Original investigation

Are female camels capital breeders? Influence of seasons, age, and body condition on reproduction in an extremely arid region

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ABSTRACT

Camels can store huge body reserves, they are the only large mammals able to survive in the hottest deserts of the planet, and thus they provide vital resource for millions of peoples. Yet the influence of environmental conditions on reproduction is not fully understood, especially under severe climatic conditions. We assessed the effect of seasons, age, and body reserves on ovarian functioning, pregnancy rate, and fetal traits in Sahraoui dromedaries form south eastern Algeria. Age and body condition were estimated in 322 females slaughtered for food consumption between November 2012 and February 2014. We examined reproductive tract, ovaries (e.g. follicles, ovarian pathologies) and fetal traits. Most females were cyclic (N = 288); analyses revealed an alternate contralateral ovarian functioning, the left ovary being the most active. Pregnancy rate was low (N = 34 pregnant females), and only the left uterine horn carried a single fetus. In both cyclic and pregnant females we found marked seasonal patterns with a reproductive peak in winter, but without cessation of reproduction during the hot and dry summer. Age and body condition positively influenced ovarian functioning, pregnancy rate and gestational age. All these factors displayed complex interactions. Overall, our analyses suggest that although body reserves are important, dromedary camels are not pure capital breeders. Instead, they exhibit a flexible reproductive strategy influenced by age and seasons. We suggest that the marked lateralization of the functioning of both the ovaries and uterus represents an adaptation that limits fecundity.

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Introduction

Camelids are large ungulates characterized by ecological and morpho-functional adaptations to very harsh conditions (Schroter et al., 1987; Elkhawad, 1992; Ulmasov et al., 1993). They can resist prolonged droughts, drastic fluctuations of ambient temperatures (both freezing and heat waves), strong dusty winds, intensive solar radiations, food shortage, unbalanced diet and lack of minerals (Faye and Bengoumi, 2002). Large body mass and the ability to store resources in their humps are involved in their buffering aptitudes against adverse conditions. Camels can survive and breed in the most arid areas of the planet with limited access to food, water, and in the absence of shelter. These characteristics explain why camels (dromedary and Bactrian camels) have been domesticated and introduced in many places where no other livestock could survive. Feral camels represent a threat to fragile desert habitats in Australia (Edwards et al., 2004), but most populations are domes-

ticated and play a pivotal role for the local economy; providing meat, milk, means of transport, workhorses and wool to millions of peoples (Faye and Bonnet, 2012). For instance, approximately 10 million dromedary camels sustain Somali communities spread in the arid areas of Kenya, Somalia and Ethiopia (Farah et al., 2004; Faye, 2015). Recent research showed that camel milk has unique characteristics; it can be stored during days at ambient temperature without becoming rancid, and it may have therapeutic effects (Dubey et al., 2016).

Most hot deserts will expand in the near future due to combined impacts of global warming and deforestation (Dai, 2013). Thus, the socio-economic value of camels is likely to increase. From this perspective, studying camel reproduction is important. Traditional extensive pastoral practices are well adapted to camel farming in poorly productive ecosystems (Farah et al., 2004; Faye, 2016). Female camels exhibit a slow-breeding strategy (Zarrouk et al., 2003). This may optimize reproductive success under unpredictable and low foraging opportunities, favoring the production of few large neonates capable to sustain harsh conditions. Substantial proportion of the resources needed for reproduction and lactation are derived from the mobilization of maternal reserves

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(Faye et al., 2001; Abdallah and Faye, 2012). Camels may therefore be considered as capital breeders (Festa-Bianchet et al., 1998; Houston et al., 2006). A positive relationship between body condition and ovarian functioning is thus expected as observed in cattle (Pryce et al., 2001). However, no mammal can exhibit a pure capital breeding strategy (Bonnet et al., 1998; Wheatley et al., 2008); thus seasonal fluctuations of resource availability should also influence reproduction (Marai et al., 2009; El-Harairy et al., 2010). Further, reproductive performances tend to increase after maturity and to decrease in oldest individuals (Erickson et al., 1976; Hussein et al., 2008). Overall, combined effect of body condition, seasons, and age should influence ovarian functioning and pregnancy in camels.

Previous studies documented significant effects of some of these factors (i.e. season, age) in Egypt, Morocco, Saudi Arabia, Nigeria, and Pakistan (Sghiri and Driancourt, 1999; Yahaya et al., 1999; Ali et al., 2007; El-Harairy et al., 2010; El-Hassan and Tingari, 2015). One study examined the effects of season, age, and body condition on ovarian structures and plasma levels of sex hormones (Hussein et al., 2008). However, the factors listed above have been examined independently, precluding the possibility to obtain an integrative view. In other words, possible interactions between age and body condition have never been assessed for example. Furthermore, reproductive characteristics vary markedly across populations (Kaufmann, 2005). The relationship between body condition and ovarian functioning has been insufficiently explored to assess to what extent maternal body reserves may offer a buffering effect against seasonal and/or annual fluctuations of resources. Overall, available information regarding possible interactions among key factors influencing reproduction in female camels is still fragmentary.

It is important to further appraise the reproductive potential of female camels under harsh conditions; notably to derive practical recommendations and to optimize stock farming. One objective of the present study was to establish baseline information regarding the effect of multiple factors on ovarian activity and pregnancy rate in camels (*Camelus dromedaries,* Sahraoui race). The study was carried out in a previously unstudied area of the Sahara, an extremely arid zone representative of future climatic challenges that will be experienced by an increasing proportion of stock-breeders (Allen et al., 2010). The description of ovarian structures included classical features (e.g. follicles), and ovarian pathologies as a proxy of dysfunctions (e.g. disturbance of ovulation or of corpus luteum development). We also examined uterine and fetal traits in pregnant females. Using a relatively large sample size (N > 300 females), we considered contrasted seasons, ages, and body condition indices. We notably examined if these factors and their interactions influence ovarian functioning, pregnancy rate and fetal traits. We thus encompass important factors that may affect fertility early during the breeding cycle and later during gestation. Food resources are scare in the study area, and summer conditions are particularly harsh (very dry and hot climate during four months). Thus, we expected a strong influence of body condition and seasons on reproductive patterns. For example, because neonates are sensitive to climatic conditions and depend on milk provisioning, parturitions should be concentrated in winter, and only females with elevated body reserves should be able to undertake reproduction. The objective of this study was to test the validity of these important, albeit incompletely assessed, predictions.

