Assessing the population performance of the black rhinoceros in Kruger National Park

Sam M. Ferreira[1*], Cathy C. Greaver[1] & Mike H. Knight[2]

[1]*Scientific Services, South African National Parks, Kruger National Park, Private Bag X402, Skukuza, 1350 South Africa.*

[2]*Park Planning and Development, Conservation Services, South African National Parks, and Centre for African Conservation Ecology, Department of Zoology, Nelson Mandela Metropolitan University, Port Elizabeth, 6001 South Africa*

Small population sizes provide several challenges to conservation managers seeking to ensure species persistence and illustrating conservation success. Black rhinoceros, *Diceros bicornis minor,* epitomizes these challenges. During October 2008 we used block surveys, estimates of availability and observer bias to calculate landscape-specific black rhino abundances in the southern parts of Kruger National Park, South Africa. We assigned age and sex to individuals, extracted an age distribution, and estimated survival and fecundity given the population growth derived from historical strip transects. The block counts, corrected for 90.3% availability bias with observers missing 3.8% of those, predicted that 627 (95% CI: 588–666) black rhinos resided in the study area. The population increased at 6.75% per annum, the result of high survival and an estimated inter-calving interval of 2.45 years. Age distributions and population growth predicts that subadult males and females have the lowest annual survival, while dependent calves and adults have the highest annual survival. Precise estimates can be obtained with a 20% study area coverage using block counts. This gives coefficient of variances allowing detection of 5% growth from surveys every two years. Detecting 2% annual decline requires bi-annual surveys for 6 years. Our results illustrate that black rhinos are performing well in Kruger National Park.

Key words: age distribution, availability bias, *Diceros bicornis,* block counts, demography, detecting trends, monitoring, observer bias.

INTRODUCTION

Black rhinos (*Diceros bicornis*), like other mega-herbivores, are locally threatened at several places (Blake *et al.* 2007; Dobson & Lynes 2008). In dealing with this challenge, conservationists often focus on reactive actions dealing with symptoms (van Aarde & Jackson 2007) such as reducing poaching effects on threatened species through several means (van Aarde & Ferreira 2009). With the last black rhino sighted in Kruger in 1936, reintroduction commenced in 1971, with a total of 81 black rhinos introduced by 1990 (SANParks 2002). For black rhino the challenge is thus first to ensure species persistence as Kruger is a stronghold for the subspecies *D. b. minor* (Emslie 2006) which has recently experienced immense poaching pressure. Understanding black rhino population dynamics and hence the potential risk of local population extinction requires several sets of information including trends derived from a time series of estimates, age- and sex-structures, as well as demographic variables such as birth and death rates.

Fixed-width transects have been used in several instances to estimate abundances of mega-herbivore species (Caughley 1977a; Khaemba *et al.* 2001). Any survey technique carries errors which influence the precision of estimates (Caughley 1974; Redfern *et al.* 2002). A key requirement of restoration of a population is to detect trends with confidence. This is particularly difficult with small populations. Detecting trends is limited by imprecision of estimates and carries trade-offs between the size of change to be detected, length of time series, intervals between estimates (Gerrodette 1987) and sample effort (Ferreira & van Aarde 2009).

In this paper we make use of a block survey (proposed by Raoul du Toit, International Rhino Foundation) equivalent to a plot-based sampling

---

*To whom correspondence should be addressed.
E-mail: sam.ferreira@sanparks.org

approach and assess observer and availability bias that contribute to imprecision of an estimate of black rhinos in Kruger. Given the imprecision, we define the optimal sampling effort that will provide the most cost-effective estimates of precision. This allows us to assess optimal survey intervals for a monitoring programme designed at detecting population trends. We provide an estimate with appropriate precision and illustrate how additional information on the sex- and age-structure of the population allows the derivation of other population variables. From these we provide an assessment of the performance of black rhinos in Kruger.

METHODS

The Kruger National Park (19 485 km²) is in the low-lying savannas of the eastern parts of the Limpopo and Mpumalanga provinces of South Africa. Mozambique abuts the park in the east, and Zimbabwe in the north. Annual rainfall ranges from 750 mm in the south to 450 mm in the north, with rain falling during October to March (Gertenbach 1980). Granite and gneiss soils dominate Kruger's western half with nutrient-rich basalt soils dominating the eastern half (Schutte 1986). Our study area focused on the region south of the Olifants River (comprising 47% of Kruger) as most of black rhino sightings were made in this area from the regular herbivore aerial survey (Kruger *et al.* 2008).

The vegetation on the southern basalts is largely wooded savanna, with the tree canopy dominated by *Sclerocarya caffra* and *Acacia nigrescens.* Mixed *Combretum* spp. and *Acacia* spp. dominate the southern granites (Gertenbach 1983).

Availability bias

We found 15 rhinos spread throughout different landscapes in the southern part of Kruger and recorded whether these were visible every 15 seconds for a total of 10 minutes. For this purpose we used a helicopter-based survey platform, the same platform used in the population survey, positioned at 350 feet above ground. This design eliminates any other biases and help to isolate availability bias in the estimation thereof. Our sample comprised five adult males, six adult females, two subadults of 1–2.5 years of age and two calves of <1 year of age.

Observer bias

Our survey made use of 3 × 3 km blocks flown systematically with flight paths covering 100% of each block. To assess observer bias, we randomly chose 33 blocks spread throughout the landscapes in southern Kruger, and allowed front and back seat observers to record rhino observations independently from each other. We could isolate communications through individual headsets to a scribe. This allowed us to record incidences where only the front observer noted rhinos (N_f), incidences where only the back observer noted rhinos (N_b), and incidences where both observers noted rhinos (N_{fb}) from a particular side of the helicopter. We defined the proportion of rhinos missed by both observers (k) adapted from Seber (1982) as follows:

$$k = \frac{N_f N_b}{(N_f + N_{fb})(N_b + N_{fb})} \, . \qquad (1)$$

Because both sides of the helicopter had observers looking for rhinos and the way flight paths were spaced, observers had two chances to see the same rhino. Both observers thus need to miss a rhino on the first and second run which was estimated by k^2.

Population survey

Field surveys were conducted during October 2009. A trial survey suggested that blocks should be 3 × 3 km in size and flown at 350 feet along transects 300 m apart at a speed of 50 knots and would typically take 20 min to survey. Surveys were conducted between 07:30 and 13:00 along transects flown in an east–west direction to minimize the effects of sun glare.

