Food, family and female age affect reproduction and pup survival of African wild dogs

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Abstract

Understanding factors that affect the reproductive output and growth of a population of endangered carnivores is key to providing information for their effective conservation. Here, we assessed patterns in reproduction for a small population of endangered African wild dogs (*Lycaon pictus*) over 90 pack years. We tested how availability of prey, pack size, pack density, rainfall, temperature and female age affected the age of first litter, litter size and pup survival. We found that females bred younger when pack density, availability of prey and pack size were large. We also found that fecundity increased significantly with age while the population was male biased only for one, two- and four-year olds. Larger litters were produced by larger packs, suggesting strong reproductive benefits of grouping related to cooperative hunting and food provisioning for helpers and alpha females. We also found an interaction between breeding female age and pack size where older females in large packs raised a high proportion of pups. Additionally, large litters and large packs were important for raising a greater number of pups to six and 12 months respectively, suggesting that while litter size is important for pup survival, the benefits of a large pack are only realised when pups are older and mobile with the pack. Collectively, these results illustrate the novel finding that prey availability is critically important in initiating reproduction in wild dogs and that the number of non-breeding helpers, female age and litter size are essential to pup survival.

Key words: helpers, litter size, *Lycaon pictus*, prey availability, pup survival

Significance Statement

Variation in socio-environmental conditions strongly affect reproduction. We studied how the temporal variation in such conditions affected reproduction for African wild dogs across 23 years. We specifically aimed to test how long-term variation in food supply in conjunction with various socio-environmental conditions affected this endangered species' ability to reproduce and raise offspring. Our result of larger groups producing larger litters and raising more pups strengthen previous conclusions of the critical importance of group size for wild dogs. However, reproduction is strongly dependent on when individuals can first reproduce and, for the first time, we illustrate that prey availability is the lynchpin upon which reproduction is initiated in this endangered species. We also highlight the importance of maternal age and initial large litter sizes in raising pups.

Introduction

The conservation of large carnivores relies on an understanding of vital rates as fundamental population information. How these vital rates affect population growth and persistence is therefore important for developing effective conservation strategies (Macdonald and Sillero-Zubiri 2004). Radio-tracking collars on individual carnivores within and across populations have allowed for the collection of high resolution data to understand vital rates and estimate population size and trends across a range of ecological contexts (Boitani and Powell 2012).

Successful reproduction in canids (i.e. litter size and pup survival) is positively related to the availability of prey for grey wolves (*Canis lupus*) (Fuller et al. 2003) and coyotes (*Canis latrans*) (Gese 2004). Access to prey for canids is driven by prey availability and vulnerability (Mech et al. 1998). For example, the population of grey wolves in Alaska's Denali National Park was positively related to the abundance of prey (Mech et al. 1998).

Conversely, reproductive success can be reduced when prey availability is low (Fuller et al. 2003). Prey species, including larger prey, are also more vulnerable to predation by larger groups of canids (Macdonald et al. 2004), highlighting the positive effect of communal hunting on increased resource intake per capita. Additionally, larger groups outcompete smaller groups of conspecifics with regard to inter-group encounters, foraging success, breeding site selection, avoidance of threats, and defence of resources and have better reproductive success (Creel et al. 2004; Ausband et al. 2018). In canids, offspring often make up the majority of the group and population composition (Fuller et al. 2003). As a result, annual changes in group and population size depends on offspring survival (Fuller et al. 2003).

Female fertility is also an important driver of reproduction. Age of first breeding depends on food supply where, in grey wolves, greater access to food results in females breeding younger (Fuller et al. 2003). However, a high abundance of food generally results in higher carnivore densities (Fuller et al. 2003) and likely increased competition for mates and food. Consequently, at high prey densities, age of first breeding could be delayed due to high conspecific densities between reproductive groups. Such interactions will likely have important consequences for reproduction and ultimately population growth. For cooperatively breeding canids that rely on non-breeding helpers for reproductive success, but compete with neighbouring groups for resources, it is important to understand how conspecific density and its effect on food acquisition might affect reproductive output.

Ensuring the survival of offspring is key to group success and consequently to population growth (Creel et al. 2004; Davies-Mostert et al. 2015). Like reproduction, offspring survival is generally positively related to available food. For example, an increase in available prey biomass resulted in increased pup survival of grey wolves (Fuller et al. 2003). Prey availability is in turn related to rainfall variability, especially in savannah systems (East 1984). Consequently, any study investigating factors affecting reproduction must also consider rainfall variability. Pup survival is also positively affected by group size (Creel et al. 2004; Ausband et al. 2018), low breeder turnover (Ausband et al. 2018), experienced breeders with familiarity of territory and defence of resources within (Borg et al. 2015) and stable group sizes (Ausband et al. 2018).

African wild dogs (*Lycaon pictus*) live in packs made up of a breeding alpha pair (Malcolm and Marten 1982) with related subordinate non-breeding helpers (Creel and Creel 2002). Packs spend three months per year raising the annual litter of pups in a den (Malcolm and Marten 1982), during which pack members return after each hunting session to regurgitate food for the lactating female, helpers and current litter of pups (Creel and Creel 2002). Females become fertile around two years old (Frame et al. 1979; Creel et al. 2004) but the average age of first litter varies between subpopulations. However, it is unknown what drives the age of first reproduction in wild dogs. Litter sizes vary significantly between populations (Creel et al. 2004) and are positively related to the number of prey herds encountered (Creel and Creel 2002), pack size (Creel and Creel 2002; Buettner et al. 2007; Gusset and Macdonald 2010) and female age (Creel et al. 2004; Davies-Mostert et al. 2015). However, interactions between prey availability, pack size and female age do not affect litter size, especially for large free-roaming populations (Creel and Creel 1998). Although litter size is not related to population density across six large ecosystems (Creel and Creel 2002), there is a proliferation of relatively small ecosystems where the density of predators and prey have increased to levels above that of free-roaming populations (Davies-Mostert et al. 2015). Consequently, what effect elevated population densities might have on reproduction in wild dogs in ecosystems with high prey availability is unknown. Moreover, as wild dogs have the highest energetic costs of gestation among all group-living carnivores (Creel and Creel 1991), how packs overcome or offset these costs with adequate food provisioning for breeding females is fundamental to pack success.

Population dynamics of wild dogs are most affected by pup survival (Creel et al. 2004; Davies-Mostert et al. 2015). A higher proportion of pups are raised to one year by middle-aged females (Creel and Creel 2002), in drier years in the Kruger National Park (Buettner et al. 2007), by packs encountering more prey herds (Creel and Creel 2002), by larger packs (Creel et al. 2004; Buettner et al. 2007) and during cooler temperatures in the denning season (Woodroffe et al. 2017). Lions (*Panthera leo*) are a threat to wild dogs with a high amount of predation recorded (Woodroffe et al. 2007). Recent evidence suggests that choice of dens by wild dogs is related to avoidance of lions (Davies et al. 2016). There are likely important interactions between these factors affecting pups raised and between ecosystems where prey availability, density, inter-specific competition, rainfall and temperature vary considerably. For small and managed populations of wild dogs, population growth is a key conservation goal (Mills et al. 1997). Therefore, understanding which factors affect survival of pups is fundamental for their successful conservation and management.

