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Mortality and female fecundity in an expanding black rhinoceros (*Diceros bicornis minor*) population

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Abstract Identifying factors that affect demographic parameters and how those factors act is vital for understanding population dynamics, especially of endangered species. Moreover, specific ideas in the population dynamics of large herbivores underpin the management of the critically endangered black rhinoceros (*Diceros bicornis*). We studied an expanding black rhinoceros population since its establishment in 1986 in the Great Fish River Reserve, South Africa, through 2008 when managed removals interrupted natural dynamics. During the study, only 13 animals died, of which nine were subadults. In a linear modelling context, we used information-theoretic methods to evaluate the influence of independent variables expected to affect demographic parameters. For females, age at first reproduction (AFR) increased with abundance, but there was no effect of abundance on adult fecundity as measured by inter-birth intervals (IBIs). We evaluated these results in the theoretical context of population dynamics of large herbivores, in particular, Eberhardt's proposal of a specific sequence in which demographic parameters first respond to increasing density. Our observations are consistent with Eberhardt's prediction that immature individuals are impacted before adults, but the relative timing and magnitude of density effects on immature individuals was unclear. Rainfall did not influence AFR or IBIs. Maternal age influenced IBIs but much of the observed variation in IBIs was not accounted for by structural variation. Studies of populations more nearly approaching a stable age distribution and carrying capacity are needed to resolve remaining uncertainties and ambiguities in the life history of the black rhinoceros in particular and megaherbivores in general.

Keywords Black rhinoceros · Demography · Density dependence · Life history · Megaherbivores

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Introduction

The performance of reintroduced populations, especially of endangered species, is of particular interest (Seddon et al. 2007). The Great Fish River Reserve, Eastern Cape Province, South Africa, is split into two sections by the Great Fish and Kat rivers. In each section, black rhinoceros (*Diceros bicornis minor*) populations were independently introduced, managed and monitored through 2008. The population in the section consisting of the Sam Knott and Kudu Reserve sectors (hereafter the SKKR population) is the older, larger and more consistently monitored of the two. The other population is in the Double Drift sector.

Since its inception in 1986, the SKKR population has been consistently monitored by ground patrols and aerial reconnaissance; each animal was ear-notched and births and deaths routinely recorded (Fike 2011). The SKKR population was effectively demographically isolated through the end of 2008. Though five subadults were exported in 2006, had these individuals remained in the population they could have

contributed likely at most three offspring by the end of 2008, all of which would have still been calves. We terminated our study at the end of 2008 due to further planned removals.

In this paper, we report on female fecundity, specifically age at first reproduction (AFR) and inter-birth intervals (IBIs), and general mortality in the SKKR population for the period 1986 through 2008. We assessed the influence of a priori chosen variables expected to affect fecundity and mortality. In particular, we explored whether demographic parameters were influenced by population size and examined the influence of rainfall, which is presumed to act on individual growth and maternal condition through an effect on primary production (Shorrocks 2007). Attributes of maternal condition were also considered as possible influences on IBIs.

The demography of populations of large herbivores has received considerable attention, especially as regards dynamics and the effects of density and environmental influences (Bonenfant et al. 2009; Owen-Smith 2010). A central idea is the threshold logistic model in which per capita growth rate remains (nearly) constant until declining rapidly to zero when carrying capacity is approached rather than declining linearly as in the logistic model (Fowler 1981, 1987; McCullough 1992).

Ultimately, one wants to understand the influences on demographic parameters that drive changes in population abundance. For example, Eberhardt (2002) proposed the following sequence of responses to increasing population density: first, decreased survival of immature individuals; then increased AFR; then decreased reproductive rate of adult females; and finally decreased survival of adults. More generally, this sequence of responses might result from any persistent effect that increases resource limitation (Trimble et al. 2009).

These ideas have received substantial empirical support (Bonenfant et al. 2009; Owen-Smith 2010), leading to the application of the threshold logistic model in the management of black rhinoceros (Diceros bicornis). The aim is to maintain populations at secure levels below a point at which density dependence diminishes population growth rate by translocating the excess to establish new populations (Emslie 2001). Eberhardt's sequence may thus provide a useful approach to detecting the onset and magnitude of density dependence. For megaherbivores, however, Owen-Smith (1988: p. 264) suggested that density would act principally on fecundity, with little effect on mortality. This difference might result because megaherbivores experience a stronger trade off between investment in growth and reproduction than other large herbivores, leading to a greater density effect on AFR than on mortality of immature individuals (Bonenfant et al. 2009: p. 339). We employed this theoretical context to evaluate our results on reproductive performance and mortality. We will report on population growth rate itself elsewhere.

Few long-term studies of expanding megaherbivore populations have been reported (but see Gough and Kerley 2006). Reintroductions provide rare opportunities to study the growth of megaherbivore populations (Hrabar and du Toit 2005), as may populations recovering from severe poaching (Walpole et al. 2001; Brodie et al. 2011), but the long-term data required to adequately test alternative hypotheses are challenging to collect, even without the poaching that threatens rhinoceros species. Further supporting material is provided in Online Supporting Information: page, table and figure references to which are prefixed by 'S'.

Methods

Study area

The SKKR study site is 220 km^2, located in the Thicket Biome as described in Lent and Fike (2003), Ganqa et al. (2005) and Ganqa and Scogings (2007). Monthly rainfall was recorded at three locations in SKKR: Kamadolo (1983–2008); Retreat (1985–1986 and 1990–2008); and Botha's Post (1989–2002 and 2006–2007) (Fike 2011). For each location, the mean (over years) rainfall of each calendar month was compared to the grand mean (over all months and years) monthly rainfall; for each location, the months May–September, inclusive, were below average and the remaining months above average. We therefore defined the dry season as May through September, the wet season as October through April and a seasonal year as a dry season followed by a wet season. Single wet and dry seasons are typical of southern Africa and result from the behaviour of the Intertropical Convergence Zone (Shorrocks 2007).

Differences in rainfall between the three locations were associated with differences in altitude and aspect (Fike 2011). For all analyses, we used the average over the locations for each month as our rainfall measure (see S1–S5 for further justification). For the 23 seasonal years beginning in May 1986, the mean annual precipitation was 452 mm (range, 253–609; CV=18 %); mean monthly rainfall for dry season months was 21 mm (range, 0–168; CV= 123 %); and for wet season months, the mean monthly rainfall was 49 mm (range, 1–194; CV=71 %) (Table S1).

Reintroductions

The SKKR population was established through multiple releases between June 1986 and December 1997 (Table 1, Fike 2011). Five animals died soon after release without contributing to the population and were excluded from the study. In the only example of migration during the study period, a female aged about four when imported into the Double Drift sector in 2000 immigrated into the SKKR

Table 1 Release history; *F* female, *M* male; crosses indicate animals (five) that died soon after release without contributing to the population and are not included in this study; population size is at release excluding released animals

Year	Subadults	Adults	PopSize
1986	1 F; 0 M	1 F; 2 M(x)	0
1989	3 F(x); 3 M(xx)	0 F; 0 M	3
1990	0 F; 1 M	2 F(x); 0 M	8
1992	1 F; 0 M	0 F: 1 M	11
1997	7 F; 6 M	0 F; 0 M	26

population just prior to giving birth to her first calf in August, 2003; this female and all her offspring were included in the SKKR population as of that date.

Data

Data sets for our analyses were always the statistical population of interest, not samples drawn from larger populations to which inference might be made, so for descriptive statistics, we computed the population standard deviation (PSD) for data and quote the mean (±PSD).

Each birth and death date was assigned an estimate of uncertainty (EU) at the time of recording as follows: EU=5, at most 1 week; EU=4, 1 week to 1 month; EU=3, 1 to 3 months; EU=2, 3 to 6 months; EU=1, 6 to 12 months; and EU=0, more than 1 year. We analysed data based on the nominal dates but also assessed the impact of EUs on descriptive statistics and analyses.

Working in months (EU=5 was taken to be zero error), if x is the maximum uncertainty in the female's birth date, y the maximum uncertainty in its first calf's birth date, then $z = x + y$ is the net (maximum) uncertainty in AFR, i.e. the minimum and maximum values assignable are AFR $-z$ and AFR $+z$, respectively. Similarly, with Z equal to the sum of the maximum uncertainties in the consecutive birth dates defining an IBI, the minimum and maximum values assignable to the IBI are IBI $-Z$ and IBI $+Z$, respectively.

Life stages

Three life stages are recognised for black rhinoceros: calf, indicating dependence upon the mother; subadult, independent but not reproductively mature; and adult, reproductively mature. These behavioural definitions, while biologically meaningful, are not sufficiently precise for assigning mortality to the appropriate stage and to avoid inflating fertility rates. After consulting Owen-Smith (1988), Emslie et al. (1995) and Skinner and Chimimba (2005), we adopted the following definitions. The calf–subadult transition occurs at observed separation from the mother, at the birth of the

mother's next calf, or the calf's fourth birthday, whichever comes first. The subadult–adult transition occurs for females at first calving or at the seventh birthday, whichever comes first, and for males at the eighth birthday. For rhinoceros born in the SKKR population (natives), the mean age (in months) that female calves became subadults was 28.0 (±5.9; $n=45$), that male calves became subadults 29.5 (±6.9; $n=33$) and that female subadults became adults 76.9 (±8.3; $n=19$). Gestation in the black rhinoceros is 15 months and longevity in captivity is over 30 years (Owen-Smith 1988; Skinner and Chimimba 2005).

Analyses

No female that first calved in SKRR died of old age during the study. Because all individual reproductive histories were incomplete and most relatively short, we chose the collection of IBIs to assess adult female reproductive performance. Statistical analyses were performed with Statistica 8.0 (Statsoft) or with R 2.10.1 (2009-12-14 © 2009, The R Foundation for Statistical Computing) when indicated.

For the chosen demographic parameters, we focused on evaluating evidence for the influence of potential explanatory variables. To avoid data dredging, we made a priori choices of variables based on expected biological relevance (Owen-Smith 1988; Walpole et al. 2001; Hrabar and du Toit 2005). We limited the number of variables we included in the analyses to respect the size of our data sets (Burnham and Anderson 2002: p. 245).

Lacking clear choices of rival a priori hypotheses to explain variation in AFR and IBI, we used the model selection framework based on the Akaike Information Criterion (AIC), specifically AIC_c (Burnham and Anderson 2002) to rank all 2^n linear models that can be built with n independent variables, thereby providing a set of models that is balanced with respect to the occurrence of the independent variables. From this ranking, we computed the relative importance of each variable as the sum of Akaike weights over the models in which that variable occurs (Burnham and Anderson 2002, § 4.4). These quantities, together with ΔAIC_c and model descriptive statistics, were used to evaluate the influence of the independent variables on IBI and AFR (for a similar approach to analyses, see Converse et al. 2006; Trimble et al. 2009). Depending on the results of these analyses, we planned to test whether including nonlinearities and/or interactions improved the modelling.

To model AFR, we considered only native females, excluding imports because translocation might have delayed their first reproduction and their birth dates were estimated with EUs of 1 or 0. We limited the number of independent variables to two due to data set size (16): population size (PopSize) measured at the month of first conception and a measure of rainfall. Hrabar and du Toit (2005) examined the

influence of cumulative rainfall over several consecutive time periods leading to first conception; we compromised with the cumulative rainfall over the 15 months ending with the month of first conception ($Rain_{15}$).

The net uncertainty Z in IBI also affects the computation of predictor values, notably rainfall measures, in models of IBI. We first restricted the data to the subset IBI74 of those IBIs with Z at most 9 months (which excluded three IBIs, leaving 74 observations). There were 26 maternal identities in IBI74, so we included maternal identity as a random factor (Gelman and Hill 2007: p. 276). We restricted our choice of fixed effects to five: population size and maternal age, each measured at the mid-point of the IBI to reduce dependence on the net uncertainty Z; the average monthly rainfall during the IBI (inclusive of both birth months); the cumulative rainfall over the 6 months prior to the birth month initiating the IBI; and the sex of the calf whose birth initiated the IBI. We expect these variables to reflect the principal influences operating during or just prior to an IBI. We repeated all analyses conducted for IBI for the subset IBI48 of IBIs for which $Z \leq 4$. As this subset contained only 48 observations, we omitted the 'sex' variable. We used the R package nlme for the IBI analyses.

With ρ^2 and σ^2 denoting the restricted maximum likelihood estimates of the variance of the random factor and error term, respectively, in a given mixed model, the intraclass correlation $\rho^2 / (\rho^2 + \sigma^2)$ measures the correlations between IBIs induced by the random factor (maternal identity) within the model (Gelman and Hill 2007).