Material and methods

Reproductive cycle of female camels

Previous studies offer a robust background on ovarian activity of the one humped camel (*C. dromedarius*) (Musa, 1979; El-Wishy,

1987; Zhao et al., 1994; Skidmore et al., 1994; Tibary and Anouassi, 1996; Skidmore, 2005; Basiouni, 2007; El-Harairy et al., 2010; Dholpuria et al., 2012). In this monotocous seasonal breeder, ovulation is induced by the presence of semen in intravaginal folds, and possibly stimulated by copulation (Zarrouk et al., 2003; Abdallah and Faye, 2012). The annual reproductive cycle is nearly polyestrous (Akral and Khanna, 1995). Females display repetitive cycles of follicle growth and regression without cyclical corpus luteum. Three main phases have been described: growth, maturity and regression. Two months after the onset of the breeding season, follicular growth is limited to the emergence of small follicles (<4 mm in diameter) at the periphery of the ovaries. Following this first recruitment phase, several follicles (3–6) continue to grow until the emergence of one or two large dominant follicles which become mature (5–17 mm in diameter; including 5–10 mm medium size follicles and 11–17 mm pre-ovulatory follicles). The dominant follicle undergoes a stagnation stage for 5–7 days. In 50% of unmated females, regression occurs until disappearance in the ovarian stroma. In other unmated females (50%) the largest follicle continues to grow attaining a large size (30–65 mm); this cyst-like follicle cannot ovulate spontaneously however, it regresses thereby permitting the expression of the next follicular growth waves an average of 18 days later (Zarrouk et al., 2003). In mated females, following ovulation, the mature follicle is usually transformed into a functional corpus luteum. It is unclear whether active follicular waves persist during non-breeding season as observed in other ungulates such as sheep (Souza et al., 1996), or if the ovaries become quiescent during the non-breeding season as in mares for example (Boeta et al., 2006).

Study area

This study was conducted in Wilaya d'El Oued district, northeast of the Algerian Sahara (33°22′16.8″N–6°50′52.7″E; altitude ~63 m ASL). The area receives less than 75 mm of rainfall annually, the climate belongs to the very arid desert type (supplementary Fig. A). Drought extends over 4 months, often more, and peaks during a very hot summer (>40 °C in July on average, range 16 °C to 51 °C). Winter is harsh with regular negative ambient temperatures at night (<6 °C in January on average, range −5 °C to 27 °C). Most of the region is represented by an immense landscape of sand dunes (great eastern erg) and by vast tabular rocky zones (Hamada). Few depressions (chotts) are seldom filled-up by water and form temporally salted lakes. Overall, in grazing areas the vegetation is sparse (supplementary List 1). Few narrow valleys benefit from local favorable conditions and provide permanent water ponds. Overall, limited foraging resources available to camels peak in winter and are minimal in summer (Chehma et al., 2010).

Sample collection

In herds, females are kept in extensive system with several males all year round. No animal was intentionally killed for this study. We opportunistically benefited from individuals slaughtered for commercial meat production; this enabled us to examine an abundant material. This method has been widely used in camels (Marai et al., 2009 for a review) and in other mammalian species (Grandi et al., 2010). A total of 322 females aged between 5 and 20 years were studied from November 2012 to February 2014. Following dissection they were assigned to two main categories: 288 non-pregnant (i.e. cyclic) and 34 pregnant females. We considered three main 4-month climatic seasons that characterize the area: November to February (N = 157, cold and relatively wet winter), March to June (N = 83; dry and relatively mild spring), and July to October (N = 82, extremely dry and hot summer). The age was estimated by teeth inspection (Schwartz and Dioli, 1992; Bello et al.,

2013). Using sequential teeth eruption and the degree of wearing of the tabular surface, individuals can be assigned to different age classes (e.g. permanent central incisors emerge in 5 year old females and are deeply worn in 12 year old camels). A crude body condition index (BCI) based on the conformation the rib cage, ischial and coxal tuberosities was scored pre-mortem (Faye et al., 2001). BCI is highly correlated with the mass of the carcass and with the fat status of individuals (i.e. mass of hump; Faye et al., 2001; Kamili et al., 2006) and thus reflects fat and protein storages that are essential for reproduction in a capital breeder. BCI ranks from 0 for very lean individuals (e.g. ischium and shoulder very prominent) to 5 for individuals with well-developed muscles, hump, and abundant under skin fat deposits (Faye et al., 2001). In practice our sample did not include very young, very lean nor very fat females (e.g. BCI = 0 or 5). Overall, individuals were assigned to three age categories (5–10 years, 11–15 years, and >16 years) and three classes of body condition (BCI < 3, 3 < BCI < 4, BCI > 4; Faye et al., 2001).

Ovarian measurements and follicular structures

The ovaries were immediately examined after slaughter in non-pregnant females. The ovarian stroma (i.e. excluding protruding large follicular structures) was measured with a caliper: two orthogonal maximal diameters in the sagittal plane for the length (L), the width (W) of the ovary, and then thickness (t). Some of these variables were correlated (e.g. L *versus* W, r = 0.428, P < 0.001, N = 576), thus we multiplied the three dimensions (LxWxt) to obtain a single broad estimate of the volume of the stroma (ovaries were irregular in shape; using ellipsoids did not change the results). The total mass of each ovary was recorded with an electronic scale (KERN PBS 6200-2 M); including the mass of the stroma plus all other ovarian structures.

All visible ovarian structures were examined macroscopically, measured (larger diameter), and classified according to previous studies (Osman, 1965; El-Wishy, 1987; Skidmore et al., 1994; Hussein et al., 2008). Smooth and black periphery ovaries were considered as inactive (Osman, 1965; El-Wishy, 1987; Hussein et al., 2008). We distinguished follicular *versus* luteal structures. Follicular structures were classified in two main groups: small size (<5 mm) and larger growing follicles (5–17 mm). This second class included medium size (5–10 mm) and pre-ovulatory follicles. Further, follicles in the process of regression were characterized by their thick and opaque follicular wall. Enlarged (cystic) follicles were ≥18 mm in diameter. The different luteal structures (e.g. hemorrhagic, large or opaque, in regression) were also recorded. The proportion of females carrying active ovaries and the proportion of females with various ovarian structures were calculated to assess the seasonal variation of the ovarian activity.

Ovarian abnormalities

Ovarian pathologies are usually associated with repeated breeding, early embryonic death, and abortion (Al-Eknah and Ali, 2001; Ali et al., 2010; Al-Afaleq et al., 2012). We recorded different lesions (e.g. para-ovarian cysts, ovarian hydrobursitis, ovarian teratoma). Ovario-bursal adhesions and cystic degeneration that are responsible for an important number of infertilities in camels (Musa, 1979; Al-Eknah and Ali, 2001; Ali et al., 2010; Al-Afaleq et al., 2012).

Abnormalities were investigated in a subsample of 165 of the 288 non-pregnant females used for ovarian examination. Each season, 55 females were randomly selected and their genital tract inspected. Macroscopic abnormalities of the ovaries and of surrounding tissues were examined and photographed. Inactive ovaries (smooth and black periphery ovaries) were discarded from these analyses due to the difficulty to tease apart pathological from normal cases at this stage.

Pregnant females

In pregnant females (N = 34) we measured: corpus luteus diameter (cm), the volume (L x h, cm^3) of left and right uterine horns, the length of the uterine body (cm), placental volume (d x h, cm^3), and main fetal dimensions (cranial diameter, shoulder height, humerus length, eye diameter). Age of pregnancy (GA) was calculated as follow: GA = (TCL + 36.80)/0.501; GA = gestational (days), TCL = total conceptus length (Ali et al., 2015). Gestation length usually ranges from 360 to 400 days, 380 days on average (El-Wishy, 1987; Skidmore et al., 1994). Therefore, the estimated parturition date was calculated as the date of slaughtering +380 days minus GA. Because fetal size was used to calculate GA, all fetal morphological variables were highly correlated among them and with GA (0.81 < r < 0.99, all P < 0.001).