Prey availability has been suggested as an unlikely limiting factor in wild dog dynamics compared to interspecific competition (Creel and Creel 1998). However, more recent evidence suggests that wild dog density is related to higher biomass of preferred prey (Hayward et al. 2007), and prey availability is important in wild dog reproduction in driving den site changes in a recovering population (Ford et al. 2015). How prey availability might interact with other factors to potentially drive wild dog reproduction (age of first reproduction, litter size, and pup survival) is unknown. In this study, we describe the long-term patterns in reproduction for a small population of wild dogs that has attained a high density concurrently with a high prey availability. We tested multiple hypotheses that should affect the age of first breeding for females, litter size and pup survival to six and 12 months (Table 1). These hypotheses included how preferred prey availability, pack size, population density, rainfall, temperature, female age and various interactions affected the age of first reproduction, litter size and pup survival to six and 12 months of age. Based on Table 1, we predicted that the age of first litter and litter size would be positively affected by high prey availability and large pack sizes where breeding females will offset costly gestation (Creel and Creel 1991) with good food intake from efficient hunting (Creel and Creel 2002). Subsequently, larger litters should have more pups surviving (McNutt and Silk 2008; Woodroffe 2011; Woodroffe et al. 2017) where this should be strongly mediated by older females (Creel et al. 2004; McNutt and Silk 2008) and in larger packs (Creel et al. 2004; McNutt and Silk 2008; Woodroffe et al. 2017).

Methods

Study site

We conducted the study in Hluhluwe-iMfolozi Park (HiP), KwaZulu-Natal province, South Africa (28º13’04.2”S 31º57’07.7”E; Fig. 1). HiP is 896 km^2 and fully enclosed with predator-proof fencing. It is comprised mainly of thornveld savannah. Rainfall in HiP is spatially heterogeneous along a gradient from north to south with the northern areas (Hluhluwe) receiving a mean of 63% more rain per annum than the southern areas (iMfolozi). Overall, the park receives rainfall varying from 200 – 1200 mm per annum (Ezemvelo KZN Wildlife, unpublished data). Rainfall occurs during the hot and humid months between October and March with colder, dry climatic conditions from April to September. HiP supports a wide range of herbivore species including the preferred prey of wild dogs such as impalas (*Aepyceros melampus*), nyalas (*Tragelaphus angasii*), and greater kudus (*Tragelaphus strepsiceros*) (Hayward et al. 2006). These have all attained high densities (le Roux et al. 2017), which is suggested to be the primary reason for the recovery of the large carnivore guild including lions, leopards (*Panthera pardus*), spotted hyaenas (*Crocuta crocuta*), cheetahs (*Acinonyx jubatus*), and wild dogs (Somers et al. 2017).

Wild dogs in HiP

Wild dogs were reintroduced to HiP in 1980, when 22 individuals were artificially bonded to one another to form one pack (Maddock 1999). After the initiation of the managed metapopulation approach in South Africa (Mills et al. 1997) there were subsequent augmentations of two, four and eight individuals in 1997, 2001 and 2004 respectively (Somers et al. 2008). The population fluctuated greatly between 1980 and 1996 (Maddock 1999; Somers et al. 2008), after which it grew rapidly to 68 adults and yearlings recorded at the onset of the 2016 denning season. Data collected from 1981 to 1992 were *ad hoc* sightings from the Natal Parks Board archives based on staff reports. Data collected between 1992 and 1995 were based on direct observations and photographs (Maddock 1999). Data from 1996 to 2016 were collected in an intensive monitoring programme to investigate artificial augmentation of the population from the managed metapopulation (Mills et al. 1997). All these data used belong to Ezemvelo KZN Wildlife (EKZNW) and are stored in HiP. The intensive monitoring of packs was enabled due to VHF and GPS satellite tracking collars (a range of makes and models) being fitted to at least two individuals per pack. All wild dogs were darted 10 – 30 m from a vehicle by a qualified veterinarian, using either a fentanyl and zylazine or a zoletil and meditomadine drug combination. Wild dogs were darted, handled and collared in accordance with EKZNW guidelines. Each wild dog is identifiable from unique coat patterns, allowing individual and group resolution recording of (1) group size, (2) identity of individuals in the pack, (3) age and sex breakdown of pack members, (4) pregnancies, (5) dominance status of individuals, (6) births and (7) denning status recorded on a weekly basis. Using these data, we compiled life history tables for the period June 1993 (onset of the 1993 denning season) to June 2016 (onset of the 2016 denning season) which accounted for 23 years and 90 pack years of data. It was not possible to record data blind because our study involved focal animals in the field.

Population characteristics. We defined a wild dog ecological year from 1 June to 31 May, as the period between two consecutive denning seasons (June is the mean, median and modal month of denning; Fig. 2). We defined age in years and also into three broader age classes for useful comparisons with other populations: pups (<1 year), yearlings (1-2 years) and adults (>2 years). A pack was defined as a group with at least one adult male and one adult female. We also determined the proportion of males within the population for each age class. Pack and population size were calculated as the sum of yearling and adult wild dogs. Population and pack density were calculated as the population size and number of packs per 100 km^2. We determined individual female survival on a monthly basis and assigned dead or alive to each female at the start of each month, restricting this dataset to individuals born between 1992 and 2015.

Reproduction. We used VHF collars, GPS collars and direct observations to determine timing and location of denning, recording the birth month of all litters between 1996 and 2016. The mean age of first observation of pups in the population was 2.78 ± SE 0.23 months. Therefore, we classified litter size as the number of pups produced at three months old and recorded the sex ratio within each litter at this same time. We also counted the number of surviving pups for each litter at six and 12 months old to determine the proportion of pups raised (i.e. pup survival). When birth month was unknown (n = 2 of 67 litters), we used the size of pups at first observation and last observation date of the pregnant female prior to denning to back-trace birth month. Each litter size was also assigned the age of the breeding female (years), natal pack size, population size and number of packs in the park. Following Creel and Creel (2002), Creel et al. (2004) and Davies-Mostert et al. (2015), we calculated age-specific fecundity as

$$P_B \times LS_B \times PF_E$$

where P_B was the proportion of females of age B (years old) that bred, LS_B was the mean litter size produced by females of age B (years) and PF_E was the proportion of females in the litters.

Lions

We utilised historical data from Somers et al. (2017) and the consolidated EKZNW database of the estimated minimum annual lion population size in HiP for the period 1992 to 2015. Some annual estimates were missing from the dataset and we used the mean of the previous year's estimate and the following year's estimate if a single year's estimate was missing (n = 1). When data for two or more consecutive years were missing, we used linear regression to incorporate the time period before and after to determine population size (three data gaps missing 2, 2 and 5 annual estimates respectively; Supplementary Fig. 1). The population of lions in HiP has maintained a very high density over the study period (mean annual 9.29 ± SE 0.32 per 100 km^2, range = 6.36 – 12.72).

Prey availability

We utilised population size estimates from EKZNW's biennial herbivore census to estimate availability of preferred prey biomass for wild dogs in HiP. This census programme estimates herbivore population sizes using distance-sampling along established transects every two years in the dry season (Fig. 1; see le Roux et al. (2017) for further details). From this we extracted the estimates for wild dog preferred prey species; impalas, nyalas, kudus, warthogs (*Phacochoerus africanus*), wildebeests (*Connochaetes taurinus*) and zebras (*Equus quagga burchellii*) (Hayward et al. 2006). Using average female body weight from Owen-Smith (1988) (impala = 44 kg, nyala = 63 kg, kudu = 107 kg, warthog = 58 kg, wildebeest = 193 kg, zebra = 265 kg), we calculated park-wide biomass per annum per species using the function

$$B = N(w * 0.75)$$

where B is the amount of available biomass, N is the estimate from the distance sampling, w is the mean female body weight and 0.75 is the correction factor to account for younger individuals in the population. We then summed the six herbivore species' biomass per annum as a total park-wide estimate of available preferred prey biomass. Finally, we expressed this as biomass density by dividing the park-wide preferred prey biomass by the area size to ensure equal scale to densities of both wild dogs and lions (kg.100 km^{-2}). Herbivore census data were available for 1986 – 1988, 1991, 1994 and biennially after that and we filled the yearly gaps utilising the same methods described for the lion data. We only used data for the periods from 1991 to 2016.

