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Original Article

Reproductive biology of *Gazella arabica*: predictors of offspring weight and short- and long-term offspring survival

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Abstract

Reproductive traits are central to organismal fitness, and so the factors influencing patterns of reproduction and offspring survival are at the heart of biology. Making use of breeding data collected over 16 years at the King Khalid Wildlife Research Centre in Saudi Arabia, we investigated the reproductive biology of Arabian gazelles *Gazella arabica*. Offspring survival was mainly a function of birth weight, with heavier offspring having higher survival rates than lighter offspring. However, while sons were heavier than daughters, daughters had higher survival rates. We could not find evidence that giving birth to sons negatively impacts offspring weight in the following year. We uncovered large narrow-sense heritability (h^2) in offspring weight at birth, while maternal effects (m^2) on birth weight were of lesser importance. However, maternal effects on offspring survival were strong until weaning age, while paternal effects dominated survival to sexual maturity and first reproduction. We propose that variation in maternal postnatal care might overshadow the effects of maternal inheritance of birth weights, while the overall strong heritability of weight at birth and the paternal effects on survival illustrates strong variance in sire fitness based on genetic quality, suggesting a role for sexual selection by female mate choice in wild populations.

Key words: Arabian gazelles, heritability, life-history evolution, offspring mortality, sex differences, ungulates.

While fitness has many different components, the decisions surrounding an individual's reproductive tactic play a central role in determining its fitness (Stearns 1992; Roff 2002). Thus, quantifying offspring quality and evaluating parental contributions to it are integral to the study of interindividual fitness variation, and for understanding the population dynamics and life-history evolution of a given species (e.g., Gaillard et al. 1998). Parental contributions *sensu* Evans (1990) include the heritability of parental quality measures but also the amount of parental resource allocation and investment provided to offspring after parturition. Ungulates are hereby characterized by high levels of energy allocation into each reproductive bout (Pélabon et al. 1995). While male ungulates usually only contribute very limited paternal care (Kleiman and Malcolm 1981; Bowyer et al. 2020), the energy allocated by females into maternal care, by comparison, is immense, and the highest fitness costs associated with maternal investment are incurred during lactation (e.g., Clutton-Brock et al. 1989; Froy et al. 2016).

One of the strongest measures of offspring quality is offspring survival (also expressed as offspring mortality). Although offspring mortality is mainly driven by environmental factors such as predation, disease, parasitism, or resource availability, both parental and offspring attributes (i.e., birth mass, birth date, sex, parental age, or parental care) also play a vital role during early life stages (e.g., Clutton-Brock et al. 1985; Gaillard et al. 2000; Johnstone-Yellin et al. 2009; Gilbert et al. 2020; Desforges et al. 2021). In this context, offspring weight is often used as a good representative of offspring size, and large offspring usually have a higher survival rate than smaller-sized offspring (e.g., Gaillard et al. 2000; Riesch et al. 2013), and life-history theory predicts offspring size to increase in low-quality environments (e.g., Rollinson and Hutchings 2013a, b). Offspring sex is another important component of offspring quality, since offspring mortality is usually higher in male than female ungulates (e.g., Cassinello and Gomendio 1996; Gaillard et al. 2000; Riesch et al. 2013; Kentie et al. 2020). Moreover, in species with variable litter sizes, offspring mortality usually increases as a function of litter size (e.g., Gaillard et al. 2000; Riesch et al. 2013). While most ungulates tend to give birth to singletons (Hamlett and Wislocki 1934; Kingdon 2013), some species like Saharan

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Barbary sheep (*Ammotragus lervia sahariensis*; Cassinello and Gomendio 1996) or sand gazelles (*Gazella marica*; Riesch et al. 2013) are known to produce larger litters at relatively high frequencies and, consequently, show higher mortality rates.

Surprisingly, even though all true gazelles (genus *Gazella*) are listed as vulnerable or endangered by the IUCN (http://www.iucnredlist.org), relevant data on dynamics and trade-offs governing reproductive life histories in this group are largely lacking (but see Riesch et al. 2013; Shalmon et al. 2020), hampering the implementation of such information in conservation and management plans (Child and Grainger 1990; Dunham et al. 2001; Wronski et al. 2012). In recent decades, ex-situ conservation has become increasingly important by providing genetic reservoirs against extinction and by breeding endangered species for future reintroductions. Moreover, ex-situ collections can be useful in a wider spectrum of conservation activities, such as conservation education, capacity building, and the production and assimilation of research materials, to better understand complex natural phenomena such as the life history and reproductive biology of threatened species (Zimmermann et al. 2007). Making use of the captive breeding program conducted at the King Khalid Wildlife Research Centre (KKWRC, Saudi Arabia), we investigated patterns of offspring size, sex ratio, and offspring survival in Arabian gazelles *Gazella arabica*. Arabian gazelles are sexually dimorphic, polygynous browsers that prefer rocky, hilly habitats with moderate vegetation (Vesey-Fitzgerald 1952; Wronski et al. 2010a; Lerp et al. 2013a, b). KKWRC essentially represents a common-garden (i.e., low-density, *ad libitum* food, and basically no predation) environment, in which veterinarians also largely control the occurrence of disease and parasitism (see Methods section for details). This effectively removes most environmental factors known to affect offspring mortality in wild populations (Gaillard et al. 2000; Owen-Smith et al. 2005), and so we argue that this system is particularly well suited to investigate the innate fitness consequences of differences in offspring sex and offspring weight at birth, as well as maternal provisioning and pedigree effects. Some environmental factors at KKWRC (i.e., temperature or precipitation), however, were beyond our control, and should, therefore, still have a measurable impact on *G. arabica* life histories (see below). While some studies have shown that in captivity, inbreeding could become a major factor of offspring survival (e.g., Ralls and Ballou 1982; Quilicot and Baumung 2016), inbreeding does not appear to be a major contributor to offspring mortality at KKWRC (Soares et al. 2015).

