Population recovery of black rhinoceros in north-west Namibia following poaching

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Abstract

Curtailing overharvest, whether illegal or legal, is often a critical conservation objective. Yet even if overexploitation can be stopped, subsequent rates of population recovery can be highly variable due to Allee effects, alterations to age and sex structure and disruptions of animal social systems. Moreover, understanding the influence of density dependence can be difficult but important for long-term management. Here, we investigate the dynamics of black rhinoceros *Diceros bicornis* in the Kunene region of Namibia as they recover from illegal hunting. We use multi-strata mark–recapture models to examine survival and stage-transition rates from 1992 to 2005. Survivorship estimates ranged from 0.793 for calves to 0.910 for adult males and 0.944 for adult females. The annual reproductive rate in adult females was estimated at 0.315. Model selection showed that these vital rates were time invariant, suggesting that Allee effects and transient dynamics did not have an important effect upon population dynamics, even in the early stages of recovery. Relative population density increased significantly from 1992 to 2005 once illegal hunting had ceased in Kunene. However, the best-fit models did not include relative density in the estimation of survival or stage-transition rates. We then used the vital rates generated from our mark–recapture analysis to build matrix projection models that assessed overall population dynamics. The female-only model gave a population growth rate estimate of $\lambda = 1.011$. Two-sex models suggest that the growth rate of the population could range from 0.990 to 1.012. The relatively slow growth rate of this population, even without hunting or density dependence, could stem from the low productivity of the region. Adult females had the highest reproductive value and their survival had the highest elasticity among vital rates. Translocating adult females would lead to the fastest initial population growth rate in founder populations but would have the most impact on the source population.

Introduction

Excessive hunting is one of the most critical threats to large vertebrates worldwide (Milner-Gulland & Bennett, 2003; Walsh *et al*., 2003). Large mammals are being removed at rates far exceeding sustainable levels in Africa (Fa & Brown, 2009) and the Neotropics (Peres & Palacios, 2007), and are already lost from most locations in south-east Asia (Corlett, 2007). The rapid destruction of many animal populations has led to increased effort to reduce the impact of hunting (Bennett *et al*., 2007), or in certain situations, to curtail it altogether (Milner-Gulland, Beddington & Leader-Williams, 1992).

The goal of controlling hunting is to allow the impacted populations to recover (Stevick *et al*., 2003). However, recovery may be far less straightforward that it seems. On the one hand, we could assume that, in the absence of human-induced mortality, low-density animal populations would grow at rates determined by their intrinsic rate of increase, *r* (Birch, 1948). The intrinsic rate of increase is relatively easy to assess indirectly, as it can be estimated allometrically from life-history parameters such as body size (Fenchel, 1974; Blueweiss *et al*., 1978). Nevertheless, populations released from harvest can behave in very unpredictable ways. Following decades of overfishing, the Atlantic cod *Gadus morhua* population crashed in 1993 (Bundy &

Fanning, 2005). Yet, despite a subsequent moratorium on fishing, populations did not recover as expected possibly because the entire trophic structure of the community had been altered (Bundy & Fanning, 2005). Even at the population-scale and ignoring impacts on the rest of the food web, responses to the cessation of harvest can vary greatly for several reasons. First, hunting can depress the population size enough to induce Allee effects – reduced population growth rates at low abundance (Petersen & Levitan, 2001). Second, hunting can disrupt the age and sex structure of the population, leading to transient rather than asymptotic population growth following release from harvest (Koons *et al.*, 2005; Koons, Rockwell & Grand, 2006). Finally, hunting can disrupt the social structure of the population with lasting consequences for long-term population growth. For example, population recoveries of different species of ungulates in a protected area in Thailand were highly dependent on the social behavior of the particular species. Thus, muntjac *Muntiacus muntjak* and gaur *Bos gaurus* recovered relatively quickly while sambar *Rusa unicolor*, whose mating system had been disrupted by hunting that specifically targeted mature males, remained rare (Steinmetz *et al.*, 2010). Overcoming Allee effects and the disruption to the age ratio, sex ratio or social system in the harvested population can take highly variable periods of time. Thus, the recovery patterns of formerly hunted animal populations may be very difficult to understand or predict.