Of the 15 animals that died during the study, nine were subadults (Table S9). We constructed Cox proportional hazard models for the 95 subadults of the study, with sex, the average monthly rainfall during an individual's period as a subadult, the individual's age and the population size as covariates; the last two variables were measured at the time at which an individual became a subadult. However, we concluded that due to the small number of mortalities, the resulting models

did not provide robust explanations of subadult mortality (see S22–S25 for details). We also compared the duration of subadulthood for those individuals that, during the study, reached adulthood versus those that died as subadults.

Results

Age at first reproduction

The 16 natives that calved during the study period gave birth with a mean AFR of 80 ($\pm$14) months; 13 % calved before age 5 years, 31 % before age 6, 63 % before age 7, 81 % before age 8, 94 % before age 9 and 100 % by age 9.25. Including the net uncertainty z, AFR ranged from 58 ± 2 to 111 ± 3 months. At the end of 2008, three females had not calved by the age of 7 years and were natives aged 116 ± 6, 88 ± 3 and 87 ± 3 months.

For the net uncertainty z of native AFRs: $E(z)=2.88$, so $E(AFR \pm z)=80.1 \pm 2$; $PSD(z)=1.80$ and $cov(AFR,z)=1.45$, so $PSD(AFR)=14.3$ and $PSD(AFR+z)=14.5$. Thus, EUs made little difference to these descriptive statistics.

Figure 1 displays scatter plots of AFR against the two variables chosen for the modelling. Results of the modelling are presented in Table 2 (also Table S2). The relative importance of PopSize was 0.933 and of $Rain_{15}$ was 0.161. Replacing $Rain_{15}$ with the cumulative rainfall over 27 months leading to first conception did not change the results (Table S3).

To assess the robustness of the modelling to the net uncertainly z in AFR, we increased smaller AFRs by their z value and decreased larger AFR values by their z value and repeated the entire modelling exercise. While the trend of increasing AFR with PopSize was weaker, it nevertheless persisted and the overall results were little changed, demonstrating their robustness to the uncertainties in AFR (Fig. S3, Table S4). Finally, for the AFR data, a simple nonlinear trend of the form $IBI=c+(PopSize)^n$ ($n=2$, 3 or 4) was just

Fig. 1 Scatter plots of age at first reproduction versus population size and cumulative rainfall over the 15 months ending with the month of first conception ($Rain_{15}$)
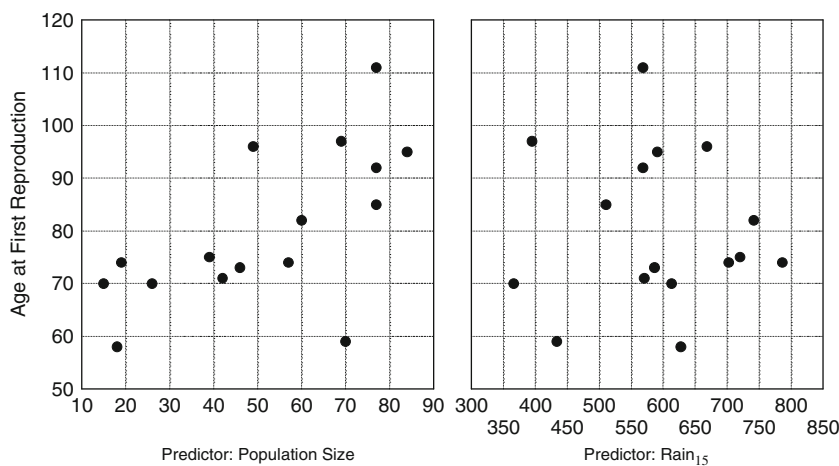
Table 2 Results of the linear modelling for age at first reproduction (K = number of model parameters; L is the maximised likelihood; R^2_a the adjusted R^2 of the model)

Model	K	$-2\log(L)$	ΔAIC_c	Akaike weight	R^2_a
PopSize	3	122.053	0	0.785	0.366
PopSize + Rain$_{15}$	4	121.744	3.327	0.149	0.331
Null	2	130.455	5.325	0.055	0
Rain$_{15}$	3	130.436	8.383	0.012	−0.070

as likely as judged by AIC_c as the linear trend ($n=1$) (Table S5).

Inter-birth interval

IBIs were measured in months. There were 77 IBIs recorded, with a mean of 29.0 (±7.9) and mode of 24. As $E(Z)=4.51$, $PSD(Z)=3.41$, $cov(IBI,Z)=0.84$, then $E(IBI\pm Z)=29.0\pm4.5$ and $PSD(IBI+Z)=8.7$. The correlation between Z and IBI was 0.03, too small to suggest Z varied systematically with IBI.

The longest IBI was 74, the final IBI of an imported female that gave birth in 1992, 1994, 1997 and finally in 2003. At the final birth, this female was estimated to be about 28 years of age and she died in 2005; her final calf itself (unsexed) died during 2003. The shortest IBI was a seemingly anomalous 14, the third IBI of a native female that calved five times, in 5/00, 8/02, 11/04, 1/06 and 10/08 (uncertainties of birth dates at most 3 months, and only 1 month for the third). Both extreme IBIs had net uncertainty $Z=4$.

For each analysis, there was no substantive difference in the results between the data sets IBI48 and IBI74, so we only report for the latter. Figure 2 presents scatter plots of IBI against the continuous fixed effects for the IBI74 data (see Table S6 for descriptive statistics). The mean of IBIs initiated by a female birth was 28.8 (±8.7; $n=42$) and of IBIs initiated by a male birth 29.4 (±8.7; $n=32$).

Table 3 records the structural model parameters for the global model while Table 4 displays the models within four AIC_c units of the top ranked model (see Table S7 for the complete ranking). The relative importance of maternal age was 0.887, of population size 0.281, of average rain (during IBI) 0.245, of rain prior to IBI 0.250 and for the birth sex initiating the IBI 0.271. The intraclass correlation of maternal identity was less than 10^{-7} in each model; indeed, for each model, the deviance ($-2\ln(L)$, where L is the maximized likelihood) differed from the deviance of the model with same fixed effects but no random factor by less than 10^{-3} so that the difference in AIC_c between these models was effectively due to the additional model parameter in the mixed model. Additive models were not improvements over the linear models and provided no compelling evidence for nonlinearities (Fig. S4).

Fig. 2 Scatter plots of inter-birth interval (IBI) versus each of four continuous predictors for the IBI74 subset of IBIs (net uncertainly $Z\leq9$). Prior rain is the cumulative monthly rainfall over the 6 months preceding the IBI; average rain is the average monthly rain during the IBI
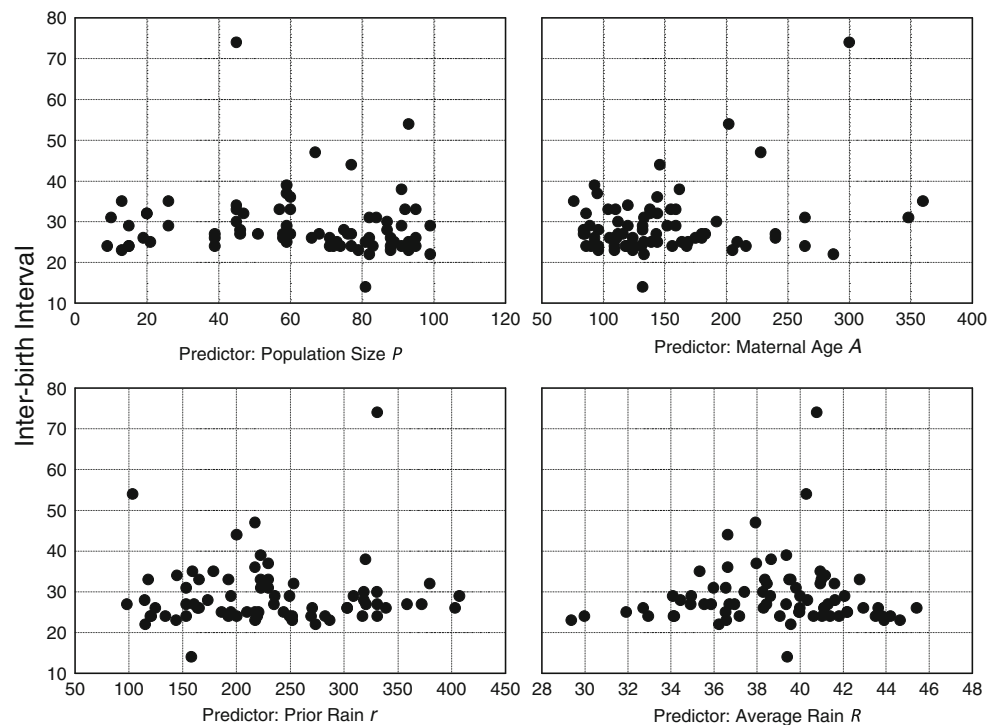
Table 3 Structural model parameters for the global linear-mixed model for the IBI74 data with maternal identity as random factor and five fixed-effect predictors: maternal age A; population size P; prior rain r (the cumualtive monthly rain over the 6 months preceding the IBI); average rain R (the average monthly rain during the IBI); and sex s, the birth sex of the birth initiating the IBI. The continuous predictor values were mean-centred and divided by twice their standard deviations to standardise the comparison of regression coefficients including that of the binary predictor s per Gelman and Hill (2007: pp. 56–57)

Predictor	Coefficient	SD	Predictor	Coefficient	SD
Intercept	28.5	1.2	Average rain R	0.7	1.9
Mat age A	4.6	1.9	PopSize P	−1.3	1.9
Prior rain r	0.8	1.9	Prior sex s	1.3	1.9

As maternal identity was not influential, we computed statistics for the global model with fixed effects only (Table S8); in particular, the adjusted R^2 was only 0.027, indicating extremely poor fit to the data. It appears that our chosen variables explain little of the variation in the IBI74 data. As a check, we preferred a nonparametric approach. As De'ath and Fabricius (2000) argued that regression trees are ideally suited for modelling ecological data that may be complex and unbalanced and involve nonlinear relationships or interactions, we conducted a regression tree analysis of IBI with the three variables of the highest relative importance as predictors. This analysis revealed that maternal age was influential due to the few longer IBI's occurring at higher maternal ages and detected no influence from the other variables (S14–S18).

The only other direct influence on IBI we could readily measure to account for the unexplained variation was the prior IBI, reflecting maternal condition, but the correlation of the 52 pairs of consecutive IBIs was only −0.01. Finally, a post-analysis check found no evidence of an influence of rainfall for up to 3 years prior to IBIs (S18–S19).

Table 4 Ranking of the linear models for IBI74 within four AIC_c units of the top model; notation for predictor variables as in Table 3

Predictors	$-2\log(L)$	K	ΔAIC_c	Akaike weights
A	511.224	4	0	0.256
A, P	511.812	5	1.890	0.100
A, s	510.852	5	1.930	0.098
A, r	511.070	5	2.148	0.088
A, R	511.157	5	2.235	0.084
A, P, s	510.342	6	3.792	0.038
Base	517.282	3	3.821	0.038

L is the maximised log-likelihood, K the number of parameters in the model, including intercept and the two variance terms. The base model is the model with just these three terms, i.e. no fixed-effect predictors

Mortality

The only known calf mortality was an unsexed calf, estimated to have been born in April 2003 at the end of the longest IBI and dead before the end of that year. Its mother was about 28 years of age at the time and died in December 2005 without calving again.

Three calving sequences with unusually long IBIs raised the issue of unobserved calf mortalities (S21). Due to the lack of any evidence to the contrary and absence of predators, these long IBIs were best interpreted as indicating variable female fecundity rather than calf mortality.

There were five adult deaths: three (two females, one male, all imports) presumed to be due to old age; one native bull euthanised (at age 13.75 years) due to injuries received from other bulls; and one imported bull of unknown causes almost 6 years after release (age at least 10 years).

Nine subadults died: five female and four male; two of the females were imports; none of the other seven were first born. Eight of these deaths occurred after 1999, four after 2004 and all male subadult mortality after 2002. The mean ± SE duration of subadulthood for those subadults reaching adulthood ($n=44$) was 50.0 ± 1.9 months and for those subadults that died 13.0 ± 3.4 months. The t test returned $p < 10^{-6}$ (even when allowing for unequal variances), a result robust to the uncertainties arising from EUs (S25–S26).