We asked 5 specific questions (Table 1). Question 1 asked about the general reproductive biology of *G. arabica*. This includes an evaluation of sex ratio at birth as well as the temporal distribution of births across a calendar year and allows comparison of these patterns to those of the close relative, *G. marica*. Question 2 asked what factors influence weight at birth in Arabian gazelles. Weight at birth is known to have a strong impact on juvenile competitiveness and survival across vertebrate taxa (e.g., Gaillard et al. 2000; Kühl et al. 2007; Riesch et al. 2012) and often differs between the sexes with males usually being heavier at birth than females (e.g., Cassinello and Gomendio 1996; Gaillard et al. 2000; Riesch et al. 2013). We, therefore, also predicted to find this pattern for *G. arabica* (prediction 1), expecting female reproductive tactics to be dependent on temperature and precipitation. Specifically, suboptimal birthing environments—as experienced during the dry summers and autumns in Saudi Arabia—should result in females producing heavier offspring to maximize offspring survival (prediction 2; Gillespie et al. 2008; Wilson et al. 2009). Question 3 asked if prior production of a son might have negative effects on reproduction in subsequent years. Previous research in other taxa, including humans, has shown that producing sons incurs a much higher cost on mothers than producing daughters (but see Douhard et al. 2019), and can negatively affect maternal survival probability (e.g., Gomendio et al. 1990), the timing of subsequent reproductive bouts (e.g., Clutton-Brock et al. 1981), the survival of subsequent offspring (e.g., Berube et al. 1996), and the weight at birth of subsequent offspring (e.g., Rickard 2008). We, therefore, predicted that females that had given birth to a son in the previous year would produce offspring with reduced weight at birth in the subsequent year (prediction 3). Question 4 asked if juvenile mortality patterns were sex and weight specific. Based on previous work in other ungulates (e.g., Gaillard et al. 2000; Kühl et al. 2007), including the

Table 1 Summary of our study questions, predictions, analytical approaches, and the main associated results

Question	Prediction	Approach	Result
1. What is the general reproductive biology of *G. arabica*?	N/A	χ^2-test, Linear Mixed Models and Generalized Linear Mixed Models	Even sex ratio at birth with only singletons being produced. Two peaks for birth rates across the year but no effect of precipitation or temperature on monthly birth rates. In addition, birth weight differed among months.
2. What factors influence weight at birth?	Male calves should be heavier than female calves	Linear Mixed Models	Support for our prediction.
3. Did prior production of a son negatively affect reproduction in subsequent years?	Reduced offspring weight at birth in the year following the birth of a son	Linear Mixed Model	No support of our prediction.
4. Are patterns of juvenile mortality sex- and weight-specific?	Daughters should have higher survival than sons and greater birth weights should translate into higher survival	Cox Regressions	Only the second part of our prediction was supported.
5. To what extent can life-history differences between individual offspring be ascribed to paternal genetic quality and maternal effects?	N/A	Animal Models	Some, but relatively low contributions of paternal genetic quality and maternal effects.

closely related sand gazelle (Riesch et al. 2013), and theory (e.g., Trivers and Willard 1973; Schindler et al. 2015), we predicted that females would have higher survival than males (prediction 4) and that offspring weight at birth would have an additional strong influence on survival, whereby greater birth weights ought to translate into increased survival (prediction 5). Finally, question 5 asked to what extent life-history differences between individual offspring can be ascribed to paternal genetic quality (given that *G. arabica* males do not provide offspring care; Grau 1974; Habibi 1991), as well as maternal effects (including maternal genetic quality, maternal postnatal provisioning, and maternal environmental effects). To tease apart those effects, we calculated heritability estimates for a key life-history trait (birth weight) using an animal model approach (Wilson et al. 2010), and we included mother and father ID in our statistical analyses on calf survivorship to compare the relative contributions of maternal and paternal effects during different developmental stages (at weaning age, at sexual maturity, and at the age of first reproduction). Our long-term data will help to better understand the life history and reproductive biology of desert-dwelling gazelles, not only in captivity, but also in their natural habitats, and will therefore facilitate the conservation of threatened gazelle species in the future.

Materials and Methods

Study animals and their maintenance

Arabian gazelles *G. arabica*, which are close relatives to the mountain gazelles *G. gazella* in the Levant, inhabit mountainous regions on the Arabian Peninsula. They likely adapted to more regular rainfall patterns and more constant food supply, compared to gazelle species inhabiting open terrain (e.g., *G. marica*; Vesey-Fitzgerald 1952; Wronski et al. 2010b; Bärmann et al. 2013, 2014; Lerp et al. 2013a, b). In captivity, female Arabian gazelles reach sexual maturity at around 5–7 months, but the first parturition in the wild—usually a singleton—occurs at the age of 18–24 months (Mendelssohn et al. 1995). Life expectancy in captivity is 13 years, but rarely more than 8 years under natural conditions. Males reach sexual maturity at 15–20 months, but successfully reproduce at the age of 3 years, that is, when they are able to occupy and defend a territory (Mendelssohn et al. 1995). According to the IUCN red list, *G. arabica* is considered "Vulnerable" (C2a(i) ver 3.1) with an overall population size of less than 10,000 mature individuals (IUCN SSC Antelope Specialist Group, 2017).

We investigated fitness differences between offspring (n = 494; from 162 different dams and 85 different sires) recorded over almost 16 years (between March 1997 and December 2012) at KKWRC in Saudi Arabia. The captive breeding scheme at KKWRC mostly serves conservation purposes, that is, reintroduction into protected areas. It consists of some 60 rectangular pens each measuring approximately 100 × 50 m. Trees, tree logs, earth mounds, and a metal shelter provide refuge from aerial predators (i.e., migrant eagles such as the steppe eagle *Aquila nipalensis* or the Eastern imperial eagle *A. heliacal,* or Eagle owls *Bubo ascalaphus*) and protection from climatic extremes such as cold winter winds and strong sun radiation in summer. Gazelles are fed *ad libitum* on dried alfalfa (*Medicago sativa*) and 200–300 g Superlac concentrate per animal and day (Arasco, Saudi Arabia; for details, see Kichenside and Lindsay 1997; Mohammed et al. 2002); each pen is also equipped with a mineral lick. Hence, the breeding conditions at KKWRC can be regarded as a seminatural common-garden rearing experiment, where all animals were exposed to the same climatic conditions, while resource availability was not a limiting factor, and predation was minimized. As the main aim of KKWRC is protecting desert ungulates from further decline or extinction on the Arabian Peninsula, working through the concerns of animal health and welfare, a pragmatic approach to ethical concerns was aspired, that is, allowing trade-offs between the goods at stake (e.g., animal welfare, species viability, veterinary screening, and ecological integrity). During the entire study period, the ethical guidelines of KKWRC, Saudi Wildlife Authority (now National Center of Wildlife), or any other international law on the care and use of wild animals kept in captivity were followed. For further details regarding the breeding, animal health, and welfare management at KKWRC, see Kichenside and Lindsay (1997), Mohammed et al. (2002), and Soares et al. (2015, 2021).