We surveyed 221 blocks each 3 × 3 km in size that were randomly distributed across 19 different landscape types south of the Olifants River (Fig. 1). This represented coverage of 21.7% of the total 9162 km² comprising Kruger south of the Olifants River. To systematically search each block, we started at the downwind side of a block, flew east–west transects to minimize sun-glare while progressively moving across the block with subsequent transects. The design allowed us to keep track of rhinos while surveying a block and, together with the manoeuverability of the helicopter, we could minimize double counting. We recorded black rhinos within sample blocks, but also any others encountered while moving between blocks. Those within blocks were used for estimating population size, while the total sample was used for the definition of the population structure.

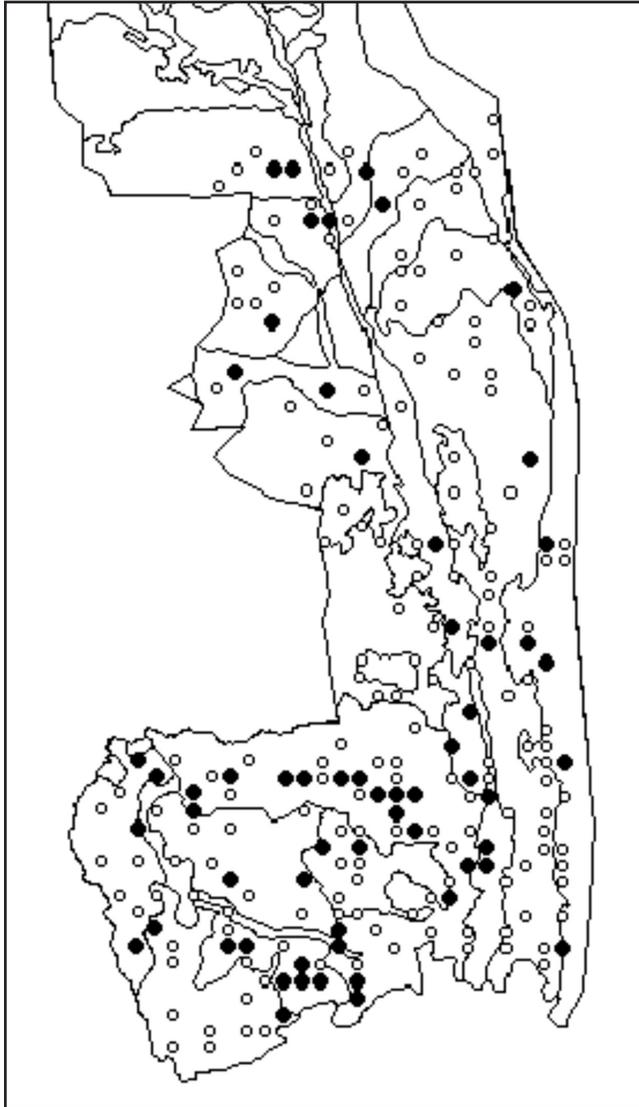We anticipated that the densities of black rhinos would be spatially variable between different land-

Fig. 1. The distribution of blocks surveyed during September – October 2009. The filled blocks indicate those that had black rhino present during the survey in 2009.

scapes because landscapes provide different levels of resources important to black rhinos. We thus estimated black rhino abundances separately for each landscape using the sample quadrant analytical approach (Jolly 1969) and corrected these for availability and observer biases.

We estimated population growth in two ways. In the first instance we used data extracted from black rhino observations during large herbivore surveys (see Kruger *et al*. 2008 for survey methods) across Kruger starting in 1988 and ending in 2007. This comprised a time series of 20 indices of black rhino abundances. We plotted the natural logarithm of abundance indices against time and estimate the slope and its confidence intervals extracted from linear regression as the exponential population growth rate (Caughley 1977b). In the second instance we constructed a model $N_{t+1} = N_i e^r + N_{i,t}$ where N_i is the expected population size and $N_{i,t}$ is the number of rhino introduced at time t with r the exponential growth rate. We used maximum likelihood (Edwards 1972) to estimate r for an expected population equal to the estimated population and its confidence intervals in 2009.

We assigned sex and age classes to each of the 155 black rhino individuals encountered. Given that the number of black rhinos typically encountered on a block were few, we could easily complete a block survey, keep track of movements, and return to confirm ages and sexes if needed. We used standard age classes (A: <0.25 years, B: 0.25–1 year, C: 1–2 years, D: 2–3.5 years, E: 3.5–6.9 years, and F: 7 years and older, Emslie *et al.* 1995) using sizes of calves relative to adult cows.

We smoothed the age distribution using an expansion technique developed for elephants (Ferreira & van Aarde 2008). Black rhinos can live up to 45 years of age in captivity (Jones 1993), while those in the wild may live shorter. We assumed that in our case black rhinos may live as long as in captivity because of the protection afforded to them in Kruger. The shape of an age distribution is defined by rate (*a*) at which the frequency of individuals in an age class decays with age. This allowed us to estimate survival rates (*s*) given that $s = \lambda a$ (Eberhardt 1988) using the estimated population growth from the time series of 20 black rhino abundances converted to $\lambda = e^r$, where *r* is the exponential growth rate.

The above procedures allowed definition of variables (n_x – the number of females in age class *x*; s_x – annual survival rate in age class *x*, and λ, the finite population growth rate) that allowed us to estimated the most likely calving interval (*c*) from Udevitz & Ballachey (1998) by first estimating (m_x) where

$$\lambda = \sum_{x=0}^{w} \frac{n_x}{n_0} s_x + \sum_{x=0}^{w} \frac{n_x}{n_0} s_x m_x \qquad (2)$$

and m_x was assumed to be age-independent once cows started calving. We also assumed equal sex ratio's at birth that define $m_x = 0.5/c$ which allowed us to estimate calving interval (*c*).

Optimal surveys

Designing a monitoring programme depends on the objectives. Regional black rhino management objectives aim to have populations increase at a minimum of 5% per annum in the short to medium term (Brooks & Adcock 1997). We thus wish to design a monitoring programme that will detect such change. In other cases detecting a decline is most important for threatened species. We thus wish to design a second programme that will detect 2% decline. Detecting such changes carries trade-offs between the survey intervals, the time or

length of a time series that it will take to detect a change and the coefficient of variance of a population estimate (Gerrodette 1987). The coefficient of variance in turn can be controlled by the effort that surveyors put in when counting (Ferreira & van Aarde 2009).