Of particular concern in assessing a population's recovery from hunting is determining when density dependence becomes apparent. At this point, population growth may slow. Certain conservation strategies call for translocations so as to reduce density dependence in the host population and promote meta-population structure that lowers the overall extinction risk (Armstrong & Seddon, 2007; Dimond & Armstrong, 2007). Yet, understanding how population density affects vital rates such as survival, growth and fecundity, as well as changes in abundance, can be difficult to do. For example, the shape of the relationship between density and a given vital rate may change across vital rates or populations, while some vital rates may be more strongly affected than others (Morris & Doak, 2002). And all of these need to be estimated from datasets that are often of short duration, comprise a small sample size or contain significant sampling error (Ludwig, 1999; Fieberg & Ellner, 2000).

Here, we assess population dynamics of a large ungulate recovering from intense illegal hunting, the black rhinoceros *Diceros bicornis*. Black rhinos were extremely heavily hunted for their horns and their total population across Africa was reduced by an estimated 95–97% from 1970 to 1987 (Leader-Williams, 1992; Berger & Cunningham, 1994; Emslie & Brooks, 1999; Muya & Oguge, 2000). However, illegal hunting of black rhinos was successfully controlled across parts of their range by the 1990s (Emslie & Brooks, 1999; Walpole *et al.*, 2001) and some populations have grown rapidly since then (Emslie, 2008). The last known rhino poaching incident in the Kunene region of north-western Namibia, was in 1994 (B. Brell, pers. obs.). Very little is known about rhinoceros population dynamics,

making it difficult to predict the potential impacts of Allee effects, transient dynamics or disrupted age and sex ratios on population recovery rates. Our study is one of the first analyses of a long-term demographic dataset for any species of rhino and spans 14 years and 259 known individuals. By following known individuals within the population as it recovered from 1992 to 2005, we have been able to measure vital rates across a range of population densities and thus assess the effects of density on vital rates.

This paper has three objectives: (1) to test for Allee effects and/or impacts of altered sex and age structure on population growth rates in the early stages of recovery; (2) to determine whether the population has begun to show signs of density dependence, and if so, to assess how strong the effects are and the mechanisms by which they manifest; (3) to assess individual vital rates and overall population growth rate in the Kunene black rhino population over the 14-year time period following the control of illegal hunting. In order to accomplish these objectives, we first use multi-strata mark–recapture models to estimate the vital rates of black rhinos in the Kunene. We then use these vital rates to build matrix projection models that allow us to characterize the dynamics of the population and assess the factors influencing population growth rates.

Methods

Study system and species

The Kunene black rhino population in Namibia is the most extreme desert-dwelling ecotype of black rhino, and is the largest free-ranging population of any species of rhinoceros persisting outside of formal protected areas. Consequently, the African Rhino Specialist Group has recognized the Kunene black rhino population as a 'Key 1' population (Emslie & Brooks, 1999). The Kunene population ranges across *c*. 20 000 km^2 of rugged terrain dominated by basalt and schist foothills and mountains interspersed with gravel plains. The area receives *c*. 150 mm of rainfall per year, and key resources such as fresh-water springs and vegetation are distributed unevenly across the landscape (Hearn, 2000). Land tenure in the region is currently a mixture of state-administered tourism concessions along with community-managed communal lands. The recent boom in nature-based tourism in Namibia has increased support from the government and local communities for wildlife conservation, particularly for flagship species such as the black rhino.