Statistical analysis

In most cases the ovaries did not contain simultaneously all follicular structures (see results). We used contingency tables to analyze the proportions of ovaries with different ovarian structures to compare their occurrence among age and body condition categories, and across seasons. Continuous variables (e.g. ovary mass) were not normally distributed (P < 0.01 in all Shapiro-Wilk normality tests), even following transformations. Yet, a careful inspection of the data set revealed that in almost all cases it is was free from outlier and the distribution was quasi-normal. Analyses of variance (GLM) were used to assess the influence of the main factors (e.g. seasons) on these variables. Where appropriate (e.g. correlations or analyses of variance) we inspected the normal probability plot of the residuals to ensure that it did not deviate from a normal distribution (i.e. showing a pattern close to linearity) thereby indicating that the error terms were normally distributed in the analyses. Several variables were established as classes (body condition, age) and therefore we used non-parametric analyses for these tests. Statistics were performed with Statistica.13 (Dell Inc., 2015, Dell Statistica version 13. software.dell.com.).

Results

Global ovarian functioning

In a monotocous species, the ovaries of not-pregnant females should function through an alternate pattern of contralateral ovulation between successive cycles (Check et al., 1991). In each female, we examined which ovary (right *versus* left) contained at least one of the different follicular structures identified. We found a clear indication that the proportions of these structures were not randomly distributed between contralateral ovaries, thereby suggesting the alternate pattern of ovulation (Table 1, Fig. 1). In many females (~50%) both ovaries contained at least one small follicle (<5 mm diameter). But this proportion felt to less than 20% in all the other cases and reached very low levels (<3.5%) in the follicular structures more closely related to ovulation (e.g. ovulatory follicles). In other words, following recruitment and selection, in an overwhelmingly majority of the cases a single ovary was carrying a well-developed follicle.

Further, we tested to what extent the mass of the right and left ovaries were correlated. We considered winter, spring and summer separately to factor out the strong seasonal effect on ovarian functioning (see below). We found little or no evidence for a correlation between the mass of the right and left ovary (Fig. 2). The only significant correlation was weak, less than 8% of the variance being

Table 1

Statistical support for the Fig. 2, summarizing contingency tables comparing the proportion of ovaries that contained at least one of the ovarian structures studied (N = 288 female camels). F stands for follicle; CL stands for *corpus luteus*; Cyst means cystic. Each contingency table considered the two ovaries separately generating four situations: both ovaries positive, both negative, right positive, and left positive. The second column (Chi^2) provides the outcome. The third column (Chi^{2}b) provides the outcome from the comparison of the right *versus* left ovary. For example, for small follicles, in most cases the ovaries contained at least one structure without difference between left and right ovaries. While for ovulatory follicles most ovaries were negative, but the proportion of positive left ovaries was greater compared to right ovaries (Fig. 2). For cystic follicles the number of positive cases for the two ovaries was very low (N = 4), yet the proportion with both ovaries negative was significantly higher (Chi^2 = 221.334, P < 0.001).

Ovarian structure	Chi^2	Chi^{2}b	df	P
Small F 1–4 mm	24.979		1	*0.001*
		0.000	1	1.000
Medium F 5–10 mm	17.644		1	*0.001*
		2.1538	1	0.142
Ovulatory F > 10 mm	12.836		1	*0.001*
		4.3556	1	*0.037*
Regressing F	5.720		1	*0.017*
		3.840	1	*0.050*
CL	26.831		1	*0.001*
		1.837	1	0.175
Cyst F 25–60 mm	1.236		1	0.266
		8.163	1	*0.004*

explained (Fig. 2). This suggests that although the respective mass of both ovaries vary in a comparable way across seasons (correlation between left and right ovary mass, seasons pooled: r = 0.683, r^2 = 0.466, $F_{1, 286}$ = 249.399, P < 0.001) they rather follow an independent pattern within season. Interestingly the left ovary was the only one to weigh regularly more than a 20 g threshold (Fig. 2), and was significantly more often active (in terms of follicle development; Table 1 and Fig. 1). In winter the left ovary tended to be heavier compared to the right one while the opposite pattern was observed in summer; in spring the data were scattered (Fig. 2).

This complex contralateral functioning, where one ovary is involved in the production of a single ovulatory follicle, and where the left and right ovaries exhibit a peculiar pattern, means that the two ovaries should be considered as a single system rather than as a duplicated system. This enabled us to pool the two ovaries of each female to consider how the global ovarian functioning was influenced by other factors. In other words, the contralateral patterns observed means that any possible pseudo replicate effect due to the
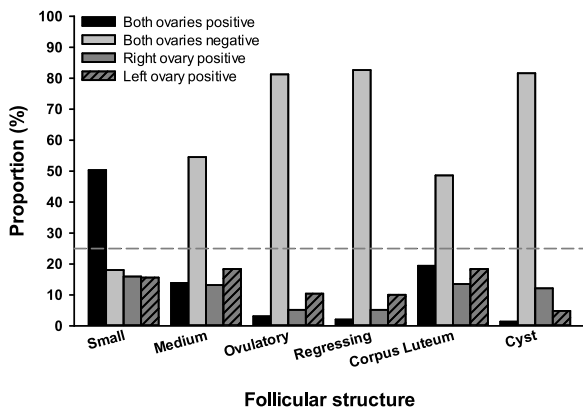

Fig. 2. Relationship between the mass of the left (Y-axis) *versus* right (X-axis) ovaries assessed during three seasons in 288 female camels: winter (r = 0.104, r^2 = 0.011, $F_{1, 142}$ = 1.555, P = 0.214, white circles); spring (r = 0.074, r^2 = 0.006, $F_{1, 70}$ = 0.389, P = 0.535, light grey circles); summer (r = 0.269, r^2 = 0.073, $F_{1, 70}$ = 5.480, P < 0.022, dark grey circles). The mass of the ovary includes the stroma and other structures (follicles, luteal structures). The regression line (black line) is displayed for the significant correlation in summer. Three reference lines (dashed grey lines, set at 20 g or at equivalence) facilitate comparisons between contralateral ovaries.

presence of two ovaries per female was negligible in the analyses based on the presence of developed ovarian structures.

Seasonal variations of ovarian size and mass

We found clear seasonal effects on the size and on the mass of the ovaries: ANOVA with seasons as the factor, the volume of the stroma of the ovaries ($F_{2, 285}$ = 58.505, P < 0.001), or the total mass of the ovaries ($F_{2, 285}$ = 771.890, P < 0.001) as the dependent variables (Figs. 2 and 3). We observed a progressive increase from winter to summer of the stroma volume of the ovaries (Fig. 3a), but the total mass of the ovaries decreased over time (Fig. 3b). The development of follicles or of corpora lutea (CL) was accompanied by a decrease of the volume of the ovarian stroma.

Seasonal variations of ovarian structures

In order to take into account the contralateral ovulation pattern we first examined the proportion of females with one or two ovaries classified as active (i.e. follicles ≥5 mm or large ovarian structure like CL) *versus* inactive (i.e. smooth ovaries or follicles ≤4 mm). Almost all females (N = 280, 97.2%) provided consistent results with both ovaries being either active (N = 181) or inactive (N = 99). Thus, for each female we considered the ovaries as being active (N = 189 females with one or two ovaries active) *versus* inactive (N = 99, two ovaries inactive). Discarding the 8 individuals with only one active ovary from the pool of females with two active ovaries did not change the statistical significance of any result.

