Density-dependent regulation of the critically endangered black rhinoceros population in Ithala Game Reserve, South Africa

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Abstract   Ensuring the persistence of populations of endangered species requires an understanding of, and response to, the causes of population declines. Species occurring in small populations are vulnerable to stochastic problems that are environmental, demographic, or genetic in nature and can reduce survival as much as the deterministic threats of habitat degradation. Critically endangered black rhinoceros (*Diceros bicornis*) populations declined throughout Africa since 1960, with numbers steadily increasing at a continental level, but remaining lower than three generations ago. However, size, demographics, trends, and factors affecting these, are poorly known. We used 18 years (1990–2008) of long-term sightings data from Ithala Game Reserve, KwaZulu-Natal, South Africa, to determine population estimates, growth rate and fecundity over time, as well as sex and age structure and age-specific probabilities of survival. Calf survivorship between the ages of 0 and 1 year was 74% for females and 94% for males. Age-specific survivorship for both sexes was significantly higher from yearling to subadult age-classes (1–6 years) than for adults (7–30 years). The most frequent cause of mortality was attributed to unknown causes while fighting injuries was recorded as the second most common cause of mortality, particularly among subadult and adult males. There was no significant difference in the sex ratios at birth, although the proportion of females in the population was 0.58. There was strong evidence for density-dependent regulation, with density in conception year a key driver of population performance (birth rate). The population does not appear to be at ecological carrying capacity; however, social effects are delaying conception. To mitigate density-dependent social effects, we recommend an adaptive management strategy of pre-selecting individuals for removal from the reserve, so as to maintain stability in the social organization of the population.

Key words: birth rate, *Diceros bicornis*, Ithala Game Reserve, population estimate, sex ratio, survivorship.

INTRODUCTION

Persistence of species occurring in small populations is often at risk from unpredictable changes in birth and death rates (Akçakaya 2002), random variations in sex ratios (Mysterud *et al.* 2000), environmental fluctuations (Benton & Grant 1999), and random genetic processes (Shaffer 1981). Small populations are more vulnerable to an extinction vortex when stochastic (Lande 1993) events exacerbate each other at low population sizes (Caughley 1994).

For instance, a rise in the frequency of mating between close relatives leads to reduced heterozygosity (Harmon & Braude 2010) that results in reduced fecundity (Lande 1988) and increased mortality (Saether & Heim 1993). This causes the population to become smaller yet. These events, and the loss of evolutionary adaptability of the species to environmental changes (Lande 1988), may ultimately result in its extinction (Gilpin & Soule 1986).

The recovery or persistence of small populations (Stacey & Taper 1992), and hence typically rare species (Caughley 1994) cannot occur without considering factors affecting the adaptability (Willi & Hoffmann 2008), demography (Nilsson & Ericson 1997) and genetic traits (Ashley *et al.* 1990) of populations. This remains challenging because stochastic (Akçakaya 2002) rather than deterministic (Benton & Grant 1999) drivers often influence demographics and their effects remain uncertain.

Intensive management often attempts to overcome stochasticity by translocating rare and endangered species (Van Houtan *et al.* 2009) to establish self-sustaining populations that require minimal long-term management (IUCN 1998). The critically endangered black rhinoceros (*Diceros bicornis*) (Emslie 2012), hereafter referred to as black rhino, is a case example where translocations into, and then subsequently out from, new populations, form part of key tactical strategies

aimed at improving and maintaining regional black rhino population growth (Brett & Adcock 2002).

However, a trade-off exists in establishing a balance between removals from source populations and introductions into new founder populations. This trade-off can be risky when exploiting relatively small populations to found new populations (Swart *et al.* 1990). A range of species recovery programmes (Griffith *et al.* 1989) and conservation strategies exist for threatened species. However, conservationists seldom assess the success of strategies using robust information (Gusset *et al.* 2008).

Erratic variance in growth (Caughley 1994), biased sex ratios (Berkeley & Linklater 2010), environmental changes (Schroder *et al.* 2005), restricted dispersal (Rachlow & Berger 1998), disease effects (Jolles *et al.* 2006), and genetic problems, such as inbreeding depression (Gakahu 1989), may weaken the ability of the population to recruit to a safe number again (Caughley 1994).