Field surveys

In order to better understand the ecological needs and population dynamics of Kunene's black rhinos, a small, local non-governmental organization, Save the Rhino Trust, has maintained detailed individual-based sighting records since the late 1980s. The first well-documented surveys on the region's black rhino population were conducted in 1983 (Loutit, 1983) and again in 1986

(G. Owen-Smith, unpubl. data). A standardized database containing individual rhino profiles and sighting information was first developed in 1997 (Brett, 1997) incorporating systematically collected sighting data from 1992 to its status of over 5000 individual sightings in 2005. Typically, the rhino tracking operations use teams of three to four trackers that are vehicle based, although camels are used in roadless areas. Tracking occurs throughout the year, and surveys are rotated across eight eco-zones within the range (Hearn, 2000). When fresh tracks are observed either crossing the road or at fresh-water springs along survey routes, trackers continue their search by foot. When the rhino is spotted, vital information such as individual identification, body condition, location and reproductive condition are recorded, while a photograph is taken of each rhino sighted. Information from each sighting is entered into the Kunene black rhino database (Brett, 1997).

Population models

We used these long-term sighting records of individual rhinos to estimate vital rates using multi-strata, open-population models in program MARK 5.1 (Cooch & White, 2001). We collapsed all sightings from a given year to 1 January of that annum, and used a 14-year run of data from 1992 to 2005. For any given year, sighted individuals were assigned to one of the following six life-stages: neonate calf, juvenile male or female (1–4 years old), adult male or female (5 + years old) or mother-with-neonate. The multi-strata model partitions the variance in individual capture histories into separate components representing detectability, apparent survival (i.e. actual survival and fidelity to the study area) and stage-transition rates. We first tested the goodness-of-fit of the global model to the data using the median-$\hat{c}$ method (Cooch & White, 2001). We then used model selection to determine the most parsimonious detectability function, testing for effects of stage, population density and time while holding survival and transition functions constant (see Table 1). Using the best-fit detectability model, we then ascertained the most parsimonious survival function, and finally the most parsimonious stage-transition function. We fixed biologically impossible stage transitions to zero and set the detectability of calves equal to that of mothers-with-neonates.

To address objective 1, we tested for Allee effects or transient dynamics such as those arising from altered sex and age ratios in the early stages of recovery, by assessing whether vital rates changed over the 14-year study period. We did this by explicitly testing time-structured models of survival and stage transition in the mark–recapture model set.

To address objective 2, we tested for density dependence by assessing whether vital rates changed with increasing relative density using density-structured models in the mark–recapture model set. We analyzed the abundance of rhinos over time in the most data-rich portion of the study area, Zone 6, which provided 31% of the total sightings over the 14-year study period. We incorporated relative

Table 1 Model selection results from multi-strata, open-population mark-recapture models

Model	QAIC$_c$	QAIC$_c$ weight	Number of parameters	Quasi-likelihood deviance
Detectability (*p*) functions				
s (stage) *p* (time) ψ (stage)	2893.8	0.735	22	2277.6
s (stage) *p* (density) ψ (stage)	2896.9	0.155	11	2303.4
s (stage) *p* (stage) ψ (stage)	2898.6	0.068	13	2301.0
s (stage) *p* (stage × density) ψ (stage)	2899.8	0.037	17	2294.0
s (stage) *p* (.) ψ (stage)	2903.6	0.005	11	2310.1
s (stage) *p* (stage × time) ψ (stage)	2929.4	0.000	52	2248.9
Survival (*s*) functions				
s (stage) *p* (time) ψ (stage)	2893.8	0.718	22	2277.6
s (density) *p* (time) ψ (stage)	2897.3	0.129	19	2287.3
s (.) *p* (time) ψ(stage)	2897.8	0.098	19	2287.8
s (stage × density) *p* (time) ψ (stage)	2898.9	0.056	27	2272.3
s (time) *p* (time) ψ (stage)	3240.4	0.000	27	2613.8
s (stage × time) *p* (time) ψ (stage)	3274.2	0.000	64	2567.1
Stage-transition (ψ) functions				
s (stage) *p* (time) ψ (stage)	2893.8	0.982	22	2277.6
s (stage) *p* (time) ψ (stage × density)	2901.8	0.018	26	2277.3
s (stage) *p* (time) ψ (.)	3034.0	0.000	19	2424.0
s (stage) *p* (time) ψ(density)	3036.0	0.000	20	2424.0
s (stage) *p* (time) ψ (stage × time)	3254.5	0.000	49	2580.7
s (stage) *p* (time) ψ (time)	3391.0	0.000	31	2756.8

