis et al. 1965). The burrows provide a refuge for food storage and also enable Libyan jirds to regulate their body temperature, whereas the humidity in the burrow prevents excessive water loss. Previous histological studies, in the semi-arid regions of the Sahara, have revealed that in both male and female Libyan jirds the reproductive season is confined to a brief period in spring and extending to the beginning of summer (Smaï 1998; Belhocine et al. 2007). With a gestation period of around 20 days, the offspring are produced in spring or summer, which coincides with the limited rains and thus maximum food availability for this region of the Sahara. In these areas, rainfall is limited but consistently occurs during the spring and summer seasons.

In this particular study where there was an absence of rainfall, we aimed to investigate the pattern of reproduction in the Libyan jird from the dune fields of central Saudi Arabia by collecting specimens on a monthly basis to assess the gross morphology and histology of the gonads and the circulating reproductive hormones. We posited that reproduction in the Libyan jird would be highly dependent on temperature and had some form of endogenous timing from previous years of reproduction when rainfall was present. We thus predicted that the Libyan jird would cue their reproductive season into the cooler season of winter and early spring since rainfall usually falls in those months, whereas the gonads would regress and hormone titres would reduce during the warmer months of summer and autumn. Finally, we predicted that the male and female Libyan jirds would synchronise reproductive activation during the winter and early spring period in the absence of rainfall.

As the effects of global warming begin to be observed, many regions will experience climatic conditions that will drastically change daily temperatures and also bring about a decrease in precipitation. This desertification will have dire effect on animals living in these areas, especially small mammals, as climate has a

greater effect on them due to their smaller body size and surface to volume ratio. An understanding of the behaviour and physiology of small mammals that inhabit desert regions presently could be pivotal in understanding the possible changes that will arise in small mammals which may be faced with future extremes. Due to the harsh and difficult conditions, which results in challenges in research, in deserts, there is a dearth of knowledge in both physiology and behaviour of small mammals that inhabit these regions. In this study, we hope to increase baseline knowledge that can be used to assess changes to populations as a result of global warming in the future.

Materials and methods

Animal capture

Sampling took place in central Saudi Arabia, on the outskirts of the city of Riyadh, Riyadh Province (24.7136°N, 46.6753°E). The study site was selected for being the preferred habitat type of the Libyan jird, comprising sandy plains interspersed with a number of sandy wadis. Animals were captured from November 2014 through to October 2015 with the specific aim of capturing 10 animals/month over 12 consecutive months. Using locally made wire live animal traps, 40 traps baited with bread, peanut butter, and oats were distributed randomly across the study site. To ensure the survival of the animals, trapping started 1 h before sunset and ended early morning the next day during the summer, whereas traps were set early in the morning and collected before sunset during the winter. Non-focal species were released at the study site, whereas our study species was transported to the animal facility at the Department of the Zoology Department, King Saud University, for further processing.

Collection, handling, and further processing of the Libyan jirds were authorised by the Saudi Wildlife Authority and the research protocol was approved by the Animal Ethics Committee of the University of Pretoria (ethics number ECO17-16), which follows the South African National Standards for Animal Welfare and Research. The animal experimentation was conducted in accordance with the *Guide for the Care and Use of Laboratory Animals* (1996; published by National Academy Press, 2101 Constitution Avenue Northwest, Washington, DC 20055, USA).

Weather data were obtained from the weather service Weather Underground (<https://www.wunderground.com>); the total precipitation, mean temperature per month, and mean maximum and minimum temperatures per month were gathered for the area around the King Khalid International Airport, which is the regional airport of Riyadh Province and is approximately 20 km from the capture sites. Photoperiodic data were obtained from the weather service ClimaTemps (<https://www.ClimaTemps.com>); the number of minutes of daylight per day over an entire calendar year was gathered for the area around the King Khalid International Airport.

Dissections

Captured animals were weighed to the nearest 0.01 g using a digital scale (Sartorius U4600P balance 1200 g). The individuals were then euthanised with an overdose of ether in a glass chamber. Once expired, whole blood was extracted with a 3.0 cm³ (1 mL) syringe with a 25 gauge × 5/8 inch needle by exsanguination from the heart. The blood was then placed in an Eppendorf tube with 0.1 mL of heparin and centrifuged at 3000 r/min for 15 min. A pipette was used to extract 100 μL of plasma and placed into an Eppendorf tube to be stored at -20 °C for later hormonal analysis. The reproductive organs were dissected out and placed into Bouin's fixative and were removed 24 h later, rinsed, and placed in 70% ethanol.

Histology

Excess fat and connective tissue were cut off from the gonads, which then were subsequently weighed to the nearest 0.001 g on a

scale (Adam Equipment PW 254 PW Series Analytical Balance, 250 g capacity, with 0.0001 g accuracy). The maximum length and width of the gonads were recorded using digital callipers (Mitutoyo American Corporation, Aurora, Illinois, USA). The measurements for the paired gonads were averaged and used to determine the mean gonadal volume using the equation for the volume of an ellipsoid ($V = 4/3 \cdot \pi \cdot a \cdot b^2$), where a is one-half the maximum length and b is one-half the maximum width (Woodall and Skinner 1989).

Gonads underwent a process of dehydration with a series of ethanol baths of increasing concentrations (70%, 80%, 90%, 96%, and 100%) and xylene, after which they were embedded in wax. Sections were randomly taken from the testes using a rotary microtome set to cut at 7 μm (Mitutoyo American Corporation, Aurora, Illinois, USA), whereas the entire ovary was cut with a thickness of 6 μm . All cuts were mounted with gelatine onto slides in consecutive order and then dried for 48 h in an oven at 36 °C. Once dry, the slides were stained with haematoxylin and eosin. Testes sections were examined for round seminiferous tubules with a light microscope (Diaplan, Ernst Leitz Wetzlar GmbH, Germany) and photographed at a magnification of $\times 10$ with a digital camera (Moticam 1000 1.3 M Pixel USB 2.0; Motic China Group, LTD., Xiamen, People's Republic of China) connected to the microscope. The diameter of 50 seminiferous tubules from each testis was measured using the programme Motic Images Plus 2.0 ML (Motic China Group, LTD., Xiamen, People's Republic of China). The reproductive status of the ovaries was assessed by examining and counting the number of follicles and corpora lutea in all serial sections throughout both ovaries of each female under a light microscope at magnifications of $\times 100$, $\times 200$, and $\times 400$. The follicular stages were classified according to Bloom and Fawcett (1964) as primordial follicles, primary follicles, secondary follicles, tertiary follicles, Graafian follicles, and corpora lutea. Primordial follicles were counted in every tenth section only, whereas all other follicle stages were counted throughout the entirety of each ovary as described in Medger et al. (2010).