Ideally, removals from the source population should be such that they do not reduce that population's productivity (Emslie & du Toit 2006), and should maintain the population at a level below which density dependent effects (Hrabar & du Toit 2005) would occur. Conversely, it may take some time for newly established populations to develop as future source populations. Founder effects and genetic drift can reduce the genetic diversity of the introduced population, which may reduce the potential for the introduced population to adapt (Kliber & Eckert 2005) to the new environment.
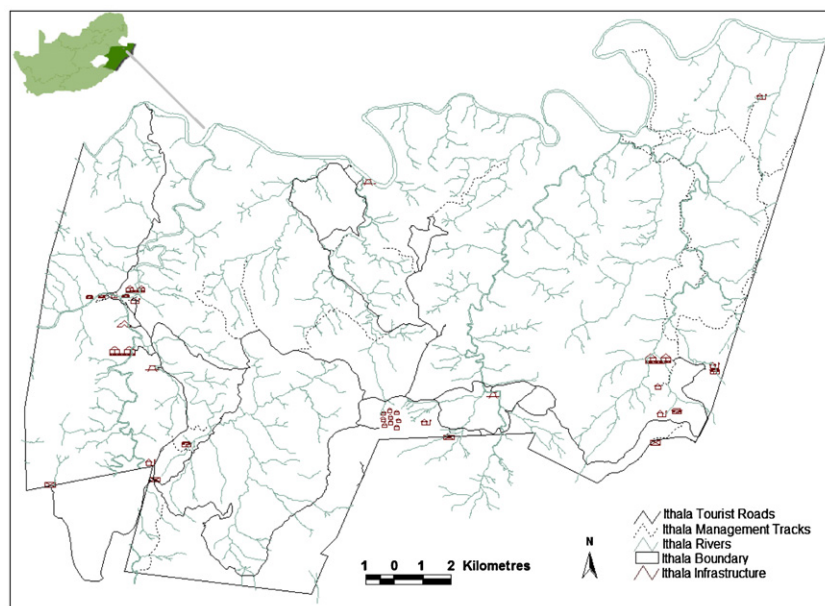
In order to evaluate some of the potential constraints in small, managed, black rhino populations, we examine Ithala Game Reserve in northern KwaZulu-Natal, South Africa, an important donor population that forms part of the African Rhino Conservation Action Plan (Emslie & Brooks 1999). Our aim was to evaluate whether the selective harvesting technique used up to now is optimal, by evaluating whether there are density-dependent effects constraining the growth of the population.

More specifically, the objectives were to: (i) Determine the population size and growth rate for each year; (ii) Calculate the birth rate for each year; (iii) Assess the influence of a range of factors on birth rate, including rainfall, population density, sex and age structure; (iv) Determine the age-specific probabilities of survival of the population; and (v) Assess if there are any density-dependent effects constraining the population growth. Through identification of these, or other key constraints on productivity, we may provide guidelines as to which variables the population is most sensitive to and hence how management can manipulate those for most effective persistence and translocations.

METHODS

Study area

Ithala Game Reserve (hereafter referred to as Ithala) is 297 km^2 and situated in northern KwaZulu-Natal, South Africa (27°30′S, 31°25′E) (Fig. 1). Elevation ranges from

Fig. 1. The locality of Ithala Game Reserve within the KwaZulu-Natal province, South Africa, and the multitude of rivers and streams throughout the reserve.

350 m a.s.l. on the Pongola River, which forms the northern boundary, to 1550 m a.s.l. on the southern escarpment plateau. Long-term mean annual rainfall is 791 mm, falling mainly during the summer (October to March). Summers are warm to hot (daily average of 18–30°C), with winters being warm to mild (15–25°C) (Porter 1983). Frosts do not occur, but low (near freezing) temperatures occur during cold windy spells on winter nights.

Five tributaries of the Pongola River flow through the reserve, resulting in topography varying from undulating grassland to cliff faces (Wiseman *et al.* 2004). Factors such as slope and abundance of paths, which affect the accessibility of a given area, have an important influence on the degree to which certain areas of the reserve are utilized by black rhino (Kotze & Zacharias 1993). Sourveld vegetation occurs on steeper slopes, with sweetveld on dolerite ridge tops (Brooks & Adcock 1997). *Acacia karroo* and *Acacia nilotica* woodland exists primarily on old croplands (Kotze & Zacharias 1993). Prior to proclamation as a game reserve in 1973 (KwaZulu Natal Nature Conservation Management Act 1997), the land was used for agricultural purposes (Wiseman *et al.* 2004). Since proclamation as a reserve, various browsers and mixed feeders were introduced (Wiseman *et al.* 2004).

Ithala black rhino monitoring history

The introduction of 34 black rhino into Ithala took place between 1973 and 1985. This formed part of the efforts of the 'Natal Parks Board' (now Ezemvelo KZN Wildlife) directed at expanding the donor rhino populations of Hluhluwe iMfolozi Park and Mkhuze Game Reserve to other potential rhino reserves in KwaZulu-Natal (Henwood 1989).

The entire adult black rhino population was individually marked and recognisable through unique ear notch patterns, ear tears or horn configurations (Brooks 1989). Calves were marked prior to them becoming independent from their mothers, but usually when they were between three and four years old. Until then, they were recognized through their association with individually marked females. This enabled the management staff to account for every individual in the population based on sightings alone.

Sightings from daily field ranger patrols in the reserve formed part of the intensive monitoring programme. Field rangers patrolled various areas of the reserve on a daily basis and recorded particulars of each rhino in their field data booklets. They reported the sightings information to the section rangers who maintained files on the life history of each animal. At monthly reserve meetings, a summary of the rhino sightings of the month were presented to the reserve manager and any changes to the population were discussed and updated. Sighting records were captured in the Animal Population Management Database (maintained by Ithala research staff) including information such as birth date (if known), sightings, mortalities, translocations and calving history (if it is female).