Models were first assessed for the most parsimonious detectability (*P*) function, then survival (*s*) and finally stage-transitions (ψ) using corrected quasi-likelihood Akaike Information Criteria (QAIC$_c$). Terms in parentheses indicate the structure imposed on each function for a given model: 'stage' refers to life-history stage, 'density' to population density (km^{-2}) and '.' denotes no structure.

population density as a covariate into the mark–recapture models, and converted counts of known individuals into estimates of abundance in year t $(\hat{N}_t)$ using Lincoln–Peterson closed-population estimators. We used February and March, the two consecutive months with the most number of rhino sightings, as the first and second sampling occasions, respectively. Then

$$\hat{N}_t = \frac{(M_t + 1)(C_t + 1)}{(m_t + 1)} - 1 \qquad (1)$$

where M and C were the numbers observed on the first and second occasions, respectively, and m the number observed on the second occasion that had also been seen on the first. Detectability in year t (p_t) was then estimated as $C_t/\hat{N}_t$. We regressed the estimates of detectability against time and used the predicted values from this relationship $(\hat{p}_t)$ to estimate population size from the minimum number of rhinos known alive each year (see supporting information). Use of these regression-based detectability estimates accounted for temporal trends in detectability but smoothed out the annual variance, much of which probably arose from sampling error.

To address objective 3, we then used the estimates of survival and stage transitions generated from the multi-strata mark–recapture models to build a matrix projection model for black rhinos, using the techniques described by Fujiwara & Caswell (2002), which allowed us to assess stage-specific vital rates and overall population growth rate. Specifically, we built a post-birth census model where the fertility element was defined as the annual probability of transition from adult female to mother-with-neonate (Fig. 1a). Most matrix models of large mammals are female-only, and this is usually quite reasonable because a single male could potentially fertilize a large number of females (Fujiwara & Caswell, 2002; Morris & Doak, 2002). However, at some point relative male abundance has to become important. All individuals are limited in their potential movements, and with large animals such as rhinos that exist at very low population densities, a single male could not possibly copulate with every female in the population (Ginsberg & Milner-Gulland, 1994). Therefore, in addition to the female-only model, we also utilized two-sex models where birth rates were dependent on the sex ratio (Fig. 1b). We used the minimum mating function (Bessa-Gomes, Legendre & Clobert, 2010; Legendre, 2004), which sets an upper limit on the population-wide offspring production equal to the number of adult male–female pairs, while accounting for polygyny. The number of mating pairs in year t (c_t) is given by

$$c_t = \min(N_{\text{females},t}, N_{\text{males},t} \times h) \qquad (2)$$

where h is the 'harem size' or the average number of females that a reproductively successful male fertilizes (Bessa-Gomes *et al.*, 2010). Genetic evidence from a small black rhino population in the Save Valley Conservancy, Zimbabwe, suggests that male reproductive success is variable, and can range from one to three calves per year (Garnier,
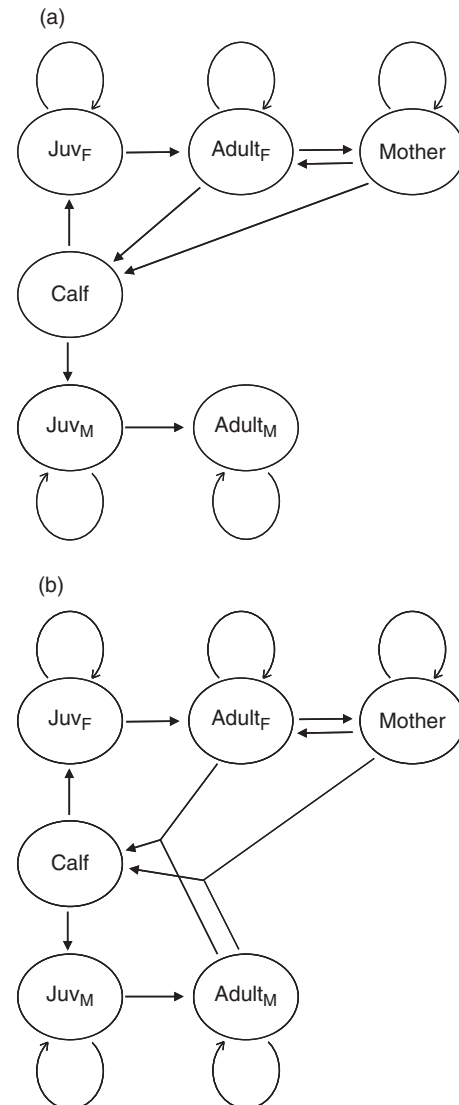