Discussion

Rainfall has been documented to influence demographic parameters in many populations of large herbivores though some populations only respond to drought conditions (Owen-Smith 2010). Gough and Kerley (2006) reported that for the African elephant (*Loxodonta africana*) in the nearby Addo Elephant National Park, birth rates, but neither AFR nor mortality, were influenced by rainfall. For the Pilanesburg black rhinoceros population, Hrabar and du Toit (2005) reported a negative influence of the July–June rainfall on the mean of IBIs for which the conception of the terminating birth fell in the same July–June period, an association between low rainfall and mortality in 'juveniles' (<3 years old), but no impact on AFRs. We found no evidence for the influence of rainfall on mortality, AFR or IBI in the SKKR population. The influence of rainfall presumably depends on the quantity and variation in both annual and seasonal rainfall and availability of surface water and forage, especially in the dry season, conditions that vary substantially across black rhinoceros and elephant habitat. However, Rasmussen et al. (2006) have argued that the normalised differential vegetation index (NDVI), a measure of primary production, has greater explanatory power than rainfall in modelling the response of demographic parameters to varying resources.

We found a positive trend of AFR with increasing population size. It is less clear at what level abundance began to act on AFR as linear and simple nonlinear trends could not be distinguished by the data, so AFR may not have begun to increase until population size reached 50–60 (Fig. 1). We will address whether the increase in AFR affected population growth rate when we report on the latter elsewhere. We found no evidence for any trend of IBI with population size. Hrabar and du Toit (2005) also reported a tendency for AFR to increase with abundance and no effect on IBI.

Other than death from old age, mortality was concentrated in the subadult stage. Three of four male subadult mortalities resulted from aggression by bulls and all occurred in the last 6 years of the study while eight of the nine subadult mortalities occurred in the last 9 years of the study, though no robust analysis is available to support the idea that subadult mortality increased with abundance. Subadults that survived their first year of independence tended to reach adulthood indicating that subadults were most vulnerable following separation from their mother. Ferreira et al. (2011) reported that mortality in the large black rhinoceros population south of the Olifants River in Kruger National Park was also largely restricted to subadults; Hrabar and du Toit (2005) found all mortality of immature individuals to be restricted to 'juveniles' (<3 years old), with no clear relation to abundance, while Brodie et al. (2011) reported that survival was lowest for neonate calves (<1 year) in north-west Namibia.

Hence, the expanding SKRR population conformed to the prediction of Eberhardt's sequence that density impacts immature before mature individuals. The small number of mortalities of calves and subadults might be construed as evidence for Owen-Smith's (1988: p. 264) prediction that density will impact megaherbivores primarily through fecundity rather than mortality but the response of the SKKR population to higher levels of density would be necessary to confirm this impression. Wittemyer et al. (2007) and Trimble et al. (2009) reported evidence for Owen-Smith's suggestion contra Eberhardt for the response of African elephant to variation in forage quality (as measured by NDVI). Compared to elephant and white rhinoceros (*Ceratotherium simum*) (an influential example in Owen-Smith's thesis), however, the greater asociality of black rhinoceros may increase vulnerability of immature black rhinoceroses so that their mortality is a more important component of demography. This issue remains unresolved.

Density feedback is typically thought to act on large herbivores through resource limitation, resulting in reduced individual growth, thereby increasing pre-adult mortality, and diversion of investment from reproduction to growth and maintenance, and thereby delaying AFR and reducing adult fecundity (Bonenfant et al. 2009). Our study area is considered to be excellent black rhinoceros habitat (Ganqa

et al. 2005). Van Lieverloo et al. (2009) studied the diet composition and preference of the SKKR population (data collected 2004) and concluded that these black rhinoceroses met their nutritional and energetic requirements without selective feeding, suggesting no resource limitation at that time, when AFR was already increasing (PopSize about 77). Ferreira et al. (2011) argued that subadult mortality in their study was socially driven rather than due to resource limitation. It is both ecologically interesting and of importance to management if density operates in rhinoceros populations not only through resource limitation but also density-dependent socially mediated cues (Bronson 1989: p. 163).

Organisms are expected to adapt to resist changes in those demographic parameters to which fitness is most sensitive (Pfister 1998; Gaillard and Yoccoz 2003; Rotella et al. 2012). The characterisation of long-lived, large herbivores as 'slow' on the 'fast–slow continuum' of mammalian life histories, together with the associated pattern of demographic elasticities (Heppell et al. 2000), suggests that this expectation may underlie the order in which demographic parameters respond to density (Bonenfant et al. 2009: p. 338). Perhaps evolutionary canalisation of demographic parameters does not fix the exact order of the response to density of certain demographic parameters, such as AFR and mortality of immature individuals, across varying habitat in a species' range. The considerable variation in habitat over the range of black rhinoceros and elephant offers an interesting opportunity to explore this possibility.

Because individual reproductive histories were incomplete, we chose individual IBIs as our unit of interest and found maternal identity not to be influential. We found evidence only for an influence of maternal age on IBI, largely due to the longest IBI occurring at a maternal age of 25 years. Owen-Smith (1988: p. 205) reported that for black rhinoceros populations from East and southern Africa, the percentage of adults ranged from 56 to 82. The SKKR population was still a young population at the end of 2008, consisting of 24 % calves, 35 % subadults and 41 % adults. Data from a more mature population, with a more representative distribution of maternal ages, are required to elucidate if IBI typically increases with maternal age and, if so, whether continuously or only discontinuously towards the end of life, a kind of incipient senescence.

Birth sex did not influence the subsequent IBI, which accords with the results reported by White et al. (2007) for white rhinoceros and Lee and Moss (1986) for African elephant (interestingly, their observations on IBIs were irrespective of any differential suckling behaviour between male and female calves).

The variation in IBI was largely unaccounted for structurally while population size accounted for about 41 % (unadjusted R^2) of the variation in AFR (comparable to the 45 % reported by Hrabar and du Toit 2005). We hypothesise

that the unaccounted-for variation in these parameters for the SKKR population was indeed not structural but due to demographic stochasticity, which has rarely been quantified in populations of large herbivores (Owen-Smith 2010: p. 107). Reintroduced populations are by their nature initially small, as are many extant black rhinoceros populations. Trimble et al. (2009) appealed to demographic stochasticity to explain why smaller elephant populations differed from the trends they generally observed.

Even allowing for EUs, the ranges, means of and variation in AFRs and IBIs of the SKRR population are nevertheless consistent with data reported for other populations (Owen-Smith 1988; Skinner and Chimimba 2005; Walpole et al. 2001; Hrabar and du Toit 2005; S26–S27). Disregarding the net uncertainty Z, the mean SKKR IBI of 29.0 months (CV 27.2 %) is shorter than that reported in most studies, which with the mode of 24 months, indicates a high rate of reproduction. There were eight IBIs with $Z=0$ (22; 23; and six of 24 months), all but one of which terminated after 2004, unambiguous evidence of continuing frequent reproduction. For the period 1998–2008 (after the introductions), annual population growth averaged 10.5 % (PSD=6.5 %); the number of calves born per adult female per year averaged 43.0 % (PSD 18.9 %); and annual mortality averaged 1.8 % (PSD=1.2 %). These statistics indicate excellent population performance according to the criteria in Emslie (2001). The considerable variance in the first two statistics reflects the uneven distribution of maternal ages still manifest from founder effects. The near absence of calf mortality indicates that female reproductive performance for the SKKR population could be tracked solely by AFR and IBI. Population size roughly quadrupled during the study period and average density reached about 0.5 rhinoceros/km². Owen-Smith (1988: p. 224) reported average densities for black rhinoceros as high as 1.4 rhinoceros/km², but most were less than 0.5. While it is unclear how closely the SKKR population approached carrying capacity, the high growth rate and average density achieved indicated that the SKKR population was a good study population for our purposes, the constraint on duration aside. The SKKR population was unusual only in that demographic, rather than environmental, stochasticity appeared dominant.

Our study of the expanding SKKR population confirms that increasing AFR provides an early warning sign of density feedback in large herbivore, including megaherbivore and especially black rhinoceros, populations and thus provides a practical indicator for managers wishing to detect density feedback prior to an impact on IBIs. We suggest that fecundity will be subject to considerable demographic stochasticity in expanding populations, at least prior to pronounced density feedback. It remains to be determined how sensitive mortality of immature black rhinoceroses is to density; the class of immature individuals most susceptible to mortality appears to vary across habitat. Even longer studies of expanding populations of megaherbivores, especially the highly endangered and managed black rhinoceros, that more nearly approach stable stage distributions and carrying capacity are required to elucidate the response to density.

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SUPPLEMENTARY INFORMATION for "Mortality and female fecundity in an expanding black rhinoceros (*Diceros bicornis minor*) population" by Law, Fike and Lent. European Journal of Wildlife Research.

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METHODS

Rainfall

As noted in the manuscript, rainfall was recorded monthly, though with some missing records, at three locations (denoted Kam, Ret, and BP here) in the study area (see Fike 2011 for full details). We employed the average across the locations for each month for a monthly rainfall figure for our analyses. Our motivation was that no single station is more representative of rainfall for the study area than any other and that the spatial average reflects better the rainfall regime given that rainfall local to each rhino home range was not available. There are perhaps two concerns that might be raised as regards the spatial average. First is that the three stations might experience different seasonal and/or annual patterns that the spatial average would obscure and that the seasonal and annual patterns in the spatial average may not reflect process patterns in rainfall. Spatial variation in rainfall in the study area is associated with variation in altitude and aspect (Fike 2011), and there is no suggestion that the three stations experience micro-local climatic differences that would lead to significantly different seasonal and/or annual patterns. In particular, the definition of wet and dry seasons we adopted in the manuscript was consistent for each station separately. Figure S1 displays the three time series of monthly rainfall together with the time series of monthly averages over locations. The four time series appear to conform over time. Figure S2 provides evidence that the three time series are indeed highly positively correlated. The exact pairwise correlations of monthly rainfall for all months were: 0.92 for Kam/Ret; 0.86 for Kam/BP; and 0.89 for Ret/BP.