Climate data

Rainfall. We utilised the EKZNW database of monthly rainfall (mm) from two stations in HiP, one in the far north and the other in the far south (Fig. 1). This was done to characterise the variation in rainfall across the entire park as variation in rainfall in savannahs strongly affects bottom up processes (East 1984). We calculated the three significant rainfall aspects relevant to wild dog pup survival following Buettner et al. (2007) to allow for comparisons to the largest population of wild dogs in South Africa, these included: total park rainfall, six months pre-denning rainfall and two-year running mean. All rainfall measurements for these three metrics were averaged between the two stations to incorporate the variation in rainfall across the park. The northern station had a complete set of data, while we had to extrapolate data for 19 non-consecutive months for the southern station from other nearby stations (< 22 km; Fig. 1) that were likely to have similar rainfall. For three non-consecutive monthly estimates in the south, there was no rainfall data collected or available from nearby stations. To fill this gap, we used the mean annual rainfall for the southern station for that month from all previous years. We utilised data for the period 1992 to 2015. As all three rainfall measures were correlated (total park & 2-year: $r = 0.73$, $n = 25$ years, $p < 0.01$; 2-year & preden: $r = 0.52$, $n = 25$ years, $p < 0.01$; total park & preden: $r = 0.52$, $n = 25$ years, $p < 0.01$), we retained only total park rainfall as this measure affects prey vulnerability during pregnancy (first litter and litter size), denning (pups raised to six months) and post-denning (pups raised to one year) in wild dogs. For the effects of rainfall on first litter and litter size, we evaluated total park rainfall for the pregnancy period preceding birth by 69-72 days (i.e. gestation period; (Van den Berghe et al. 2012)) while for pup survival we used total park rainfall for the year in which the litter was born.

Temperature. We utilised temperature data from the South African Weather Service station at Riverview, 22 km east of the park boundary. We extracted the maximum daily temperature and averaged it across the expected pregnancy period for each litter. We also calculated the average daily maximum temperature for denning for each litter to estimate its effect on pup survival.

Statistical analyses

We utilised multiple non-parametric tests and model evaluation procedures. In all model evaluation procedures, collinearity between independent variables for each analysis was assessed prior to analysis using variance inflation factors (VIF) and Spearman rank correlation tests. Where high levels of correlation (Spearman's rho > 0.5) were found between variables, one was discarded from the analysis, ensuring that all variables had VIF values ≤ 2 in the final statistical models. We discarded a variable if it was predicted to be less important than the variable with which it was correlated (Table 1). Predictor variables were rescaled and centred in all models prior to analysis. We did not include dominance as a variable in the pup survival models due to the small number of subordinates that gave birth (n = 3). Population density and pack density were highly correlated in all model evaluations, and so we retained pack density as the pack is the fundamental unit of wild dog reproductive behaviour. The density of packs is likely to affect wild dog behaviour more than the density of individuals and is thus a valid index for population density and intraspecific competition.

Reproduction. We created seven *a priori* candidate models to test how pack size, pack density, prey biomass, rainfall and temperature affected the age of a female's first litter (Table 1). We used generalised linear mixed-effects models (GLMMs) with Poisson distribution and specified female age (years) at her first litter as the response variable, while pack size, pack density, prey biomass density, rainfall and temperature and the two-way interactions of prey biomass density with pack size and pack density were set as explanatory variables as *a priori* expectations (Table 1). Although prey biomass and pack density were slightly correlated ($r = 0.53$, $n = 29$, $p < 0.01$) we decided to retain both variables in the model evaluation as there is strong evidence to suggest that these variables both individually influence the age of first litter (Table 1). We controlled for the random effect of year in all models.

We also used linear regression models to test the effect of female age and survival on fecundity. To investigate if there was a sex-bias in this population, we used exact binomial tests from birth to eight years old. We collapsed the age categories for eight years and above into a single category as the sample size for individuals older than eight were small ($n_{males} = 1$, $n_{females} = 4$). For the test of sex-bias at birth, we only included data from litters with complete sex breakdown information (n = 33 of 67 recorded litters).

We created ten *a priori* candidate models to test whether female age, pack size, pack density, prey biomass, rainfall, temperature and lion density affected litter size (Table 1). We used GLMMs with a Poisson distribution and set litter size as response while female age, pack size, pack density, prey biomass, rainfall, temperature, lion density and the two-way interactions of pack size with female age and prey biomass and the interaction of pack density with prey biomass were set as predictor variables as *a priori* expectations (Table 1). We controlled for variation in the same females across years by nesting female identity into sample year and set this term as the random effect.

Pup survival. To test which factors affected the proportion of pups raised to six and twelve months we created two sets of 13 *a priori* candidate models. In all models, we set the proportion of pups surviving as the response. We then tested whether female age, litter size, pack size at birth, pack size at six or twelve months, pack density at birth, pack density at the age of interest, prey biomass, lion density, all three rainfall categories and temperature (Table 1) affected the proportion of pups raised to six and 12 months. We dropped multiple variables due to collinearity with the final global model for each survival response (six or twelve months) containing female age, litter size, pack size at the age of interest, prey biomass, lion density, total park rainfall and temperature in both model sets. Pack density was correlated with rainfall ($r = -0.51$, $n = 63$, $p < 0.01$) and lion density ($r = 0.63$, $n = 63$, $p < 0.01$) and so we dropped pack density as we had weak *a priori* reason for its inclusion relative to rainfall and lion density (Table 1). We used GLMMs with a binomial distribution, a logit link, weighted all models by the number of pups born to account for differences in litter size and tested all explanatory variables and the two-way interactions of pack size with litter size, prey biomass, lion density, rainfall and female age and the interaction of rainfall and temperature as *a priori* expectations (Table 1). We controlled for pack identity rather than female identity as females changed pack affiliations multiple times in their lives (DGM, unpublished data). We also tested which factors affected the number of pups raised to six and 12 months. We did this by creating the same 13 candidate regression models from the proportion of pups raised to six and 12 months but we specified the number of pups raised as response and Poisson distribution GLMMS (as number of pups raised is a count). For all four model sets, we used data from pups born from 1996 to 2015.

We used model selection based on Akaike Information Criterion corrected for small sample size (AIC*c*). When several models were selected ($\Delta AICc \leq 2$), following Burnham and Anderson (1998), we performed modelaveraging correcting for model weights to provide model-averaged coefficients and confidence intervals. All statistical analyses and figures were performed in RStudio, desktop version 0.99.879 (RStudio Team 2015) for Windows, using functions in the packages *dunn.test* (Dinno 2016), *stats* (RStudio Team 2015), *lme4* (Bates et al. 2015), *car* (Fox and Weisberg 2011), *MuMIn* (Barton 2013), and *ggplot2* (RStudio Team 2015).

Data availability

The datasets generated and analysed during the current study are available in the figshare repository, 10.6084/m9.figshare.7791164.

Results

Reproduction

We recorded 67 litters from 25 different females across the 90 pack years from 1996 to 2016 (Table 2). Other reproduction trends are presented in Table 3. The majority of litters were born during the dry, cool winter months between April to October (n = 65 litters), while only two litters were born in the hot, wet summer months (Fig. 2). The top models for factors affecting the age of a female's first litter (Table 3) included pack density, prey biomass and pack size (Supplementary Table 1). Specifically, females bred younger when there was a high pack density (Table 4, Fig. 3a), a high availability of food (Table 4, Fig. 3b) and when the female was part of a large pack (Table 4, Fig. 3c).