Figure 1 Life-cycle diagram illustrating the structure of the black rhinoceros matrix projection model used here. 'Juv' stands for 'juvenile', subscripts M and F stand for male and female, respectively. (a) Standard model where fertility is entirely dependent on females. (b) Two-sex model where fertility is dependent on the relative numbers of males and females, linked through a minimum mating function.

Bruford & Goossens, 2001). Therefore, we tested two extreme harem size scenarios: $h = 1$, representing monogamy, and $h = 4$ representing facultative monogamy (*sensu* Clutton-Brock, 1989).

We measured the population growth rate (λ) as the dominant eigenvalue of the projection matrices. We used Monte Carlo simulations to generate λ confidence intervals (CI) by randomly drawing vital rates from β distributions determined by the maximum-likelihood estimated mean and variance for each rate. For each of 10 000 iterations, we generated projection matrices from the β-random vital rates

and calculated λ for each. We then sorted the λ arrays and used the 250th and 9750th values as 95% confidence limits (Caswell, 2001).

Results

The relative density of black rhinos in Kunene region Zone 6, estimated using equation 1 as described above, increased between 1992 and 2005 (Fig. 2); because of the relationship between relative density and time, we did not test any density × time interactions in our mark–recapture models. The variance inflation factor of the global mark–recapture model, $\hat{c} = 1.329$, was associated with a significant lack of fit between model and data ($P < 0.001$). To correct this, we adjusted the test statistics in future model runs to account for the extra-binomial variation; therefore we relied on quasi-likelihood information criteria to compare mark–recapture models. Initial model runs gave survival estimates of mothers-with-neonates equal to 1. Because this is biologically unrealistic, in subsequent analyses we fixed the survival of mothers-with-neonates equal to the survival of adult females without neonates. Initial model runs also gave extremely low juvenile → mother-with-neonate transition probabilities ($\sim 10^{-13}$). In subsequent model runs, we fixed this transition to zero to afford more accurate estimation of the remaining vital rates. While calves in our model analysis are sex independent, the gender of 121 (97%) of the 125 calves was known. The observed calf sex ratio did not differ from parity ($\chi^2 = 1.397$, d.f. = 1, $P = 0.237$), and thus we fixed the calf → juvenile transition probabilities to 0.5 for both males and females.