Age-classes were assigned to rhinos based on horn development and size of calves relative to adults (following Hitchins 1970; refined by Emslie *et al.* 1995). Data of the introductions to the Ithala black rhino population (*n* = 34) from 1973 to 1985 included the sex and ages of introduced individuals (females: *n* = 17; males: *n* = 16; unknown sex: *n* = 1). Historical paper records were filed (G. Root, pers. comm., 2008), and in later years imported to the Animal Population Management Database.

There have been no further introductions to the population since 1985. In 1990, the start of the study period, the black rhino population consisted of 35 adults (males: *n* = 16; females: *n* = 19), nine subadults (males: *n* = 6; females: *n* = 3), one yearling (males: *n* = 1; females: *n* = 0) and one juvenile (males: *n* = 1; females: *n* = 0). During 11 January 1991 to 7 October 2008, a total of 39 black rhino (males: *n* = 23; females: *n* = 16) were successfully removed from Ithala.

The total population in 2008 consisted of 23 adults (males: *n* = 8; females: *n* = 15), nine subadults (males: *n* = 6; females: *n* = 3), eight yearlings (males: *n* = 2; females: *n* = 6), and three juveniles (males: *n* = 2; females: *n* = 1).

Data analysis

Prior to 1990, historical records were incomplete – search effort was low and inconsistent. We collated 7363 sighting records from 1990 to 2008, but after removal of incomplete sightings and duplicate entries, our cleaned dataset totalled 7046 sightings of 123 identifiable individuals. The sightings records contained detailed information of births, calves that became independent of their mothers, known mortalities, one dead and several live removals.

We estimated population size using the minimum number alive per year (White *et al.* 1982). This was facilitated by the process of tracking an individual's life history. We calculated historical annual population growth rates $r = \ln(N_{t+1}) - \ln(N_t - N_{r,t \to t+1})$ where N_{t+1} is the population estimate for the subsequent year; N_t the population estimate for the current year and $N_{r,t \to t+1}$ the number of rhino removed during the current year (adapted from Caughley 1977).

We obtained detailed records of mother–calf relationships with accurate age estimates of offspring since 1990. Age at sexual maturity was the mean age at which females in the population gave birth for the first time. We used the weighted average function to calculate the average calving interval (average number of years between consecutive births for each rhino female) from the inter-calf intervals of all females (*n* = 16) with more than one calf. We determined the mean birth rate as the number of calves born in the year, divided by the number of adult females (≥7 years old) at the end of that year.

We used the chi-squared function to test for disparities in the sex ratios. To determine the peak birth events we used the detailed records of mother–calf relationships (1990–2008) which details the spread of birth dates in the population per annum. We used a model selection approach (Johnson & Omland 2004) to assess influences on birth rates, and included the effect of rainfall and population density on birth rate.

We obtained rainfall records from the Thalu field office at Ithala, and used the monthly rainfall data to distinguish between wet and dry seasons. This enabled us to determine if the variability in birth rate was associated with population density, rainfall, or both. Rainfall in this case served as an indicator of resource quality (Bourgarel *et al.* 2002).

We ran separate models for each of the peak birth months of March, April, May and July and also combined these representing alternative hypotheses for the effects on birth rate as follows: (i) R_{15}: Rainfall 15 months before the birth event; (ii) R_{27}: Rainfall 27 months before the birth event; (iii) D_c: Population density in the conception year; and (iv) D_b: Population density in the birth year. We then used Akaike's Information Criterion for small sample sizes (AIC_c) to rank models for each peak birth month from the most- to the least-supported model, given the data. We calculated the difference between the lowest-observed AIC value and the value for the current model (AIC_i), and Akaike weights (w_i) as measures of model support (Johnson & Omland 2004) where the estimated best model had an $\Delta AIC_c = 0$.

The ages of rhino born on the reserve, especially since 1992, are known within 1–4 weeks. We used Analyses of Variance (ANOVA) to determine any significant variability in the sex and age structure of the black rhino population at Ithala for each year. We distinguished four age-classes, namely: juvenile (<1 year), yearling (1–2 years), subadult (2 to <7 years), and adult (≥7 years).

We then explored age- and sex-specific probabilities of survival by constructing a life table (Caughley 1977) of every age-class, the number of deaths, the survivors remaining and the rate of mortality where: (i) The age at the beginning of an interval, symbolized x; (ii) f_x is the number of animals aged x in the population; (iii) l_x gives the probability at birth of an individual to survive to any age x and is termed 'survivorship' or simply 'survival'; (iv) Mortality (d_x) is the probability of dying during the age interval $x, x + 1$. This is the frequency of mortality calculated as the difference between two consecutive values of l_x with use of the following formula: $d_x = l_x - l_{x+1}$; (v) We used the ratio d_x/l_x to estimate the age-specific mortality rate q_x; and (vi) p_x is the survival rate of a proportion of animals alive at age x that survive to age $x + 1$.

The proportion of individuals in age-classes affects the demographic parameters (Chung 1994). A life table articulates the patterns of changing mortality rates with age, which is a concise summary of certain vital statistics of a population (Deevey 1947).

We used a two-tailed t-test to initially compare survivorship (the probability at birth of an individual to survive to any age x), and survival rate (the proportion of animals alive at age x that survive to age $x + 1$), of males and females of all age-classes in the population. Given that we used the mean and standard deviation, we applied the norm inverse function to extract random values from the sex-specific survival distribution.