Pens either hold breeding groups or single-sex groups, with each breeding group being composed of 1 male and 8–14 females. Juveniles were separated from breeding pens at approximately weaning age (3 months; Mendelssohn et al. 1995) and held in single-sex groups consisting of 8–20 individuals. For breeding purposes, single males were cohabited with female groups for about half a year, after which they were retransferred to their original bachelor herds, and another male was assigned to the respective breeding group once all offspring had reached the weaning age. Assignment of males to breeding groups was based on the smallest possible relatedness coefficient obtained from the Animal Records and Keeping System (ARKS) developed by the International Species Information System (ISIS/CMS; Flesness 2003). ARKS was used to produce routine pooled inventories and individual pedigrees for all individuals included in this study. Individuals were distinguished by neck collars with different color combinations. Upon birth, each calf at KKWRC is sexed, weighed (using a hand-held weighing scale), and given a unique ID number; at the same time, the IDs of the mother and father are noted, which can be used to trace back the mother's and father's birth information as well as the information on any previous parturitions. Daily routine checks of the entire breeding stock provided continuous information on the survival/ death of juvenile gazelles.

Statistical analyses

All Linear Mixed Models (LMM) using Gaussian distributions were fit with the {lme4} library (Bates et al. 2015). Generalized Linear Mixed Models (GLMM) with non-Gaussian distributions were fit using the {glmmTMB} library (Brooks et al. 2017). LMM and GLMM models were fit using restricted maximum likelihood (REML) and model diagnostics were performed using the {DHARMa} library (Hartig 2022). Significance of fixed effects was assessed with the function *Anova* in the {car} library (Fox and Weisberg 2019) using *F*-tests with Kenward–Rogers degrees of freedom estimation and type II sums of squares for LMMs (except for models with significant interactions where type III sums of squares were used instead) and Wald χ^2 tests for GLMMs. All LMM and GLMM were run using R (4.2.0, 2022). To estimate the heritability of weight at birth, we used "animal models" fit in the {MCMCglmm} library (Hadfield 2010) using R (4.0.3, 2020). Finally, we analyzed the survivorship of calves using mixed-model Cox regressions implemented in the {coxme] library (Therneau 2012) using R (3.1.3, 2014).

Reproductive biology

We first evaluated if births were distributed nonrandomly across months using a χ^2-test, where the expected probability of births in each month (i.e., assuming an even distribution across months) was 0.083. Because we found the distribution of births in each month to differ from random expectations, we downloaded climate data from WorldClim (Hijmans et al. 2005) at 2.5-min resolution to determine if the number of births per month was associated with average monthly mean precipitation and temperature at KKWRC using a GLMM with a Poisson error distribution (as our response variable was count data) with "year" fit as a random effect. We additionally asked if birth weight significantly differed among calendar months using an LMM with "year" as a random effect. As making pairwise post-hoc comparisons between all 12 months is not practical, we visually examined this pattern (see *Results*) and investigated the causes for variation in birth weight in more details below.

Environmental and biological predictors of weight at birth

Using birth weight as a proxy for maternal energy allocation of all individuals for which we had accurate information on birth weights and the mother's date of birth (n = 438), we investigated differential maternal allocation as a function of "age of mother at parturition" (we did not correct for maternal longevity to account for the selective disappearance of poor quality mothers which may have masked any age-related changes *sensu* van de Pol and Verhulst 2006), "offspring sex," "mean monthly precipitation," and "mean monthly temperature" (climate data was obtained from WorldClim, see above) by means of an LMM that incorporated "weight at birth (kg)" as the dependent variable. We included "dam ID," "sire ID," and "year" as random effects. We tested for the presence of significant interactions between our independent variables during data exploration. As there were no significant interactions (all $P > 0.05$), we did not include them in our final model (Crawley 2007). We additionally evaluated if weight at birth was influenced by the sex of the previous calf born to a female (i.e., evidence for differential "costs" of producing a male or female offspring). To do so, we fit another LMM using "offspring sex," "sex of previous calf," and their interaction as independent variables. We again included "dam ID," "sire ID," and "year" as random effects. To test for a relationship between birth weight and the mean number of births per month, we further investigated the relationship between the "number of mean monthly births" and "mean monthly birth weight" by means of an LMM with "year" included as a random effect. Finally, we examined weight at birth across the temporal scale of our dataset. To do so, we ran a linear model with "year," "offspring sex," and the interaction between "year" and "offspring sex" as independent variables. We did not include dam or sire ID as random effects in this model because they have a nonrandom association with "year," preventing the model from converging. Variance inflation factors in the analyses reported here were <2, suggesting that problems arising from potential multicollinearity were negligible (e.g., Quinn and Keough 2002).

Heritability of weight at birth

We estimated the genetic architecture of offspring birth weight with the "animal model" approach (*sensu*, Wilson et al. 2010). To do so, we fit mixed-effects models using the {MCMCglmm} library (Hadfield 2010) incorporating pedigree information to partition the total phenotypic variation in offspring birth weight into the components explained by additive genetic effects (i.e., h^2: narrow-sense heritability), maternal effects (m^2), and environmental effects. Our dataset for analysis consisted of 84 sires, 161 dams, and 494 individuals with known birth weight and parentage (3 individuals were missing sire identity). We first fit an intercept-only model with the random effect of "dam ID," an inverse-gamma prior, and a multigenerational pedigree (made using the *insertPed* function from the {MasterBayes} library [Hadfield et al. 2006]). Because of some initial autocorrelation, we used 300,000 iterations with a burn-in of 20,000 and a thinning interval of 100 iterations in our final model. We found low autocorrelation in the final model and our results were similar when alternatively using a stronger prior. We next fit the previous model but also included an extra random effect of "year," because of an observed trend in birth weight over time (see Results). We increased the number of iterations to 500,000 with a burn-in of 50,000 and a thinning interval of 100 iterations in this model. Again, there was low autocorrelation in our final model, and the results were similar when alternatively using a stronger prior. The animal models were run using R (4.0.3, 2020).