One female gave birth three times in 13 months: June 2007, December 2007 and July 2008. The entire June 2007 litter died underground. However, this female gave birth to 10 pups in December 2007 (Fig. 2) and then again the following dry season when she gave birth to five pups in July 2008. Fecundity increased significantly with senescence ($F_{(1,7)} = 29.75$, $p < 0.01$; Fig. 4a) but female survival had no effect on fecundity ($F_{(1,6)} = 0.02$, $p = 0.90$).

We observed four instances of multiple births per pack in a denning season: (1) two sisters from the "Ume" pack in 2007 gave birth, (2) the same two sisters from the "Ume" pack in 2008 became pregnant. However, only the alpha female was confirmed to have given birth while it was likely that the beta female also gave birth. The beta female dispersed the following year during the mating season and formed a pack with a single male who was reintroduced into the park; (3) three sisters from the "Shiyane" pack in 2010 were observed mating, with two of the females becoming pregnant and both giving birth; (4) two sisters from the "Sokhwezela" pack in 2013 were observed mating and falling pregnant but the beta female split from the pack with three female siblings and an older related female prior to giving birth. From the first three events, we also observed that pups from dominant and subordinate females were brought together into a single den where we could not track pup survival specific to the breeding female's dominance status.

There was no bias in the sex ratio of litters (118 of 210 pups were males; exact binomial test; $p = 0.08$). The proportion of males across age classes varied, with the population biased towards males for one-year olds (197 of 343 yearlings were males; exact binomial test; $p = 0.01$), two-year olds (141 of 238 2-year olds were males; exact binomial test; $p = 0.01$) and four-year olds (59 of 97 4-year olds were males; exact binomial test; $p = 0.04$; Fig. 4b). Male bias peaked at four-years old where the population was 61% male biased (Fig. 4b). Although the population became slightly dominated by females from seven years old (Fig. 4b), this was not significant (20 of 32 ≥7-year olds were females; exact binomial test; $p = 0.22$).

The top model for factors affecting litter size (Table 3) included only pack size (Supplementary Table 2), where larger packs produced larger litters (Table 4, Fig. 5).

Pup survival

The top model for factors affecting the proportion of pups raised to six months and one year (Table 3) included the interaction of female age and pack size at the age of interest (six months: Supplementary Table 3, one year: Supplementary Table 4). Older females were able to raise a higher proportion of pups to six months when they were part of larger packs (Table 4, Fig. 6a), while pack size did not affect young female's ability to raise pups to six months (Fig. 6a). Generally, larger packs raised more pups to one year (Table 4, Fig. 6b) but this relationship was particularly strong when the breeding female was older (Table 4, Fig. 6b).

The top model for factors affecting the number of pups raised to six months (Table 3) included only litter size (Supplementary Table 5), where more pups were raised to six months when from larger litters (Table 4, Fig. 7). The top models for factors affecting the number of pups raised to one year (Table 3) included litter size and the interaction of litter size and pack size (Supplementary Table 6). Generally, more pups survived to one year from larger litters (Table 4), but more pups were raised to one year by larger packs when the litter size was large (Table 4, Fig. 8).

Discussion

Wild dogs in HiP bred in the dry season synonymous with wild dog populations elsewhere in southern Africa (Creel and Creel 2002; Buettner et al. 2007). Reproductive seasonality is common in other canid species such as Ethiopian wolves (*Canis simensis*) (Sillero-Zubiri et al. 1998) and grey wolves (Fuller et al. 2003). In dry seasons with an increase in forage scarcity, ungulate body condition can be reduced (Marshal et al. 2012) making them more vulnerable to predation. Wild dog denning in the dry season therefore suggests a link between their reproduction and prey vulnerability. In the Serengeti, only 60% of litters were born between March and June, in the late rainy season (Frame et al. 1979). This suggests that wild dogs in open and less seasonal ecosystems display reduced seasonality likely due to good year-round prey availability. Aseasonal breeding in our study occurred when litters were lost, with females cycling again later in the year (n = 2), providing *in situ* evidence for mono-oestrus in wild dogs (Boutelle and Bertschinger 2010).

Dominant female wild dogs successfully monopolised breeding for multi-years as indicated by the low mean annual proportion of breeding females and few beta female births. This suggests a low degree of shared maternity (Malcolm and Marten 1982; Creel et al. 1997) in line with the wild dog monogamous mating system (Creel and Creel 2002). However, social components of mating systems often differ to actual mating outcomes (Kappeler and van Schaik 2002), where extra-pair copulations occur within monogamous carnivores to increase individual fitness. Our observations, albeit few, suggest that successful extra-pair copulations occurred within this population of wild dogs as recorded previously in this population (Spiering et al. 2009) and others (Frame et al. 1979; Creel and Creel 2002).

Fecundity increasing linearly with age is similar to that observed for other populations in southern Africa (Creel et al. 2004; Davies-Mostert et al. 2015) but differs to those in northern Botswana and Selous Game Reserve (Tanzania) that have a tendency for a decrease in litter size for older breeding females (Creel et al. 2004). Irrespective of the regional differences, it is apparent that as age increases, so too does fecundity. Moreover, this pattern, coupled with the probability of dominance increasing with age (DGM, unpublished data), low anthropogenic mortality (Somers et al. 2017) and avoidance of inter-specific competition (Darnell et al. 2014) could explain the rapid population growth of wild dogs in HiP.

Wild dog litters were not sex-biased suggesting natural selection on breeding females to produce equal sex litters. Consequently, natural selection should then favour inter-sexual similarities in spatial philopatry and dispersal if mortality was not sex-specific, which is the case for this population (DGM, unpublished data). There was a slight male-bias in the younger age classes (one, two and four year olds), which varies from an adult male bias found elsewhere across the species range (Frame et al. 1979; Creel and Creel 2002). This could then have influenced the observations in this population of female biased early dispersal with male philopatry (DGM, unpublished data).

Wild dog reproduction is well studied across a range of ecosystems, but our study provides the only account of factors affecting females' age at first litter. We found that, on average, a female wild dog first gives birth between 3 and 3.5 years old and primiparity is reduced when there is high prey availability, large pack sizes and high pack density. In grey wolves, high prey availability increased the prey capture opportunities and nutritional levels (Mech et al. 1998). Although we do not have data on prey capture rates across temporal variation in prey availability, we suggest similar conclusions. Assuming increased capture rate, alpha females should then have increased nutritional intake, to satisfy the physiological and metabolic requirements of pregnancy and gestation allowing them to breed younger. Under low prey availability conditions, females are unable to meet the high energetic costs of gestation (Creel and Creel 1991) and will forego reproduction for energy conservation. These conclusions are related to limited inter-pack competition, so it is interesting that high pack density also resulted in young breeding females. However, even at high densities with extensive spatial overlap between neighbours, packs avoid each other via temporal partitioning (Creel and Creel 2002). High population densities could decrease dispersal time in mate finding to ensure rapid pack formation, home range establishment and breeding. Increased numbers of non-breeding helpers enable packs to kill larger prey, over shorter chase distances, with increased probability of a kill and a greater chance of multiple kills (Creel and Creel 1995, 2002). Consequently, larger packs should have higher capture rates and nutritional intake, providing better for alpha females to meet the costs of pregnancy and gestation. Moreover, irrespective of prey availability, larger packs had younger breeding females than smaller packs as indicated by no interaction between pack size and prey availability in the top model set. This suggests a more indirect causal link between the age of first litters and prey, which is mediated in larger packs' abilities to outcompete smaller packs (Creel and Creel 2002). Smaller packs then have to tolerate higher lion densities and less safe dens sites that could delay first breeding. Essentially, we suggest that a high number of non-breeding helpers (pack size) is key to the youngest breeding females.