Hormone analysis

Blood plasma progesterone levels for the Libyan jird females were determined using Coat-a-Count Progesterone kits (Diagnostic Products Corporation). The antiserum is highly specific for progesterone. Cross-reactivity of the antibody was $\leq 0.5\%$, except for 17α -hydroxyprogesterone (3.4%), 11-deoxycorticosterone (2.4%), 5β -pregnan-3,20-dione (3.2%), and 5α -pregnan-3,20-dione (9%). The plasma progesterone assay was validated by tests for parallelism. After log-logit transformation of the data (Chard 1978), the slopes of the lines were compared and found not to differ significantly from the reference preparation (ANOVA: $F_{[1,2]} \leq 0.001$, $p = 0.989$). The sensitivity of the assay was 0.36 nmol/L and the intra-assay coefficient of variation was 1.5%.

Testosterone for the Libyan jird was assayed from blood plasma samples using Coat-a-Count Testosterone kits (Diagnostic Products Corporation). Cross-reactivity of the antibody was $\leq 5\%$ with dihydrotestosterone and 19-hydroxyandrostendione and 1% with aldosterone, androstendione, cortisol, corticosterone, oestrone, methyltestosterone, and progesterone. The plasma testosterone assay was validated in the Libyan jird by undertaking tests for parallelism. After log-logit transformation of the data (Chard 1978), the slopes of the lines were compared and found not to be significantly different from the reference preparation (ANOVA: $F_{[1,2]} \leq 0.001$, $p = 0.992$). The sensitivity of the assay was 20 ng/L. Intra-assay coefficient of variation was 8.8%.

Statistical analyses

Due to the low number of animals captured in some months for analyses, we pooled data across seasons into four intervals of equal length starting with the month when captures were initiated: winter (December–February), spring (March–May), summer (June–August), and autumn (September–November).

Climate

Mean, maximum, and minimum temperatures per month and photoperiodic day length (min) per month were found not to be normally distributed even after a log transformation was performed (Shapiro–Wilk (S–W) test: $p \leq 0.0001$). A Spearman's rank correlation test was performed to discover the relationship between photoperiod per month and mean, maximum, and minimum temperatures.

Body mass

Body mass was found to be normally distributed (S–W test: $p = 0.054$). However, body mass consequently failed the test for homogeneity (Levene's test: $p = 0.015$) and further transformation failed to homogenise the data. A generalised linear model (GLZM) was conducted on body mass of Libyan jirds, with gamma log-link distribution, to assess the effects of season and sex and their interactions, as the main factors, and mean, maximum, and minimum temperatures and photoperiod per month, as covariates. Least significant difference (LSD) was used for post hoc comparisons.

Reproductive parameters

Reproductive parameters consisted of gonad (testicular and ovarian, respectively) mass, volume, corrected gonad mass, male and female plasma reproductive hormones (plasma testosterone and plasma progesterone, respectively), seminiferous tubule diameter (male reproductive parameter), and number of corpora lutea (female reproductive parameter). Gonad (testicular and ovarian, respectively) mass was corrected for body mass using the following formula: gonad mass (g) / body mass (g). Both gonad mass and corrected gonad mass were included in all the statistical analyses. Both gonad mass and corrected gonad mass were tested for normality and were observed not to be normally distributed (S–W test: $p \leq 0.001$); log transformation failed to normalize the data (S–W test: $p \leq 0.001$). Seminiferous tubule diameter satisfied the criteria for normal distribution (S–W test: $p = 0.124$); however, it failed the Levene's test for homogeneity, even after log transformation (Levene's test: $p = 0.017$), thus non-parametric tests were conducted on the seminiferous tubule diameter. A log transformation produced a normal distribution in the plasma progesterone data (S–W test: $p = 0.125$) and homogeneity of plasma progesterone data was confirmed with a Levene's test (Levene's test: $p = 0.102$); however, no other reproductive parameter data, even after log transformation, satisfied the criteria for parametric data (S–W test: $p \leq 0.001$). Consequently, we employed a general linear model (GLM) to analyse the effects of season on log progesterone with season as the independent variable. All other reproductive parameters were not normally distributed and, consequently, we employed GLZM with a gamma distribution and a log-link function and season as the independent variable. We additionally included body mass, photoperiod (number of minutes of daylight per day), and mean, maximum, and minimum temperatures (°C) per month as a covariate for all reproductive parameters in the models. LSD was used for post hoc comparisons. Model accuracy was presented as adjusted R^2 .

All statistical analyses were implemented using the SPSS version 24.0. Results are presented as mean \pm SE and were found to be significant at $p \leq 0.05$. Parameter estimates (b) were presented for each covariate.

Results

Climate

During the 12 month study period, no rainfall was recorded at the study area (Table 1). The highest mean temperatures were recorded during the months of summer (June–August), with the mean peak temperature of the 12 month study period occurring during August at 38 °C (Table 1); the lowest mean temperature was found in winter (December–February), with January having the

Table 1. Weather conditions, photoperiod length, and number of captured Libyan jird (*Meriones libycus*) per season in Riyadh, Saudi Arabia, during the study period.