Holding survival and stage-transitions constant, with both structured by 'stage', we determined that the best-fit detectability function included 'time' as a covariate (see Table 1). We then used this detectability function to ascertain that the most parsimonious survival and transition functions were structured by stage but did not include relative population density or time. The maximum-likelihood estimates of survival and stage transitions (Fig. 3) show that estimates of calf survival was the lowest, at 0.793 (95% CI = 0.658–0.884). Furthermore, the only significant
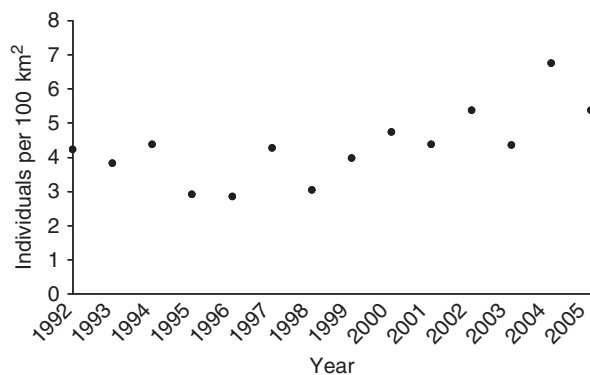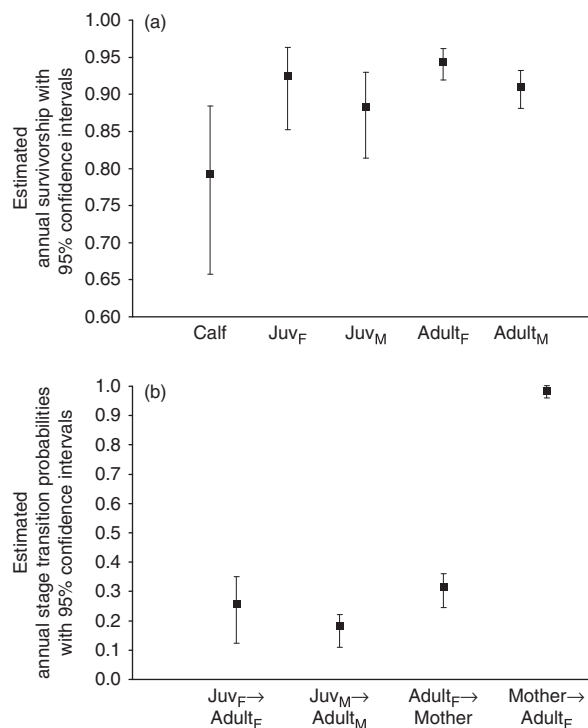

Figure 3 Estimated annual survival (a) and stage-transition rates (b) for black rhinoceros of different life stages; 'Juv' stands for 'juvenile', subscripts M and F stand for male and female, respectively.

difference, comprising non-overlapping 95% CI, was between adult female survival (0.944; 95% CI = 0.920–0.962) and calf survival. The transition rate from adult female to mother-with-neonate was 0.315 (95% CI = 0.265–0.369), and this also served as the annual fertility estimate for adult females. The probability that mothers-with-neonates returned to the adult female stage in the following year was very high, at 0.985 (95% CI = 0.901–0.998).

We estimated the population growth rate for black rhinos in the Kunene region in three ways: as $\lambda = 1.011$ (95% CI = 0.991–1.030) using the female-only model; as $\lambda = 0.990$ (95% CI = 0.967–1.013) using the two-sex model where $h = 1$; as $\lambda = 1.012$ (95% CI = 0.993–1.031) using the two-sex model where $h = 4$ (Fig. 4). Survivorship of adult females showed the highest elasticity, at 0.239 (Fig. 5).

Discussion

Population recovery from harvest can be very unpredictable because overhunting can lead to Allee effects (e.g. Petersen & Levitan, 2001); alter the age and sex structure of the population leading to transient growth (Koons *et al.*, 2006); or disrupt animal social systems (e.g. Steinmetz *et al.*, 2010). We investigated population dynamics of a desert-dwelling black rhino population over 14 years following the successful control of poaching in the Kunene region of north-west Namibia. Our mark–recapture analysis showed no support
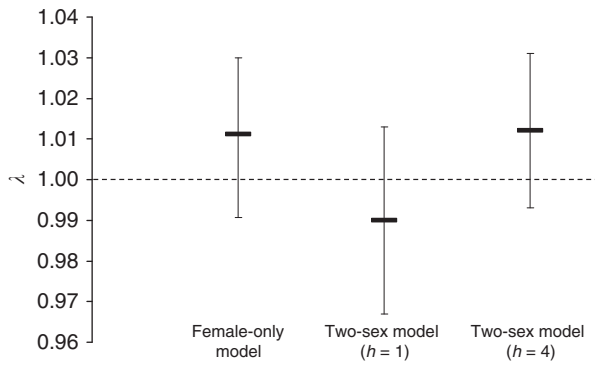

Figure 2 Relative black rhino density in Zone 6 of the Kunene region.