To ascertain the fraction of individuals that survive to reproductive maturity, we used a two-tailed t-test assuming unequal variances to compare survival rate of only the juvenile to subadult males and females. To determine if survival of adults affects the fitness of the population, we used a two-tailed t-test assuming unequal variances to compare survival rate of only adult males and females.

RESULTS

Since introductions started during 1973, there was a steady increase in population size, with the highest estimate ($n = 53$) reached in 1997. The observed population estimates (Fig. 2a) began to stabilize primarily because of the inception of the harvesting strategy in 1998, when 11 black rhino were removed from the population, the largest annual translocation operation from Ithala to date.

Population growth rates, corrected for the effects of removals and introductions, were negatively associated with population density ($F_{1,16} = 13.76$, $P = 0.01$, $r^2 = 0.46$) (Fig. 2b). The average growth rate was 4.9% from 1990 to 2008. The mean birth rate (Fig. 2c) over the study period was 0.12, but this increased significantly over time ($F_{1,17} = 8.23$, $P = 0.01$, $r^2 = 0.33$). The estimated age at first calving for the Ithala black rhino females was $6.5 \pm SE\ 0.42$ years ($n = 18$), with an average inter-calving interval of $3.2 \pm SE\ 0.04$ years ($n = 61$).
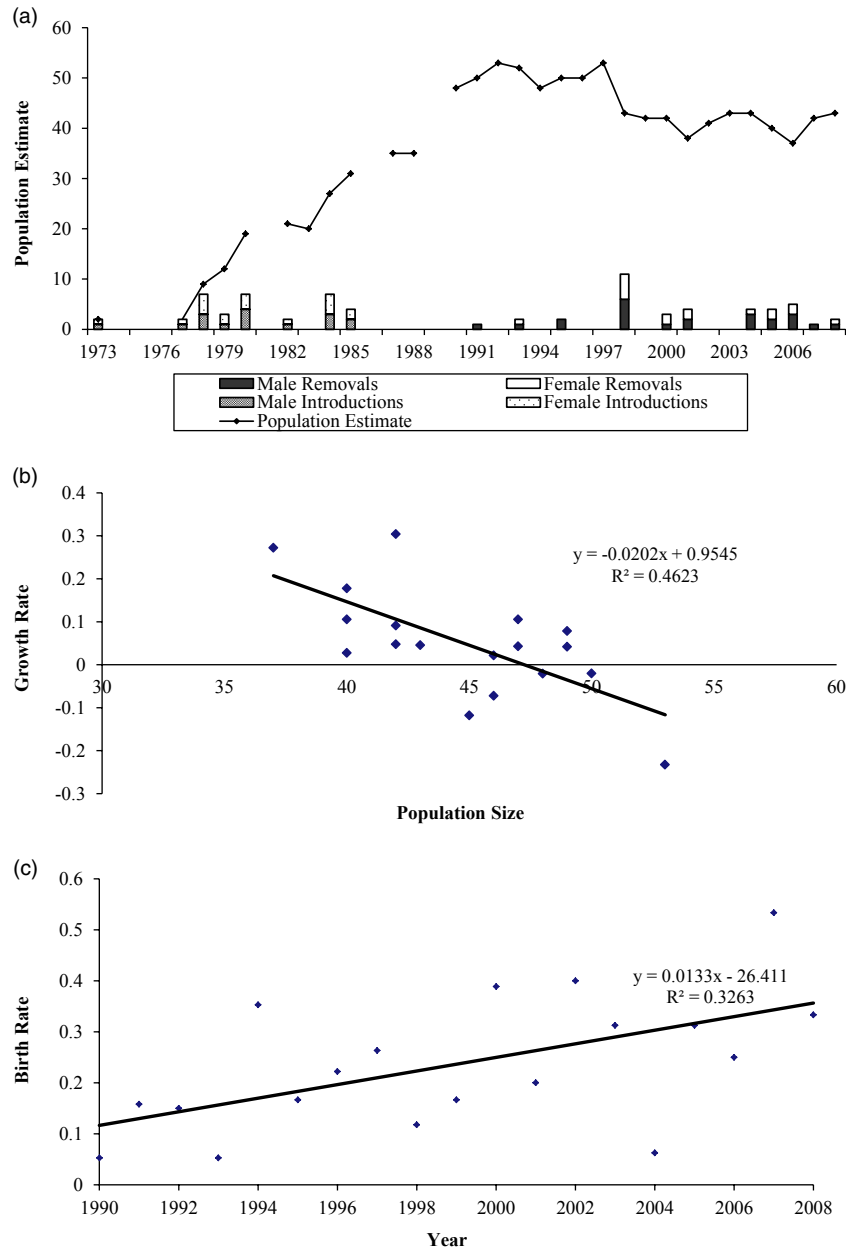
There was no significant difference in the sex ratio at birth ($X^2_{0.54,1} = 0.362$, $P = 0.55$). Population density in the conception year D_c was consistently included as a variable in the most likely model explaining variation in birth rates (Table 1). Births were mostly explained by population density at conception, and the lag effect from rainfall on birth rate, particularly where we observed peaks in births (Fig. 3) as a secondary variable.