Season	Month	Female (pregnant)	Male	Temperature (°C)			Total precipitation (mm)	Photoperiod (min of light per day)
				Mean	Mean minimum	Mean maximum		
Summer	June	6	3	37	27	42	0	817
	July	4	8	37	28	44	0	809
	August	3	5	38	29	44	0	778
Autumn	September	6	4	35	25	40	0	795
	October	2	3	30	23	36	0	691
	November	6	9	21	13	26	0	714
Winter	December	4	6	18	9	23	0	697
	January	5 (1)	6	15	7	22	0	646
	February	5	5	20	12	25	0	677
Spring	March	6 (1)	4	23	16	29	0	718
	April	5	5	28	20	33	0	762
	May	4	5	34	26	40	0	799

lowest mean temperature of 15 °C (Table 1). The lowest temperatures were found in the months of winter, with a mean minimum temperature of 9.15 ± 0.502 °C (Table 1), whereas the highest mean minimum temperature of 28.13 ± 0.180 °C was observed in summer (Table 1). Additionally, the highest temperatures were found in the months of summer, with a mean maximum temperature of 43.63 ± 0.202 °C (Table 1), whereas the lowest mean maximum temperature was 23.24 ± 0.304 °C observed in winter (Table 1). The longest photoperiods (minutes of light) observed were those of summer with 800.81 ± 4.044 min of light, on average (Table 1), whereas the shortest photoperiods were observed during winter with 673.12 ± 5.393 min of light, on average (Table 1). There was a significant positive correlation between photoperiod per month and mean, maximum, and minimum temperature per month ($r \geq 0.884$, $n = 11$, $p \leq 0.0001$), as the photoperiod (minutes of daylight) increased so does the temperature (Fig. 1).

Body mass

In total 63 male and 56 female Libyan jirds were captured during the study period (Table 1).

The GLZM accuracy was relatively weak for the observed data; however, it was the best-fitting model that could be achieved (adjusted $R^2 = 0.202$).

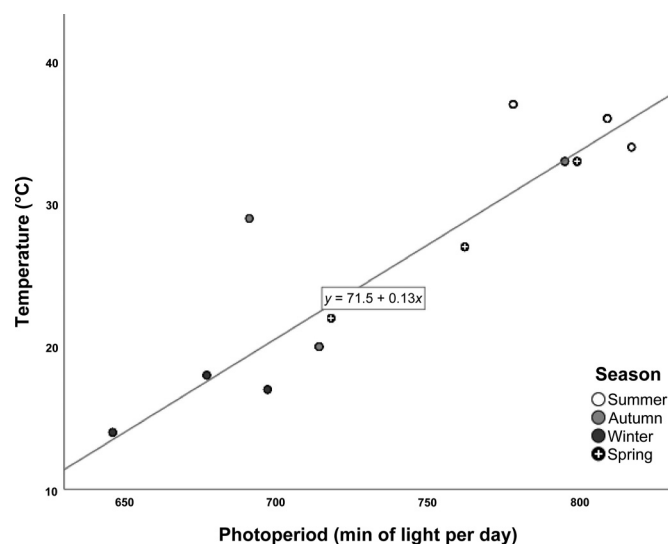
On average, throughout the year, males (114.938 ± 5.0351 g) were observed to be heavier than females (98.297 ± 4.224 g), but this was found to be not significant (GLZM: Wald $\chi^2_{[1]} = 3.15$, $p = 0.076$). Libyan jirds in autumn and winter appeared to have higher body masses, but the model did not find season to affect body mass significantly (GLZM: Wald $\chi^2_{[3]} = 4.42$, $p = 0.219$; Fig. 2A). Additionally, the interaction between sex and season (GLZM: Wald $\chi^2_{[3]} = 4.47$, $p = 0.215$) and maximum temperature yielded no significant effect on body mass (GLZM: Wald $\chi^2_{[1]} = 4.47$, $p = 0.215$). Contrastingly, photoperiod (Fig. 2B), mean temperature (Fig. 2C), and maximum temperature (Fig. 2D) significantly affected Libyan jird body mass (Wald $\chi^2_{[1]} \geq 5.72$, $p \leq 0.008$). The times during the year with longer photoperiods (longer days) were observed to have individuals with lower body masses (Fig. 2B). Although both maximum and mean temperatures displayed similar trends, hotter periods of the sample year had the lowest recorded body masses of male female Libyan jirds (Figs. 2C and 2D).

Male reproductive parameters

Testicular mass

The GLZM accuracy was relatively strong for the observed data and thus we are confident in the model strength (adjusted $R^2 = 0.707$). There were significant differences in relative testicular masses of Libyan jirds between seasons (Wald $\chi^2_{[3]} = 13.48$, $p = 0.004$). Testicular mass was significantly lower in summer (0.18 ± 0.04 g) than in

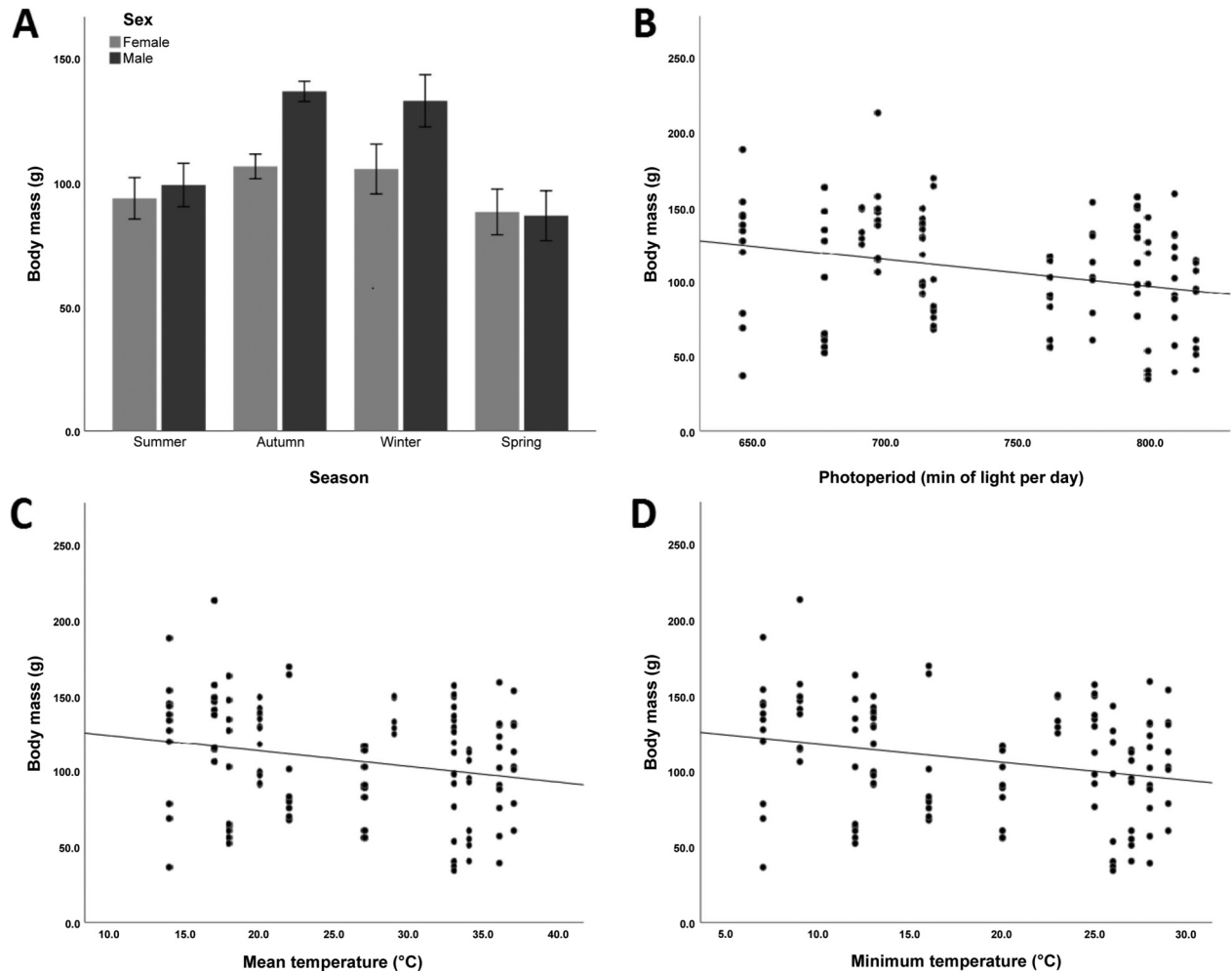
Fig. 1. The correlation between mean temperature (°C) and photoperiod (min of light per day) over the four seasons in the areas around Riyadh, Saudi Arabia.