Figure S1. Time series of monthly rainfall for the three stations Kam, Ret, and BP, together with that of their mean for each month.
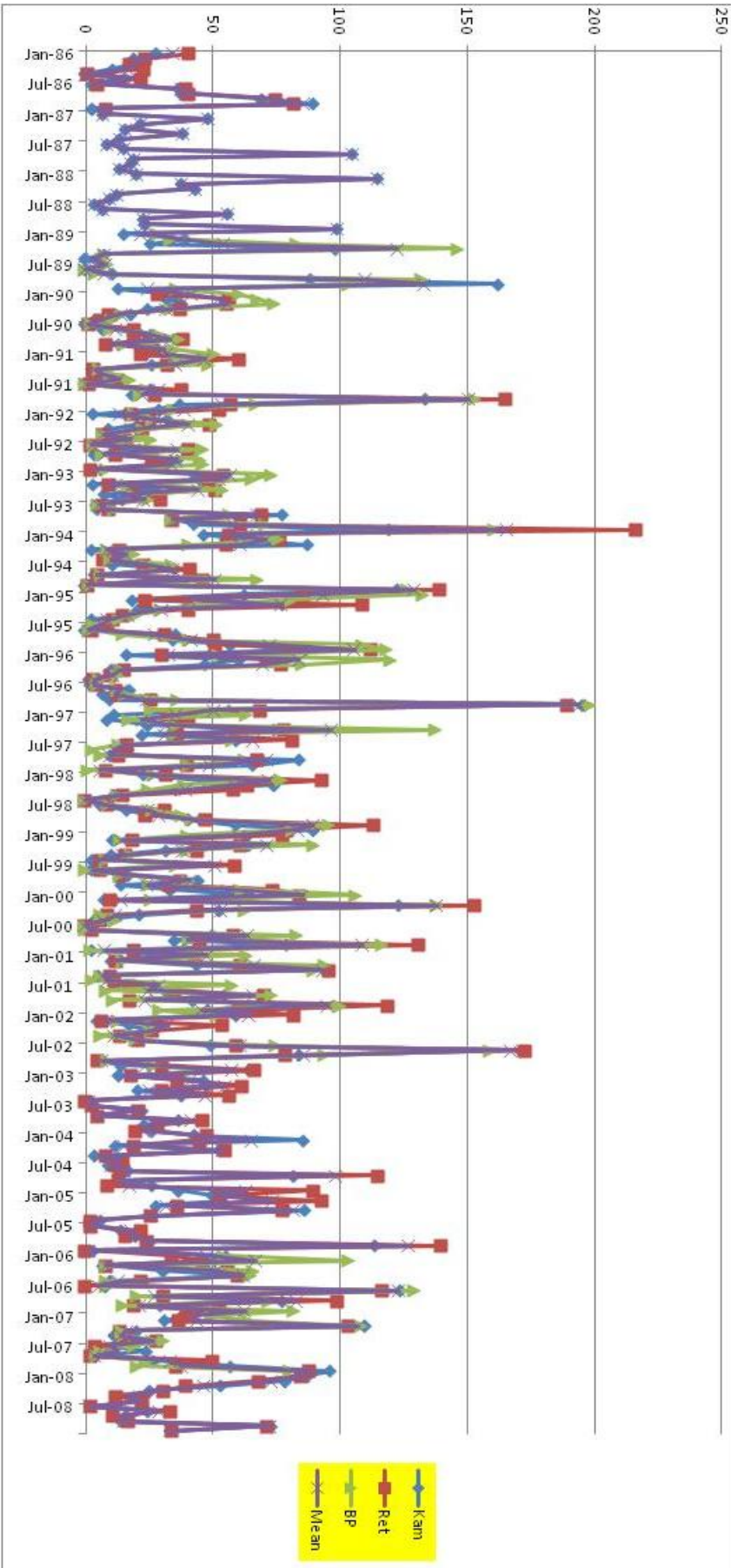
Figure S2. var1 = monthly rainfall at Kam, var2 = monthly rainfall at Ret, and var3 = monthly rainfall at BP, for those months (180) for which rainfall was recorded at all three stations. The diagonal displays frequency histograms for each variable, the squares below the diagonal are pairwise correlations, and the squares above the diagonal are scatter plots with fitted regression lines.
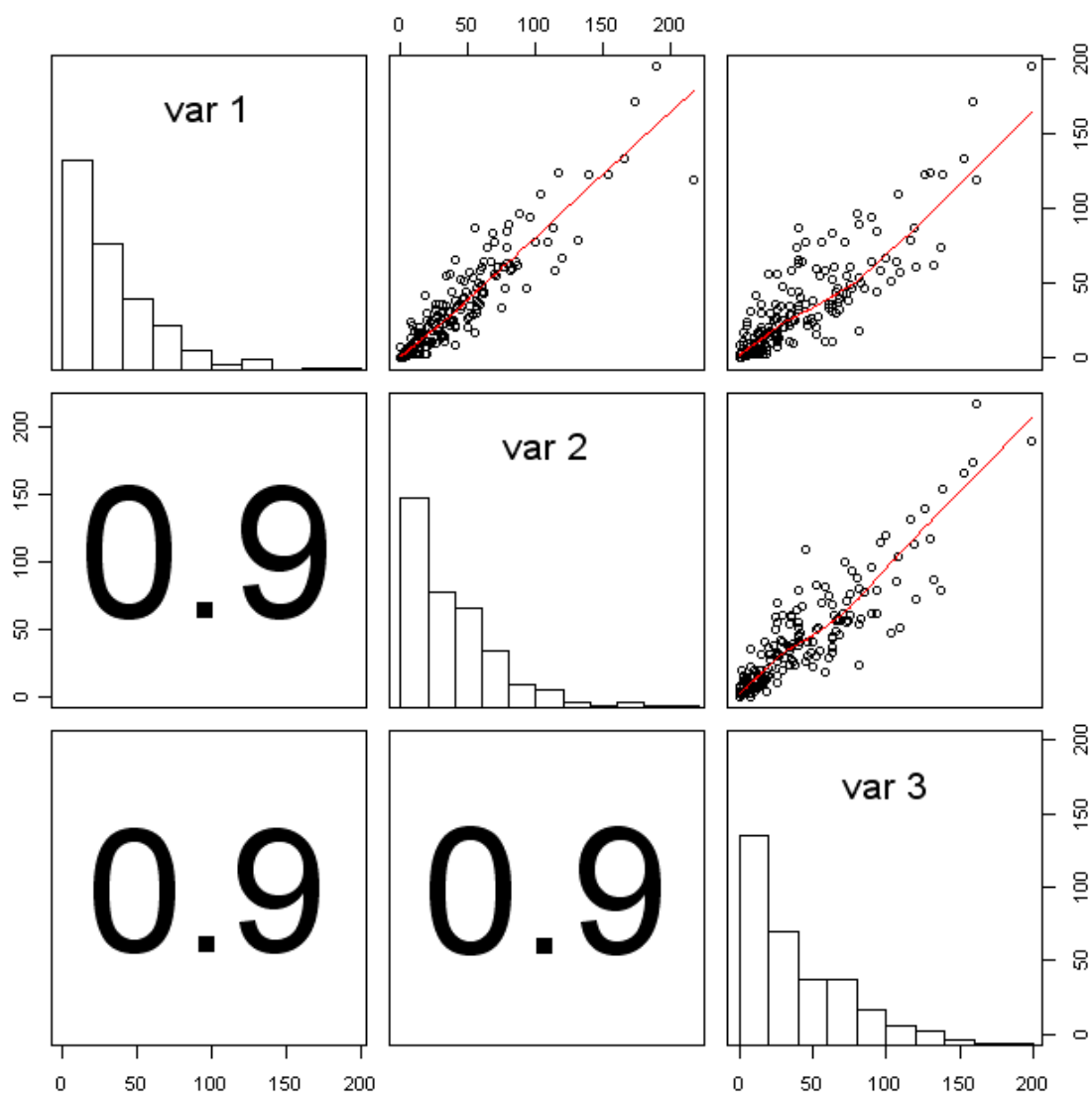
Furthermore, variance-inflation-factors (VIFs, Zuur et al. 2007, p. 469) are 6.9 for the regression of Kam monthly rainfall on that of Ret and BP, 8.41 for the regression of monthly rainfall of Ret on that of Kam and BP, and 5.0 for the regression of monthly rainfall of BP on Kam and Ret (equivalently, R^2 values for the regressions of one time series on the other two are at least 0.8). Finally, for the three time series of monthly rainfall, both for the 180 months for which measurements were available at all three locations and for the entire collection of data (276 months, but with missing data) we conducted dynamic factor analysis (Zuur et al. 2007, §17.4), which models each (normalised) time series in a set of n synchronized time series as a linear combination of k random walks ($k < n$) plus a Gaussian error term. The covariance matrix R of the k error terms and the loadings of the random walks are determined by maximum likelihood methods. We used the R package MARSS for this purpose. For the two data sets, we considered four models each. We considered $k = 1$ and 2, the unconstrained covariance matrix in which R is not diagonal and also the constrained form in which R is diagonal (though not necessarily with equal diagonal entries). For both data sets, AIC_c favoured the models with R unconstrained other those with R diagonal, the latter being more than 80 AIC_c units above the former (not surprisingly given the high degree of correlation between the rainfall time series). For a given form of R, AIC_c ranked the models by increasing value of k. For the data set of 180 months for which all stations had a rainfall record, model($k=1$, R unconstrained) was 4.2 AIC_c units lower than model($k=2$, R unconstrained) while for the data set of all months this difference was 3.6. The model parameters for model($k=1$, R unconstrained) for the full data set are:

loadings for the common trend: -0.0084; 0.0018; -0.0006;

covariance matrix: $R_{11} = 0.99$; $R_{22} = 1.04$; $R_{33} = 0.92$; $R_{12} = 0.94$; $R_{13} = 0.81$; $R_{23} = 0.86$;

The very small loadings indicate the random walk is actually unimportant and that the three rainfall time series are best viewed as highly positively correlated fluctuations without any significant trends. This result is exactly what we would expect for the normalised rainfall time series.

Altogether, these results indicate that these three time series should not be regarded as independent but rather highly positively correlated. Thus, we conclude that taking the average of monthly rainfall across the three stations has not compromised the seasonal and annual patterns in rainfall.

The other concern is that the missing data in the rainfall records may compromise the spatial averages, especially when data were only available from one station. For the 23 years of the study, 1986 – 2008, data was available from all three stations for 15 years, from two stations for 6 years, and from only one station for just two years, 1987 – 1988, early in the study and thus less critical to our analyses. Rainfall was measured at Kam every month of the study period while the remaining stations contributed to most months. There is no actual instance of two different months for which rainfall was recorded from two different and no common station.

We conclude therefore that using the average across stations is a reasonable strategy that takes advantage of all the rainfall data available rather than relying on that of a single station and that seasonal and annual patterns have been preserved in the spatial average.

To parametrize data by years, one can begin with the calendar year 1987 or with the dry season of 1987 (there were no births or mortalities prior to May 1987 other than failed imports; the prior wet season and the dry season of 1986 is designated year zero for convenience); the n'th seasonal year starts with May 86+n, and ends with Apr 86+n+1.

We called a year normal (N) if the annual rainfall was within one SD of the mean, wet (W) if wetter than this range, and dry (D) if drier than this range. Table S1 records the results for both calendar and seasonal years (using their respective statistics).

Table S1. Wet (W), Normal (N), and Dry (D) years. Each seasonal year begins in May of the calendar year above it in the table and ends in April of the following year. The calendar year 2008 had normal (N) rainfall.

Calendar Year	86	87	88	89	90	91	92	93	94	95	96
	D	D	N	N	D	N	D	W	N	N	N
Seasonal Year	0	1	2	3	4	5	6	7	8	9	10
	D	N	N	N	D	N	D	W	N	N	N
Calendar Year	97	98	99	00	01	02	03	04	05	06	07
	N	N	N	N	N	W	D	N	N	W	N
Seasonal Year	11	12	13	14	15	16	17	18	19	20	21
	N	N	N	N	N	W	D	N	N	W	N

W. L. Linklater (pers. comm. 2011) informed us that the oldest aged black rhino in the Rhino Management Group's data set was 31, a female that had recently calved, and that the longest lived black rhino in captivity, according to the 2005 international rhino studbook, was 37. Linklater (2007) reported an average of 460 days for gestation in the black rhino based on records in the literature. Since we used month as our unit of time, we employed the customary figure of 15 months for black rhinoceros gestation.

RESULTS

Age at First Reproduction (AFR)

We note that the Shapiro-Wilk test returned $p = 0.601$ for the residuals of the global model, indicating, along with the Q-Q plot, that the residuals as a whole, at least, are consistent with a normal distribution. The correlation between PopSize and $Rain_{15}$ was -0.2.

Table S2. The 'global' model for AFR modelling. PopSize is population size at conception; $Rain_{15}$ is the cumulative rainfall for the 15 month period ending with the month of first conception. R^2_a is the adjusted R^2; b denotes an estimated partial regression coefficient and β its standardized value. Each is followed by its SE. Also recorded are the statistics for the usual F-test for the regression model and for the intercept and each predictor the statistics for the standard t-test for the null hypothesis that the model parameter is zero. These statistics are quoted for descriptive purposes as an indication of model quality, not for hypothesis testing for model selection.

Model	R^2_a		F		df	p
PopSize+$Rain_{15}$	0.331		4.704		1,14	0.029
	β	SE	b	SE	t	p
Intercept			51	19	2.721	0.017
PopSize	0.66	0.22	0.42	0.14	3.063	0.009
$Rain_{15}$	0.11	0.22	0.013	0.026	0.504	0.623

Table S3. Modelling results for AFR with $Rain_{27}$, the cumulative rainfall over the 27 months leading to first conception, in place of $Rain_{15}$.

Model	K	-2log(L)	ΔAIC_c	Akaike weight	R^2_a
PopSize	3	122.053	0	0.788	0.366
PopSize + $Rain_{27}$	4	121.845	3.428	0.142	0.326
Null	2	130.455	5.325	0.055	0
$Rain_{27}$	3	129.975	7.922	0.015	-0.040

The relative importance of the two predictors of PopSize is 0.930 and of $Rain_{27}$ is 0.157.

To assess the robustness of the modelling exercise to the net uncertainty z in AFR values, for a low AFR value, we added its z to the AFR, while for high AFR values, we subtracted its z from the AFR. This modification of AFR values produces the maximal reduction in trends in AFR that might result from uncertainty in birth dates. We repeated the main modelling exercise, with these modified AFR values (modAFR) replacing the nominal AFR values.

Table S4. Modelling results for modAFR.

Model	K	-2log(L)	ΔAIC_c	Akaike weight	R^2_a
PopSize	3	118.717	0	0.693	0.269
Null	2	124.838	3.044	0.151	0
PopSize + $Rain_{15}$	4	118.541	3.461	0.123	0.222
$Rain_{15}$	3	124.815	6.098	0.033	-0.070

The relative importance of PopSize is 0.816 and of $Rain_{15}$ is 0.156. Figure S3 presents scatter plots of the modified AFR data.