The proportion of females with active ovaries varied significantly across seasons (N = 288 females; Chi^2 = 11.22, df = 2, P < 0.005): the proportion increased from winter (N = 99 active among 144, 68.8%) to spring (N = 54 active among 72, 75.0%) and decreased in summer (N = 36 active among 72, 50.0%). The proportion of females with inactive ovaries (smooth and black periphery ovaries) directly mirrored this trend and was notably higher in summer (N = 36/72, 50%). We explored this pattern more precisely.

Fig. 1. Proportions (Y axis) of ovarian structures (X axis) observed in left and right ovaries of female camels (N = 288). Four exclusive situations were possible: both ovaries positive (black), both negative (light grey), or only one positive. We then distinguished cases were the right ovary was positive (dark grey) from cases where the left ovary was positive (hatched bar). The horizontal dashed grey line indicates 25% to facilitate comparisons (equal distribution of positive cases among the four situations). Associated statistics are provided in the Table 1.
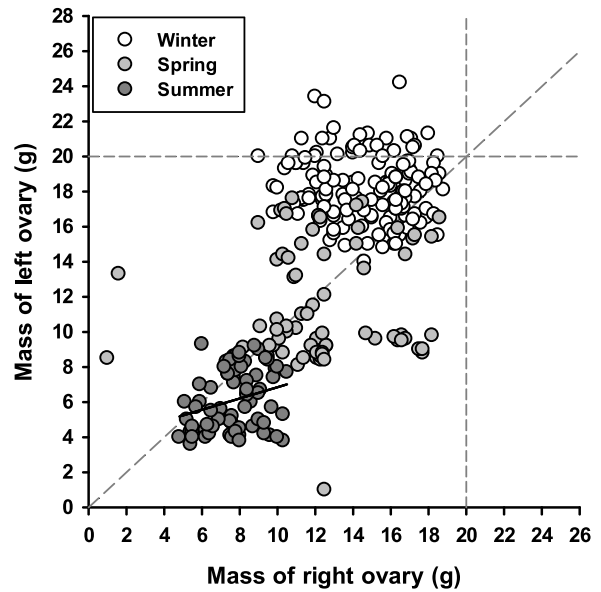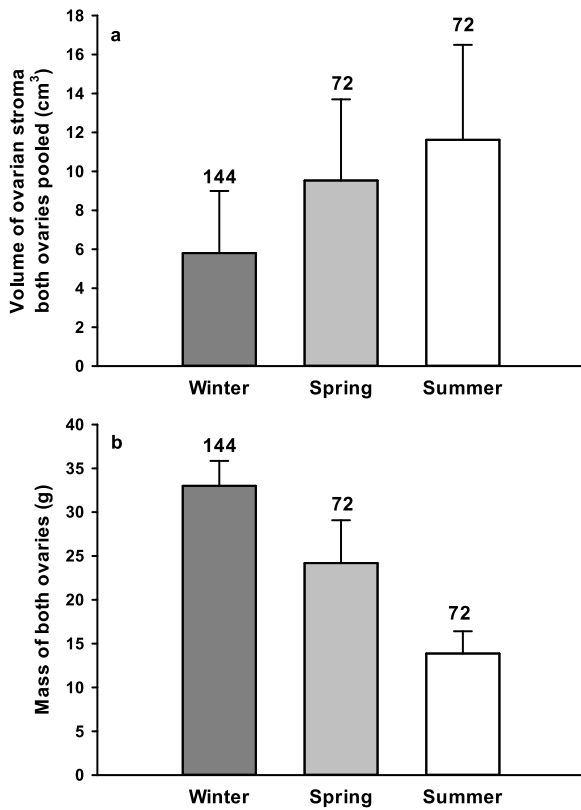
Fig. 3. Seasonal changes of the mean ovarian stroma volume (top graph a), and of the mean mass of the ovaries (bottom graph b) during winter (dark grey), spring (light grey), and summer (white) in 288 female camels. Means are expressed with their SD, sample sizes are provided. See text for statistics.

The proportion of small follicles (<5 mm), of larger follicles and of other ovarian structures found in the ovaries varied across seasons (Fig. 4), and these variations were not random (Table 2). While the number of small follicles increased from winter to summer, the number of larger structures decreased concomitantly (Fig. 4 and Table 2). Dominant follicles (11–17 mm) were not observed in summer. The overall number of females carrying cystic follicles was relatively low (N = 53), but the proportion was nonetheless highest in spring (30.6%) compared to winter and summer (17.4% and 8.3% respectively). The number of CL was higher in winter (62.5% of the females carried one CL) compared to spring and summer
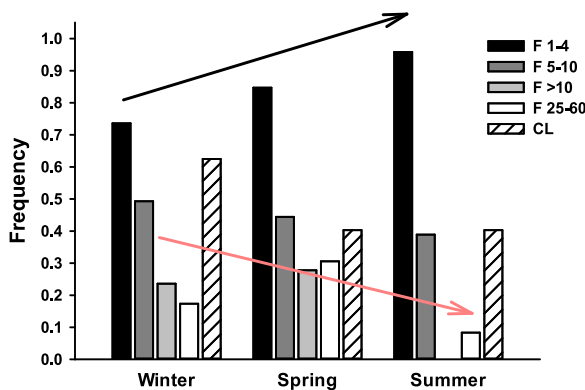
Table 2

Statistical results for Fig. 4. Possible seasonal effects on the proportion of female camels (N = 288) where various ovarian structures (first column) have been detected (positive) or not (negative) were examined using contingency tables and chi squared tests. Three seasons were considered (winter, spring and summer). F stands for follicle; CL stands for *corpus luteus*.

Structure	Positive	Negative	Chi^2	df	P
Small F 1–4 mm	236	52	16.522	dl = 2	*p<0.001*
Medium F 5–10mm	131	157	2.142	dl = 2	p = 0.343
Ovulatory F > 10mm	54	234	22.701	dl = 2	*p<0.001*
Regressing F	50	238	23.330	dl = 2	*p<0.001*
CL	148	140	14.233	dl = 2	*p<0.001*
Cyst F 25–60 mm	53	235	12.047	dl = 2	*p = 0.002*

(40.3% of the females). Overall the ovaries tended to progressively carry a lower number of large ovarian structures (large follicles, CL) from winter to summer while the recruitment of new small follicles increased.

Effect of age, body condition and seasons on ovarian activity

The three categories of body condition were not distributed equally among the three age classes (contingency table: Chi^2 = 335.62, df = 4, P < 0.001; Fig. 5). Notably, almost all young females exhibited a low body condition index. This situation precluded distinguishing the respective influence of age *versus* body condition across the full spectrum of age and body condition classes. Consequently, we performed a set of restricted (i.e. more focused) analyses.