Litter sizes were similar to the large free-roaming population in Selous (Creel and Creel 2002; Creel et al. 2004) and the recovered population in Laikipia (Woodroffe 2011), but were smaller than the rest of the managed metapopulation (Davies-Mostert et al. 2015), and the majority of large populations in northern Botswana (McNutt and Silk 2008), Kruger (Creel et al. 2004) and the Serengeti. We found larger litters were produced by larger packs. As pack size increases, foraging success increases through the killing of larger prey, chasing prey over shorter distances, increased probability of capturing prey and multiple kills (Creel and Creel 1995, 2002). This should increase the nutritional intake for pack members including the alpha female as a high number of non-breeders helpers regurgitate meat, which occurs during gestation (Malcolm and Marten 1982). Therefore, as reproductive success is related to pack size in our study and others (Creel and Creel 2002; Gusset and Macdonald 2010), the benefits of grouping outweigh the costs related to efficient communal hunting and pack and alpha female provisioning (Rasmussen et al. 2008; Gusset and Macdonald 2010).

Pup survival is the most important parameter in wild dog population dynamics (Creel et al. 2004), making understanding factors affecting it crucial for a population of wild dogs and especially one that is closely managed. The proportion of pups surviving in this population was high (to six months: 0.80, to one year: 0.69), similar to populations in the Selous (Creel and Creel 2002) and Laikipia (Woodroffe 2011). We found pup survival to be enhanced when older breeding females were part of larger packs. This effect was particularly strong for survival to six months. Den site selection is critical to reproduction in wild dogs (Davies et al. 2016) and it is likely that older females have more experience in selecting suitable sites. Additionally, when older females had more non-breeding helpers, as in large packs, there is more assistance in prey catching, regurgitation for pups and the lactating female at dens, guarding offspring at dens and giving priority access at kills to pups once they have left the den (Creel and Creel 1995, 2002; Forsmann et al. 2018). Subordinate and yearling wild dogs regurgitate for pups more than dominants and adults (Forsmann et al. 2018), which should confer positive maintenance benefits to dominants and adults that are less required to directly provision regurgitated meat for pups. We suggest this gives flexibility for non-breeding adults and the alpha males to increase pup guarding while alpha female’s energy goes into milk production. Essentially, pup survival is dependent on both communal hunting and alloparental care (Creel et al. 2004).

We also found that larger litters resulted in more pups being raised to six months as found in other studies (McNutt and Silk 2008; Woodroffe 2011; Woodroffe et al. 2017). An increased reproductive effort to produce larger litters and raise more offspring is associated with diminished life spans (Partridge and Harvey 1985) in accordance with the cost of reproduction hypothesis (Risch et al. 1995). Indeed, wild dogs in HiP have very short life spans (average 2.5 years, DGM unpublished data). The production of large litters to ensure the survival of at least some offspring suggests a strategy to offset the multiple limiting factors on wild dog populations (Creel and Creel 1998). Interestingly, for pups surviving to one year, larger packs were able to raise more pups if the litter was large indicating a delayed helper effect in pup survival. On average, large packs have large litters, due mainly to effective food provisioning to the pregnant females, then it is likely that these packs will have high recruitment with associated positive benefits for the individuals (increased resource intake rate per capita) and for the pack (communal and efficient hunting). Whether investigating the proportion or number of pups raised it is apparent that pack size is critical to wild dog reproductive success.

Generally, two further conclusions can be made about pup survival from our study: (1) a prominent geographic variation and (2) a limited effect of lions. Regarding geographic variation, our results differ to those in Kruger (Buettner et al. 2007) where multiple rainfall metrics affected pup survival to nine months while pack size only affected survival to one year. Despite the threat of lions to pup survival (Woodroffe et al. 2007), their effect was limited, but we retain a precautionary conclusion in this regard, as we had an annual estimate for lion density whereas monthly estimates may have revealed a clearer effect. Irrespective, wild dogs in HiP appear to have local adaptations to living in an area of a high density of lions, which could include maintaining larger pack sizes that allow more helpers to assist in care for pups.

Compliance with ethical standards

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Conflicts of interest

The authors declare that they have no conflict of interest.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of The University of Pretoria under the approved Animal Ethics Committee, project number EC006-14.

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Figure and table captions

Fig. 1 Location of Hluhluwe-iMfolozi Park on a 1:50 000 topographic section (insert) within northern KwaZulu-Natal, South Africa. The insert also shows the location of the two main weather stations (●), the secondary weather stations (♦) and the herbivore transects (dashed lines). The boundary of the park is also shown (narrow solid line) as well as the district road bisecting the park (thick solid line)

Fig. 2 The frequency distribution of litters born per month for wild dogs in HiP

Fig. 3 Factors affecting the age at which female wild dogs first produce pups in HiP, affected by the (a) pack density, (b) available prey biomass density, and (c) pack size. Shaded regions show the 95% confidence intervals

Fig. 4 (a) Relationship between female age and fecundity, the trend line shows the linear regression, and (b) relationship between age and sex-bias in HiP population, with a line of equal proportion of males and females (i.e. 1:1) and with 95% confidence intervals shown as dashed lines. The calculation of age-specific fecundity can be found in the methods following Creel and Creel (2002), Creel et al. (2004) and Davies-Mostert et al. (2015)

Fig. 5 The positive effect of pack size on litter size at den emergence in wild dogs in HiP, Shaded regions shown are the 95% confidence intervals

Fig. 6 The interaction of female age and pack size affecting the proportion of wild dog pups raised to (a) six months and (b) one year in HiP. Shaded regions shown are the 95% confidence interval

Fig. 7 The positive effect of litter size at den emergence on the number of wild dog pups raised to six months. Shaded regions shown are the 95% confidence interval

Fig. 8 The interaction of litter size and pack size on the number of wild dog pups raised to one year. Small litters comprise between two and seven pups while large litters were between eight and 14 pups. Shaded regions shown are the 95% confidence interval

Table 1 An *a priori* summary of the variables expected to affect the age of a female's first litter, litter size and pup survival in wild dogs. Within the hypotheses, upward arrows (↑) denote increases in a variable while downward arrows (↓) denote decreases in a variable. Measures and units per variable are in parentheses

Table 2 Descriptive reproduction data for the 25 females that bred in HiP from 1996 to 2016

Table 3 Descriptive reproduction variables from breeding female wild dogs illustrating the mean, standard error (SE) and range for each variable

Table 4 Average effects of explanatory variables from the top models explaining the age of first litter for females, litter size, the proportion and number of pups raised to six months and to one year based on the model evaluation procedure