Figure S3. Scatter plots of the modified AFR (modAFR) values versus population size (*P*) and the cumulative rainfall over the 15 month period ending with the month of first conception (Rain$_{15}$).

Predictor: Population Size

Predictor: Rain$_{15}$
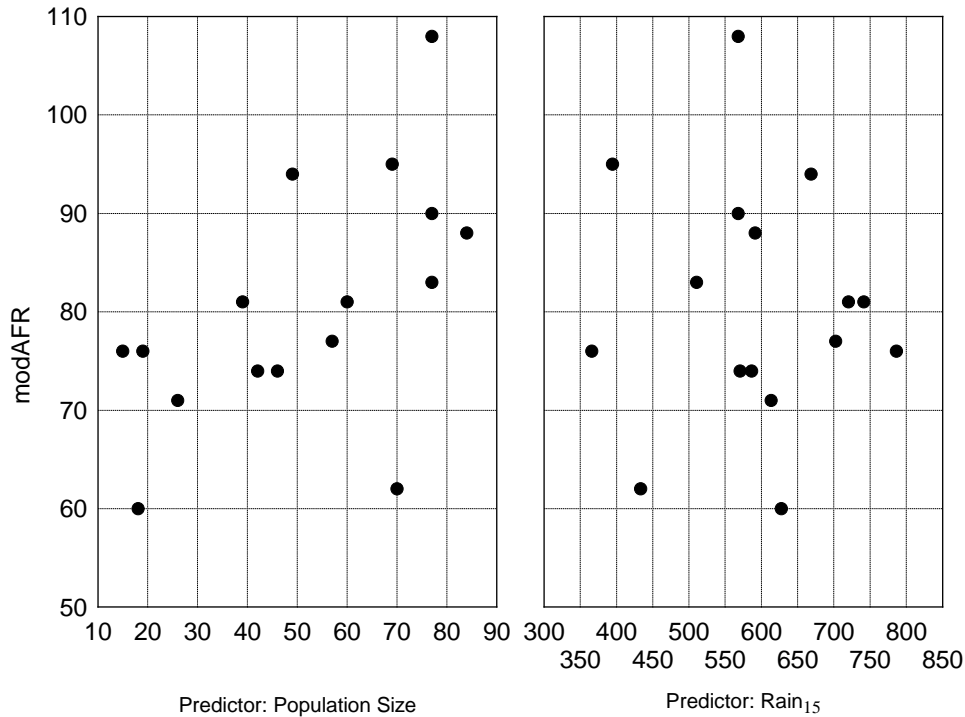
We note a further descriptive statistic. Let $n|m$ denote that, in a specified period of time, n females calved before the age of 7 years and that m females reached the age of 7 years without calving. Then for the three five-year periods 1993 – 1998, 1999 – 2003, and 2004 – 2008, the data are 4|1, 4|3, and 2|7 respectively, where, taking into account EUs, we have recorded only those females which can be unambiguously assigned to the two categories. We excluded from the period 1999 – 2003, 3 females that, according to nominal birth dates, calved before the age of 7 years and one that didn't (all imports with EUs of 1 for their birthdates) while from the period 2004 – 2008 we excluded one female that calved around the age of 7 years (give or take a month or two). These exclusions do not appear to alter the impression that a greater proportion of females reached the age of 7 years without calving in the last 5 years than previously.

Based on the scatter plot of AFR versus PopSize in Fig. 1, we conducted a post-analysis exploration of departures from linearity for AFR as a function of PopSize. Models were of the form AFR = $F(P)$ + e (*P* denoting PopSize), where the error term *e* is assumed to be from N(0,σ). The log-likelihood for this model is

$$\ln(L) = -\frac{\sum_i e_i^2}{2\sigma^2} - \frac{N}{2}\ln\left(2\pi\sigma^2\right),$$

where the summation is over the data, N is data set size, and $e_i = y_i - F(P_i)$, where y_i is the i'th observed response and P_i the corresponding population size. Maximum likelihood estimation of the structural parameters in F is equivalent to least squares estimation of these parameters. Maximum likelihood estimation of σ yields

$$\sigma^2 = \frac{RSS}{N},$$

where RSS denotes the estimated sum of residual squares:

$$RSS = \sum_i \left(y_i - F(P_i)\right)^2,$$

with the estimated values of the structural parameters substituted into F. The resulting maximized log-likelihood satisfies

$$-2\ln(L) = N\ln(2\pi \frac{RSS}{N}) + N.$$

For candidate models we considered polynomials, in particular all 15 possible linear combinations of P, P^2, P^3, P^4 (together with a constant term), the polynomial with all terms up through degree five, and an exponential of the form: $F(P) = b_0 + \exp(b_1 + b_2 P)$ (estimated using Statistica's nonlinear estimation module with least squares as the loss function to determine the parameters). Table S5 records the results obtained.

There are no surprises here. All models have very similar -2ln(L) values, so the ΔAIC_c values reflect the number of parameters in the different models (equal to the number of structural parameters, including intercepts, in F plus one for σ), and the models are grouped by AIC_c into subsets with models with the same numbers of parameters (the model exp has three structural parameters and is ranked least likely by AIC_c of such models). Within these subsets of models, AIC_c does not effectively discriminate between models. We interpret these results as suggesting that over the range of PopSize in our data, AFR is just as likely to be a small power of PopSize as linear, but that there is insufficient data to distinguish these functional forms, and the data is unlikely to support more complicated nonlinearities.

Table S5. Results of Nonlinear Modelling of AFR = $F(P)$.

Model	-2ln(L)	ΔAIC_c	Model	-2ln(L)	ΔAIC_c
$M(P^2)$	121.8106	0	$M(P^2, P^3)$	121.8106	3.6363
$M(P^3)$	122.0382	0.2276	$M(P^3, P^4)$	121.9370	3.7627
$M(P)$	122.0533	0.2427	exp	122.0411	3.8668
$M(P^4)$	122.3994	0.5888	$M(P^2, P^3, P^4)$	121.4557	7.6450
$M(P, P^4)$	121.6873	3.5131	$M(P, P^3, P^4)$	121.4874	7.6768
$M(P, P^3)$	121.7419	3.5676	$M(P, P^2, P^4)$	121.5113	7.7007
$M(P, P^2)$	121.7974	3.6221	$M(P, P^2, P^3)$	121.5420	7.7313
$M(P^2, P^4)$	121.8059	3.6316	$M(P, P^2, P^3, P^4)$	121.4254	12.9481
			quintic	121.0352	19.2245

Inter-Birth Intervals (IBI)

The shortest IBI of 14 has net uncertainty of 4 months. The calf was first seen 26 December 2006 and assigned a birth date of January, 2006, with EU 3 (i.e., an uncertainty of at least a month but less than 3 months). It was ear notched on 7 May 2007 and its age then assessed to be consistent with the assigned birth date. The previous calf was first seen 26 November, 2004, assigned a birth date of November, 2004, with an uncertainty of at most one month, and ear notched in March 2006 when its age was assessed to be consistent with the assigned birth date. Walpole et al. (2001) and Hrabar and du Toit (2005) reported IBIs as short as 20 months. The authors would be very interested to hear of any reliable records of

IBIs of less than 20 months. Are there records of premature births, presumably from captivity, for which the calf survived without management assistance?

Table S6. Descriptive statistics for the continuous predictors in the linear modelling of the IBI74 data. All pairwise correlations were at most 0.2 and all variance-inflation factors at most 1.04, hence there was no concern regarding correlations between the continuous predictors.

Variable	Mean (±PSD)	Range
Maternal Age	150 (± 61)	[76, 360]
Population Size	63 (± 27)	[9, 99]
Average Rain	38.8 (± 3.4)	[29.4, 45.4]
Prior Rain	230 (± 77)	[98, 407]

Table S7. Model selection results for the subset IBI74 of IBIs satisfying $Z \leq 9$, with maternal identity as random factor and five fixed-effect predictors: maternal age A; population size P; prior rain r (the cumualtive monthly rain over the six months preceding the IBI); average rain R (the average monthly rain during the IBI); and sex s, the birth sex of the birth initiating the

IBI. *K* is the number of parameters in the model, including intercept and the two variance terms. The base model is the model with just these three terms, i.e., without fixed-effect predictors.

Predictors	-2log(*L*)	*K*	ΔAICc	Akaike weights
A	511.224	4	0	0.256
A, P	511.812	5	1.890	0.100
A, s	510.852	5	1.930	0.098
A, r	511.070	5	2.148	0.088
A, R	511.157	5	2.235	0.084
A, P, s	510.342	6	3.792	0.038
Base	517.282	3	3.821	0.038
A, r, s	510.636	6	4.085	0.033
A, P, R	510.668	6	4.118	0.033
A, P, r	510.695	6	4.145	0.032
A, R, s	510.806	6	4.255	0.031
A, R, r	510.989	6	4.438	0.0279
P	516.716	4	5.491	0.016
R	517.146	4	5.922	0.013
r	517.179	4	5.954	0.013
s	517.189	4	5.964	0.013
A, P, r, s	510.170	7	6.063	0.012
A, P, R, s	510.275	7	6.118	0.012
A, P, R, r	510.537	7	6.430	0.010
A, R, r, s	510.577	7	6.470	0.010
P, R	516.456	5	7.534	0.006
P, s	516.559	5	7.637	0.006
P, r	516.647	5	7.725	0.005
R, r	517.025	5	8.104	0.004
r, s	517.061	5	8.139	0.004
R, s	517.066	5	8.145	0.004
A, P, R, r, s	510.039	8	8.450	0.004
P, R, s	516.318	6	9.768	0.002
P, R, r	516.372	6	9.822	0.002
P, r, s	516.467	6	9.917	0.002
R, r, s	516.923	6	10.373	0.001
P, R, r, s	516.211	7	12.104	0.001

Note that the lowest ranked model is the model excluding only maternal age.

Additive Models

For the IBI48 and IBI74 data, additive mixed models constructed using the R package mgcv yielded the same general conclusions as the linear mixed models and yielded no compelling evidence for nonlinearities. Additive mixed models had a negligible intraclass correlation; models were ranked similarly to the linear models, with some evidence for an influence of maternal age. Fig. S4 presents plots of mgcv-fitted additive models for IBI74 against fixed effects individually. The weak nonlinear behaviour of IBI versus population size and average rain (during the IBI) is particularly influenced by a small number of longer IBIs, and is unlikely to be biologically meaningful. The regression tree analysis below also picks out this behaviour for population size and, as below, we argue that this nonlinearity results from over fitting of the data.