We first evaluated whether lower efforts can provide similar estimates to what we achieved with ~21% coverage of the study area. For this purpose, we sought the survey effort at which predicted estimates were within 10% of the estimate obtained through 21% coverage of the study area and defined these as accurate estimates (Thompson 1992). At the same time we evaluated the survey efforts at which percentage confidence limits (PCL is the 95% confidence interval as a percentage of the estimate – Barnes 2002) were lower than 20%. We thus randomly sub-sampled the 221 blocks to achieve a range of survey efforts and calculated population estimates and confidence intervals using Jolly's (1969) method.

The desired efforts obtained through the analyses above, defined the likely coefficient of variance extracted from the effort-related predicted PCLs. We then used Gerrodette's (1987) inequality

$$\left[\ln(1+r) \right]^2 n(n-1)(n+1)$$
$$\geq 12 \left(z_{\alpha/2} + z_\beta \right)^2 \left\{ \frac{1}{n} \sum_1^n \ln \left[\frac{cv^2}{(1+r)^{i-1}} + 1 \right] \right\}, \qquad (3)$$

where *r* is the exponential growth rate set at 0.05 (*i.e.* 5% increase per annum) or –0.02 (*i.e.* 2% decline per annum), *n* is the number of surveys $z_{\alpha/2}$ and z_β the inverse of the standard normal distribution at α and β, *i* is the interval between surveys in years and *cv* the coefficient of variance. Values of α reflect minimizing making a Type I error (concluding there is a trend when in fact there is none), while $1 - \beta$ reflect minimizing making a Type II error (concluding there is no trend when in fact there is). We varied survey intervals to define trade-offs between intervals, number of surveys and time to detect trends. We used the shortest time to detect trends as an optimal survey interval given the coefficient of variance that desired survey efforts will produce.

RESULTS

Availability bias

On average, rhinos were visible for 90.3% (95% CI: 82.7–97.9%) of the time. This means that an estimate needs to be corrected by a factor of 1.11 (95% CI: 1.02–1.21).

Table 1. Black rhino population estimates for 19 different landscapes south of the Olifants River in Kruger National Park. The number of blocks sampled in each landscape (*n*), estimates of the Lower (LCL) and Upper (UCL) 95% confidence limits are provided.

Landscape type	Area (km^2)	*n*	Estimate	LCL	UCL
Lowveld Sour Bushveld of Pretoriuskop	372	10	57	28	86
Malelane Mountain Bushveld	473	14	30	12	48
Combretum collinum/Combretum zeyheri woodland	450	10	46	19	73
Thickets of the Sabie & Crocodile River	1241	45	145	106	184
Mixed *Combretum/Terminalia sericea* woodland	1483	35	60	38	82
Combretum/Colophospermum mopane woodland of Timbavati	400	10	36	15	57
Olifants River Rugged Veld	222	5	11	5	17
Acacia welwitschii thickets on Karoo sediments	486	11	62	40	84
Kumana Sandveld	115	2	0	0	0
Punda Maria Sandveld on Cave Sandstone	37	0	–	–	–
Sclerocarya birrea subspecies *caffra/Acacia nigrescens* savanna	1350	28	12	4	20
Dwarf *Acacia nigrescens* savanna	343	7	13	3	23
Thornveld on gabbro	730	11	93	59	127
Bangu Rugged Veld	207	4	0	0	0
Combretum/Acacia nigrescens Rugged Veld	225	3	10	2	18
Combretum/Colophospermum mopane Rugged Veld	92	3	8	2	14
Colophospermum mopane shrubveld on basalt	38	0	0	0	0
Lebombo South	779	18	44	26	62
Lebombo North	120	3	0	0	0

Observer bias

Based on 54 rhino observations encountered on 33 blocks chosen for observer bias assessments, observers were missing 3.8% of rhinos available to be seen. This means that estimates corrected for availability bias also needs an additional correction factor of 1.04. Note that the method provides a point estimate with no confidence intervals.

Population estimate

We encountered black rhinos on 60 blocks (27% of blocks surveyed). In total 155 black rhinos were encountered. Of these 125 were within blocks and 30 in close vicinity to blocks. Population estimates differed between landscape types (Table 1) with 627 (95% CI: 588–666) black rhinos estimated to live in Kruger south of the Olifants River in 2009.

The black rhino estimate is substantially higher than the 286 (95% CI: 75–497) estimated in 2007 when only areas south of the Sabie River were included and no biases were accounted for (Judith Kruger, SANParks, pers. comm.). If we assume biases for fixed-wing platforms of observation is

the same as that for helicopter platforms (typically fixed-wing based platforms suffer excessively from biases; Caughley 1974), estimates corrected for biases observed in our study suggest 329 (95% CI: 84–572) black rhino most likely occurred south of the Sabie River in Kruger during 2007. When we constrained our data to south of the Sabie River, we estimated 437 (95% CI: 382–492). The uncertainty associated with the estimates particularly during 2007 limits a reliable derivation of annual population growth. Historical trends derived from the longer time series of strip transect estimates was an exponential growth of 0.069 (95% CI: 0.041–0.098) for the total population in Kruger. Exponential growth given introductions and the estimated population size in 2009 was 0.066 (95% CI: 0.064–0.068). The number of landscapes in which observers noted black rhinos also increased over time (Fig. 2).

Demographic profile

We noted 35% of individuals 7 years and younger (Fig. 3). Although 53% of individuals older than
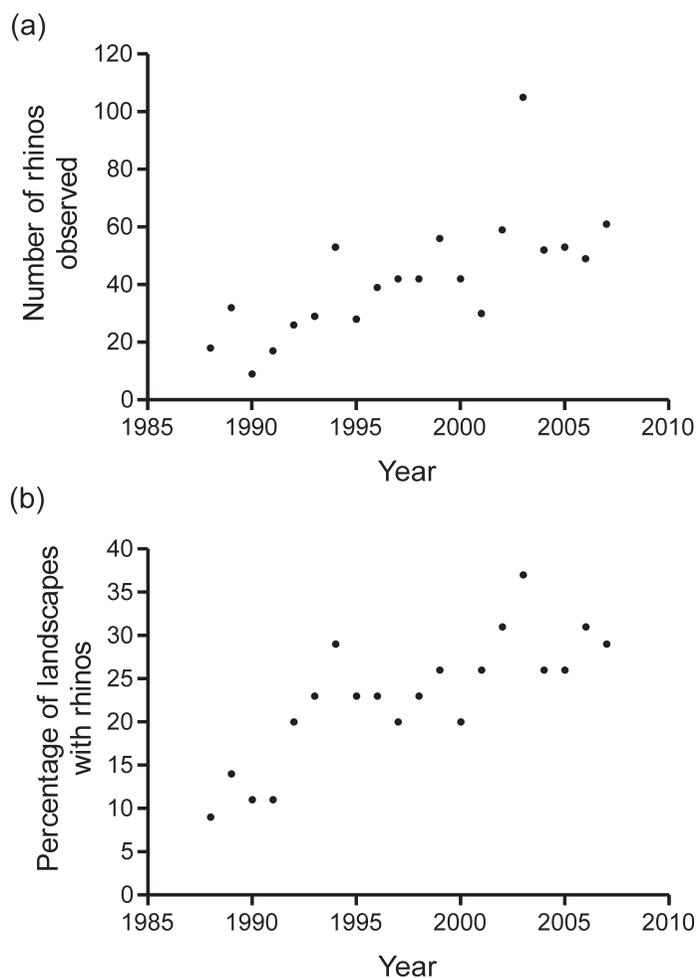
(a)