spring (0.92 ± 0.23 g) (LSD: $p = 0.013$), but similar to that of autumn (1.08 ± 0.12 g) and winter (2.06 ± 0.24 g) (LSD: $p \geq 0.801$ for both). Autumn testicular mass was significantly higher than that of spring (LSD: $p = 0.021$) but showed no difference with winter testicular mass (LSD: $p = 0.930$). Additionally, winter and spring testicular masses were not significantly different (LSD: $p = 0.081$). Testicular mass was found to increase with body mass (Wald $\chi^2_{[1]} = 39.85$, $p \leq 0.0001$). Testes mass was not significantly affected by mean, maximum, and minimum temperatures per month (Wald $\chi^2_{[1]} \geq 0.035$, $p \geq 0.424$). Similarly, it was observed that photoperiod did not affect testicular mass (Wald $\chi^2_{[1]} = 2.76$, $p = 0.096$).

The model describing corrected testicular mass did not describe the data observed as precisely as the previous model (adjusted $R^2 = 0.598$); however, it was the best-fitting model to the data. Corrected testicular mass to body mass showed similar results to testicular mass; the season and body mass had significant effects on corrected testicular mass (season: Wald $\chi^2_{[3]} = 14.56$, $p = 0.002$; body mass: Wald $\chi^2_{[1]} = 8.83$, $p = 0.004$; Fig. 3A). Summer was found to have Libyan jirds with the lowest corrected testicular mass in comparison with spring (LSD: $p = 0.009$; Fig. 3A). Likewise, autumn corrected testicular mass was found to be significantly lower than spring (LSD: $p = 0.018$; Fig. 3A). Winter was observed to have similar corrected testicular mass in comparison with the other three

Fig. 2. (A) Seasonal and sex variation of body mass (mean \pm SE) over the four seasons and the inverse relationship between body mass and (B) photoperiod (min of light per day), (C) mean temperature ($^{\circ}$ C), and (D) minimum temperature ($^{\circ}$ C) of Libyan jird (*Meriones libycus*) in the areas around Riyadh, Saudi Arabia.



seasons (LSD: $p \geq 0.099$ for all three seasons; Fig. 3A). Additionally, summer and autumn were found to have similar corrected testicular mass (LSD: $p = 0.759$; Fig. 3A). Similar to that of testes mass, corrected testicular mass was not significantly affected by mean, maximum, and minimum temperatures per month (Wald $\chi^2_{[1]} \geq 0.018$, $p \geq 0.102$). Additionally, it was observed that photoperiod did not affect testicular mass (Wald $\chi^2_{[1]} = 2.68$, $p = 0.405$).