Figure 4 Estimated Kunene black rhino population growth rate (with 95% confidence intervals) based on different matrix model structures.

for models where survival or stage transitions varied over time. This suggests that neither Allee effects nor transient dynamics reduced survivorship or reproduction to any detectable degree in this population early in its recovery. In contrast, Allee effects were reported for black rhinos in Pilanesberg, South Africa (Hrabar & du Toit, 2005), where maternal success increased with density up to 0.085 rhinos km^{-2}. In Pilanesberg, female age structure and adult sex ratio changed during the early stages of population growth, which could have resulted in the observed Allee effects (Hrabar & du Toit, 2005), although it was not reported whether trends in maternal success translated into impacts on overall population dynamics. The reason that Allee effects were not observed in the Kunene could be due to smaller changes in age and sex structure during the early stages of population growth, or else that those changes in age and sex structure did not detectably manifest at the population level.

Interestingly, despite the increasing relative density of Kunene rhinos over 14 years (Fig. 2), we did not detect any important density-dependent effects in the Kunene black rhinos. It may be that density has not yet reached levels at which it negatively affects vital rates across the whole population, although smaller areas within the current range might still be experiencing density-dependent effects that were not detectable at the scale of our analysis. The continued monitoring of the Kunene rhino population might provide important information on density dependence. Our population growth rate estimates and temporal trends in relative density both suggest that population density will continue to increase over the near term, but at a much lower rate than the intrinsic rates of increase known to be possible for rhinos, which generally range from 4 to 11% (Okita-Ouma *et al.*, 2009). If density does continue to rise in the Kunene, density dependence may begin to affect particular vital rates at some point. Determining exactly how density dependence affects population dynamics will be critical for managers (Morris & Doak, 2002). For example, an understanding of density dependence is necessary to accurately estimate long-term population size, environmental
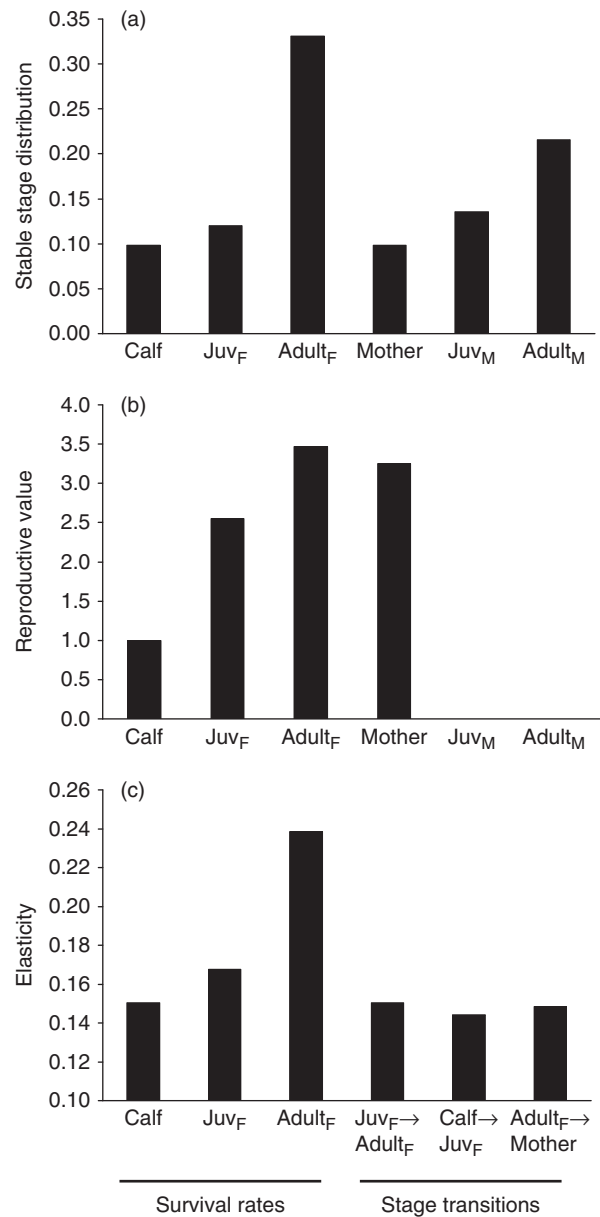