Survivorship of calves

We analyzed the survival of 438 calves born between March 1997 and December 2012 with a binomial (i.e., survived/not survived) coding at 3 different times: (1) 3 months after birth (approximation of weaning age, which is reported to be 3 months in the wild; Mendelssohn et al. 1995), (2) at 1 year of age (i.e., sexual maturity), and (3)—for females only (n = 40)—offspring survival to the first reproduction using mixed-model Cox regressions implemented in the {coxme] library (Therneau 2012), in which "weight at birth," "month of birth," "age of mother at parturition," and "offspring sex" were included as independent variables, and "dam ID" and "sire ID" as random effects (fit using maximum likelihood). However, "offspring sex" was not included in analysis (3) because this analysis was restricted to female survival. We further excluded females from analysis (3) that were alive up to the end of our records but had not yet given birth as well as females that left KKWRC for reintroductions or were transferred to other collections. We controlled for the false discovery rate (Benjamini and Hochberg 1995) when reporting the significance of these multiple comparisons. During data exploration, we tested for the presence of significant interactions between our independent variables. As there were no significant interactions (all $P > 0.05$), we did not include them in our final models (Crawley 2007). Variance inflation factors in the analyses reported here were <2, suggesting that problems arising from potential multicollinearity were negligible (e.g., Quinn and Keough 2002). Survival analyses were run using R (3.1.3, 2014).

Results

Reproductive biology

All 494 births recorded between 1997 and 2012 were singleton births. Sex ratios of calves (males: females) did not differ from evenness overall (0.95: 1; $\chi^2 = 0.29$, $df = 1$, $P = 0.59$, $n = 494$) or within individual months (all $P > 0.05$, correcting for the false discovery rate). In contrast, the distribution pattern of monthly birth events was slightly bimodal (χ^2 =

52.79, df = 11, P < 0.0001, n = 494), with birth peaks in March and April (22%), and then again between July and December (57%; Figure 1A). Mean temperature and precipitation were significantly correlated—months with greater mean precipitation tended to experience cooler mean temperatures (Spearman rank correlation, r_s = –0.74, n = 12, P = 0.006). However, the mean number of births per month was not significantly related to either mean monthly precipitation (χ^2= 0.78, df = 1, P = 0.38) or mean monthly temperature (χ^2 = 1.37, df = 1, P = 0.24). Weight at birth significantly differed between months ($F_{1, 423.36}$= 2.04, P = 0.023). In visualizing this pattern (Figure 1B), calves born in the summer (i.e., June, July, and August) had lower mean weights at birth compared to calves born during months of the winter and spring (i.e., December, March, and April).

Environmental and biological predictors of weight at birth

When comparing offspring weight at birth as a measure of maternal allocation, the LMM revealed a significant effect of offspring sex ($F_{1, 384.13}$= 6.79, P = 0.01); males were heavier at birth than females (Figure 2A). However, the age of mother at parturition ($F_{1, 351.07}$= 1.74, P = 0.19) had no significant influence (Figure 2B). There were weak and nonsignificant

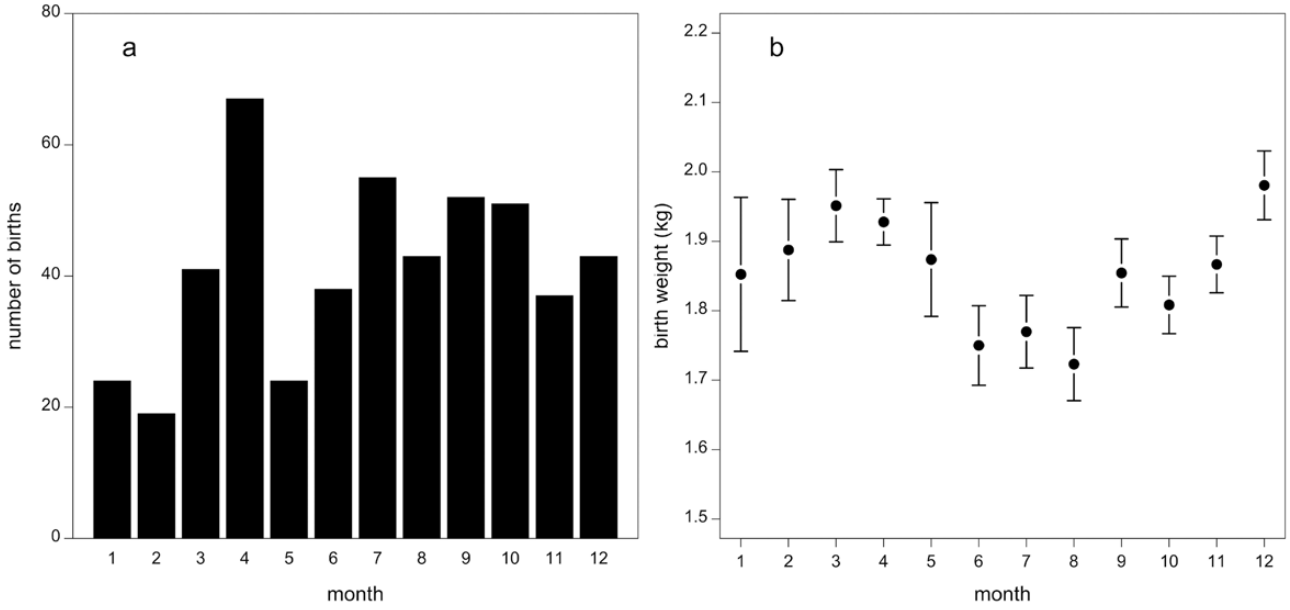

Figure 1 Monthly distribution of births (A), n = 494), and the monthly distribution and standard error of mean birth weight (B).