Testicular volume

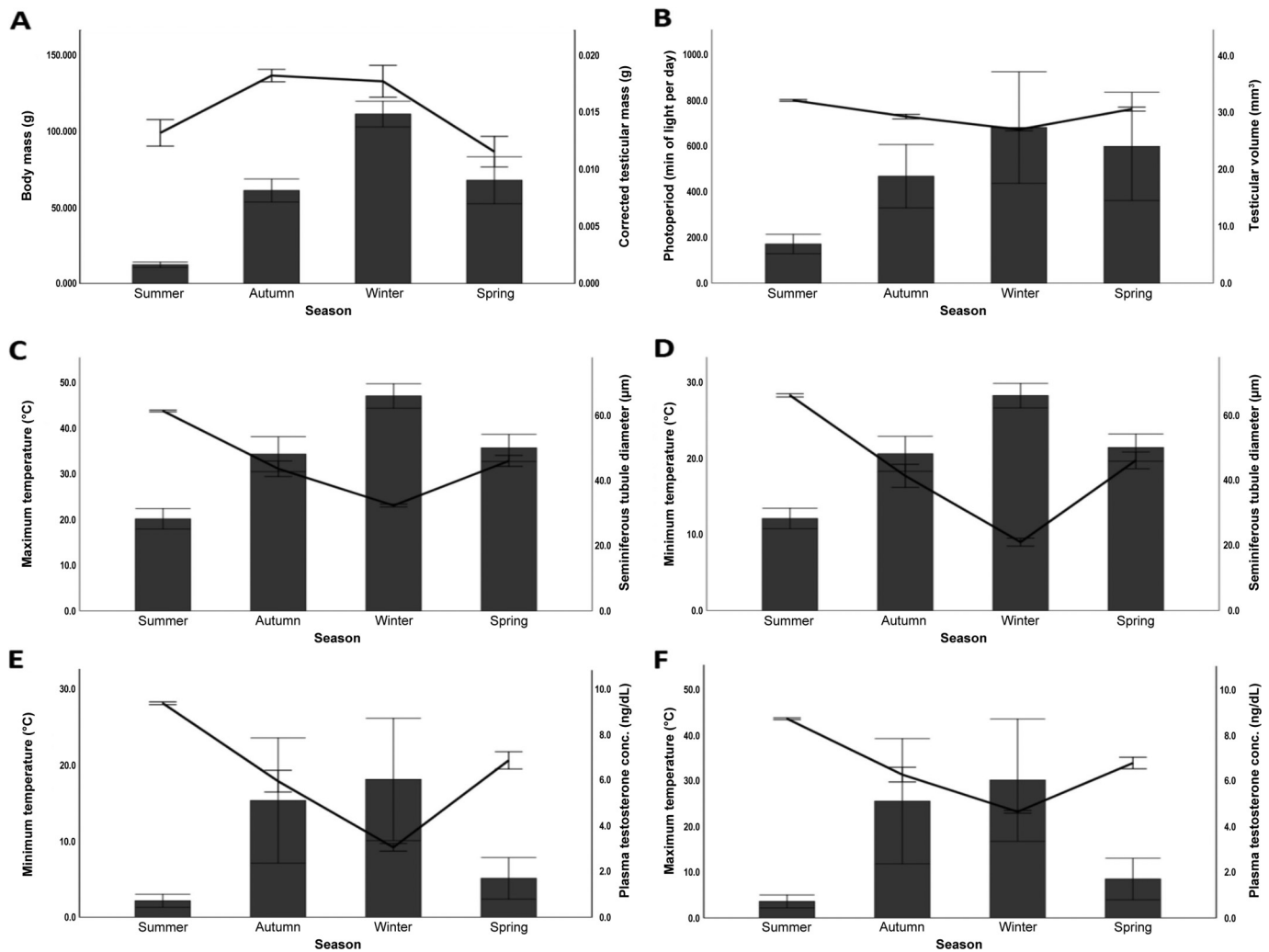
This GLZM fitted the observed data but did not have a relatively high accuracy; however, it was the best-fitting model that we could employ for the data (adjusted $R^2 = 0.293$). There were significant differences in relative testicular volume between seasons (Wald $\chi^2_{[3]} = 36.82$, $p \leq 0.0001$; Fig. 3B). The testicular volume in autumn was observed to be significantly larger compared with those in summer and spring (LSD: $p \leq 0.048$; Fig. 3B), but smaller than those in winter (LSD: $p = 0.004$; Fig. 3B). Testicular volume in winter was found to be larger than in spring and summer, respectively (LSD: $p \leq 0.017$; Fig. 3B), whereas summer and spring were found to have similar testicular volume (LSD: $p = 0.471$; Fig. 3B). Photoperiod had a significant effect on testicular volume (Wald $\chi^2_{[1]} = 6.67$, $p = 0.01$), with an increase in photoperiod accompanied by a decrease in testicular volume (Fig. 3B). Testicular volume was found not to be affected by body mass (Wald $\chi^2_{[1]} = 0.706$, $p = 0.401$). Testicular volume was found to not be affected by mean, max-

imum, and minimum temperatures per month (Wald $\chi^2_{[1]} \geq 0.284$, $p \geq 0.188$).

Seminiferous tubule diameter

The GLZM fitted for the seminiferous tubule diameter data was not as accurate as those of testicular mass and volume but was better than the model fitted for corrected testicular mass, thus we are confident in the model results (adjusted $R^2 = 0.622$). There were significant differences in seminiferous tubule diameters between seasons (GLZM: Wald $\chi^2_{[3]} = 12.37$, $p = 0.006$; Fig. 3C). The males in summer were observed to have significantly smaller seminiferous tubule diameters compared with those in autumn and spring (LSD: $p \leq 0.05$ for both; Fig. 3C). Libyan jirds had larger seminiferous tubule diameters in autumn than in spring (LSD: $p = 0.05$; Fig. 3C). Spring was observed to have similar seminiferous tubule diameters compared with those in summer and winter (LSD: $p \geq 0.140$ for both; Fig. 3C). Body mass played a significant role in seminiferous tubule diameter (GLZM: Wald $\chi^2_{[1]} = 12.44$, $p \leq 0.0001$). Larger individuals were found to have greater seminiferous tubule diameters. Additionally, both maximum (Fig. 3C) and minimum (Fig. 3D) temperatures were found to play a significant role in seminiferous tubule diameter (GLZM: Wald $\chi^2_{[1]} \geq 5.14$, $p \leq 0.023$), where there were larger seminiferous tubule diameters during the cooler seasons (Figs. 3C and 3D). Both mean temperature and photoperiod did not play any significant role in seminiferous tubule diameter (GLZM: Wald $\chi^2_{[1]} \geq 0.30$, $p \geq 0.330$).

Fig. 3. Seasonal variation in the following reproductive parameters (mean \pm SE): (A) testicular mass corrected for body mass and body mass; (B) testicular volume and photoperiod (min of light per day); (C) seminiferous tubule diameter and maximum temperature; (D) seminiferous tubule diameter and minimum temperature; (E) plasma testosterone concentration and minimum temperature; (F) plasma testosterone concentration and maximum temperature of the Libyan jird (*Meriones libycus*) and mean temperature in the areas around Riyadh, Saudi Arabia. Reproductive parameters represented by a bar graph and covariates by a solid line.