Figure 5 Proportion of individuals in each stage at stable distribution (a), reproductive value of different stages (b) and analytical elasticities across female vital rates (c). 'Juv' stands for 'juvenile', subscripts M and F stand for male and female, respectively.

carrying capacity and population trends. Moreover, translocation strategies can be made particularly effective if animal removals are conducted in a way that reduces density dependence in the donor population (Todd, Nicol & Koehn, 2004).

Another productive line of future research would involve a further examination of the role of males in rhino population dynamics. Males are clearly important at some level (Ginsberg & Milner-Gulland, 1994), but our currently limited data on male reproductive success (Garnier *et al.*,

2001) afford only imprecise estimates of their importance to population dynamics. For example, the two harem size scenarios that we examined resulted in quite different estimates of population growth rate, from 'likely declining' at $h = 1$ to 'likely increasing' at $h = 4$. An important consideration, although not one that has received much attention in the literature (see Caswell, 2001; Sundelöf & Åberg, 2006), is that h could very plausibly vary with male density. As the ratio of males to females declines in the population, we might expect the reproductive success rate of a given individual male to increase. However, given the paucity of data that allow us to estimate even static measures of h, it will be very difficult indeed to assess the factors influencing variation in h.

Our female-only matrix models suggest that the Kunene black rhino population grew at 1% per year from 1992 to 2005. This relatively slow rate of growth could be attributable to the extreme aridity and low productivity of the region (Hearn, 2000). Our population growth rate estimates may be useful for understanding the dynamics of this population as it continues to recover from intense poaching. Moreover, our models could prove useful for informing management decisions regarding translocations of individuals and/or trophy hunting. The Rhino Custodianship Program of the Namibia Ministry for Environment and Tourism (MET, 2003) currently manages the country-wide population of *D. b. bicornis* in accordance with continental-scale recovery goals (Emslie *et al.*, 2009). The main objective of Namibia's National Rhino Policy (MET, 2003) is to maximize growth rates through strategic removals in high-density areas while increasing the range and population size through translocations within the historical range. New population centers are being established because 'custodians', including Namibians on both private and communal lands, now have the opportunity to benefit economically from having black rhino back on their lands in exchange for providing protection and monitoring. Long-term management goals are to re-establish a connected population of at least 2000 black rhino in suitable habitat across Namibia, develop both consumptive and non-consumptive sustainable use policies and to achieve better overall co-ordination for protection and management of rhino in Namibia. Such ambitious goals may benefit tremendously from long-term black rhino monitoring data. In the north-west Kunene region, where annual black rhino translocations into communal lands are ongoing, Save the Rhino Trust continues to manage the largest and longest-running database on any black rhino population in Africa. This source of long-term rhino demography and movement data has the potential to be a very useful tool for biological management. We know, for example, that adult females have the highest reproductive value and that survivorship of these individuals has the highest elasticity of any vital rate. These findings, consistent with those for other long-lived animals (Pfister, 1998), suggest that translocating adult females would ensure the highest initial population growth rate in the founder communities but would have the most impact on the growth rate of the source population.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Estimates of detectability over time ($\hat{y} = 0.009x - 16.720$; $R^2 = 0.131$).

Figure S2. Trends in relative density estimates from three different estimation methods: Lincoln-Peterson mark-recapture, minimum number known alive (MKNA), and MKNA corrected by detectability. MKNA/detectability values are reported in the main text, figure 2

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