Ithala black rhino have produced 59 females. Of these, 22 have become reproductive and calved successfully while the remaining 37 consisted of non-reproductive females known to have died ($n = 12$), been translocated ($n = 11$), or were still too young (in 2008, $n = 14$) to reproduce. The female population (in 2008, $n = 25$) consisted of 15 reproductive females of seven years and older, while the male population (in 2008, $n = 18$) had eight sexually mature males (Fig. 4).

There was a significant change in the sex and age structure of the population over time, with a significant decrease in both male ($F_{1,17} = 40.6$, $P = 0.01$), and female ($F_{1,17} = 12.8$, $P = 0.01$) individuals >7 years over time (Fig. 5).

Forty-eight black rhino mortalities were recorded from 1990 to 2008 (Fig. 6), with juveniles (<1 year) ($n = 8$), yearlings (1–2 years) ($n = 4$), subadults (2 to <7 years) ($n = 14$), and adults (≥7 years) ($n = 22$) dying. The most frequent cause of death for adults were recorded as 'unknown' ($n = 11$) and old age ($n = 5$), while juvenile mortalities were mostly attributed to exposure or cold ($n = 3$). Fighting injuries were a common cause of death for subadult to adult males ($n = 5$) and females ($n = 1$). A fighting injury was also recorded for a female ($n = 1$) in the yearling age-class. Cause of death was established through post mortems by the wildlife veterinarian where possible, and in some cases the injuries were so severe that mortality could only be attributed as fighting injuries.

Fig. 2. Black rhino population (a) observed estimates since the introduction in Ithala in 1973 (b) growth rates (c) birth rates from 1990 to 2008.

Analysis of age-specific survivorship (l_x) for males and females (Fig. 7) indicated a significantly higher survivorship from yearling to subadult age-class (1–6 years) ($t = -3.53$, d.f. = 5, $P = 0.01$) than for adults (7–30 years) ($t = 5.31$, d.f. = 33, $P = 7.279$). The mean sex-specific survival (Table 2) was significantly different for females (87%) than males (95%) in the 0–1 year age-class ($t = -2.70$, d.f. = 20, $P = 0.01$). However, in the 5–6-year-old age-class, although not significantly different, subadult males, had lower

survival (92%) than females (100%) ($t = 5.37$, d.f. = 19, $P = 3.43$).
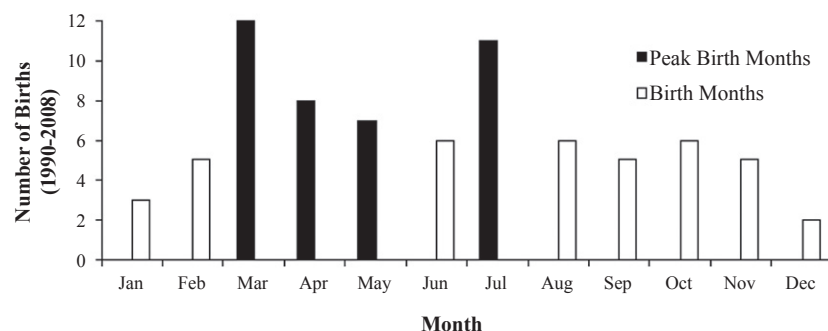
DISCUSSION

The Ithala black rhino population is relatively young, with the older individuals all <30 years. Although there were records of animals dying from old age, these were very few and we could not determine

Table 1. The effect of rainfall and population density on birth rate in peak birth months March, April, May, and July

Model	n	K	Fstat	r^2	ΔAIC_c	W_i	n	K	Fstat	r^2	ΔAIC_c	W_i
			March births						April births			
R15	10	1	0.3	0.036	8.682	0.009	5	1	0.086	0.028	0.334	0.225
R27	10	1	2.373	0.229	7.713	0.015	5	1	0.599	0.167	**0**	**0.266**
Dc	10	1	2.373	0.52	5.651	0.042	5	1	0.279	0.085	0.202	0.24
Db	10	1	0.056	0.007	8.811	0.009	5	1	0.018	0.006	0.383	0.22
$R_{15} \times D_c$	10	2	4.621	0.569	8.401	0.011	5	2	0.208	0.172	6.652	0.01
$R_{15} \times D_b$	10	2	0.134	0.037	11.89	0.002	5	2	0.218	0.179	6.635	0.01
$R_{27} \times D_c$	10	2	4.702	0.573	8.358	0.011	5	2	1.305	0.566	5.248	0.019
$R_{27} \times D_b$	10	2	1.408	0.287	10.59	0.004	5	2	0.355	0.262	6.403	0.011
$R_{15} \times D_c + D_b$	10	3	84.14	0.977	**0**	**0.705**	5	3	0.995	69.67	15.45	1E-04
$R_{27} \times D_c + D_b$	10	3	41.03	0.954	3.014	0.156	5	3	1.998	0.857	22.84	3E-06
$R_{15} \times R_{27} \times D_c + D_b$	10	4	54.33	0.978	5.862	0.038	5†	4				
			May births						July births			
R15	6	1	0.053	0.013	1.331	0.202	9	1	0.006	9E-04	2.463	0.11
R27	6	1	9E-06	2E-06	1.365	0.199	9	1	1.619	0.188	1.654	0.164
Dc	6	1	2.754	0.408	**0**	**0.393**	9	1	6.159	0.468	**0**	**0.376**
Db	6	1	0.079	0.019	1.314	0.204	9	1	0.198	0.027	2.358	0.116
$R_{15} \times D_c$	6	2	1.585	0.514	13.53	5E-04	9	2	3.186	0.515	3.067	0.081
$R_{15} \times D_b$	6	2	0.093	0.058	13.54	5E-04	9	2	0.086	0.028	5.785	0.021
$R_{27} \times D_c$	6	2	1.529	0.505	13.53	5E-04	9	2	2.783	0.481	3.33	0.071
$R_{27} \times D_b$	6	2	0.044	0.028	13.54	5E-04	9	2	0.703	0.19	5.073	0.03
$R_{15} \times D_c + D_b$	6	3	110.5	0.994	16.53	1E-04	9	3	3.534	0.68	6.248	0.017
$R_{27} \times D_c + D_b$	6	3	80.78	0.992	16.53	1E-04	9	3	3.355	0.668	6.385	0.015
$R_{15} \times R_{27} \times D_c + D_b$	6	4	41.44	0.994	20.2	2E-05	9	4	2.123	0.68	13.44	5E-04