(b)

Fig. 2. Trends observed in observations of black rhinos during annual aerial surveys between 1988 and 2007. Observation increased (**a**) as did the number of landscapes (**b**) in which black rhinos were observed.

7 years were female, the sex ratio did not differ significantly from unity ($\chi_1^2 = 0.36$, $P = 0.54$). Note that 5.7% of adult females had calves younger than 0.25 years.

Smoothed age distributions (Fig. 4) together with population growth rate (*i.e.* 0.0675, the mean of the two methods of estimation) suggest that calves survived well during the first year, but appeared to have a higher chance of dying when they become less dependent on cows (Table 2). Subadult animals had the worst survival with males in this age class having the lowest survival. Once rhinos reach adulthood, survival was high.

Given the age structure, observed growth rates and survival, and assuming that black rhino cows have their first calf at the age of seven (Hitchins & Anderson 1983), we estimated that cows will

have calves once every 2.45 years (95% CI: 1.5–4.0 years).

Optimal surveys

Population estimates varied considerably at low coverage of the study area. Population estimates were within 10% of the estimate obtained through ~21% coverage of an area when surveyors covered 15–20% of the area (Fig. 5a). Percentage confidence limits in contrast required less effort. In this case PCLs were lower than 20% at between 10–15% coverage of the area (Fig. 5b). These suggest that 20% coverage of an area will provide accurate and precise estimates (see Thompson 1992 for definitions).

At 20% coverage PCLs typically were 12.5% of the population estimate. That translates to a
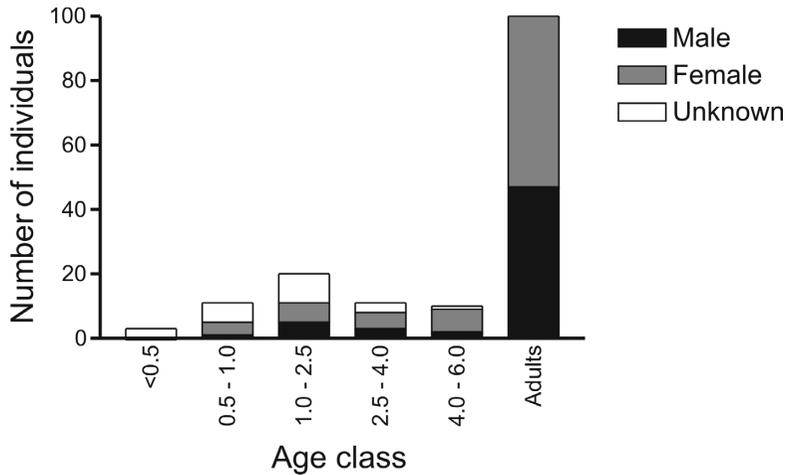
Fig. 3. Age and sex structure defined from a sample of 155 black rhino in Kruger National Park in 2009.
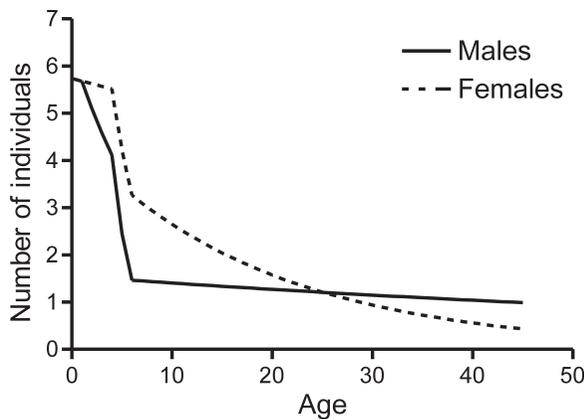

Fig. 4. Smoothed age distribution for the black rhino population in Kruger during 2009.

typical coefficient of variance of 3.2%. At survey intervals of 1 and 2 years it would take 2 years to detect a 5% annual increase and by that time the population would have had a total change of 10.3%. At survey intervals of 1 and 2 years it would take 6 years to detect a 2% annual decline. By the time of detection a total change of –11.4% would

Table 2. Sex-specific annual survival rates for black rhinos extracted from age distributions and population growth rates.

Age in years	Males	Females
0–1	0.99	0.99
2–4	0.94	0.99
5–6	0.64	0.82
Adults	0.99	0.99

have taken place (Table 3). Optimal intervals would thus be 2 years.

DISCUSSION

The persistence of some mega-herbivores carries significant challenges for conservationists. Rhino species epitomize these. The illegal trade in animal products fuelled poaching and had dire consequences for some species (Dobson & Lynes 2008). Species with low fecundity and population growth rates are likely to be more sensitive to disturbances such as predation and poaching effects (Grange *et al.* 2004). Many mega-herbivore populations plummeted in Africa and Asia (Emslie & Brooks 1999; Douglas-Hamilton 2009), and poaching led to the near extinction of both black and white rhinos (Emslie & Brooks 1999).