The mean age of the sampled females decreased from winter to summer (mean age class shifting from 2.2 to 1.8; Kruskal-Wallis H_2 = 17.00, P < 0.001, N = 288). Consequently, we considered each age class separately to examine changes of body condition over time. Across seasons, we observed a complex pattern where the mean body condition of young females was low and remained stable (Kruskal-Wallis H_2 = 2.25, P = 0.324, N = 78), was intermediate and decreased in the medium age class (Kruskal-Wallis H_2 = 6.27, P = 0.043, N = 117), but was high and tended to slightly increase (not statistically significantly) in the oldest females (Kruskal-Wallis H_2 = 4.43, P = 0.109, N = 78; Fig. 6). In each season, the mass of the ovaries did not differ among the age classes (Kruskal-Wallis H_2 were respectively 3.78, 4.58 and 1.32 in winter, spring and summer; 0.101 < P < 0.515; Fig. 6). Similarly, considering each season

Fig. 4. Seasonal pattern of ovarian functioning in 288 female camels. The frequency of different types of follicles found in the ovaries varied across seasons. The frequency increased from winter to summer for small follicles (black arrow), but tended to decrease for larger structures (grey arrow). F means follicle and CL stands for *corpus luteus*. Associated statistics are provided in the Table 2.
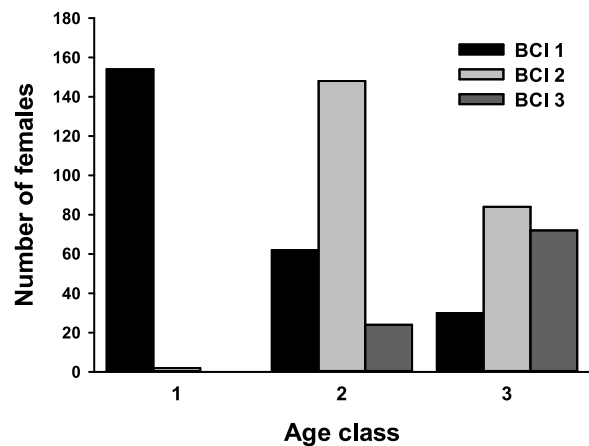

Fig. 5. Distribution of the numbers of female camels (N = 288) in function of the age classes (3 classes, X-axis) and body condition (3 classes indicated with black and grey pattern). Age classes (1: 5–10 years; 2: 11–15 years, and 3: >16 years) were determined using rostral dentition (Bello et al., 2013). Body condition index (BCI) was based on morphological traits and scored as recommended by Faye et al. (2001).
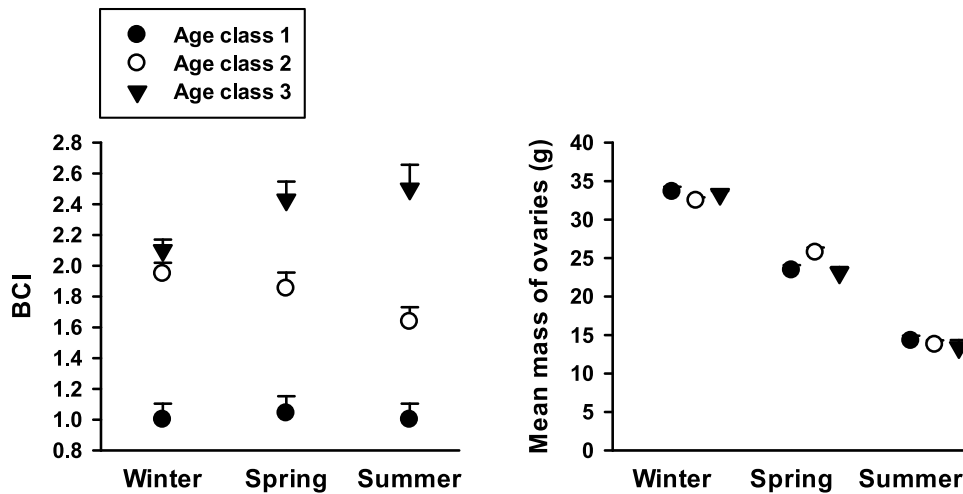
Fig. 6. Seasonal variations of body condition (BCI, Y-axis, left panel) and ovary mass (g both ovaries pooled, Y-axis, right panel) in function of the three age classes (white and black symbols) in 288 female camels. BCI exhibited a complex seasonal pattern while the mass of the ovaries decreased in a similar way in the three age classes (1: 5–10 years; 2: 11–15 years, and 3: >16 years).

Table 3
Prevalence (%) of different pathological conditions observed in the ovaries of 165 slaughtered female camels. The last column (proportion) provides percentages calculated on the 22 affected females.

Type of disorder	N	Prevalence (%)	Proportion (%)
Follicular cyst	8	4.8	36.4
Hemorrhagic cyst	3	1.8	13.6
Luteinized follicular cyst	2	1.2	9.1
Par ovarian cyst	1	0.6	4.6
Ovarian teratoma	1	0.6	4.6
Oophoritis	1	0.6	4.6
Ovarian bursitis / hydro-bursitis/ pyo-bursitis	6	3.6	27.3

separately, we observed a lack of age effect on the size of the ovaries ($0.310 < P < 0.721$).

Considering the three age classes, the three categories of body condition, and the different ovarian structures identified (5 main types) generated a high number of possibilities for the proportions of positive *versus* negative examinations. To limit the inflation of the results we selected the most salient effects. For simplicity we extracted and compared the highest proportion of positive examinations (i.e. presence of ovarian structures) per season, age and body condition classes (Fig. 7). We used these series of proportions to factor out the uneven distribution of body condition classes among the different age classes. Disregarding seasons, the main trend was driven by age and body condition: the proportion of positive examinations (a proxy for ovarian activity) increased in older individuals with higher body condition index (all $P < 0.05$, detailed results not shown for conciseness).

Ovarian abnormalities

Table 3 summarizes the abnormalities observed in 22 non-pregnant females among the 165 selected (prevalence 13%). Ovarian cysts (follicular + hemorrhagic + luteinized cysts) and clearly pathological conditions of ovarian bursa (ovarian bursitis, hydro bursitis, pyo-bursitis) were the most commonly observed categories of abnormalities.

Season, age and BCI did not influence the occurrence of abnormalities (Chi^2 = 1.99, df = 2, P = 0.370; Chi^2 = 0.74, df = 2, P = 0.690; and Chi^2 = 3.09, df = 2, P = 0.213 respectively). However only one female among 25 that displayed a high BCI (>4) showed an abnor-
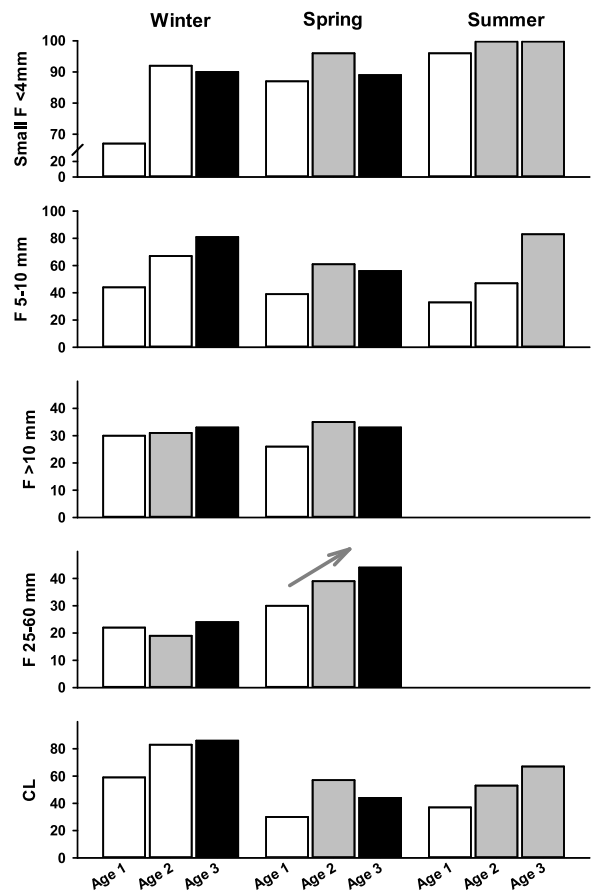