Figure S4. IBI as additive models of each continuous predictor for the IBI74 data.
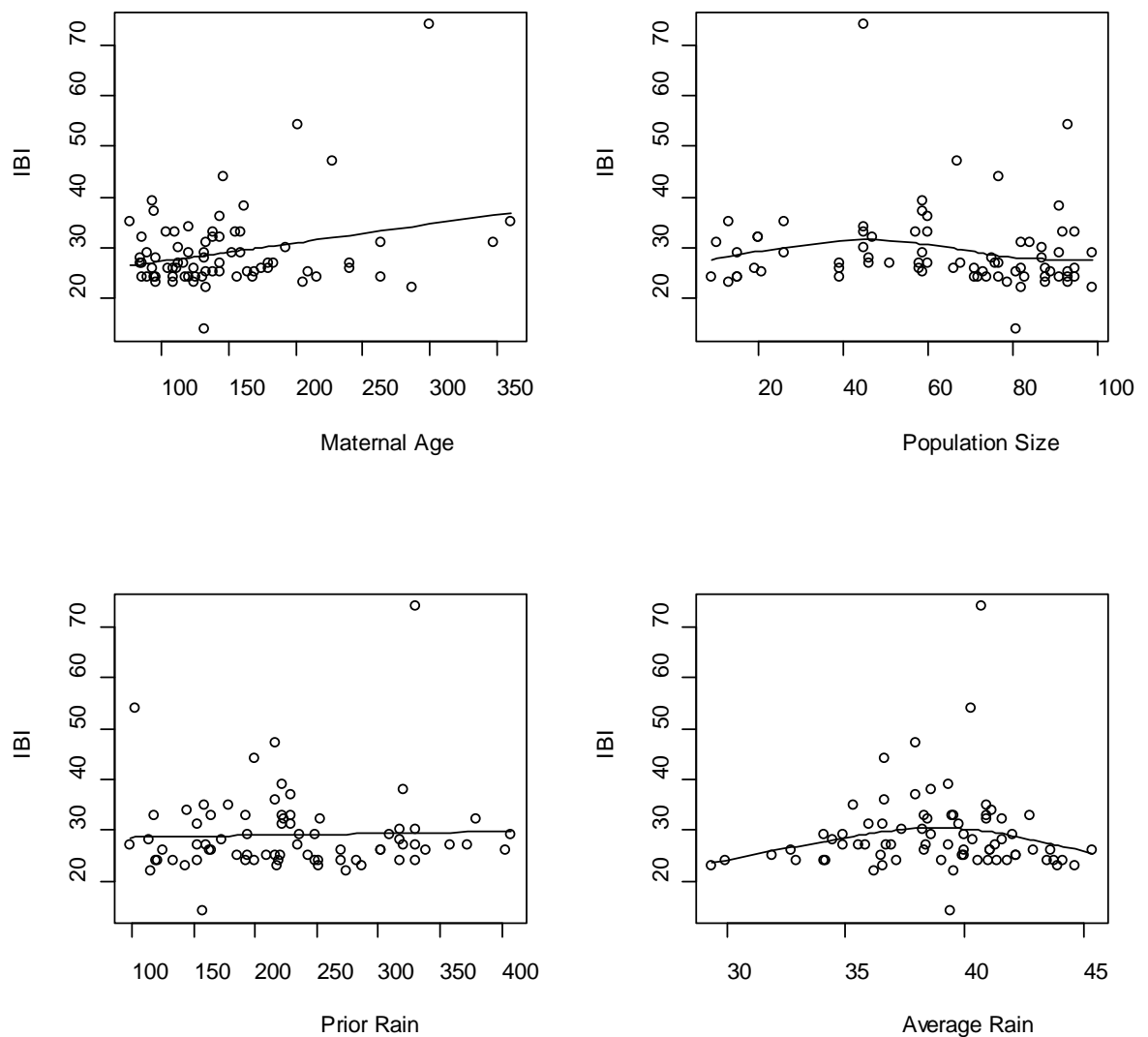
Table S8. Descriptive statistics for the 'global' model for the subset IBI74 without maternal identity as random factor. Variable symbols as for Table S7; statistical notation as in Table S2.

Model	R^2_a		F		df	p
$M(A, P, R, r, s)$	0.027		1.379		5, 68	0.236
	β	SE	b	SE	t	p
Intercept			20.27	11.31	1.792	0.078
A	0.28	0.12	0.037	0.015	2.432	0.0176
P	-0.08	0.12	-0.025	0.035	-0.705	0.483
R	0.04	0.12	0.10	0.27	0.347	0.730
r	0.05	0.12	0.005	0.012	0.414	0.680
s (Female)	-0.08	0.12	-0.64	0.95	-0.678	0.500

Regression Tree Analysis

Because maternal identity as a random factor was not influential, we could supplement our analyses with a regression tree analysis with IBI as response and maternal age A, population size P, and the 6 months cumulative rainfall prior to the start of the IBI r as explanatory variables. De'ath and Fabricius (2000) argue that regression trees are ideally suited for modelling ecological data that may be complex and unbalanced and involve nonlinear relationships with interactions so we used it to check that the linear modelling (and additive modelling) did not overlook any influences of these variables. We used the R package 'tree' to perform the regression tree analysis. A regression tree is built by splitting the data into two subsets according to a criterion such as those IBIs for which $A < 197$ and $A > 197$ (assuming no $A = 197$). For each subset, the sum of squares of the response variable (in the usual sense of the sum of squares of mean-centred values) is refered to as the deviance. The initial splitting is chosen to minimize, over all possible bifurcations of each explanatory variable, the sum of the two deviances. Once the intial splitting is made, the procedure is repeated for each of the subsets formed, and this process repeated until some stopping criterion is met. The various subsets of data that are not further split are called terminal nodes of the tree. For each terminal node the sum of squares of the response variable can be computed and their sum is called the total deviance of the tree. The total deviance D may be

viewed as the variation in the response variable unexplained by the tree. If S denotes the sum of squares of the entire data set, then

$$1 - \frac{D}{S}$$

is an anlogue of R^2, the coefficient of determination in linear regression. The following expression, where n is the data set size and p the number of terminal nodes, is the analogue of R^2_a, and thus takes into account model complexity:

$$Q = 1 - \frac{D/(n-p-1)}{S/(n-1)}.$$

The regression tree analysis for the IBI74 subset produced a tree with eight terminal nodes. Each terminal node is labelled with the mean of the IBI values grouped into that terminal node and the data set size for that terminal node, while the bifurcations are lablled by the splitting criterion, e.g, the criterion MaternalAge < 197 (MaternalAge = A; PopSize = P; PriorRain = r; program R requires no spaces in variable names) defines the left branch of the first bifurcation. Note that each terminal node has rather small data set size and the quantity Q for this tree is 15.2%, suggesting the tree has overinterpreted the data.

Figure S5.Regression tree for IBI74 data.
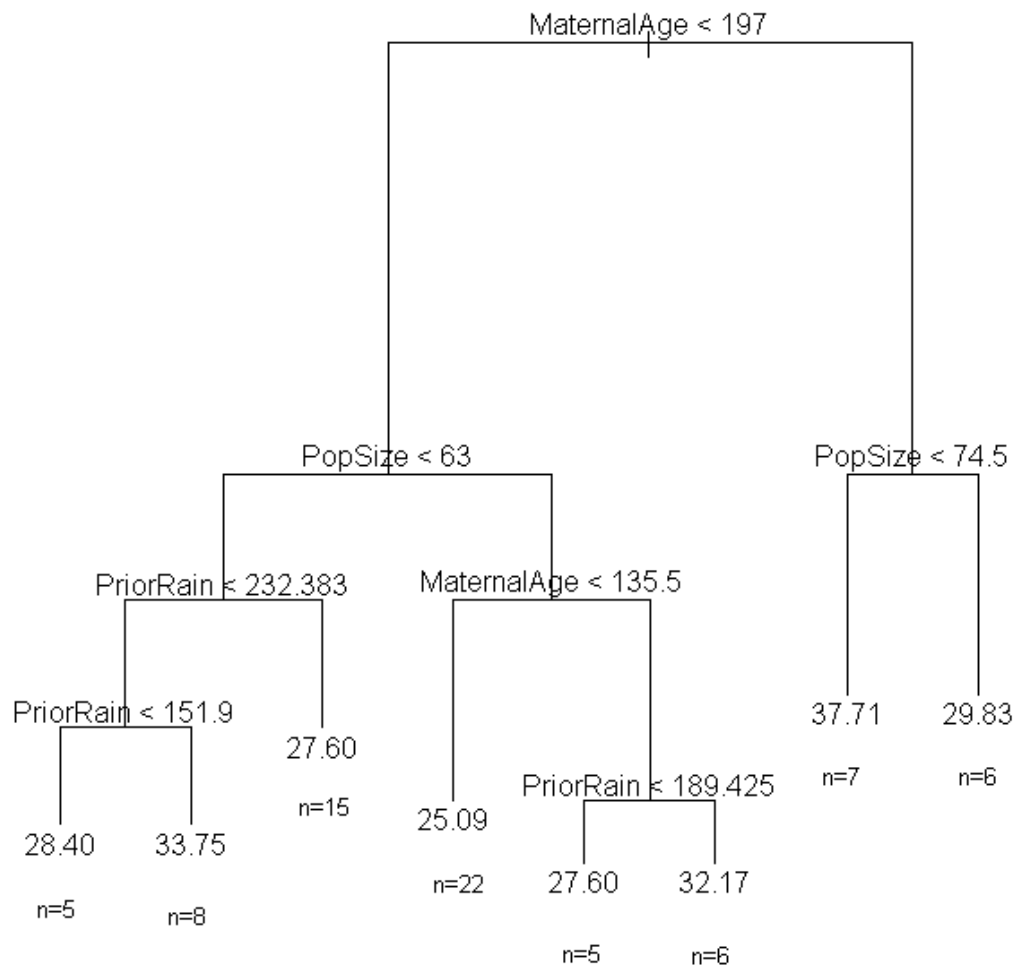
The package 'tree' includes an algorithm for pruning a given tree to yield smaller trees nested within the given tree; in particular, the algorithm attempts to produce a best tree of each smaller size than the given tree. In the present case, the pruning algorithm yields nested trees with number of terminal nodes:: 7 ($Q = 15.2\%$), 6 ($Q = 14.4\%$), 5 ($Q = 13.0\%$), 3 ($Q = 8.9\%$) but no tree with only 4 terminal nodes. The best tree with 5 terminal nodes is given in Figure S6.

Figure S6. The tree of Fig. S5 pruned to 5 terminal nodes.
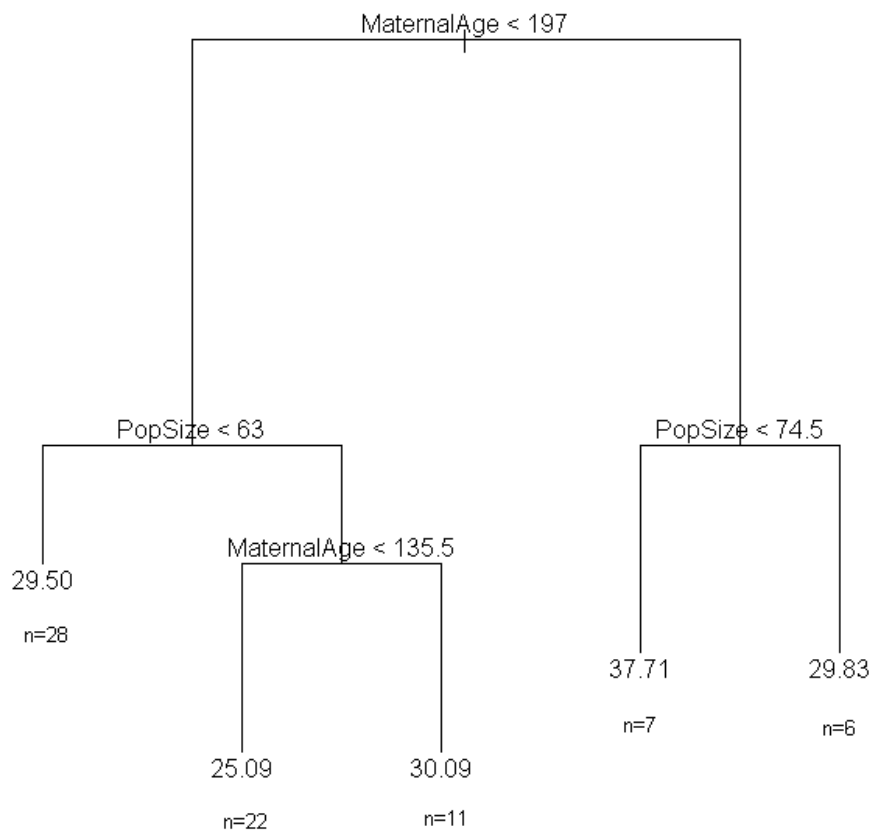
The first bifurcation splits IBIs according as maternal age is less than or greater than 197 months. The former 61 IBIs have a mean of 28, while the latter 13 IBIs have mean of 34. This split reflects the influence of maternal age on IBI. Consistent with the scatter plot of Fig. 2, this influence is through a small number of observations of longer IBIs at higher maternal ages. Indeed, the subset of 13 IBIs with $A > 197$ includes the three longest IBIs of 74, 54 and 47. We suggest a more mature population with a more representative distribution of maternal ages is required to clarify whether the influence of maternal age is biologically real (we suspect it is) and what form it takes (a functional inverse relationship of IBI on maternal age or a pronounced effect only at high maternal ages, i.e., a kind of incipient senescence effect).

The next bifurcations are based on criteria involving population size P but in both cases the mean IBIs of terminal nodes are larger at lower population sizes. Hence, these splittings are not a density dependent effect, at least not the expected one. In the scatter plots of Fig. S7 there is evidence of a trend for IBI to increase with population size within node 1, but this trend does not continue for higher population sizes in nodes 2+3 (and disappears for the IBI48 data subset).