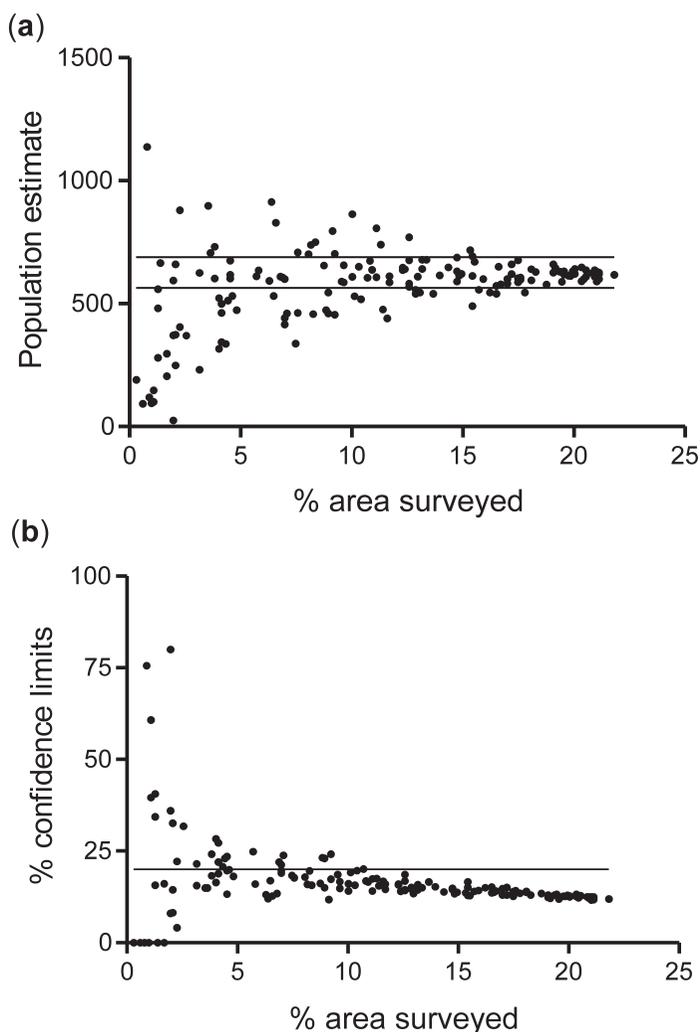Concerted efforts flipped the negative trends in

(a)

(b)

Fig. 5. Effects of survey effort on estimates of population size (**a**) as well as% confidence limits (**b**). At 15–20% survey of the area population estimates will be within 10% (horizontal lines) of the estimate, while a % confidence limit of less than 20% will be achieved by surveying 10–15% of the area.

some instances (Emslie 2002, 2004, 2006) as a result of several initiatives directed at reducing extinction risks by increasing rhino numbers (Mills *et al.* 2006) and expanding their present distribution back into the historical distribution of both African species (Sherriffs 2007; Knight & Kerley 2009). Actions involved increased anti-poaching activities and re-introductions (Taylor 2003; van der Westhuizen 2003; Linklater *et al.* 2011) that are often augmented by focal actions such as providing temporary safe areas (Emslie & Brooks 1999), or active husbandry to maximize birth rates (Knight 2001; Patton *et al.* 2008). The restoration of rhino populations thus carry the challenge of

reducing local extinction risks in areas within their historical distribution after introductions.

Evaluating this challenge often use individual histories to derive several population variables (Patton & Jones 2007). However, at some point, individual focal sampling may become time consuming, costly and inefficient (Walpole 2002) given the objectives of maintaining 5% population growth (Brooks & Adcock 1997) and the size that populations reach. Several white as well as black rhino populations are now of such size that registration studies (*e.g.* Patton & Jones 2008) may carry too much cost to offset the benefit gained from the information gathered. Our results illus-

Table 3. Survey trade-offs for black rhinos in Kruger National Park when surveyors cover 20% of an area wishing to detect 5% increase (**a**) and 2% decrease (**b**) in the population.

(**a**)	Number of years between surveys (i)	Number of surveys required (n)	Number of years to detection $[i(n-1)]$	Total change $[(1 + r)^{i(n-1)} - 1]$
	1	3	2	10.3%
	2	2	2	10.3%
	3	2	3	15.8%
	4	2	4	21.6%
	5	2	5	27.6%
	6	2	6	34.0%
	7	2	7	40.7%
	8	2	8	47.7%
	9	2	9	55.1%
	10	2	10	62.9%

(**b**)	Number of years between surveys (i)	Number of surveys required (n)	Number of years to detection $[i(n-1)]$	Total change $[(1 + r)^{i(n-1)} - 1]$
	1	7	6	−11.4%
	2	4	6	−11.4%
	3	4	9	−16.6%
	4	3	8	−14.9%
	5	3	10	−18.3%
	6	2	6	−11.4%
	7	2	7	−13.2%
	8	2	8	−14.9%
	9	2	9	−16.6%
	10	2	10	−18.3%

trate that block sample techniques, particularly if biases and sources of error can be assessed, may support the efforts of conservationists wishing to evaluate the success of reintroductions.

Availability or concealment bias (Caughley 1974; Redfern *et al.* 2002) is a common source of error that detracts conservationists from obtaining accurate or precise estimates. Availability is primarily affected by vegetation features. Note that the detection of available animals may also depend on horizontal distance that individuals are from an observer as well as group and body size (*e.g.* Kruger *et al.* 2008). We did not explicitly check detectability bias primarily because we used narrow strips and black rhinos typically were noted in small groups. Availability bias may thus primarily increase when foliage density increases. Counters often address this by making corrections, but seldom are such corrections objective. In our case, we estimated that black rhinos are only available to

be seen for ~90% of the time on average over all landscapes, at our strip density, flight height and speed for helicopters. However, we acknowledge that this is unlikely to be constant as the landscapes in Kruger have very different vegetation features (Gertenbach 1983). At present, sample sizes do not allow estimation of landscape-specific availability bias, but if this could be done, population estimates may be more precise.

Observer bias, another source of error when estimating black rhino population sizes, is also a common bias in most animal surveys (Caughley 1974) and seldom if ever accounted for in African large mammal surveys. Counters thus rarely correct for this bias – population estimates tend to be lower than expected as a result. Differential observer recording (Seber 1982; Borchers *et al.* 1998) allowed us to estimate that observers will on average miss 3.8% of visible black rhinos. This is unlikely to differ between landscapes because

availability bias should drive landscape differences. However, the variance in observer bias is likely to increase when the number of observers participating in the overall survey increases. That then should induce wider confidence intervals for the ultimate population estimate which will carry more challenging trade-offs when conservationists wish to detect (Gerrodette 1987) or evaluate the achievement of positive population growth rates. Counters should thus design surveys that minimize the number of observers, but include estimation of observer bias in their approach (Borchers *et al.* 1998).