Fig. 7. Proportions (%) of positive examinations for five main ovarian structures in function of seasons, age classes (3 categories noted Age 1 to Age 3) and body condition index (3 BCI categories indicated with a white, grey and black scale) in 288 female camels (see Table 2). On the X-axes, F stands for follicle and Cl for *corpus luteus*. In each season, the proportions of positive examinations tended to increase with age. All the bars in the left part of each panel (13/13) are white and thus pertain to young females with a low BCI. Most bars situated in the right are black (10/13) and pertain to old females with a high BCI. Most bars in the middle are grey (9/13) and correspond to intermediate females in terms of age and body condition. The grey arrow shows a typical example for this trend. In summer some data were lacking.

Table 4
Seasonal mean values for several traits recorded in 34 pregnant female camels (five first lines) and in their fetus (five last lines). CL stands for *corpus luteum*. Means are provided ± SD, sample size is provided in bracket for each season. Results from the comparison among seasons (ANOVA: F, df and P values) are provided for each trait in the two last columns (significant effects italicised).

Source	Winter (N = 13)	Spring (N = 11)	Summer (N = 10)	$F_{2, 31}$	P
Gestational age (d)	130.0 ± 96.0	116.5 ± 28.9	190.6 ± 53.4	3.50	*0.043*
CL (cm)	1.82 ± 0.24	1.86 ± 0.17	1.91 ± 0.33	0.40	0.671
Left uterine horn (cm^3)	295.9 ± 494.8	262.2 ± 235.4	732.8 ± 403.0	4.54	*0.019*
Right uterine horn (cm^3)	695.0 ± 959.2	699.0 ± 413.3	1244.4 ± 621.6	2.02	0.149
Length of uterine body (cm)	23.2 ± 20.1	21.5 ± 7.4	31.5 ± 11.6	1.399	0.262
Placenta volume (cm^3)	1998.3 ± 3419.5	2563.8 ± 1199.8	3148.9 ± 1426.9	0.676	0.516
Cranial diameter (mm)	23.6 ± 35.1	18.6 ± 10.6	45.8 ± 19.5	3.50	*0.043*
Shoulder height (cm)	15.5 ± 24.5	12.1 ± 6.1	28.8 ± 11.4	2.91	0.070
Humerus (cm)	3.5 ± 4.8	3.1 ± 1.7	7.2 ± 2.8	4.4	*0.021*
Eye diameter (cm)	0.82 ± 0.23	1.75 ± 0.73	0.69 ± 0.45	4.24	*0.024*

mality (4.0%) while this proportions was respectively 11.9% (N = 7 among 59) and 17.3% (N = 14 among 81) in females with low or intermediate BCI.

Pregnancy

The total number of pregnant females was 34, representing an average pregnancy rate of 10.6% in our sample (N = 322 adult females). The proportion of pregnant females did not change significantly across seasons (8.3% in winter; 13.3% in spring and 12.2% in summer; Chi^2 = 1.74, df = 2, P = 0.420). The mean gestation age (GA) was 143.5 ± 73.3 days (ranging from 69.6 to 381.1 days across seasons) and was higher in summer (Table 4). Mean values of most uterine and fetal traits were higher in summer compared to winter and spring (two seasons that were relatively similar in terms of mean values; Table 4), albeit seasonal differences were not always significant (Table 4). Post-hoc tests revealed a lack of difference between winter and spring and confirmed the fact that summer differed from the two other seasons in many cases (not all results are shown for conciseness). A strong variability was observed for most fetal or uterine traits (cf. the elevated SD in Table 4). Mean CL diameter did not change across seasons (Table 4).

Females from the lower BCI group tended to be pregnant less often than females from the two other groups (respectively 6.1%, 14.0% and 12.8% of pregnant females with increasing BCI category), however this effect was not significant (Chi^2 = 4.70, df = 2, P = 0.095; yet, small sample size limited the power of this analysis). Ages did not influence significantly pregnancy rate (respectively 9.3%, 7.90% and 14.7% with increasing age category; Chi^2 = 3.07, df = 2, P = 0.215).

We examined the influence of maternal characteristics (age and BCI) on uterine and fetal traits. Because these traits are highly correlated we used only gestational age (GA). We also considered the effect of seasons and the interactions between maternal and seasonal factors. Mean GA was significantly higher in older females, and it increased from winter to summer without significant interaction between age and seasons (Fig. 8 and Table 5). Mean GA was

Table 5
Effect of age, season, and body condition (BCI) on gestational stage (a proxy of fetal development status) recorded in 34 female camels. ANOVAs were performed sequentially, first using age and then BCI, as independent variables because several cells were empty (e.g. no old female with very low body condition). This table provides statistical results for the Fig. 8. Significant effects are italicised.

Source	F	Df	P
Age (Ag)	7.261	2,25	*<0.03*
Season (S)	3.543	2,25	0.044
Interaction (Ag × S)	0.522	4, 25	0.722
Body condition (BCI)	36.648	2,25	*<0.001*
Season (S)	6.022	2,25	*<0.01*
Interaction (BCI × S)	4.656	4, 25	*<0.01*

more elevated but was not significantly influenced by seasons in females with a high BCI; mean GA was lower in females with intermediate and low BCI, and it increased from winter to summer (Fig. 8 and Table 5).

Most estimated parturition dates fell in winter (N = 25, 73.5%), seldom in spring (N = 8, 23.5%), and rarely in summer (N = 1, 3%); these proportions differed from a random distribution across seasons (Chi^2 = 114.96, df = 2, P < 0.001). In young females (Age 1, N = 8), 50.0% of the estimated birth dates did not fall in winter. This proportion was 30.0% in females from the Age-2 category (N = 10), and 12.5% in older females (N = 16). Regarding BCI, the proportions of non-winter births were, respectively, 50.0%, 15.8% and 28.6% in females from the low (N = 8), medium (N = 19) and high (N = 7) BCI groups. We found no significant difference among these proportions regarding age or BCI categories, either considering categories simultaneously (all P > 0.412) or separately (all P > 0.096). Sample size was small for these analyses however (N = 34 pregnant females for 3 seasons and 6 age/BCI classes). All embryos or fetuses were found in the left uterine horn.