Figure S7. Scatter plots of IBI versus population size for the tree of Fig. S6. In the top right panel, nodes 2 and 3 (numbered from left to right in Fig.S6) are combined.
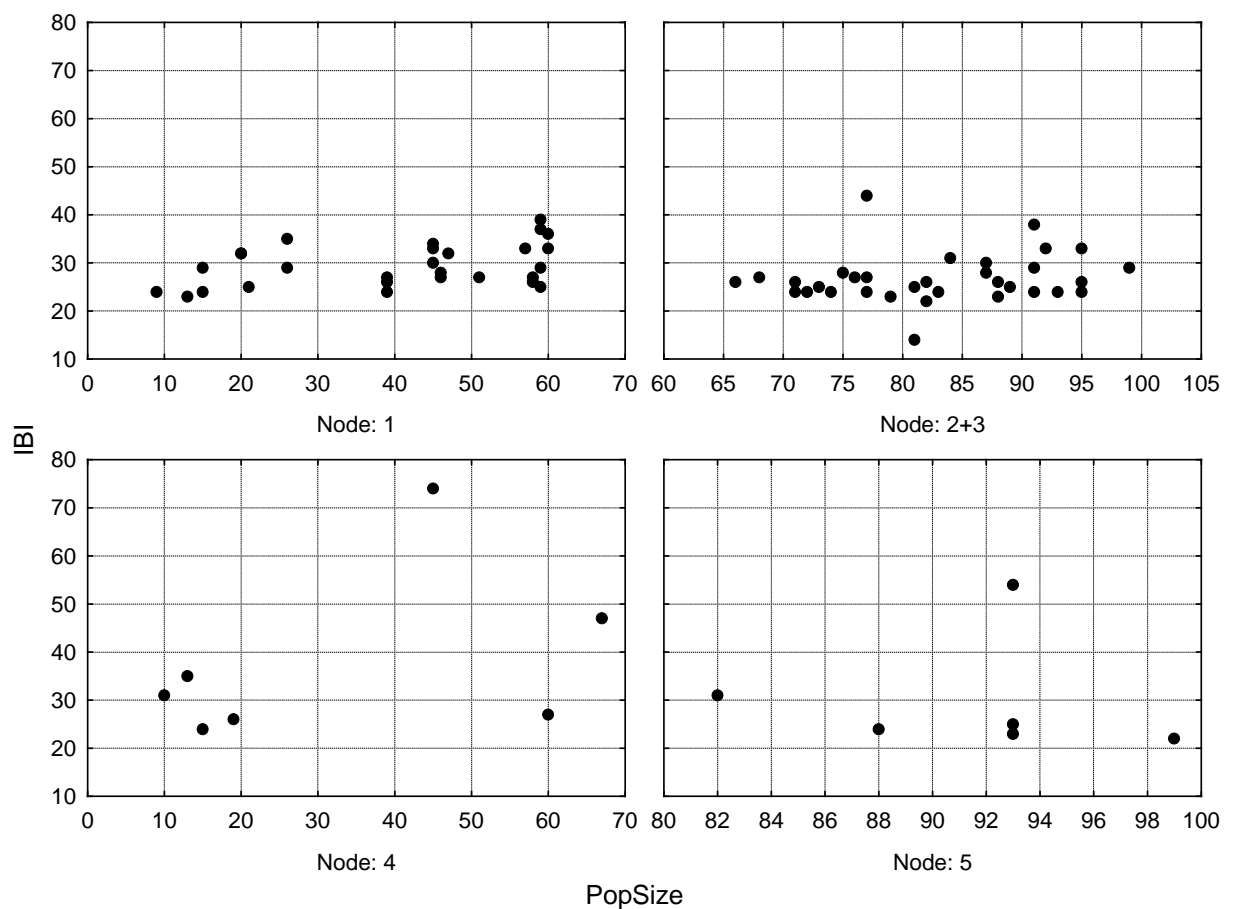

We suggest the trees are over interpreting the data, apart from identifying the influence of maternal age, which for the IBI74 data stems from the fact that the three longest IBIs occurred at high maternal age and that there were few other long IBIs.

To test for a delayed effect of rainfall on IBI, we set Rain1 to be the cumulative rainfall over the 12 month period ending with the first month of the IBI, Rain2 to be the cumulative rainfall for the 12 month period before that, and Rain3 to be the cumulative rainfall for the 12 month period before that of Rain2. With maternal age and these measures

of rainfall as possible fixed effects and maternal identity as random factor (for consistency with previous results; the influence of maternal identity was again negligible), these models had ΔAIC_c values greater than ten. Plots of IBI versus each of these fixed effects using the R package mgcv, i.e., in which the response is fitted as an additive model, do not provide any evidence for an influence of delayed rainfall on IBI either. With modRain as the mean monthly rainfall during that part of the IBI prior to the conception resulting in the birth terminating the IBI, the model with maternal age and modRain as predictors had a ΔAIC_c of 7.5 and thus was not competitive (nor was modRain alone, $\Delta AIC_c = 4.9$).

Figure S8. IBI as additive models of maternal age and rainfall in previous years for the IBI74 data.
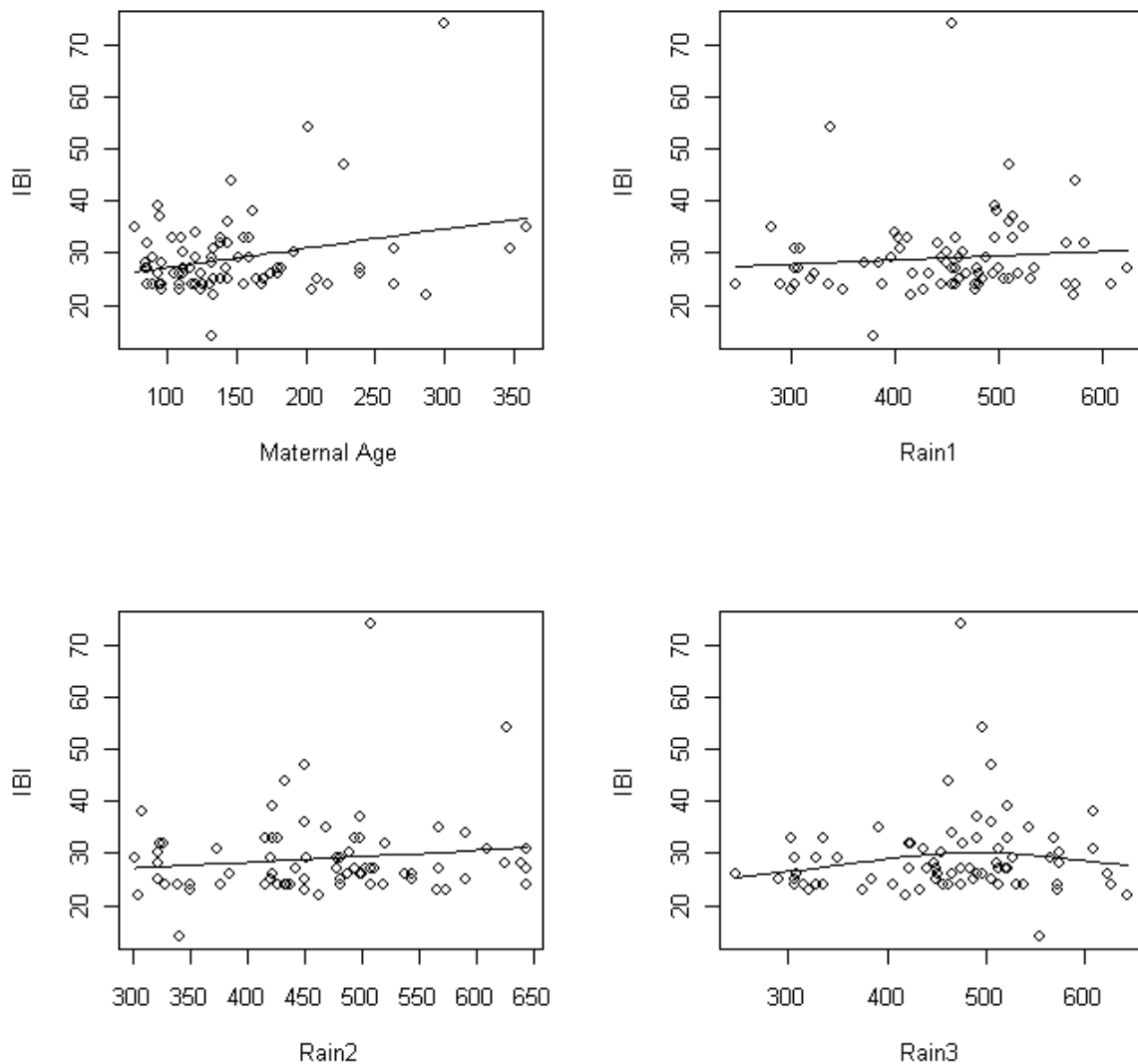
Mortality

Table S9. Mortalities. Status: I = import, with year of release; N = native; Rainfall: DS = dry season, WS = wet season. Stage: SA = subadult; A = adult. The final column indicates whether the period during which the mortality occurred (defined by how accurately the date of death is known) experienced less, more, or normal rainfall, determined by examining the rainfall records (where normal is judged to be within 1 PSD of the period mean), for rainfall data 1986 – 2008. There is no apparent pattern.

Name (status)	Sex	Stage	Age (y)	Date	Cause	Rainfall
U (N)	?	calf	< 1	between 4/03 & 12/03	unknown	normal DS; normal 10/03 - 12/03
Lucy (I; 89)	F	SA	about 5	1/91	unknown	dry 10 – 12/90; normal 1/91
Elsa (I; 97)	F	SA	about 5 – 6	in 2000	unknown	wet Jan – Apr; normal May - Dec
Yanda (N)	F	SA; as of 8/01	about 3	in 2002	unknown	dry Jan – Apr, wet DS; dry Oct - Dec
Mystery (N)	F	SA; as of 7/03	about 4	between 7/05 & 12/05	unknown	normal (but below average DS)
Chitha (N)	F	SA; as of 8/05	about 3.5	1/07	unknown	normal 10/06 – 1/07
Celani (N)	M	SA; as of 8/03	about 2.5	8/03	killed by young bull shortly after separation from mother	normal DS
Owethu (N)	M	SA; as of 9/03	about 4	2005	unknown	Wet Jan – Apr; normal DS; normal Oct - Dec

Quelea (N)	M	SA; as of 10/08	about 2	11/08	killed by rhino, shortly after separation from mother	normal DS; normal Oct - Dec
Funani (N)	M	SA; as of 4/04	not quite 3	between 4/04 & 11/04; probably 6/04	probably killed by bull	normal DS; normal Oct - Dec
Ndumu (I)	M	A	at least 10	between 1/92 & 4/92	unknown	Dry Jan - Apr
Khataza (I)	F	A	about 36	4/98	presumed old age	normal WS 97/98
Burdettski (I)	F	A	about 30	12/05	presumed old age	Nov very wet; Dec very dry
Jumbluti (I)	M	A	about 35	2006	presumed old age	Wet DS, normal Jan – Apr, Oct - Dec
Hlathi (N)	M	A	13.75	11/07	euthanized due to injuries inflicted by bulls	normal DS, normal Oct - Nov

The three calving sequences with unusually long IBIs were, (net uncertainty Z of the IBI in brackets): i) 23 (1); 24(0); 25(3); 24(4), 30(4), 47(4), 24(4); ii) 32 (4); 33 (6); 54 (4); and iii) 28 (6); 26 (9); 44 (3).

For those years in which at least one subadult died, we computed annual subadult mortality rate as the number of subadult deaths during the year divided by the number of subadult years for the given year. The latter was computed as follows. For each subadult alive during the year, we computed the fraction of that year the individual was a subadult and summed these fractions. The sum represents the total subadult exposure to mortality for that year. Fig. S9 displays the results.

Figure S9. Annual subadult mortality rate, computed as described in the text.
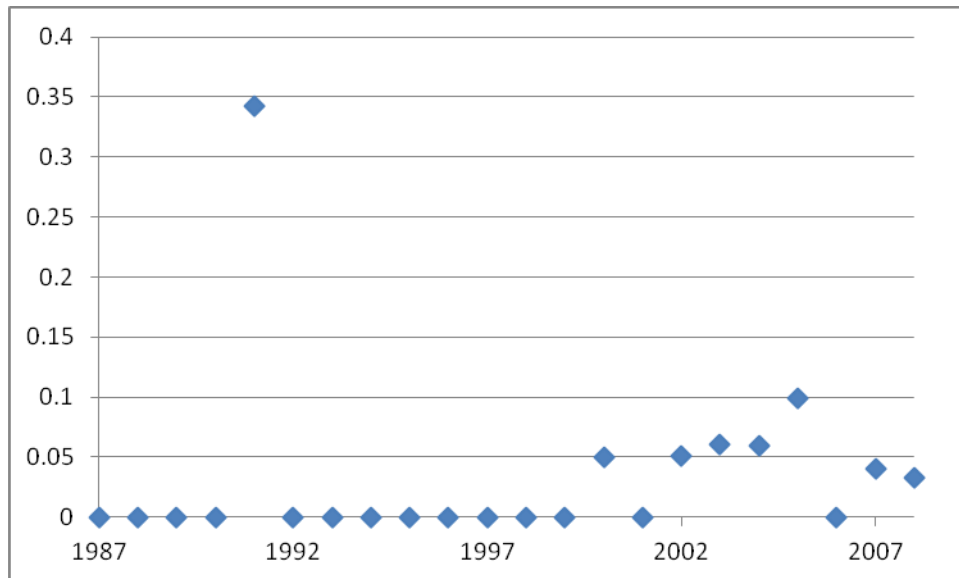
Cox Proportional Hazard Models for Subadult Mortality.