Following the corrections for the biases estimated above, between 588 and 666 black rhino lived south of the Olifants River in Kruger during 2009. This translates to a CV of 3.2%, substantially lower than what is typically obtained for megaherbivore species using sample survey designs (Blanc *et al.* 2007). The low CV most likely result from our consideration of landscape differences since our analyses stratified our data into the 19 different landscapes available to black rhinos south of the Olifants River in Kruger. Stratification of data typically allows counters to accommodate spatial differences and result in lower confidence intervals when distribution of individuals is clumped or they exhibit strong landscape selection (Salehi & Seber 2002).

Reduction in CVs through assessing biases and considering spatial realities carry some advantages given that most rhino management actions wish to achieve a population growth rate exceeding 5% per annum in the short to medium term (Brooks & Adcock 1997) and therefore need to detect that. Monitoring programmes for smaller populations usually focus on registration approaches (Patton *et al.* 2007), but this is not practical for larger populations. Given that survey efforts affect precision of population estimates (Barnes 2002; Ferreira & van Aarde 2009) surveyors of larger populations can further enhance precision of black rhino population estimates by covering at least 20% of an area if using the block count approach in similar conditions to Kruger. Detecting trends however, has different demands and trade-offs (Gerrodette 1987). For endangered species, conservationists may thus wish to detect change relatively quickly and minimize the total change by the time they have detected the change, specifically if a population is declining. In our case, detection of 5% change per annum is best achieved when black rhinos are surveyed once every two years using

the techniques and bias estimation we have described here.

Recent insurgence of rhino poaching in Kruger National Park may impose desires to detect declines even though only six black rhinos were poached since the rhino onslaught started in 2007 (SANParks, unpubl. data). Our analyses suggest that surveying every two years will also allow detection of 2% annual decline, but only within six years.

Detecting trends has several other values other than just evaluating a strategic objective. Often conservationists do well in getting estimates of population trends, but seldom do they know why such a trend is the way it is. Demographic complementarity (van Aarde & Ferreira 2009) may greatly influence the ability of conservationists to respond particularly if populations have undesirable trends. Knowledge of demographic drivers (Trimble *et al.* 2009) thus carries high value that may inform management actions better. Extraction of values can be achieved when growth rate and population age-structures are known (Michod & Anderson 1980; Udevitz & Ballachey 1998). By recording additional data such as age and sex of observed individuals while surveying to obtain population estimates, conservationists can thus extract relevant demographic variables.

In our case we do not have a repeat survey for black rhinos using the techniques developed and described here. However, we extracted trends from a time series of estimates obtained through strip transect aerial surveys (Kruger *et al.* 2008) as well as predictions of growth required to achieve our population estimate given historical introductions. Although the aerial survey observations suffer from the biases we noted above, the length of the time series is beneficial (Gerrodette 1987) and likely to reflect the average population growth experienced since 1988. Both methods converge onto similar exponential values of 6.9 and 6.6%, respectively. The trends extracted for the population carry high levels of uncertainty primarily because of influences of biases not accounted for in estimates derived from strip transect aerial surveys. In addition, landscape-specific growth rates may differ substantially.

The growth rate we noted does reflect an increase at rates similar to other populations (Cromsigt *et al.* 2002; Adcock *et al.* 2010). Caution should be made though–most comparable populations are small and population growth rates estimated for small populations suffer from stochasticity (Walpole

et al. 2001), large influences of survey errors in population estimates when populations are small (Barnes 2002; Ferreira & van Aarde 2009) and destabilized age structures for a given fecundity and survival schedule (Ferreira & van Aarde 2008). When one considers typical life-histories of black rhinos (Smith & Read 1992) and fecundity and survival schedules under optimal conditions a sustained exponential growth of ~6–7% per annum is possible as estimated through age-structured models (Caswell 2001). The black rhinos in Kruger are thus comparatively performing well in this context.

In addition, male and female sex ratios are nearly equal and for both sexes survival rates are high across all ages. Note that the sex and age structure as well as survival rates we derived may suffer from stochastic small sample effects (Thompson 1992) that inflates estimates. In several populations residing in small areas, black rhino survival tends to be high especially at low densities (Walpole *et al.* 2001; Cromsigt *et al.* 2002; Hrabar & du Toit 2005). For both sexes subadults in our study had the lowest survival, which most likely result through social interactions as young dispersing individuals may encounter older individuals more often. In the case of Kruger, little removal of black rhinos has taken place removing the influence that slow management induced colonization observed elsewhere (Linklater & Hutcheson 2010) may have on our interpretations. In several cases similar kind of socially induced rhino limitations may prevail (Gottert *et al.* 2010) and explain why black rhino introductions often have high success rates initially, but thereafter suffer set-backs particularly in small areas (Linklater & Swaisgood 2008; Linklater *et al.* 2011) – spatial restrictions impose social regulation long before resources may become limited.

In a large area such as Kruger, social limitations do play out and may also be a driver of the continued colonization of new landscapes (Stoen *et al.* 2009) not occupied by black rhinos yet as we have noted. Limitations imposed by resources as is the case in the Hluhluwe-Umfolozi Park (Reid *et al.* 2007) and Pilanesberg National Park (Hrabar & du Toit 2005) in South Africa, may play out on black rhinos in Kruger and specifically locally within specific landscape types. We do not have landscape-specific population growth rates to test this prediction – our sample of landscape-specific time series extracted for Kruger is inundated with zeros and lead to spurious landscape-specific population growth rates. However, to achieve the recorded age structure given the noted overall population growth, cows need to drop their calves once every 2.5 years. This is close to the physiological capability (Smith & Read 1992) and lower to that recorded for a population thought to be already resource limited (Patton *et al.* 2008), but similar to that recorded elsewhere (2.2–2.9 years, Adcock 2009). These results reflect a population not restricted by localized resource limitation. Our conclusion is further supported by high estimated calf survival. Large mammal populations are expected to respond through juvenile survival followed by reproductive variables and then adult survival when they approach densities that experience resource restrictions (Eberhardt 2003; Sibly *et al.* 2005).

CONCLUSION

We have estimated sampling and bias assessments that provide strong guidelines in designing surveys to help evaluate local achievement of conservation objectives concerning black rhinos (Emslie & Brooks 1999). These constraints are applicable to several other mega-herbivores (Barnes 2002; Ferreira & van Aarde 2009). We use these biases estimated for black rhinos to estimate population sizes for black rhinos. For black rhino it provides estimates with defined and defendable precision surveyed at optimal two year intervals.