†Too few parameters for the sample size. The number of parameters (K) in each model includes the intercept and each explanatory variable: R_{15} (Rainfall 15 months before the birth event); R_{27} (Rainfall 27 months before the birth event); D_c (Density in the conception year); D_b (Density in the birth year). Models with a lower ΔAIC_c and a greater Akaike weight (W_i) have more support. Values for the model with the most support are in bold. AIC, Akaike's Information Criterion.

Fig. 3. The number of births per month indicating the peak birth months of March, April, May and July.
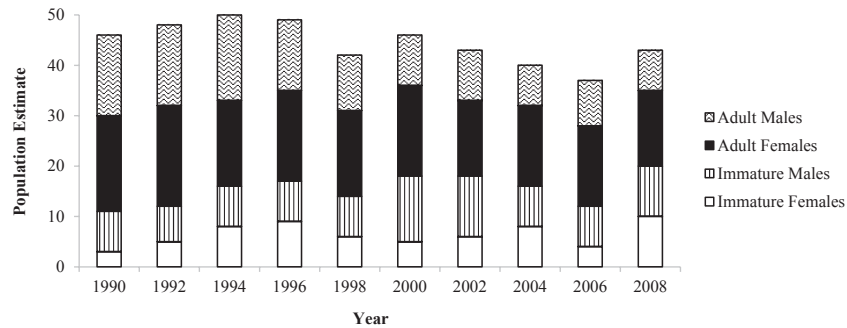
natural senescence, but we would expect a lower senescence mortality than in a population with an older age structure (Mackey *et al.* 2006). One would therefore expect an eruptive population growth rate (Caughley 1994), which should continue in the short and medium-term while the population converges to stable-state distribution (Slotow *et al.* 2008).

However, the growth rate was relatively low at <5%, with a density-related effect that is constraining conception. The birth rate was driven by population density at conception, and rainfall as a secondary variable. At Ithala, reducing the density increased population growth rate by releasing vital rates from
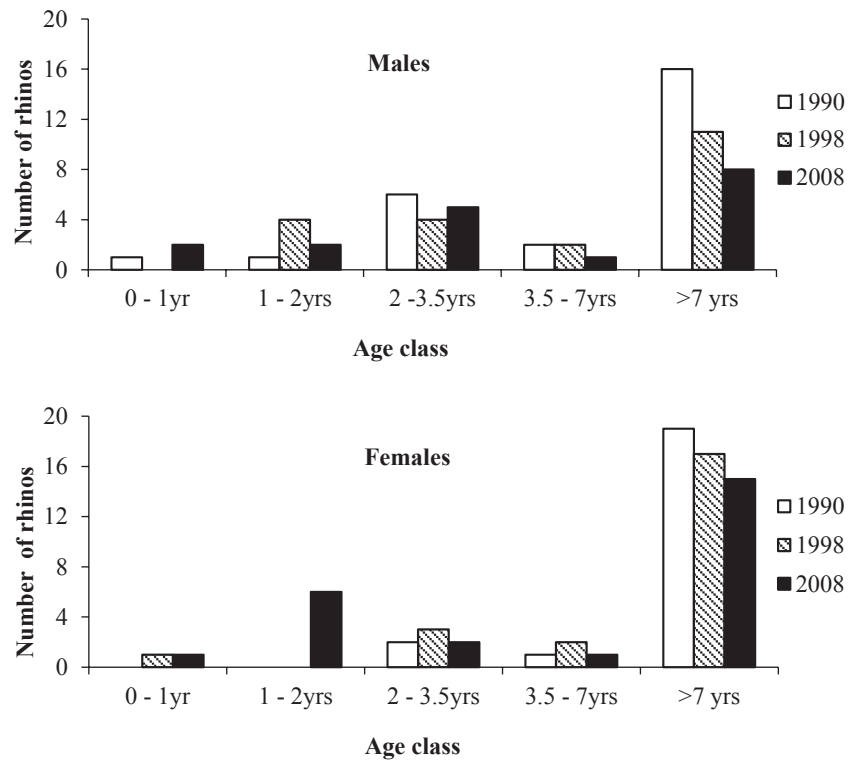
Table 2. Sex-specific survival for the Ithala black rhino population