There were 95 subadults during the study period, of which nine died, 44 reached adulthood during the study, 5 were exported (in 2006), and the remaining 37 were still alive and subadults at the end of 2008. To construct a Cox proportional hazard model, those subadults that did not die were right censored, the 44 that reached adulthood at their time of transition from subadult to adult, the five that were exported as of May 2006, and the remaining 37 at the end of 2008. For each subadult, we computed the length of time it was a subadult during the study. For animals imported as subadults, we used the import date as the beginning of their subadulthood for the Cox proportional hazard models. As covariates, we used an individual's sex (female = 0; male = 1), the age at which it became a subadult, the population size (PopSize) at the time it became a subadult, and the average monthly rainfall during the time it was a subadult (AvRain). In Table S9, we indicated rainfall proximal to each mortality but that does not itself provide a covariate for each subadult. So we employed AvRain to explore any association between rainfall and mortality. Due to the presence of a categorical predictor (sex), we normalized the continuous predictors by mean centering and dividing by twice their standard deviations (Gelman and Hill 2007, pp. 56–57). We conducted the analyses using the package 'survival' in R.

We chose as our global model the model with all six pairwise interactions of the four covariates. For this model, R provided the following test statistics, which are viewed here as a measure of model fit.

Rsquare = 0.183   (max possible = 0.563)

Likelihood ratio test = 19.14 on 10 df,   p = 0.03847

Wald test = 17.47 on 10 df,   p = 0.06469

Score (logrank) test = 25.33 on 10 df,   p = 0.00475

Fig. S9 suggested that there might be an effect of population size after 1999 on subadult mortality but we had no other preconceived expectations as to which submodels might be plausible. There are too many submodels to consider all of them with this data set. We therefore applied the R function 'step', which eliminates one term at a time based on AIC values (except that we used AIC_c), to our global model. After this process, we checked other simple models not produced in this step-down procedure to make sure we had not overlooked other models of low AIC_c score. Table S10 records results of the model comparison.

Table S10. Comparison of Cox proportional hazard models for subadult mortality. K is he number of model parameters.

Model	K	ΔAIC_c	Model	K	AIC_c
AvRain	1	0	AvRain+sex+age	3	3.17
AvRain*PopSize+PopSize*sex	5	0.32	AvRain*PopSize+sex	4	3.74
AvRain+age	2	1.14	AvRain+sex+PopSize	3	3.74
AvRain*PopSize+AvRain*sex+ PopSize*sex	6	1.43	AvRain*sex	3	3.97
AvRain+sex	2	1.84	AvRain+sex*PopSize	4	3.99
AvRain+PopSize	2	1.84	AvRain*PopSize+AvRain*sex+ PopSize*sex+age	8	4.26
AvRain*PopSize	3	2.01	AvRain+PopSize+sex+age	4	5.35
AvRain*PopSize+AvRain*sex+ PopSize*sex+age	7	2.73	null model	0	5.59

The global model (K=10) has ΔIAC_c = 9.07. Models with $K \leq 3$ but without AvRain were ranked beyond the null model. It is clear that AvRain is the dominant predictor but that

model averaging over several models that include terms might be appropriate. Statistics provided by R for the two top models were

Rsquare = 0.077   (max possible = 0.563)

Likelihood ratio test = 7.64 on 1 df,   p = 0.005711

Wald test = 10.37 on 1 df,   p = 0.001279

Score (logrank) test = 13.32 on 1 df,   p = 0.000263

and

Rsquare = 0.155   (max possible = 0.563)

Likelihood ratio test = 15.95 on 5 df,   p = 0.006981

Wald test = 15.72 on 5 df,   p = 0.00768

Score (logrank) test = 17.85 on 5 df,   p = 0.003136,

respectively, while statistics for the covariate coefficients are recorded in table S11.

Table S11. Coefficients for the two top models of table S10.

Variable	Coefficient	SE	p
Top Model			
AvRain	-1.70	0.53	0.0013
Second Model			
AvRain	-2.20	0.58	0.0002
sex	-1.05	0.93	0.2615
PopSize	0.05	0.91	0.9544
AvRain.PopSize	4.7	2.1	0.0242
PopSize.sex	4.0	1.8	0.0262

As expected, mortality varies inversely with AvRain. Every subadult that did not die experienced a wet season (even those subadults right censored at the end of 2008 experienced

at least the final (wet-season) months of 2008) and their AvRain values tend to be averages over several years (the mean ± PSD for all 95 values is 37.5 ± 4.8mm; for those that did not die 37.8 ± 3.7mm; and for those that did die 34 ± 10mm). One might expect AvRain to be a useful predictor of mortality as low values should reflect either a succession of dry years or an individual that lived as a subadult for just a few months in a dry season. Table S1 indicates there was no succession of dry years in our study. On the other hand, three of the nine subadults that died did so within two months of becoming a subadult so their AvRain values depend acutely on the few months in which they happened to be subadults. In particular, the lowest AvRain value of 12.1mm occurred for a subadult that survived for only one month as a subadult during a dry season. The next lowest value of 24.5mm occurred for a subadult that died after just two months, also within a dry season. But the third animal, dying after just one month had an AvRain value of 44.1mm as it died within a wet season. Removing the mortality with the lowest AvRain value datum from the analysis considerably weakens the results. For the global model one now has the following statistics:

Rsquare = 0.148   (max possible = 0.523)

Likelihood ratio test = 15.09 on 10 df,   p = 0.1288

Wald test = 13.71 on 10 df,   p = 0.1865

Score (logrank) test = 12.44 on 10 df,   p = 0.2569

indicating a less appropriate model of the data. From the global model, the R function 'step' leads to the model AvRain*PopSize + AvRain*sex+PopSize*sex ($K = 6$, $AIC_c = 69.79$), which is more complicated than the model obtained from 'step' with the full data set. With the restricted data set, the model with AvRain as sole covariate has $AIC_c = 70.26$ while the null model has $AIC_c = 69.56$. Thus, removing this single datum radically weakens the effectiveness of AvRain as an explanatory variable. The strong influence of this single datum indicates a lack of robustness in the previous modelling results. As already noted, with the full data set, models without AvRain were ranked beyond the null model, e.g., beginning with PopSize*sex+PopSize*age+age*sex and applying 'step' results in PopSize*sex with $\Delta AIC_c = 9.00$.

Since Fig. S9 also suggests a threshold effect in subadult mortality as of 2000, we also examined models with PopSize replaced by a simple categorical variable that distinguished between whether a subadult ceased to be at risk as a subadult of the population before 2000 or after 1999. This variable actually performed worse than PopSize, as models containing it had AIC_c values larger than the corresponding models with PopSize. In particular, the result of applying the R function 'step' to the global model with the categorical variable in place of PopSize was the model containing AvRain only.

For a dataset with more mortalities AvRain (and indeed the other covariates) may well be a useful explanatory variable but for our data set we concluded that there are just too few mortalities for the Cox proportional hazard models to be robust.

Q-Q plots of the durations of subadulthood for those 44 subadults achieving adulthood and of the nine subadults that died each suggest normality is plausible (in particular, the Shapiro-Wilk test returned $p = 0.385$ and 0.319 respectively). To assess the robustness of the t-test result reported in the manuscript to uncertainty arising from EUs, we relied on the largish number of subadults that reached adulthood to average out uncertainties and focused on the uncertainties in dates of death. Four of the nine mortalities had uncertainties in date of death. For these four data, we took the maximum uncertainty in months and added that to the nominal duration. The mean duration $\pm$ SE of subadulthood with this modified data for those subadults that died was 16.1 ± 4.3 months and for this modified data the t-test returned $p < 10^{-4}$ (even when allowing for unequal variances).

DISCUSSION

Comparison of SKKR to Other Studies.

Hrabar & du Toit (2005) did not distinguish between imports and natives and found a mean AFR of 7.25y, with a range from 6 to 8.92 years; 33% had calved before 7y, 83% before 8y and all before 9y. The SKKR population had both younger and older AFRs than the Pilanesberg population and a younger mean AFR but does not appear atypical compared to the data summarized by Owen-Smith (1988), pp. 140 – 141, who noted considerable variation, but with mean AFR for both wild and captive populations tending to occur in the sixth year. In conclusion, the AFRs of natives, despite the uncertainty due to EUs, accord well with other data on AFR for black rhino.

Hitchins and Anderson (1983) reported a qualitative correlation between AFR and density in the Hluhluwe/Corridor/Umfolozi Game Reserve Complex. Hrabar and du Toit (2005) found a tendency for AFR to increase with population size but a regression analysis was judged to be not 'significant' with a p value of 0.071 ($R^2_a = 0.402$).

Owen-Smith (1988), Table 10.1, quoted a mean IBI of 2.6y (31m) and minimum of 2.1y (25m). Skinner and Chimimba (2005) reported a range for mean IBIs at different locations in South Africa of 2.1 (25m) – 3.4y (41m) in the late 1980s and report an IBI of 23 months from Zimbabwe. Walpole et al. (2001) reported a mean IBI of 35m with a mode occurring in the range 21 – 30m, an IBI in the range 11 – 20m and another in the range 61 – 70m; Hrabar & du Toit (2005) reported a mean IBI of 2.83y (34m) with a range of 1.67y (20m) – 5.17y (62m).

Hrabar and du Toit (2005) reported a nearly 'significant' negative relationship between IBI and population size but that the most important relationship was an increase in IBI with decreasing annual rainfall and argued (p. 264) that 'Periods of low rainfall must reduce the body condition of female black rhinos by reducing the quantity and quality of their food supply...' The relationship between mean annual precipitation and primary production, both herbaceous and woody, upon which this argument is based, is reviewed by Shorrocks (2007). That no influence of rainfall on IBIs of the SKKR population was detected is therefore noteworthy. On a seasonal basis, B. Fike notes that there was no observed loss of

body condition during the dry season amongst black rhino of the SKKR population. The habitat of SKKR is regarded as high quality for black rhino (Ganqa et al. 2005; but especially van Lieverloo 2009, who concluded that black rhino in GFRR readily met their energetic and nutritional requirements without exhibiting detectable preferences for available browse) and Fike believes browse is plentiful for SKKR black rhino even during the dry season. SKKR black rhino also browse extensively on succulent Euphorbia species (Ganqa et al. 2005, Heilmann et al. 2006, and Luske et al. 2009), which are thought to be a source of water (Hall-Martin et al. 1982, Dudley 1997), especially during the dry season. It is unknown whether this habit is important for satisfying water requirements of SKKR black rhino; it may be that surface water is adequate even during the dry season. As IBIs average over two years, however, the pattern in rainfall over the years may be more relevant. Table S1 indicates that there was no pronounced succession of dry years over the study period, particularly since 1988, so it may be a contingent fact that annual rainfall has not been low enough, regularly enough, to impact IBIs of the SKKR population, especially if conditions combine to make the SKKR population robust to the effects of the typical dry season. Thus, a more comprehensive comparison between black rhino populations as regards the influence of rainfall on IBI (or other aspects of rhino biology) surely requires detailed information on the particular resources available to the different populations, the seasonal variation in these resources, and the actual historical record of annual rainfall. Such comparisons will also depend on how accurately measures of mean annual rainfall reflect local impacts of rainfall.

W. Linklater drew our attention to Grange et al. (2009), who reported evidence that artificial selection for high fertility in domesticated ungulates may result in feral populations of ungulates (e.g., feral horses) that do not follow Eberhardt's (2002) paradigm. Grange et al. reported that while adult males behaved as expected, maintaining high survival in the face of high density, female adults compromised their survival to maintain high fertility in the face of high density. It will be interesting to see whether natural selection (if allowed) will eliminate this 'aberrant' behaviour in due course.

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