Fig. 1

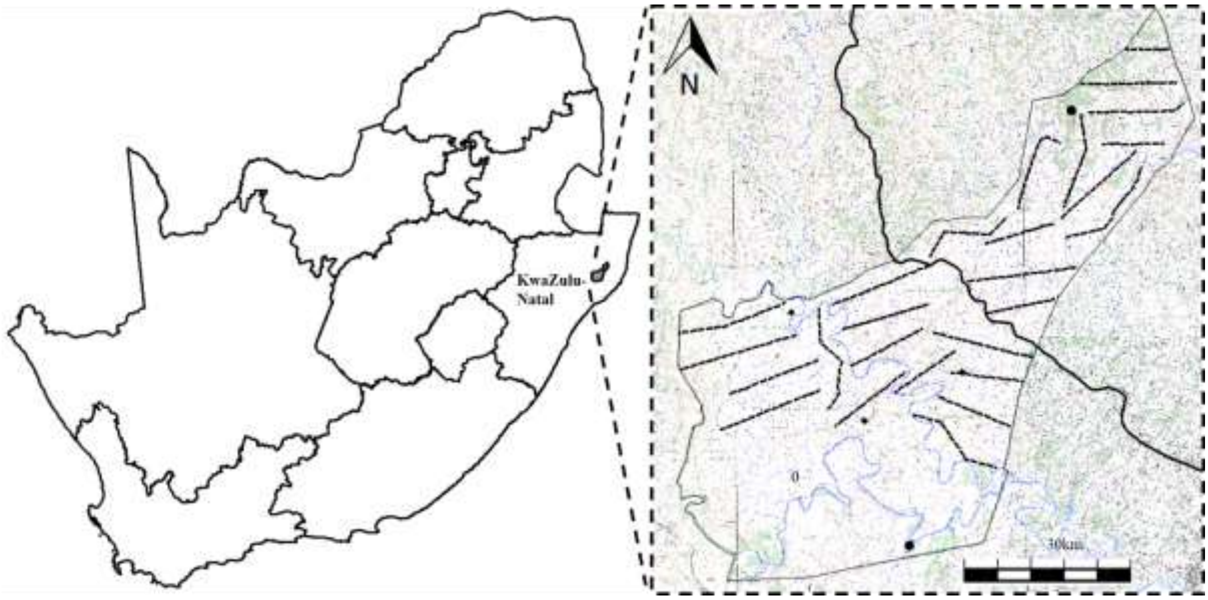

KwaZulu-Natal
N
0
30km

Fig. 2

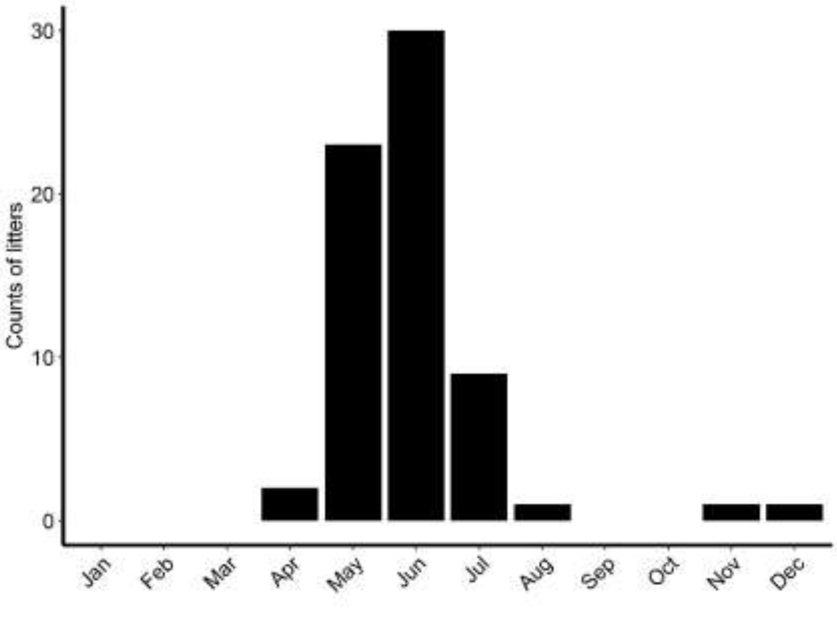

Counts of litters
30
20
10
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Fig. 3

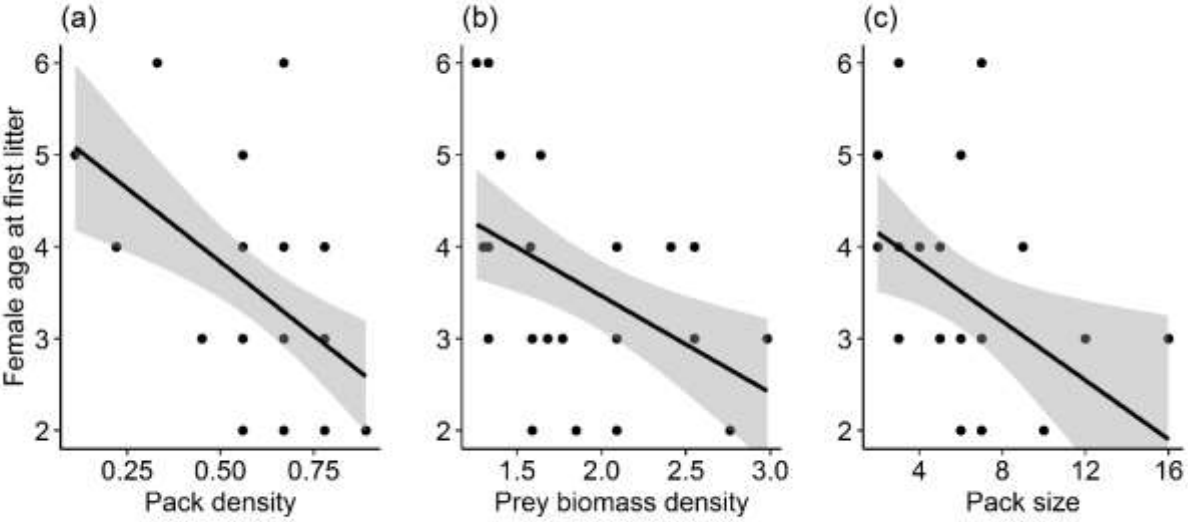

(a)
(b)
(c)
Female age at first litter
6
5
4
3
2
0.25
0.50
0.75
Pack density
1.5
2.0
2.5
3.0
Prey biomass density
4
8
12
16
Pack size