Plasma testosterone

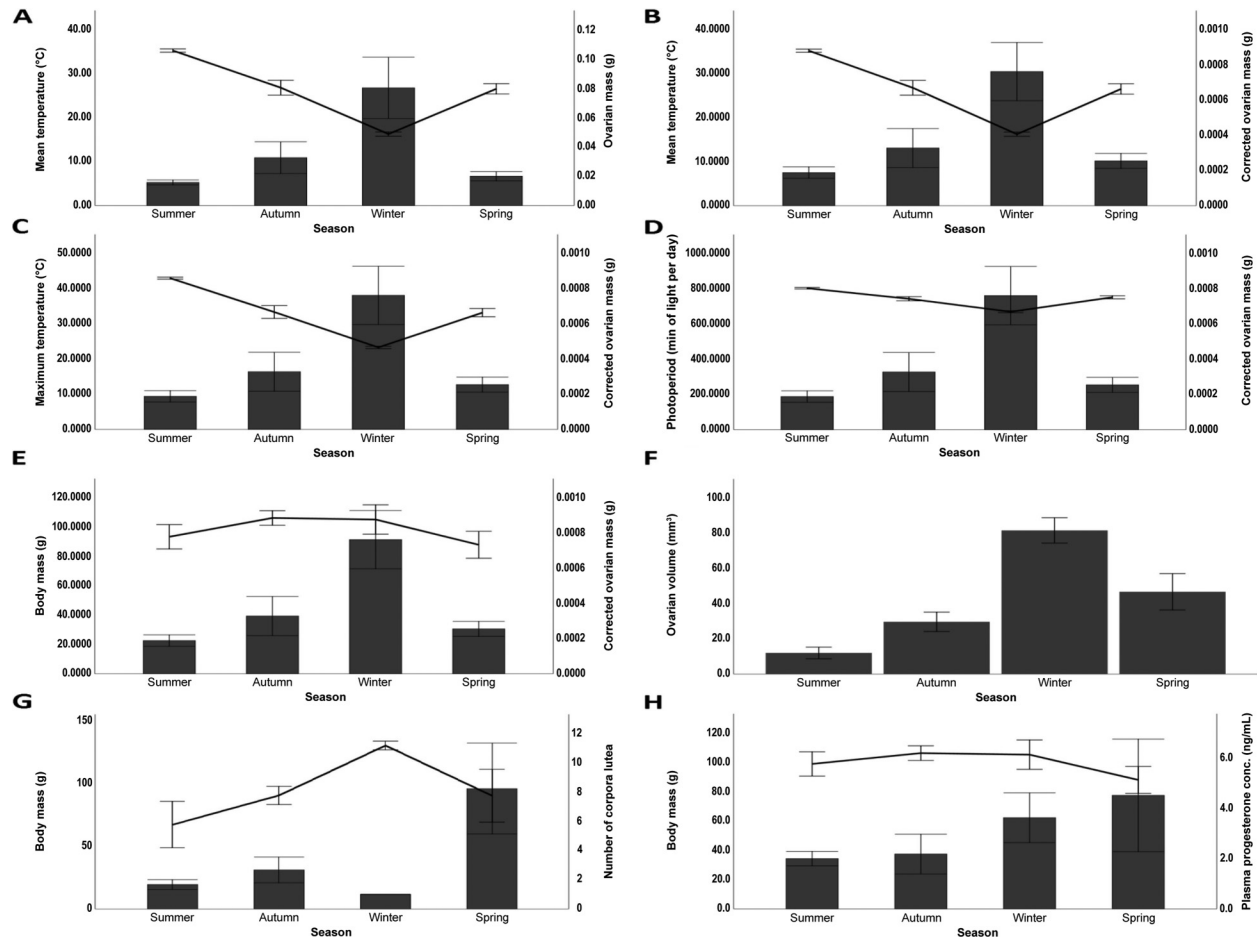
The GLZM used to analyse the plasma testosterone data set was not strongly fitted (adjusted $R^2 = 0.107$); however, the model chosen was the best fitting to explain the data. There was a significant effect of season on plasma testosterone (Wald $\chi^2_{[3]} = 26.94$, $p \leq 0.0001$; Fig. 3E). On closer analysis, plasma testosterone was found to be significantly higher in Libyan jirds in winter than in autumn and spring (LSD: $p \leq 0.026$; Fig. 3E). Summer plasma testosterone was found to be similar to that in the other three seasons (LSD: $p \geq 0.067$; Fig. 3E), additionally males in spring and autumn were observed to have similar plasma testosterone concentrations (LSD: $p = 0.698$; Fig. 3E). Both minimum (Fig. 3E) and maximum (Fig. 3F) temperatures over the sample period were found to significantly affect plasma testosterone, with plasma testosterone decreasing with an increase in both mean minimum and mean maximum temperatures of each season (Wald $\chi^2_{[1]} = 34.0$, $p = 0.46$ and Wald $\chi^2_{[1]} = 4.44$, $p = 0.035$, respectively; Fig. 3F). The mean seasonal temperature and photoperiod did not affect plasma testosterone concentration (Wald $\chi^2_{[1]} \geq 1.63$, $p \geq 0.202$). Body mass, however, did affect plasma testosterone (Wald $\chi^2_{[1]} = 5.6$, $p = 0.018$), with larger individuals having higher plasma testosterone concentrations.

Female reproductive parameters

Ovarian mass

The GLZM used to analyse ovarian mass had lower accuracy than those used to describe the male reproductive parameters; however, it was the best-fitting model (adjusted $R^2 = 0.430$). Winter appeared to contain females with the heaviest ovaries, but there were no significant differences in relative ovarian mass between seasons (Wald $\chi^2_{[3]} = 6.87$, $p = 0.076$; Fig. 4A). Body mass did not affect ovarian mass (Wald $\chi^2_{[1]} = 2.90$, $p = 0.089$). Mean temperature was observed to affect ovarian mass (Wald $\chi^2_{[1]} = 4.29$, $p = 0.038$; Fig. 4A), with heavier ovarian mass in cooler months. Similarly, the maximum temperature over the sampling period was found to have a statistical significant effect on ovarian mass, with ovarian mass decreasing with an increase in maximum temperature of each season (Wald $\chi^2_{[1]} = 6.29$, $p = 0.012$, estimated value = -0.38). Minimum temperature did not significantly affect ovarian mass (Wald $\chi^2_{[1]} = 0.66$, $p = 0.416$). Photoperiod length played a significant role in ovarian mass (Wald $\chi^2_{[1]} = 4.48$, $p = 0.034$). Periods of the sample year with shorter photoperiods were observed to have heavier ovarian masses (estimated value = 0.007).

Fig. 4. Seasonal variation of reproductive parameters (mean \pm SE): (A) ovarian mass and mean temperature; (B) ovarian mass corrected for body mass and mean temperature; (C) ovarian mass corrected for body mass and maximum temperature; (D) ovarian mass corrected for body mass and photoperiod; (E) ovarian mass corrected for body mass and body mass; (F) ovarian volume; (G) number of corpora lutea and body mass; (H) plasma progesterone concentration and body mass of the Libyan jird (*Meriones libycus*) and temperature in the areas around Riyadh, Saudi Arabia. Reproductive parameters represented by a bar graph and covariates by a solid line.