Discussion

Results on the interactions among intrinsic and environmental factors shed light on regulatory processes of reproduction of a large ungulate in extremely arid habitats. This information contributes to better understand mammalian reproductive strategies (Clutton-Brock and Harvey 1978; Saether and Gordon, 1994), notably considering the continuum between capital and income breeding strategies, or regarding the impact of environmental fluctuations on fertility (Houston et al., 2006; Parker et al., 2009). Below we first address methodological issues, then review the main results.

One limit of this study was the lack of control on the females that were brought to the abattoir. Indeed, farmers may select which individuals they sell *versus* those they decide to keep in the breeding herd. However, whatever the selection operated by farmers (or buyers), it is unlikely that the status of the ovaries was known. Similarly, females during early gestation or carrying ovarian abnormalities cannot be easily detected unless specific diagnostic is performed. No specific examination being performed by herders, the selection of most females studied was largely random. Our large sample size enabled us to examine a wide range of ages and body conditions during the three seasons that characterize the climate of the study area. Importantly, the animals examined were raised through an extensive system, and thus they were subjected to natural climatic conditions and fluctuations of food availability. Consequently, our analyses based on ovarian functioning, pregnancy rate, and ovarian pathology prevalence likely reflected the influence of endogenous and exogenous resources needed for reproduction.
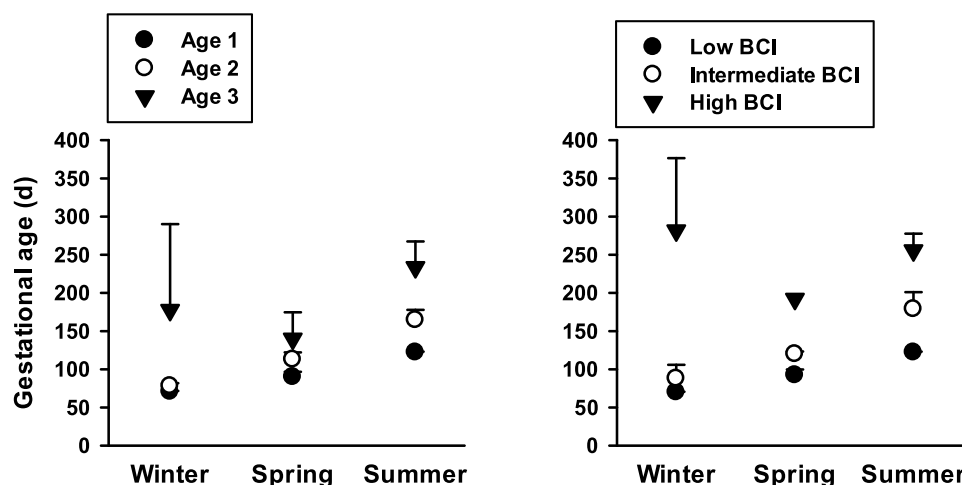
Fig. 8. Mean gestational age (±SE, Y-axis, days) of the fetus of the 34 pregnant females examined across seasons (X-axis). In the left panel, females were classified according to their age (Age 1, N = 8; Age 2, N = 10; Age 3, N = 16); and in the right panel in function of their body condition (BCI 1, N = 8; BCI 2, N = 19; BCI 3, N = 7). The high values for the SD recorded in winter in old females, characterized with a high BCI (black triangle in winter), was due to one outlier (a relatively old fetus with an estimated GA of 381 days).

Seasonal pattern

The mass and the size of the ovaries were strongly affected by seasons. Ovarian size excluded large ovarian structures, thus our results superficially provided a paradoxical pattern with opposite trends between ovarian volume and ovarian mass (Fig. 3). But the mass of the ovary included ovarian structures, and thus was an integrative index. We observed a decrease of overall ovarian mass from winter to summer, concomitant to an increase of the volume of the ovarian stroma (Figs. 3 and 6). These results echo studies in camels reporting that sexual activity increases during winter and spring (Akral and Khanna, 1995; Ali et al., 2007; Hussein et al., 2008; Marai et al., 2009; El-Harairy et al., 2010; Zeidan et al., 2011; El-Hassan and Tingari, 2015; Yahaya et al., 1999). Yet, beside a broad consistent seasonal pattern with a reproductive peak in winter, more detailed comparison among studies reveals important differences. For instance, we found strong seasonal variations of ovarian volume (Fig. 3) and in the proportion of females carrying ovulatory follicles (Table 2 and Fig. 4), but El-Hassan and Tingari, (2015) and Sghiri and Driancourt (1999), respectively, reported a lack of effect. These discrepancies cannot be explained by divergences among studies in the mean age or body condition of the animals sampled. Indeed, while we found strong and complex interactions between these factors and seasons, Ali et al. (2007) reported that age did not influence either the activity or the mass of the ovaries. Moreover, the proportion of females with active ovaries (follicles >5 mm) ranged between 74% and 89% in Morocco (Sghiri and Driancourt, 1999), but from 50% to 75% in our study, and from 46% to 87% in Pakistan (Ali et al., 2007). Overall, available data show divergences across populations distributed across a wide array of geographical and climatic situations, and thus exposed to seasonal differences in food availability.

The marked seasonal pattern observed was expected. In winter food and water are relatively abundant while climatic conditions relatively mild: individuals can invest resources into reproduction (Tibary and Anouassi, 1996; Barros et al., 2015). Nonetheless, both in current and previous studies, female camels did not exhibit a cessation of reproduction during the extremely harsh summer conditions (Marai et al., 2009; El-Harairy et al., 2010). In other mammals living in the same desert area, reproduction is strictly seasonal and it coincides with the mild season (e.g. in sand rats; Khammar and Brudieux, 1984). But among desert mammals, camels present unique traits that may explain the persistence of reproductive activity. They are the largest desert animals (body mass often

exceeds 500 kg, up to 600 kg in dromedaries and up to 1000 kg in Bactrian camels), they can accumulate very large body reserves, and gestation extends over more than one year (El-Wishy, 1987; Kamili et al., 2006). Large size confers buffering against harsh climate while large body reserves permit a temporal dissociation between foraging and reproduction. Because gestation is particularly long in camels, reproductive activity cannot be limited to early spring. In comparison, small rodents can achieve reproduction, from vitellogenesis to parturition, in few months; but they also depend on deep shelters to survive in arid habitats (Tchabovsky et al., 2004; Novillo et al., 2017).

These traits do not fully explain why reproduction is not strictly seasonal. For example, photoperiodic mechanisms may promote the establishment of a strict breeding cycle to ensure that all parturitions occur during the most favorable period for the neonates and for lactation (McAllan and Geiser, 2006; Kriegsfeld et al., 2015). Thereby, ovarian activity should be periodically inhibited to prevent possible mismatch between births and favorable climatic conditions. Our data mainly conform to this pattern, but not fully. Mean gestational ages recorded across seasons indicate that most births should occur in winter (Fig. 8). But approximately 25% of the parturitions should occur in spring and summer (rarely). Births occur throughout the year without seasonal peak in Kenya ranches (Wilson, 1986), but mostly in August in Sudan (Babiker et al., 2011). This lack of strict periodicity suggests that parturition date is not the unique determinant of reproductive timing in camels.