Fig. 4

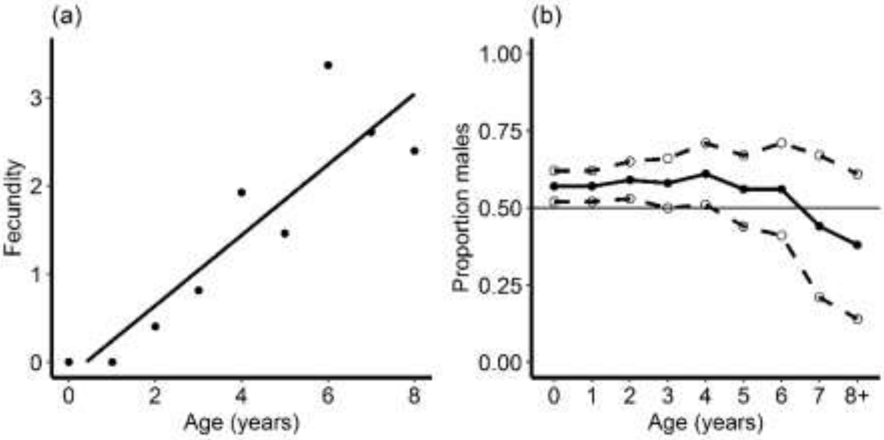
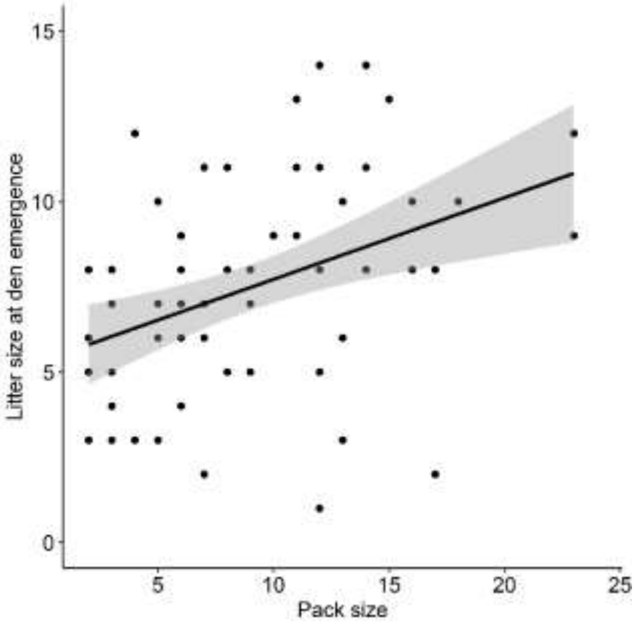
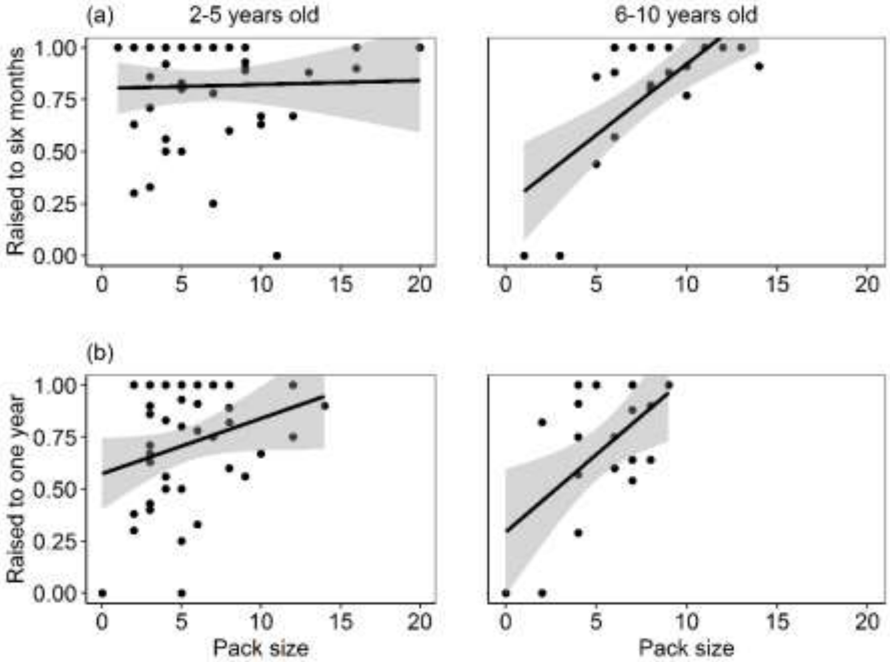

(a)
Fecundity
0
1
2
3
0
2
4
6
8
Age (years)
(b)
Proportion males
0.00
0.25
0.50
0.75
1.00
0
1
2
3
4
5
6
7
8+
Age (years)

Fig. 5



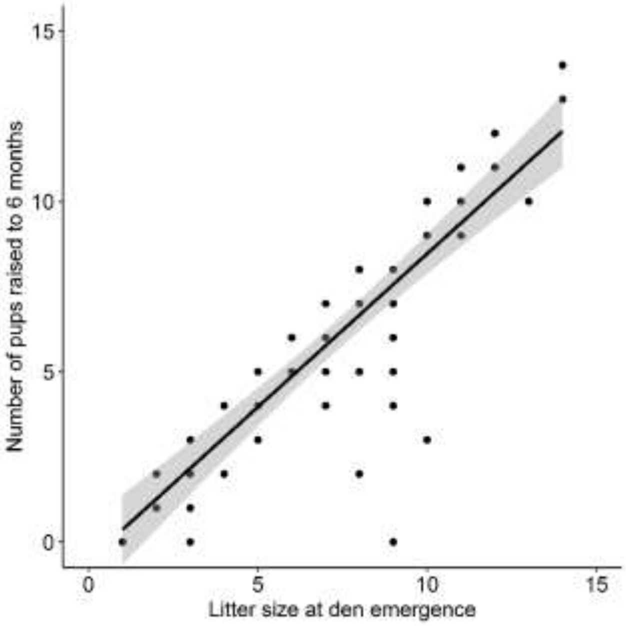
Litter size at den emergence
0
5
10
15
5
10
15
20
25
Pack size

Fig. 6



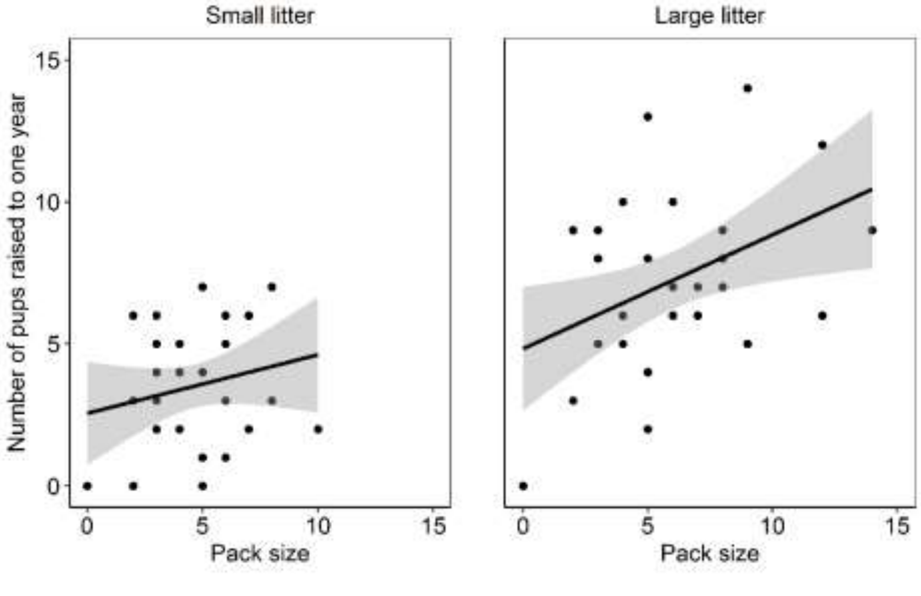
(a)
2-5 years old
6-10 years old
Raised to six months
1.00
0.75
0.50
0.25
0.00
0
5
10
15
20
(b)
Raised to one year
Pack size
Pack size

Fig. 7



Number of pups raised to 6 months
15
10
5
0
0
5
10
15
Litter size at den emergence

Fig. 8



Small litter
Large litter
Number of pups raised to one year
15
10
5
0
0
5
10
15
Pack size
0
5
10
15
Pack size

Table 1 An *a priori* summary of the variables expected to affect the age of a female's first litter, litter size and pup survival in wild dogs. Within the hypotheses, upward arrows (↑) denote increases in a variable while downward arrows (↓) denote decreases in a variable. Measures and units per variable are in parentheses