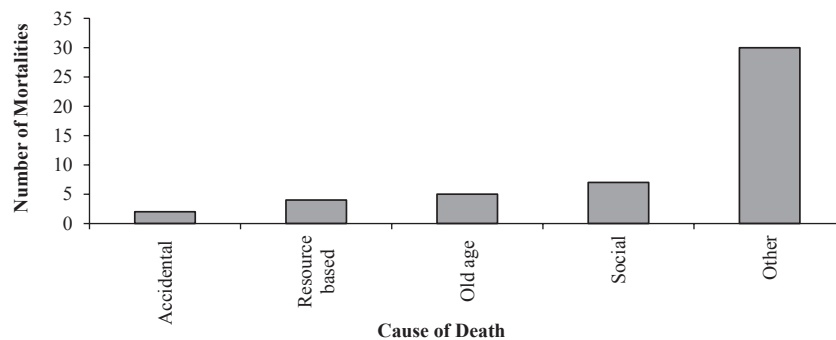| Age in years	Females (SD)	Males (SD)
0–1	87% (0.18)	95% (0.02)
2–4	96% (0.04)	94% (0.06)
5–6	100% (0)	92% (0.12)
Adults	97% (0.07)	94% (0.11)

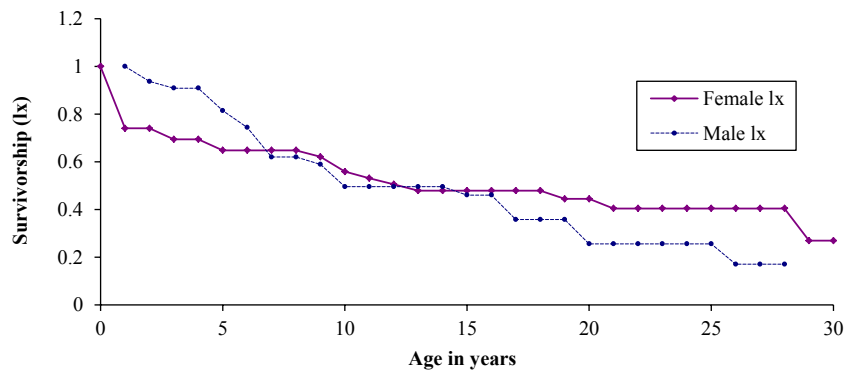Numbers in brackets are standard deviations (SD) of the mean.

Fig. 4. The number of reproductive and non-reproductive black rhino females and males from 1990 to 2008.

Fig. 5. Sex and age structure of the population for the years 1990, 1998 and 2008 respectively indicating a decline in the number of adult males and females.

Fig. 6. The number of Black Rhino mortalities recorded in Ithala from 1990 to 2008.

Fig. 7.   Survivorship curves for males and females in the Ithala black rhino population.

density-dependent limitations, thereby maximizing reproductive potential (Slotow *et al.* 2005). The population is not acting in an eruptive manner because of the density-dependence through either resource limitation or social effects.

Density-dependence because of resource depletion should first decrease juvenile survival, then decrease reproductive rates, and finally decrease adult survival (Eberhardt 2002). The demographic consequences of density-dependence include depressed female conception, increased interval between births, changes in sex ratios at birth, decreased juvenile survival, and changes in age-specific mortality (Mysterud *et al.* 2000; Wittemyer *et al.* 2007; van Aarde *et al.* 2008; Bonenfant *et al.* 2009).

Reproductive performance is also density-dependent (Albon *et al.* 1983). The age at first calving increases under conditions of resource limitations (e.g. Owen-Smith 1990) because the onset of puberty is dependent on body mass (Hamilton & Blaxter 1980). Black rhino have a 15-month gestation period and the average age at first calving has been reported as 6–9 years of age (Alibhai *et al.* 2001; Okita-Ouma 2004). In Ithala, the average age at first calving was 6.5 years, which is towards the lower end of the scale for this species. This implies that age at first calving is not a constraint on growth, and implies that resources are not the key constraint.

Although changes in sex ratios at birth have been attributed to density-dependence (Mysterud *et al.* 2000), we found no significant difference in the sex ratios at birth. Selective removals favouring males for translocation by Ithala management (males $n = 23$; females $n = 16$) and higher mortalities in male ($n = 23$) than female ($n = 14$) sexes, therefore account for the significant decrease in male individuals over time. Small populations with high proportions of sexually mature females enhance reproductive potential (Slotow *et al.* 2005).