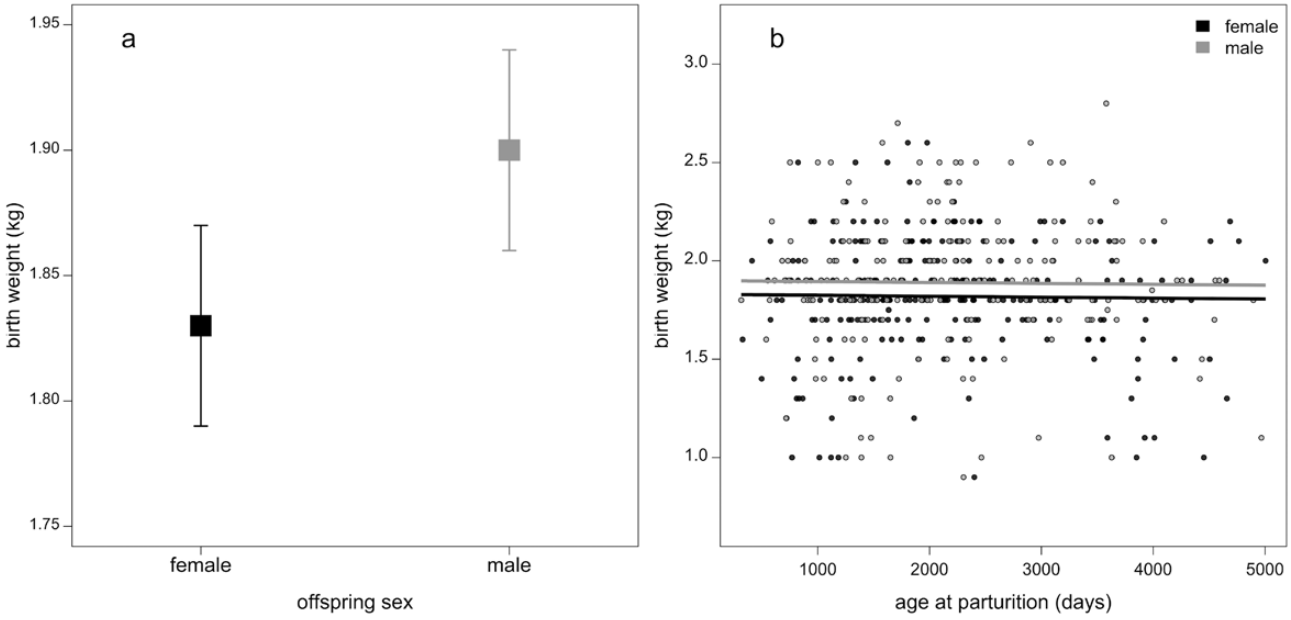

Figure 2 Sex-specific weight at birth (A), the values plotted are the estimated marginal means for females (solid) and males (shaded) with standard errors from the LMM of weight at birth (see text for details), and the nonsignificant relationship between weight at birth as a function of age at current reproduction for females (solid) and males (shaded) (B), fitted lines are from the LMM of weight at birth (see text for details). Age range ≈11 months to 14 years.

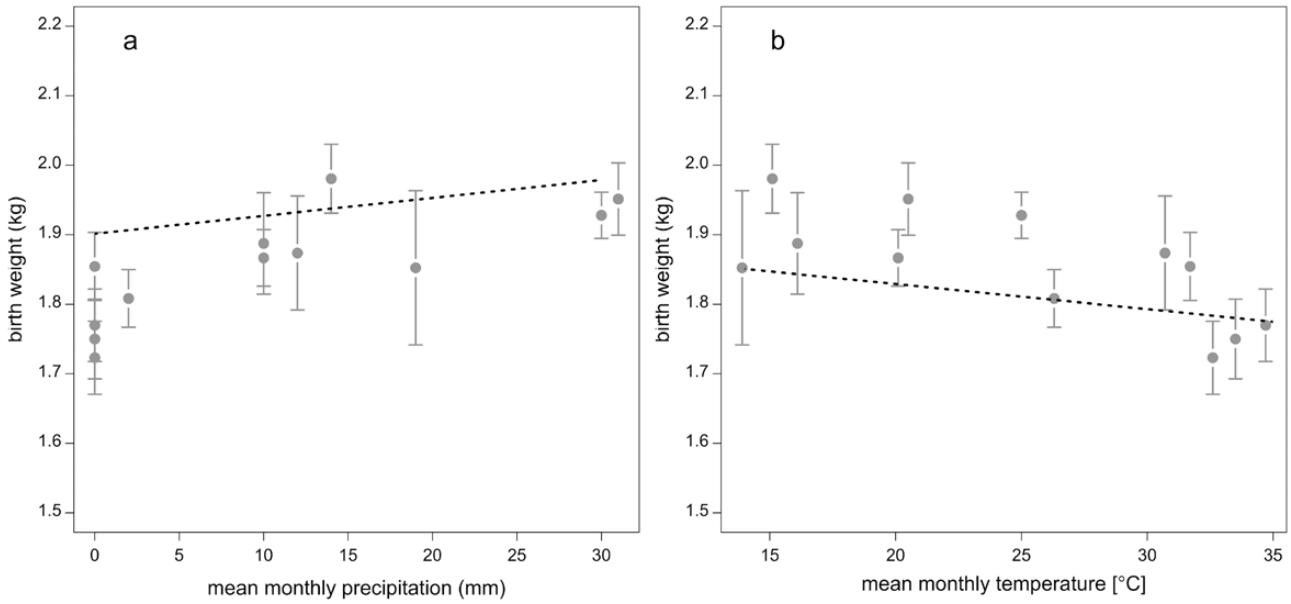

Figure 3 The nonsignificant relationship between weight at birth and mean monthly precipitation (A) and the nonsignificant relationship between weight at birth and mean monthly temperature (B). Means and standard errors and plotted, along with the nonsignificant regression from the LMM of weight at birth (see text for details).

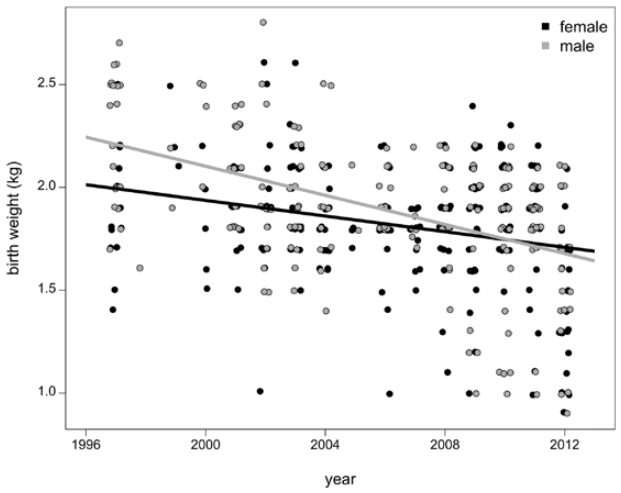

Figure 4 Temporal pattern in birth weights from 1997 to 2012 for females (solid) and males (shaded) from the linear model of sex-by-year (see text for details). Points are jittered to avoid overplotting.