Similarly, the GLZM used to analyse the corrected ovarian mass did not completely fit the observed data; however, it was the best-fitting model that we could use (adjusted $R^2 = 0.417$). As with the ovarian mass, winter appeared to contain females with the heaviest corrected ovarian mass; however, the corrected ovarian mass was not significantly different with season (Wald $\chi^2_{[3]} = 6.41$, $p = 0.093$; Fig. 4B). Additionally, minimum temperature did not affect the corrected ovarian mass (Wald $\chi^2_{[1]} = 0.756$, $p = 0.385$). Contrastingly, mean temperature (Wald $\chi^2_{[1]} = 4.03$, $p = 0.045$; Fig. 4B), maximum temperature (Wald $\chi^2_{[1]} = 5.39$, $p = 0.02$; Fig. 4C), and photoperiod (Wald $\chi^2_{[1]} = 3.89$, $p = 0.049$; Fig. 4D) did significantly affect the corrected ovarian mass. During times of lower temperatures (mean and maximum), the corrected ovarian masses were observed to be heavier. Additionally, during times of shorter day lengths, the corrected ovarian mass was found to be heavier. Body mass, additionally, affected the corrected ovarian mass (Wald $\chi^2_{[1]} = 7.75$, $p = 0.005$; Fig. 4E). As body mass of the female Libyan jirds increased, so too did the corrected ovarian mass.

Ovarian volume

mass also did not affect ovarian volume (Wald $\chi^2_{[1]} = 0.248$, $p = 0.619$). The seasonal change in photoperiod and mean, maximum, and minimum temperatures over season had no affect (Wald $\chi^2_{[1]} \geq 0.124$, $p \geq 0.280$).

Number of corpora lutea

This GLZM fitted the observe data and thus we are confident in the model results (adjusted $R^2 = 0.774$). The number of corpora lutea was significantly affected by the season of the year (Wald $\chi^2_{[3]} = 16.609$, $p = 0.001$; Fig. 4G). The greatest number of corpora lutea was found in the ovaries in the spring (LSD: $p \leq 0.031$ for all; Fig. 4G). The number of corpora lutea remained similar between the three other seasons (LSD: $p \geq 0.331$). Body mass was observed to play a significant role in the number of corpora lutea (Wald $\chi^2_{[1]} = 9.668$, $p = 0.002$; Fig. 4G), with lighter animals having more corpora lutea. The photoperiod and maximum and minimum temperatures per month were also observed to not affect the number of corpora lutea (Wald $\chi^2_{[1]} \geq 0.129$, $p \geq 0.138$).

Plasma progesterone

As with the male reproductive hormone (testosterone), the plasma progesterone GLM did not fit the observed data optimally (adjusted $R^2 = 0.103$); however, this was the best-fitting model available. On observation, spring and closely followed by winter were the seasons with the females exhibiting the highest concentrations of plasma progesterone; however, the GLM revealed no

significant change in log plasma progesterone over the four seasons ($F_{[3,48]} = 1.57, p = 0.209$), but the log plasma progesterone was found to be significantly affected by body mass ($F_{[1,48]} = 6.502, p = 0.014$; Fig. 4H); individuals with lighter body masses were observed to have higher concentrations of plasma progesterone (Fig. 4H). The photoperiod and maximum and minimum temperatures per month were also observed to not affect plasma progesterone ($F_{[1,48]} \geq 0.032, p \geq 0.209$).

Discussion

Mammals inhabiting arid environments undergo marked seasonal changes in body mass and reproductive parameters, which are generally dictated by the presence or absence of rainfall (Liu et al. 2007). During the study period that took place over an entire calendar year, there was no rainfall; thus, we attempted to investigate how reproduction is brought about in the absence of one of the more crucial zeitgebers in the desert environment. Despite the absence of rainfall, the Libyan jird was observed to exhibit some seasonal changes in both body mass and a number of reproductive parameters (gross morphology, histology, and circulating reproductive hormones) that were closely linked to temperature (maximum, minimum, and mean) and photoperiod or a combination of the two. Libyan jirds in Saudi Arabia were found to initiate breeding during the winter months and into early spring, embracing some of the coolest months with the shortest day lengths. Interestingly, the Baluchistan gerbil, Arabian spiny mouse, and Ethiopian hedgehog were found to initiate breeding in the spring months in Saudi Arabia with the presence of rainfall; however, these species did not use photoperiod as a zeitgeber (Sarli et al. 2015, 2016; Alagaili et al. 2017).

Male Libyan jirds exhibited increased testicular mass, testicular volume, seminiferous tubule diameters, and circulating plasma testosterone during the winter months. Winter days were shorter than those of the other seasons; the maximum temperatures were also lower, which was significant in the control of some male reproductive parameters. In addition, male's body mass was at its greatest during this season; this may in part be due to increased testosterone that can bring about increased mass or muscle gain and enables males to be effective at competition during mating. The rise in plasma testosterone concentration in males during the winter months promotes the development of the testes for the production of spermatozoa and the subsequent increase in the seminiferous tubule diameter. However, there is strong evidence that the males begin preparing for the breeding season (winter) during the autumn with higher levels of plasma testosterone and heavier body masses.

Seasonal changes in temperature and photoperiod are more predictable than seasonal patterns of precipitation in deserts. It is thus posited that Libyan jirds, especially males, may use temperature changes to activate the breeding season in the absence of rainfall as has been found for gerbils and hedgehogs (Henry and Dubost 2012; Sarli et al. 2015; Alagaili et al. 2017). Temperature has been found to play a prominent role in determining the initiation of reproduction in males of several species of small mammal in arid regions (Henry and Dubost 2012; Sarli et al. 2015; Alagaili et al. 2017). Lower maximum and minimum temperatures in autumn triggers a rise in plasma testosterone in hedgehogs, which in turn brings about an increase in seminiferous tubule diameter as sperm production is promoted (Alagaili et al. 2017). Increased testosterone also brings about the onset of mate searching, as well as enhanced aggression directed towards male conspecifics (Yamaguchi et al. 2013; Alagaili et al. 2017). In the presence of rainfall, the role of photoperiod becomes muted (Alagaili et al. 2017). Photoperiod has been found to be a crucial zeitgeber in regions of higher latitudes such as southern Africa, where the spiny mouse (*Acomys spinosissimus* Peters, 1852; also known as the southern African spiny mouse) is photo-responsive (Medger et al. 2012) and was observed to become

reproductively active under a greater amount of light per day (summer) (Medger et al. 2012), whereas in this study, the Libyan jird becomes active under a smaller amount of light per day (winter).