Lengthened inter-calving intervals (Laws *et al.* 1975) are also demographic consequences of density-dependence, with high densities resulting in an increase in the time between calves (Rachlow & Berger 1998). The average inter-calving interval of 3.2 years (38 months) for the Ithala population may be compared with the 3.16 years (38 months) reported by Okita-Ouma (2004), but is shorter than the 3.35 years (40.3 months) reported by Alibhai *et al.* (2001). The shorter interval between successive calves, along with the young age of first reproduction, implies that the density-dependent constraint is unlikely to be a resource limitation.

In the Ithala population, the cause of mortality for all age-classes was mostly recorded as 'unknown' where it could not be determined what the animals had died from or the carcasses were too old in order to carry out post mortems. However, in keeping with Emslie and du Toit (2006) our data indicated that fighting injuries were the second most common cause of mortality, particularly among subadult to adult males, possibly because of young dispersing males encountering older or territorial males more frequently. Adult males tend to be solitary and aggressive (Kock *et al.* 1999), and the heightened competition between males competing for territories and mating possibilities (FitzGibbon & Lazarus 1995) increases mortality rates.

Variability in juvenile survival is more sensitive to density-dependence (Gaillard *et al.* 2000). Our data indicated a major effect on the suckling calves (0–1 year) ($n = 12$), but once suckling discontinued and the calves were past a certain age, that is, 1 year, they tended to perform well. The cause of mortalities of juveniles was attributed mostly to exposure or cold, rather than malnutrition. Once individuals reached adulthood, survival was high.

Even so, our results suggest that there might be disruption of the social system or social carrying capacity that constrains the Ithala population size. The effects of social interactions and how they influence demographic processes (Ishibashi *et al.* 1998) are well known. Social interactions include intense

competition among males (Archie *et al.* 2007) for space to establish territories and, in accordance with Reid *et al.* (2007), an imbalanced social structure might cause a reduction in productivity because more energy is exhausted in maintaining home ranges, rather than in reproduction. Sizes of home ranges are also strongly influenced by social interactions (Lent & Fike 2003).

Black rhino in particular require protracted social interactions in order to breed (Emslie & du Toit 2006), and are selective in their choice of habitat (Reid *et al.* 2007). However, the spatial restrictions in smaller reserves (Rachlow & Berger 1998) such as Ithala impose higher population densities and force high rates of association upon black rhinos (Linklater & Swaisgood 2008). Increased social pressure along with territorial behaviour leads to increased fighting and higher levels of mortality (Adcock 1994; Adcock *et al.* 1998; Linklater *et al.* 2010). The mechanism of density dependence is thus through mortality that is associated with increased social interactions rather then resource limitations. However, the challenge remains the maintenance of maximum reproductive performance while keeping the Ithala black rhino population size viable (Rai 2003) to evade stochastic drivers which influence demographics.

In order to maximize the black rhino population performance, the rhino strategy for Ithala follows the guidelines and principles set in the conservation plan for black rhino (Brooks & Adcock 1997), which requires a minimum acceptable population growth rate of 5% (Goodman 2001). The plan prescribes a set harvesting rate of at least 5% per annum over time but not more than 8% (Emslie 2001). In keeping with Brooks and Adcock (1997), the Ithala black rhino population is maintained at its estimated Maximum Productivity Carrying Capacity (MPCC) (Okita-Ouma *et al.* 2008), that is, 75% of the Ecological Carrying Capacity (ECC), in order to maintain the population growth.

The appropriateness of using the carrying capacity concept in particular is not only challenged by our data, but also by other authors (O'Connor *et al.* 2007; Morgan *et al.* 2009). Decision-making around elephant numbers for instance, have moved away from a single, constant maximum density-based approach to one using indicators from the environment (Slotow *et al.* 2008). Given the age at first reproduction and inter-calving data, it does not appear that the Ithala population is at ecological carrying capacity, but that social effects are primarily disrupting the conception of females and affecting survival rates of some age-classes.

This is the likely explanation of how density-dependence is limiting the population, despite the fact that it is young and should be eruptive. This also clarifies why the population is performing below the optimum growth rate, and is at the bottom-end of the desired 5–8% growth rate. It implies that management has to think carefully about how to manage the social factors (Lent & Fike 2003) that are causing density dependence in a source population such as Ithala and this may improve the strategic and tactical planning for endangered species protection (Belovsky *et al.* 1974).

The findings of our analysis have important implications for black rhino population management at Ithala. It highlights that the density and growth of the Ithala black rhino population are indirectly driven by periodic translocations from the population. Currently this option may ensure the persistence (Rai 2003) of the Ithala population by impeding social interactions and injuries, particularly among males. Nonetheless, careful monitoring to enhance understanding of social factors (Van Dyk & Slotow 2003) particularly black rhino male behaviour should be intensified in order to allow strategic translocation of individuals in such a way that the density dependent effects are mitigated.

Our study highlights the challenges associated with managing small populations, especially in the context of many threatened large mammal species that have social systems that may be unintentionally impacted by management interventions. We emphasize that, in this context, it is essential that detailed information of the focal population is known, and that management evaluates, including through scenarios, unintended risks of interventions to population persistence or growth. Any intervention would need to be nuanced in intensity across both space and time, based on this understanding, to mitigate risk and unintended consequences.

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