trends between birth weight and mean monthly precipitation ($F_{1,406.65}$= 3.2, P = 0.074) and mean monthly temperature ($F_{1,385.06}$= 2.35, P = 0.126). Specifically, birth weight scaled positively with mean monthly precipitation ($\beta \pm SE$ = 0.003 ± 0.001; Figure 3A), and negatively with mean monthly temperature ($\beta \pm SE$ = –0.003 ± 0.002; Figure 3B). Dam ID, sire ID, and "year" explained 1%, 27%, and 12.4% of the variance components, respectively. In addition, we did not find a relationship between the mean number of births per month and the mean monthly birth weight ($F_{1,94.25}$ = 0.51, P = 0.82). We also found no effect of the sex of the previous calf ($F_{1,273.56}$ = 0.17, P = 0.68) or the interaction between the previous and current offspring's sex on offspring birth weight (current offspring's sex: $F_{1,262.74}$ = 3.69, P = 0.06; current offspring's sex × previous offspring's sex: $F_{1,261.91}$ = 1.17, P = 0.28). Finally, weight at birth declined from 1997 to 2012 (Figure 4). Male offspring, on average, weighed more than female offspring (sex: $F_{1,434}$ = 6.74, P = 0.01) and experienced a greater decline in weight over this period compared to female offspring (sex × year: $F_{1,434}$ = 6.72, P = 0.01; $\beta_{male} \pm SE$ = –0.035 ± 0.004, $\beta_{female} \pm SE$ = –0.019 ± 0.004).

Heritability of weight at birth

Our estimate of narrow-sense heritability (h^2) was high (posterior mode and highest posterior density interval = 0.556, 0.391–0.741), while our estimate of maternal effects on birth weight (m^2) was lower (0.091, 0.005–0.157). Narrow-sense heritability (0.365, 0.235–0.573) and maternal effects (0.01, 0.002–0.084) were somewhat lower when also estimating the environmental effect of year (0.137, 0.054–344). The deviance information criteria were similar between the 2 models (ΔDIC = 1.14).

Survivorship of calves

Weight at birth (β = –0.61, SE = 0.13, z = –4.54, P = 0.0001) was the only significant predictor for survival over the first 90 days of life, while offspring sex (β = 0.16, SE = 0.26, z = 0.64, P = 0.52), month of birth (β = –0.06, SE = 0.04, z = –1.45, P = 0.27), and age of mother at parturition (β = 0.1, SE = 0.13, z = 0.76, P = 0.68) had no influence. Specifically, a greater birth weight translated into higher survival rates (Figure 5A). The variance component for random effects was 0.72 for dam ID and 0.28 for sire ID. We report the variance rather than % variance for the survival analyses because mixed-model Cox regressions do not estimate the residual error. For survival through the first year of life, both weight at birth (β = –0.38, SE = 0.09, z = –4.11, P = 0.0001) and offspring sex (β = 0.38, SE = 0.16, z = 2.33, P = 0.04) had statistically significant effects. Again, greater birth weight translated into higher rates of survival (Figure 5B), but independent of their smaller body weight, female offspring had greater survival than male offspring (Figure 5D). In contrast, neither month of birth (β = –0.04, SE = 0.03, z = –1.34, P = 0.27) nor age of mother at parturition (β

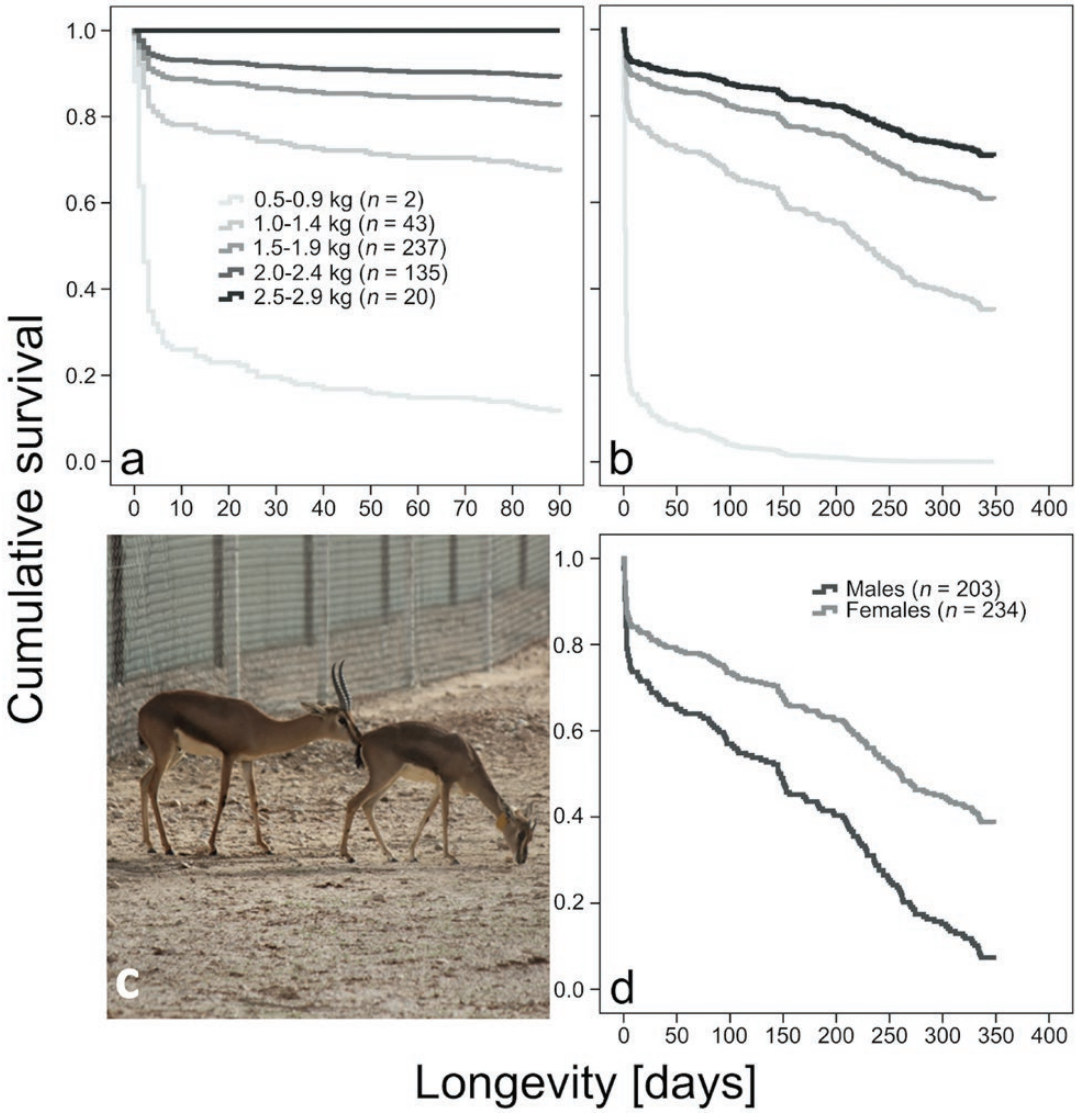

Figure 5 Survival plot indicating cumulative survival (%) over 90 days (A) and 365 days (B and D) for *Gazella arabica* offspring born and raised at KKWRC as a function of weight at birth (A and B) and sex (D). Please note that the curves for the 2 highest weight categories are on top of one another in (B). Male and female *G. arabica* at KKWRC (C); photo by Moritz Klein.