The additional information on the sex- and age-structure of the population allows the derivation of other population variables. Demographic complementarity has great potential to inform managers better, not just for black rhinos, but also for other mega-herbivores (Ferreira & van Aarde 2009) and large mammals (Ferreira & Funston 2010). The application of a block survey, calibrated by estimated biases and supplemented by population structure data, allowed extraction of demographic variables. These illustrate a healthy expanding population colonizing the rest of Kruger supporting local and regional black rhino conservation objectives.

Thompson, Nicky Groves, Khosi Maseko, Albert Smith, Craig McGloughlan and Judith Kruger assisted with observations. Grant Knight and Charles Thompson were the helicopter pilots during the survey.

REFERENCES

ADCOCK, K. 2009. Status and management of black rhino in Namibia, South Africa and Zimbabwe: January 2005 to December 2006. SADC Rhino Management Group, Port Elizabeth.

ADCOCK, K., KNIGHT, M., DU PREEZ, P., KOTTING, B., FIKE, B., HEARN, M., URI-KHOB, S., HOFMEYR, D., DELL, S., NXELE, B., CLINNING, G., DE GOEDE, N., ROSSOUW, D., GREAVER, C., HANNEKOM, C., MARCHANT, A., VAN DYK, G., ELS, R., FERREIRA, H., SHOLTO-DOUGLAS, A., WALKER, A. & YORK, G. 2010. An analysis of 18 years of SADC Rhino Management Group population history data. SADC Rhino Management Group, Port Elizabeth, South Africa.

BARNES, R.F.W. 2002. The problem of precision and trend detection posed by small elephant populations in West Africa. *Afr. J. Ecol.* 40: 179–185.

BORCHERS, D.L., ZUCCHINI, W. & FEWSTER, R.M. 1998. Mark-recapture models for line transect surveys. *Biometrics* 54: 1207–1220.

BLAKE, S., STRINDBERG, S., BOUDJAN, P., MAKOMBO, C., BILA-ISIA, I., ILAMBU, O., GROSSMANN, F., BENE-BENE, L., DE SEMBOLI, B., MBENZO, V., S'HWA, D., BAYOGO, R., WILLIAMSON, L., FAY, M., HART, J. & MAISELS, F. 2007. Forest elephant crisis in the Congo Basin. *Public Library of Science* 5: 945–953.

BLANC, J.J., BARNES, R.F.W., CRAIG, G.C., DUBLIN, H.T., THOULESS, C.R., DOUGLAS-HAMILTON, I. & HART, J.A. 2007. African Elephant Status Report 2007: An Update from the African Elephant Database. IUCN/SSC African Elephant Specialist Group, Gland.

BROOKS, P.M. & ADCOCK, K. 1997. Conservation plan for the black rhinoceros (*Diceros bicornis*) in South Africa. Rhino Management Group Report, Port Elizabeth.

CASWELL, H. 2001. Matrix population models: construction, analysis and interpretation. Sinauer Associates, Sunderland.

CAUGHLEY, G. 1974. Bias in aerial survey. *J. Wildl. Manage.* 38: 921–933.

CAUGHLEY, G. 1977a. Sampling in aerial survey. *J. Wildl. Manage.* 41: 605–615.

CAUGHLEY, G. 1977b. Analysis of vertebrate populations. John Wiley & Sons, New York.

CROMSIGT, J.P.G.M., HEARNE, J., HEITKONIG, I.M.A. & PRINS, H.H.T. 2002. Using models in the management of black rhino populations. *Ecol. Model.* 149: 203–211.

DOBSON, A. & LYNES, L. 2008. How does poaching affect the size of national parks? *TREE* 23: 177–180.

DOUGLAS-HAMILTON, I. 2009. The current elephant poaching trend. *Pachyderm* 45: 154–157.

EBERHARDT, L.L. 1988. Using age structure data from changing populations. *J. Appl. Ecol.* 25: 373–378.

EDWARDS, A.W.F. 1972. Likelihood. Cambridge University Press, Cambridge.

EMSLIE, R.H. 2002. African rhino numbers continue to increase. *Pachyderm* 33: 103–107.

EMSLIE, R.H. 2004. Rhino population sizes and trends. *Pachyderm* 37: 107–110.

EMSLIE, R.H. 2006. Rhino population sizes and trends. *Pachyderm* 41: 100–105.

EMSLIE, R.H., ADCOCK, K. & HANSEN, H.B. 1995. Fine tuning rhino management group age class system. Rhino Management Group Report, Port Elizabeth.

EMSLIE, R.H. & BROOKS, M. 1999. African rhino: status survey and conservation action plan. IUCN/SSC African Rhino Specialist Group. IUCN, Gland.

FERREIRA, S.M. & FUNSTON, P.J. 2010. Estimating lion population variables: Prey and disease effects in Kruger National Park, South Africa. *Wildl. Res.* 37: 194–206.

FERREIRA, S.M. & VAN AARDE, R.J. 2008. A rapid method to estimate population variables for African elephants. *J. Wildl. Manage.* 72: 822–829.

FERREIRA, S.M. & VAN AARDE, R.J. 2009. Aerial survey intensity as a determinant of estimates of African elephant population sizes and trends. *S. Afr. J. Wildl. Res.* 39: 181–191.

GERRODETTE, T. 1987. A power analysis for detecting trends. *Ecology* 68: 1364–1372.

GERTENBACH, W.P.D. 1980. Rainfall patterns in the Kruger National Park. *Koedoe* 23: 35–43.

GERTENBACH, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe* 26: 9–121.

GOTTERT, T., SCHONE, J., ZINNER, D., HODGES, J.K. & BOER, M. 2010. Habitat use and spatial organization of relocated black rhinos in Namibia. *Mammalia* 74: 35–42.

GRANGE, S. DUNCAN, P., GAILLARD, J-M., SINCLAIR, A.R.E., GOGAN, P.J. P., PACKER, C., HOFER, H. & EAST, M. 2004. What limits the Serengeti zebra population? *Oecologia* 140: 523–532.

HRABAR, H. & DU TOIT, J.T. 2005. Dynamics of a protected black rhino (*Diceros bicornis*) population: Pilanesberg National Park, South Africa. *Anim. Conserv.* 8: 259–267.

JOLLY, G.M. 1969. Sampling methods for aerial censuses of wildlife populations. *E. Afr. Agric. For. J.* 34: 46–49.

JONES, M.L. 1993. Longevity of ungulates in captivity. *Int. Zoo Yearb.* 32: 159–169.