Variable	Hypotheses	References
First litter		
Preferred prey available biomass (kg.100km^{-2}/10,000)	↑ prey = ↓ age	Fuller et al. (2003)
	No effect	Creel and Creel (1998); Creel and Creel (2002)
Pack size (adults and yearlings)	↑ pack size = ↓ age	Rasmussen et al. (2008); Ausband et al. (2018)
	↑ pack size = ↑ age	
Population density (no. packs.100km^{-2})	↑ pack density = ↓ age	
	↑ pack density = ↑ age	Balme et al. (2013)
Rainfall (mm)	↓ rainfall = ↓ age	Ogutu et al. (2008)
Mean daily maximum temperature (°C)	↑ temperature = ↑ age	
Prey*Population density	↑ density & ↓ prey = ↑ age	Fuller et al. (2003)
Prey*Pack size	↑ prey & ↑ pack size = ↓ age	Rasmussen et al. (2008); Ausband et al. (2018)
Litter size		
Preferred prey available biomass (kg.100km^{-2}/10,000)	↑ prey = ↑ litter size	Fuller et al. (2003); Gese (2004)
	No effect	Creel and Creel (1998); Somers et al. (2008); Gusset and Macdonald (2010)
Pack size (adults and yearlings)	↑ pack size = ↑ litter size	Creel et al. (2004)*; McNutt and Silk (2008)*; Woodroffe (2011)
	No effect	Somers et al. (2008)
Population density (no. packs.100km^{-2})	No effect	Creel and Creel (2002)
	↑ pack density = ↓ litter size	Balme et al. (2013)
Birth female age (years)	↑ age = ↑ litter size	Creel et al. (2004)*; McNutt and Silk (2008)*; Davies-Mostert et al. (2015)
	No effect	Somers et al. (2008); Woodroffe et al. (2017)
Rainfall (mm)	↓ rainfall = ↑ litter size	Buettner et al. (2007)
	No effect	Somers et al. (2008)
Lions (number.100km^{-2})	No effect	Somers et al. (2008); Gusset and Macdonald (2010)
	↑ lion density = ↓ litter size	
Mean daily maximum temperature (°C)	↑ temperature = ↓ litter size	Woodroffe et al. (2017)
Pack size*Prey	↓ pack size = ↑ litter size if ↑ prey	
Population density*Prey	↑ density = ↑ litter size if ↑ prey	Fuller et al. (2003)
Age*Pack size	↑ age & ↑ pack size = largest litter sizes	Creel et al. (2004)
Pup survival		
Preferred prey available biomass (kg.100km^{-2}/10,000)	↑ prey = ↑ survival	Hayward et al. (2007); McNutt and Gusset (2012); Ford et al. (2015)
	No effect	Creel and Creel (1998); Somers et al. (2008); Gusset and Macdonald (2010)
Pack size (adults and yearlings)	↑ pack size = ↑ survival	Creel et al. (2004); Buettner et al. (2007); McNutt and Silk (2008); Gusset and Macdonald (2010); Davies-Mostert et al. (2015); Woodroffe et al. (2017)

	No effect	Somers et al. (2008); Gusset and Macdonald (2010)
Population density (no. packs.100km^{-2})	↑ population density = ↓ survival	Balme et al. (2013)
	No effect	Creel and Creel (2002)
Rainfall (mm)	↓ rainfall = ↑ survival	Buettner et al. (2007); Woodroffe et al. (2017)
	↑ rainfall = ↑ survival	Ogutu et al. (2008); Woodroffe et al. (2017)
	No effect	Buettner et al. (2007); Somers et al. (2008); Woodroffe et al. (2017)
Birth female age (years)	↑ age = ↑ survival	Creel and Creel (2002); Creel et al. (2004)*; McNutt and Silk (2008)*
	No effect	Woodroffe et al. (2017)
Lions (number.100km^{-2})	↑ lion density = ↓ survival	Woodroffe et al. (2007)
	No effect	Somers et al. (2008); Gusset and Macdonald (2010)
Mean daily maximum temperature (°C)	↑ temperature = ↓ survival	Woodroffe et al. (2017)
Litter type (alpha only, beta only, mix)	Alpha survival > beta survival	Girman et al. (1997)
	Only one litter = ↑ survival to one year	Woodroffe et al. (2017)
	Multiple breeding females = ↑ survival	Woodroffe et al. (2017)
Litter size (number of pups)	↑ litter size = ↑ survival	McNutt and Silk (2008); Woodroffe (2011); Woodroffe et al. (2017)
Pack size*Litter size	↓ pack size = ↑ survival if ↑ litter size	
Pack size*Prey	↓ pack size & ↑ prey = ↑ survival	
Pack size*Lion density	↑ lion density = ↑ survival if ↑ pack size	Malcolm and Marten (1982)
Rainfall*Pack size	↓ rainfall & ↑ pack size = ↑ survival	Buettner et al. (2007)
Rainfall*Temperature	↑ temperature & ↓ rainfall = ↑ survival	Buettner et al. (2007); Woodroffe et al. (2017)
Age*Pack size	↓ age = ↑ survival if ↑ pack size	Creel et al. (2004)

[a] decrease for the eldest aged females

Table 2 Descriptive reproduction data for the 25 females that bred in HiP from 1996 to 2016

Female ID	Age (years) of first litter	Number of litters	Mean litter size ± SE[a]
18	5	3	6.33 ± 1.76
9703	4	5	6.40 ± 1.50
9706	4	1	12
2001	4	7	8.57 ± 1.69
2109	5	1	4
2219	3	1	7
2226	3	4	9.00 ± 1.41
2309	4	4	7.00 ± 1.22
2401	3	1	7
2402	3	1	7
2421	3	3	6.00 ± 1.53
2501	2	1	7
2505	3	4	10.75 ±1.25
2705	2	2	3.50 ± 2.50
2707	2	4	9.75 ± 0.85
2708	3	1	3
2713	4	2	4.50 ± 0.50
2727	3	6	6.83 ± 0.98
2920	6	2	7.50 ± 0.50
21001	3	1	3
MWF21001	4	1	8
21017	2	3	8.33 ± 1.45
21030	3	3	7.67 ± 0.33
21103	3	3	7.67 ± 3.18
21108	2	3	8.33 ± 1.20

[a] Only for females that had at least two litters

Table 3 Descriptive reproduction variables from breeding female wild dogs illustrating the mean, standard error (SE) and range for each variable

Variable	Mean ± SE	Range
Number of litters per female	2.96 ± 0.36	1 – 7
Age (years) of first litter	3.32 ± 0.21	2 – 6
Inter-birth interval (months) for individuals	31.30 ± 1.39	10.25 – 70.25
Inter-birth interval (months) for packs	29.39 ± 1.00	10.25 – 63.33
Annual proportion breeding females in the population	0.09 ± 0.01	0 – 0.20
Annual number pups produced in the population	23.68 ± 3.07	0 – 42
Litter size (n = 67 litters)	7.48 ± 0.37	1 – 14
Breeding female age (years; n = 25 females)	4.82 ± 0.19	2 – 10
Annual birth rate	0.68 ± 0.11	0 – 2.38
Proportion pups raised to six months	0.80 ± 0.03	0 – 1.0
Proportion pups raised to one year	0.69 ± 0.04	0 – 1.0
Number of pups raised to six months	6.08 ± 0.41	0 – 14
Number of pups raised to one year	5.27 ± 0.42	0 – 14

Table 4 Average effects of explanatory variables from the top models explaining the age of first litter for females, litter size, and the proportion and number of pups raised to six months and to one year based on the model evaluation procedure

Variable	$\widehat{\boldsymbol{\beta}}$	**SE** ($\widehat{\boldsymbol{\beta}}$)	***P***	**N models**	**Importance**
First litter					
Pack density	-0.07	0.11	0.53	2	0.39
Biomass	-0.06	0.10	0.60	3	0.33
Pack size	-0.03	0.08	0.70	2	0.21
Litter size					
Pack size	0.15	0.05	< 0.01*	3	0.97
Proportion raised to six months					
Female age: Pack size	0.81	0.21	< 0.01**	1	>0.99
Proportion raised to one year					
Female age: Pack size	0.32	0.17	0.06	1	0.88
Number raised to six months					
Litter size	0.45	0.06	< 0.01**	2	>0.99
Number raised to one year					
Litter size: Pack size	-0.03	0.05	0.59	1	0.54
Litter size	0.45	0.06	< 0.01**	2	>0.99

** $p < 0.001$, * $p < 0.01$