= −0.03, *SE* = 0.09, *z* = −0.35, *P* = 0.73) predicted offspring survival during the first year of life. The variance component for sire ID was 0.90, while it was 0.10 for dam ID. Survival to first reproduction in females was predicted by a single trait—weight at birth (β = −0.22, *SE* = 0.1, *z* = −2.24, *P* = 0.025). Month of birth (β = 0.01, *SE* = 0.03, *z* = −0.33, *P* = 0.74) and age of mother at parturition (β = −0.1, *SE* = 0.1, *z* = −0.99, *P* = 0.68), on the other hand, had no effect. Sire ID now had a variance component of 0.81 and dam ID 0.19.

Discussion

Our first question asked about the general patterns of reproduction in a captive population of *G. arabica* at KKWRC in Saudi Arabia. We found Arabian gazelles to produce a very even sex ratio at birth. Thus, we could not find any indication for secondary sex ratio adjustment in *G. arabica*, suggesting that either these gazelles are not capable of active sex ratio adjustment, or that the seminatural conditions at KKWRC (including constant group sizes and compositions) did not trigger sex ratio adjustment. This is similar to sex ratios described for wild (Cunningham and Wronski 2011) and captive sand gazelles (Riesch et al. 2013), but also for other gazelle species (Martin 2000). Future studies could investigate the influence of group composition on secondary sex ratios in this genus.

Arabian gazelles exclusively gave birth to singletons, and while there was a slight signal of seasonality in the patterns of birth events across months, this pattern was not predicted by temperature or precipitation. This means that there are some similarities but also some differences in reproductive life-history characteristics between *G. arabica*, *G. marica* (Riesch et al. 2013), and other desert-dwelling ungulates in the wild or in captivity (Rubenstein 1989; Schuler et al. 2009; Wronski et al. 2011). In both *G. arabica* and *G. marica*, male offspring are heavier at birth than females, and both female and heavier offspring have lower early mortality rates than male and lighter offspring. However, in contrast to *G. marica*, *G. arabica* never (or at the very least extremely rarely) produce twins (indeed, many ungulates predominantly produce singletons: Sæther and Gordon 1994), and birthing is much more evenly spread across

the year (for similar species-specific differences in singleton vs. twin births in other ungulates, see Coulson et al. 2000). We propose that these differences reflect the different environmental conditions both species are adapted to. Reproduction (including lactation) comes with very high energetic costs/demands, and females of iteroparous mammals face a trade-off between current reproduction and the maintenance of body condition for future reproduction (Festa-Bianchet et al. 1998; Froy et al. 2016). Being adapted to hyper-arid desert environments that are nearly devoid of vegetation, sand gazelles are faced with a high uncertainty surrounding survival and future reproduction and maximize fitness by exhibiting strong seasonality in birthing patterns as well as a high propensity for twinning (i.e., maximizing current reproduction), both of which closely track maximum food availability after winter/spring rains (see discussion in Riesch et al. 2013). Arabian gazelles, on the other hand, are adapted to the mountainous regions on the Arabian Peninsula, which exhibit more regular rainfall patterns and more constant food supply (Vesey-Fitzgerald 1952; Lerp et al. 2013a, b). Therefore, *G. arabica* can give birth year-round (with a slight decrease in birthing rates during January, February, and May) and appear to be able to maximize both offspring fitness and their own future reproductive prospect by producing exclusively singletons (Williams 1966; Case 1978; Stearns 1992).

In agreement with our prediction 1, males were consistently heavier at birth than females. This corroborates previous data from other gazelles and ungulates (e.g., Alados and Escos 1991; Lindsay and Wood 1992; Cassinello and Gomendio 1996; Gaillard et al. 2000; Riesch et al. 2013) and is congruent with the assertions of Willson and Pianka (1963) and Trivers and Willard (1973) that optimal parental investment in polygynous species should involve a greater relative investment into male offspring. Not surprisingly, body mass at birth is more correlated with male than female fitness (Clutton-Brock et al. 1988; Kruuk et al. 1999), and male offspring benefit more from extra allocation of resources than females (Trivers and Willard 1973; Schindler et al. 2015), for example, because larger males have higher reproductive success as they are superior in male–male competition (Andersson 1994). In other words, adult males need to be strong (and big) in order to successfully compete for access to females and being larger at birth, therefore, provides them with a starting advantage (but see Hewison and Gaillard 1999). However, we do not yet know how exactly male-male competition plays out in natural populations, and so we call on future studies to investigate this further and to directly compare to what extent mating success for males is directly tied to weight at birth.

In agreement with our prediction 2, calves born around the turn of the year were heavier than those born during the middle of the year, but we did not uncover significant relationships between offspring weight at birth and precipitation/temperature. This pattern largely matches that described for *G. marica* at KKWRC (Riesch et al. 2013), which also produced the heaviest offspring late in the year. This suggests that factors other than seasonality (i.e., precipitation and temperature) are driving this temporal pattern (if representative of natural populations), or that other factors (e.g., constant food supply in captivity) override responses to seasonal climatic variation in captivity (Zerbe et al. 2012; Heldstab et al. 2021). Future studies will have to investigate this further.

Contrary to our prediction 3, we found no evidence that giving birth to a son in one year negatively affected offspring weight in the following year in *G. arabica*. This is a bit surprising because differential allocation into male versus female offspring should also lead to different reproductive costs associated with producing offspring of either sex (e.g., Clutton-Brock et al. 1981; Gomendio et al. 1990; Berube et al. 1996; Rickard 2008). While this could indicate that Arabian gazelles do not pay a similar cost of producing sons, we find this explanation highly unlikely. We rather argue that this suggests that the cost of producing sons is resource dependent. Under natural conditions, when mothers might have to survive periods of extreme food shortage, the cost of producing sons is more likely to leave a strong signal than at KKWRC, where food is fed *ad libitum* throughout the year. This interpretation is also congruent with the cost of sons only being detectable in females of low social status as previously described in wild ungulates (e.g., Gomendio et al. 1990).