KHAEMBA, W.M., STEIN, A., RASCH, D., DE LEEUW, J. & GEORGIADIS, N. 2001. Empirically simulated study to compare and validate sampling methods used in aerial surveys of wildlife populations. *Afr. J. Ecol.* 39: 374–382.

KNIGHT, M.H. 2001. Current and possible population performance indicators for black rhinos. In: R. Emslie (Ed.), Proceedings of a SADC Rhino Management Group (RMG) workshop on biological management to meet continental and national black rhino conservation targets (pp. 49–56). SADC Regional Programme for Rhino Conservation, WWF SARPO, Harare.

KNIGHT, M.H. & KERLEY, G.I.H. 2009. Black rhino translocations within Africa. *Africa Insight* 39: 70–83.

KRUGER, J.M., REILLY, B.K. & WHYTE, I.J. 2008. Appli-

cation of distance sampling to estimate population densities of large herbivores in Kruger National Park. *Wildl. Res.* 35: 371–376.

LINKLATER, W.L., ADCOCK, K., DU PREEZ, P., SWAISGOOD, R.R., LAW, P.R., KNIGHT, M.H., GEDIR, J.V. & KERLEY, G.I. 2011. Guidelines for large herbivore translocation simplified: black rhinoceros case study. *J. Appl. Ecol.* 48: 493–502.

LINKLATER, W.L. & HUTCHESON, I. 2010. Black rhinoceros are slow to colonize a harvested neighbour's range. *S. Afr. J. Wildl. Res.* 40: 58–63.

LINKLATER, W.L. & SWAISGOOD, R.R. 2008. Reserve size, conspecific density, and translocation success for black rhinoceros. *J. Wildl. Manage.* 72: 1059–1068.

MICHOD, R.E. & ANDERSON, W.W. 1980. On calculating demographic parameters from age frequency data. *Ecology* 61: 265–269.

MILLS, A., MORKEL, P., AMIYO, A., RUNYORO, V., BORNER, M. & THIRGOOD, S. 2006. Managing small populations in practice: black rhino *Diceros bicomis michaeli* in the Ngorongoro Crater, Tanzania. *Oryx* 40: 319–323.

PATTON, F., CAMPBELL, P. & PARFET, E. 2007. Establishing a monitoring system for black rhinos in the Solio Game Reserve, central Kenya. *Pachyderm* 43: 87–95.

PATTON, F., CAMPBELL, P. & PARFET, E. 2008. Biological management of the high density black rhino population in Solio Game Reserve, central Kenya. *Pachyderm* 44: 72–79.

PATTON, F. & JONES, M. 2007. Determining minimum population size and demographics of black rhinos in the Salient of Aberdare National Park, Kenya. *Pachyderm* 43: 63–72.

PATTON, F. & JONES, M. 2008. Errors that occur when using photo-identification to identify individual black rhinos. *Pachyderm* 44: 35–44.

REDFERN, J.V., VILJOEN, P.C., KRUGER, J.M. & GETZ, W.M. 2002. Biases in estimating population size from an aerial census: a case study in the Kruger National Park, South Africa. *S. Afr. J. Sci.* 98: 455–461.

REID, C., SLOTOW, R., HOWISON, O. & BALFOUR, D. 2007. Habitat chances reduce the carrying capacity of Hluhluwe-Umfolozi Park, South Africa, for critically endangered black rhinoceros *Diceros bicornis. Oryx* 41: 247–254.

SALEHI, M.M. & SEBER, G.A.F. 2002. Unbiased estimators for restricted adaptive cluster sampling. *Aust. N. Z. J. Stat.* 44: 63–74.

SANPARKS 2002. Strategic plan for the conservation and management of rhinoceros (*Diceros bicornis* and *Ceratotherium simum*) within South African National Parks 2003–2013. South African National Parks, Pretoria.

SCHUTTE, I.C. 1986. The general geology of the Kruger National Park. *Koedoe* 29: 13–38.

SEBER, G.A.F. 1982. The estimation of animal abundance and related parameters. Griffin, London.

SHERRIFFS, P. 2007. Update on the Black Rhino Range Expansion Project: local community receives black rhinos. *Pachyderm* 43: 116–117.

SIBLY, R.M., BARKER, D., DENHAM, M.C., HONE, J. & PAGEL, M. 2005. On the regulation of populations of mammals, birds, fish and insects. *Science* 309: 607–610.

SMITH, R.L. & READ, B. 1992. Management parameters affecting the reproductive potential of captive, female black rhinoceros, *Diceros bicornis. Zoo Biol.* 11: 375–383.

STOEN, O.G., PITLAGANO, M.L. & MOE, S.R. 2009. Same-site multiple releases of translocated white rhinoceroses *Ceratotherium simum* may increase risk of unwanted dispersal. *Oryx* 43: 580–585.

TAYLOR, P. 2003. Black rhino translocations into Malawi. *Oryx* 37: 139.

THOMPSON, S.K. 1992. Sampling. John Wiley & Sons, New York.

TRIMBLE, M.J., FERREIRA, S.M. & VAN AARDE, R.J. 2009. Drivers of megaherbivore demographic fluctuations: inferences from elephants. *J. Zool., Lond.* 279: 18–26.

UDEVITZ, M.S. & BALLACHEY, B.E. 1998. Estimating survival rates with age-structure data. *J. Wildl. Manage.* 62: 779–792.

VAN AARDE, R.J. & FERREIRA, S.M. 2009. Elephant populations and CITES trade resolutions. *Environ. Conserv.* 36: 8–10.

VAN AARDE, R.J. & JACKSON, T.P. 2007. Megaparks for metapopulations: addressing the causes of locally high elephant numbers in southern Africa. *Biol. Conserv.* 134: 289–297.

VAN DER WESTHUIZEN, E. 2003. Reintroduction of black rhino to North Luangwa National Park, Zambia. *Oryx* 37: 403.

WALPOLE, M.J. 2002. Factors affecting black rhino monitoring in Masai Mara National Reserve, Kenya. *Afr. J. Ecol.* 40: 18–25.

WALPOLE, M.J., MORGAN-DAVIES, M., MILLEDGE, S., BETT, P. & LEADER-WILLIAMS, N. 2001. Population dynamics and future conservation of a free-ranging black rhinoceros (*Diceros bicornis*) population in Kenya. *Biol. Conserv.* 99: 237–243.

Corresponding Editor: N. Owen-Smith