Possible roles of age, body size and body condition

In birds and most mammals, notably ungulates, growth is determinate (Mumby et al., 2015). Remarkably, both female and male camels continue to grow during the first years after maturity: a relatively modest increase of skeletal body size is accompanied by a strong augmentation of body volume and body mass (Ishag et al., 2011). Perhaps increasing body size and mass in older individuals provides physical and social advantages?

If age and body size confer benefits, then BCI (and integrative index of the trophic status) and ovarian activity should be higher in older females compared to younger ones. Once the very strong influence of seasons was considered, our results revealed precisely that older females exhibited higher BCI, carried significantly more often active ovaries or large ovarian structures, and were expected to give birth more often in winter compared to younger females. A previous study suggested that older females exhibit higher BCI

and ovarian activity scores (Hussein et al., 2008); statistical tests were lacking and seasons were pooled, precluding examining the effect of age and BCI *per se* however. Our results also show that only oldest females were able to increase their BCI from winter to summer (Fig. 6). We speculate that the ability to store resources increase with age; greater experience (higher social status?) may promote maternal survival, limit abortion rate, improve parental care and neonate growth. Future studies are needed to test these hypotheses.

Underlying mechanisms for low fecundity

Fertility is strongly constrained in female camels. Maturity is delayed: puberty occurs at 3–4 years (sometimes later, Wilson, 1986), almost twice the value of similar size ungulates (e.g. in mares puberty begins at 18 months on average; Bennett and Hoffmann, 1999). Annual fecundity is low in camels (less than one calf every 2–3 years on average) but reproductive life is prolonged (until 20 years, total life expectancy exceeds 40 years) (Skidmore, 2005; Marai et al., 2009). These characteristics are typical of species displaying a slow pace of life and a slow reproductive strategy; as observed in ungulates (e.g. mountain goat) living in environments with limited resource availability (Festa-Bianchet et al., 1995).

The peculiar unbalanced pattern of the contralateral functioning of the ovaries fits well with a slow reproductive rate. One side of the reproductive tract is specialized to produce offspring: the left ovary was the most active one (this study; El-Wishy, 1987; Skidmore, 2005; El-Harairy et al. 2010 but see Tibary and Anouassi, 1996) and almost all conceptuses (>90%–100%) were found in the left uterine horn (Ismail, 1987; this study). This suggests a functional lateralization, also observed in other ungulates, albeit in a less pronounced way (Gupta et al., 2011). The mechanisms that underlie the dominant and subordinate ovarian system (Armstrong and Webb, 1997; Webb et al., 2004; Beg and Ginther, 2006; Lucy, 2007; Manjunatha et al., 2012; Monaco et al., 2015) seem to be strongly lateralized in camels.

The percentages of females with active ovaries, with one (rarely two) pre-ovulatory follicle(s), and that were pregnant were low (respectively 50%–75%, ∼18%, and ∼10%). Therefore, following follicular recruitment and dominance (Monaco et al., 2015), further drastic selective mechanisms reduce the number of follicles that eventually lead to gestation. The outcome is the infrequent production of a unique gamete, and of an even less frequent calf. Seldom poly-ovulation with multiple CL has been recorded (El-Wishy, 1987), but only one viable fetus was detected after nine weeks of gestation. Possible role(s) of the contralateral ovary remain to be deciphered (for example by investigating possible inhibition of the hypothalamo-pituitary axis). Whatever the case, we propose that the strong lateralization of the reproductive tract of female camels underlies their slow breeding rate and represents an adaption to arid deserts.

In has been assumed that female camels in poor condition are prone to ovarian pathologies and low fertility, especially under harsh environmental conditions (Benaissa et al., 2015). Our results do not support this scenario: age, season, or BCI did not influence the prevalence of ovarian abnormalities. Regardless, the observed proportions of ovarian pathologies fell broadly into previously documented range (Al-Eknah and Ali, 2001; Al-Afaleq et al., 2012; Benaissa et al., 2015). The regulatory mechanisms that adjust fertility with seasons, age and BCI may not primarily involve pathological pathways as documented in dogs (Ortega-Pacheco et al., 2007).

Are camels capital breeders?

Capital and income breeding refer to the extremes of a continuum ranging from strategies where body reserves finance reproduction to strategies where reproductive effort is financed by concomitant food intake; various intermediate strategies have been described (Warner et al., 2008; Stephens et al., 2014). Strictly speaking, pure capital breeding corresponds to organisms where reproduction is entirely fuelled (i.e. from the onset of gametogenesis to the production of independent offspring) by resources accumulated prior to reproduction (Bonnet et al., 1998). This strategy is characterized by a high BCI threshold below which reproduction is inhibited (Naulleau and Bonnet, 1996). This extreme strategy seems to be incompatible with the high metabolic rate of endotherms (Bonnet et al., 1998). Even large seals, once considered as typical capital breeders, have to feed during reproduction (Wheatley et al., 2008). Our results in female camels do not make exception. Despite a remarkable ability to store huge amounts of reserves in the hump, several females with a low BCI were reproductive while many females with a high BCI were not. Moreover, following parturition, in female camels supplemented with food, ovarian activity rapidly increased and this effect represents a typical income breeder response (Kelanemer et al. 2015). Yet, BCI positively influenced ovarian activity and possibly early pregnancy rate. Therefore female camels fuel reproduction by combining both endogenous reserves and recently acquired food, and might be classified as (not pure) capital breeders. The lack of precise measurement of the reliance of camels on capital during reproduction makes this categorization putative however (Stephens et al., 2009).

Abortions and pre-weaning mortality can reach 25.7% in camels, reproduction failures are common. Late gestation and milk production might be more demanding compared to the production of a single gamete and to the specific metabolism increase of early gestation (Wilson, 1986). Body reserves might be primarily used during these sensitive phases, to sustain the elevated energy demands of a large fetus, of parturition, and of lactation, but not to trigger ovarian activity *per se*. Old reproductive females with a high BCI should be more resistant to drought and food shortage. The increase of BCI with age we observed in females, and their ability to maintain a high BCI in summer support this view. Further investigations until weaning are needed, however, to accurately assess the influence of BCI on reproductive success.

Conclusion

In an extremely arid area, dromedary camels exhibit low reproductive rates and marked seasonal patterns. Our results exemplify the great geographic variations of reproductive phenology and breeding rate of this species (review in Marai et al., 2009; El-Hassan and Tingari, 2015). Reproduction of female camels appears to be flexible, partly driven by climatic conditions but not locked by photoperiod, influenced by age and body condition but not dependent on a high threshold of body reserves. In females, ovarian activity and reproduction extend all year-round and can be adjusted to current conditions. Flexibility is advantageous for seizing unpredictable opportunities. Indeed gestation lasts more than one year and weaning generally almost one year. Such a long reproductive period (∼2 years) cannot fit within a single favorable winter/spring season. Large body size combined with the capacity to store very large body reserves might confer sufficient flexibility to exploit the scanty fluctuating resources in desert habitats. Dromedary camels may exhibit a combined income/capital breeding strategy where body reserves buffer periodic food and water shortage from follicular recruitment to weaning. In the studied population, climatic conditions are particularly harsh and most births occur in winter, suggesting that physiological limits have been reached.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.mambio.2018.10.002.

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