Contrary to prediction 4, we did not find any significant differences in offspring survival between the sexes. However, we found offspring weight at birth to be the most important predictor of offspring survival to weaning age, sexual maturity (1 year), and female survival to the first reproduction, which is in strong support of prediction 5. The absence of any sex effects could either represent a true result (i.e., also wild *G. arabica* exhibit this pattern) or could be an artifact of the conditions at KKWRC. However, it is important to point out that *G. marica* from KKWRC did indeed exhibit a sex-specific pattern of mortality, with females having greater survival rates than males (Riesch et al. 2013). This suggests that the absence of such a pattern in *G. arabica* might indeed be a true result, but this will require further study in wild populations. Nonetheless, the fact that weight itself was the most important predictor of early survival in *G. arabica* matches similar patterns reported for other vertebrate taxa (e.g., humans: Gillespie et al. 2008; reptiles: Janzen and Warner 2009; fish: Einum and Fleming 2000; deer: Gilbert et al. 2020; gazelles: Riesch et al. 2013). Thus, it is clearly beneficial also for female *G. arabica* to invest as much as possible into offspring size to ensure the highest possible offspring survival. At KKWRC, average mortality rates during the first year of life were around 40% (if we discount the lightest weight class, which had 100% mortality), and thus, considerably lower than mortality rates reported from wild ungulates, which can exceed 60% (Milner-Gulland and Lhagvasuren 1998; Gaillard et al. 2000; Johnstone-Yellin et al. 2009; Shalmon et al. 2021). This discrepancy reflects the fact that most environmental stressors (such as disease, parasitism, resource shortage, and predation) are strongly reduced or even excluded at KKWRC. However, mortality rates of *G. arabica* are still considerably higher than those previously reported for the related *G. marica*, also reared at KKWRC under the same conditions (Riesch et al. 2013), or from other gazelle species reared in captivity (Müller et al. 2010). We tentatively argue that this may be a sign of lower behavioral stress tolerance in Arabian compared to sand gazelles: even though an attempt was made to keep human-induced stress at KKWRC to a minimum, the crepuscular and more bush-dwelling Arabian gazelles are more easily startled by external stimuli (e.g., strangers visiting KKWRC or stray dogs at the periphery of the breeding center) than the plain-dwelling sand gazelles (TW, pers. obs.).

Regarding our question 5, across both sexes, we found narrow-sense heritability (h^2) for offspring weight at birth to be relatively high compared with the average h^2 for life-history traits from several recent syntheses (i.e., h^2 around 0.3; Postma 2014; Wood et al. 2016; Moore et al. 2019), while the influence of

maternal effects (m^2) on birth weight was lower in comparison. Nonetheless, our estimate of maternal effects on birth weight was in line with a recent meta-analysis of maternal effects across taxa (i.e., m^2 around 0.1; Moore et al. 2019). We argue that while the contribution of male ungulates to parental care is largely genetic (Kleiman and Malcolm 1981), female ungulates also bear the cost of postnatal maternal care, which is known to vary according to maternal characteristics such as body mass (Hewison and Gaillard 1999; Côté and Festa-Bianchet 2001), past reproductive history (Rutberg 1986), social status (e.g., Barrette and Vandal 1986; Ceacero et al. 2012), and genotype. Since a large proportion of variation in birth weight is explained by additive genetic variance, and offspring size at birth is directly linked to offspring fitness, this opens the door for selection to act on offspring size in this species. In essence, individuals that are genetically predisposed to produce larger offspring will tend to have greater fitness, which in turn should mean that (all else being equal) the genes predisposing to larger offspring size should increase in frequency over time.

With that in mind, it is interesting to note that across the almost 16-year study period, we noticed a significant decline (not increase) in offspring birth weight in our study population. While we do not have enough data to fully dissect this pattern, we propose a few nonmutually exclusive mechanisms that might help explain this. First, this captive population is subjected to a breeding regime, so artificial and/or inadvertent selection might simply overrule natural and sexual selection on offspring size at birth. Second, long-term captivity is known to have detrimental effects on animal reproductive fitness (including offspring size at birth; Farquharson et al. 2018), also via inbreeding depression (e.g., Alados and Escós 1991; Walling et al., 2011). Nonetheless, each year, there was an influx of *G. arabica* individuals into the setup from other collections or from confiscation (TW, pers. obs.), so we think that inbreeding is likely to play a minor role at KKWRC. Third, this could be a response to rising temperatures from Global Climate Change, which has been shown to drive decreases in body size across taxonomic groups (Sheridan and Bickford 2011). Indeed, when the year of birth was accounted for in our animal models, the estimates of heritability and maternal effects modestly decreased, suggesting that changes in the environment across the years of the study affected phenotypic variation in birth weight. Unfortunately, we could not directly test for this association because the annual temperature record for the region is surprisingly sparse.

In conclusion, our study furthers our understanding of the variability in reproductive traits in true gazelles, and of the costs and benefits surrounding reproduction at different times of the year. In addition, the major objective of the captive breeding program of *G. arabica* at KKWRC is to maintain a self-sustaining population in captivity and to provide gazelles for reintroduction into the protected areas of Saudi Arabia. To improve the success of reintroductions as a conservation tool, it is imperative to release animals with a good perspective for survival in the wild (Dunham et al. 2001). It is, therefore, vital to have long-term data on the reproductive biology of the target species ideally collected from wild animals. However, collecting such data is, unfortunately, nigh impossible due to various factors such as small population sizes, remoteness and inaccessibility of the habitat, or dangerous and inhospitable conditions in the field. Collecting such data in captivity can, therefore, provide important insights into the reproductive biology and life-history traits of the species and compensate for the lack of data obtained from the wild. The data provided here will be of major importance for the management of the captive *G. arabica* populations, not only at KKWRC but also in other captive breeding programs on the Arabian Peninsula, and will thus allow to make science-informed conservation decisions in the absence of solid data from wild animals.

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Author Contributions

All authors contributed to the study conception and design. Material preparation, data collection, and maintenance were performed by Torsten Wronski, Naif A. Al Hanoosh, and Martin Plath. Data analysis was performed by Ryan Martin and Rüdiger Riesch. The first draft of the manuscript was written by Ryan Martin and Rüdiger Riesch, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability

All raw data generated or analyzed during this study are available in the Zoological Information Management System (ZIMS).

Conflict of Interest statement

All authors declared no competing interests.

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