There were few pregnancies found within this study probably because of a lack of precipitation. A lack of rainfall would result in a lack of food resources and, consequently, an inability to raise offspring. Two cases of pregnancy were recorded in winter and spring. In times of the year with lower maximum and mean temperatures and shorter winter days, ovarian mass and volume were observed to be greater than during the other months and, consequently, were at a stage where the animals were more receptive to males for breeding, if breeding occurred. The lack of precipitation in the year of study may have influenced the activation of the gonads. Contrastingly, plasma progesterone and the number of Graafian follicles indicate breeding to arise around spring. This is very similar to what was seen in the Baluchistan gerbil, Arabian spiny mouse, and Ethiopian hedgehog (Sarli et al. 2015, 2016; Alagaili et al. 2017). Although precipitation is highly unpredictable in an arid region, it is somewhat more likely to arise in spring and early summer, and subsequent to these rains, food sources are more readily available thus increasing the survival of the offspring. As in the other small-mammal species, the Libyan jird may show reproductive recrudescence for the onset of precipitation in spring and thus become activated for breeding and producing offspring. With a gestation period of 20 days if mating occurs just prior to spring or the beginning of spring, this would allow the offspring to be born during or just after the rains, which would allow the maximum likelihood for survival. The outcomes of all models conducted on the female reproductive parameters reveal that in the absence of rainfall, the normal timing of reproduction (seasons) was not followed as strictly, causing a lack of significance and low model accuracy. Other zeitgebers thus became significantly important in the control of the female reproductive system; in the presence of rainfall, we would have expected stricter reproductive patterns as seen in the Libyan jirds occurring in the Sahara of Algeria.

The Libyan jirds occurring in the Sahara of Algeria exhibited a pattern of seasonal reproduction similar to those recorded in the Baluchistan gerbil, Arabian spiny mouse, and Ethiopian hedgehog in the deserts of Saudi Arabia (Smaï 1998; Belhocine et al. 2007; Sarli et al. 2015, 2016; Alagaili et al. 2017). The climatic conditions of the Sahara of Algeria appear to be more consistent on an annual basis than that of the climatic conditions of deserts in central Saudi Arabia. During spring and early summer, water and food are usually available in the Sahara of Algeria and thus the mammals occupying this area, such as the Libyan jird and Algerian gerbil, can use the predictability of the climatic conditions and food availability to time their breeding to occur at these times of plenty, thus allowing the highest survival rate for their offspring (Smaï 1998; Belhocine et al. 2007). The Libyan jird population from central Saudi Arabia occurs in a climatically unpredictable region where rainfall often fails and, consequently, food availability is sometimes absent during spring, which is the usual period of breeding for the Libyan jird. The lack of rainfall has consequently resulted in a reduced mating success, a lower number of successful pregnancies, and a shift in the reproductive season (Smaï 1998; Belhocine et al. 2007). Changes in environmental temperature and photoperiod have been found to be more reliable than rainfall in central Saudi Arabia and, consequently, the Libyan jirds have possibly cued their breeding time to temperature and (or) photoperiod with a shift, in the absence of rainfall, to the cooler winter and early spring months compared with the Libyan jirds found in the Sahara of Algeria that breed mainly in the spring.

In the Arabian spiny mouse, many reproductive parameters are correlated to environmental temperature and not rainfall (Sarli et al. 2016). Temperature is implicated as an important cue for the regulation of reproduction in many small mammals due to the

high energetic constraints experienced during cold periods when energy expenditure for thermoregulation may constrain the energetic investment into reproduction (Bronson and Heideman 1994).

Males invest little energy and resources into reproduction and tend to utilise the more predictable environmental variable of temperature to control their reproduction (Henry and Dubost 2012; Sarli et al. 2015; Alagaili et al. 2017). Females, on the other hand, invest vast amounts of energy and resources into reproduction and offspring care, and can ill afford to reproduce and produce young during unfavourable times of the year. Although temperature and photoperiod are by far the more predictable environmental variables for the onset of reproduction due to the need for available food resources, the probable main environmental factor promoting reproduction in the female Libyan jirds would be rainfall, which is speculated to override all other environmental factors. Complete cessation of reproduction for such a short-lived rodent would put the survival of the population in jeopardy; some individuals, even in the absence of rainfall, would still breed and produce offspring using temperature change and photoperiod as the controlling breeding factors; thus, we believe that the breeding pattern of the Libyan jird shifted to the cooler months of winter and early spring in the absence of rainfall. Furthermore, the lowered accuracy levels of the best-fitting models used to explain the observed data bolsters rainfall as the prime environmental driving force. Because of the lack of rainfall data within the models, the ability for the models to accurately describe the observed data are decreased, indicating the importance of rainfall in predicting (and thus controlling) the reproductive parameters and reproduction itself in Libyan jirds.

Rainfall in arid regions is the crucial zeitgeber because rainfall is intrinsically linked to primary productivity and thus food sources for small mammals. Therefore, it is reasonable to intimately tie reproduction to rainfall. However, if this cue is removed, then the small mammals of these arid regions would depend on other zeitgebers, such as photoperiod and temperature. Temperature is a principle cue for reproduction of small mammals in arid regions, whereas photoperiod is not (Alagaili et al. 2017). Our study indicates that in the absence of a controlling environmental factor, such as rainfall, mammals will rely on more predictable environmental factors to synchronise their physiology and behaviour to the environmental conditions. In our study, it is not possible to differentiate between temperature and photoperiod as a critical environmental zeitgeber in the absence of rainfall, thus further laboratory studies are needed to unlock this mystery.

Acknowledgements

We extend our sincere appreciation to the Deanship of Scientific Research at the King Saud University through Vice Deanship of Research Chairs and King Abdulaziz City for Science and Technology (KACST) through Graduate Research Program for funding the work. We also thank HH Prince Bander bin Saud Al-Saud, former President of the Saudi Wildlife Authority, for his permission to trap the animals. N.C.B. acknowledges funding from the SARChI chair of Mammalian Behavioural Ecology and Physiology from the DST-NRF South Africa, the National Research Foundation (grant No. 64756), and the University of Pretoria. The research was cleared by the ethics committee of the University of Pretoria.

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