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# Density dependence and population dynamics of black rhinos (*Diceros bicornis michaeli*) in Kenya's rhino sanctuaries

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## Abstract

Density-dependent feedback mechanisms provide insights into the population dynamics and interactions of large herbivores with their ecosystem. Sex ratio also has particularly important implications for growth rates of many large mammal populations through its influence on reproductive potential. Therefore, the interrelationships between density-dependent factors, comprising density, sex ratio and underlying growth rates ( $r$ ) were examined for the Eastern black rhino (*Diceros bicornis michaeli*) living in three rhino sanctuaries in Kenya using four population models. The exponential and logistic models gave similar results and the former were accepted because they better portrayed the actual situation on the ground. Sex ratios in all sanctuary populations were positively correlated with  $r$  but interpreted with realization of other factors also affecting  $r$ . We caution that the results of population models should be interpreted alongside ground-truthed observations. We recommend that future translocation strategies should take into account sex and age structures of the donor population, while future studies of density dependence should take into account both biotic and abiotic factors.

*Key words:* black rhino, density dependence, population models, sanctuary, sex ratio, underlying growth rate

## Résumé

Des mécanismes de feedback de densité-dépendance chez les grands herbivores donnent un aperçu de la dynamique des populations et de l'interaction avec l'écosystème. Les

sex-ratios ont aussi d'importantes implications pour la dynamique des populations de nombreux grands mammifères, spécialement par leur influence sur le potentiel reproducteur. On a étudié ces relations croisées entre les facteurs densité-dépendants du rhino noir de l'Est *Diceros bicornis michaeli*, le sex-ratio et le taux de croissance ( $r$ ) sous-jacent dans trois sanctuaires de rhinos du Kenya en utilisant quatre modèles de population. Les modèles exponentiel et logistique donnaient des résultats similaires, les résultats du premier étant acceptés parce qu'ils représentaient la situation actuelle sur le terrain. Les sex-ratios de toutes les populations étaient positivement liés à  $r$  mais interprétés en réalisant que d'autres facteurs affectent aussi  $r$ . Nous attirons l'attention sur le fait que les résultats de la modélisation des populations doivent être interprétés tout en les confirmant par des observations sur le terrain; nous recommandons des stratégies de translocations qui prélèvent des individus dans les diverses structures de sexe et d'âge de la population d'origine; et nous suggérons que de futures études de densité-dépendance tiennent compte de facteurs biotiques et abiotiques.

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## Introduction

Density dependence can play an important role in regulating population dynamics of many species of mammals (Krebs, 2002). Thus, increasing population densities can result in a situation where birth rates decline, whereas mortality rates and emigration increase. As a result, population density can rise to a level where net growth rate equals zero when food resources are limiting (Primack,

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2002). Likewise, changes in adult sex ratios can have important implications for the population dynamics of many large mammals (Verme & Ozoga, 1981; Saltz, 2001), particularly through their influence on reproductive potential (Owen-Smith, 1988). Skewed sex ratios in large mammals may be indicative of chance in demographic factors in small populations and/or may be influenced by parental condition (Trivers & Willard, 1973). Populations with adult sex ratios skewed in favour of females in adequate food supplies would be expected to achieve a higher growth rate (Owen-Smith, 1988; Emslie, 1999). Biased adult sex ratio can also influence the effective population size and levels of genetic heterozygosity (Kimura & Crow, 1963; Lande & Barrowclough, 1987; Nunney & Elam, 1994). It is particularly important to understand how factors such as density dependence and skewed adult sex ratios can influence the population dynamics of endangered species like the black rhino (*Diceros bicornis*) managed intensively *in situ*.

Severe poaching significantly reduced many black rhino populations across Africa in the 1970s and 1980s (Emslie & Brooks, 1999). In response, black rhino Range States adopted measures to conserve them *in situ*. These measures included creation of Rhino Conservation Areas, Rhino Conservancies, Rhino Sanctuaries and Intensive Protection Zones (IPZs) (Brett, 1990; Nduku & Martin, 1993; Leader-Williams *et al.*, 1997). In Kenya, small, fenced sanctuaries with adequate protection were established on State and private lands from the mid-1980s onwards. This approach led to a significant reduction in poaching, resulting in the gradual recovery of black rhino numbers from 380 in 1987 to 458 in 2003 and 570 in 2007, thereby maintaining Kenya as the stronghold of 84% of the eastern black rhinos *Diceros bicornis michaeli* in the wild (Emslie & Brooks, 1999; Okita-Ouma *et al.*, 2008, Unpublished Report). Because Kenyan rhino sanctuaries are small and mostly fenced, they require sound biological management. For the established sanctuaries, a growth rate of  $\geq 6\%$  per annum has been set by Kenya as its policy for the recovery of its black rhino population (Okita-Ouma, Amin & Kock, 2007).

Black rhino populations can grow with a long term maximum intrinsic growth rate of  $\sim 9\%$  per annum, although young growing populations with very low adult mortality rates may grow even faster (Owen-Smith, 1988; Emslie, 1999). Metapopulation management through translocations has been the key feature of Kenya's rhino conservation strategy to achieve higher growth rates. For example, translocation records for 1992–2003 show that

Nairobi National Park (Nairobi NP) was primarily a source population that supported a total of 41 outward translocations and received one inward translocation. In contrast, Ngulia Rhino Sanctuary (Ngulia RS) was primarily a recipient population that received 16 inward translocations and supported one outward translocation. Meanwhile, Lake Nakuru National Park (Lake Nakuru NP) did not receive or support any translocations during this period.

Given the intensive programme of managing Kenya's black rhinos within sanctuaries, it is important to understand relationships between rhino density, sex ratio and growth rates in order to improve population performance and minimize genetic problems (Awise & Hamrick, 1996; Woodruff, 2001). This study analyses historical black rhino monitoring data collected over 12 years in the three State land rhino sanctuaries of Nairobi NP, Lake Nakuru NP and Ngulia RS. These data encompassed basic demographic parameters including densities, births, deaths, translocations and sex and age structures. We seek to examine how changes in population density and adult sex ratios correlate with underlying intrinsic growth rates over time by using the most appropriate density dependence model and testing the hypothesis that increasing adult sex ratios in favour of females are positively correlated with intrinsic growth rates hereinafter also referred to as underlying growth rate. We conclude by recommending the best model for predicting underlying growth rates of intensively managed black rhino populations, and the interventions necessary for improving underlying growth rates for these populations.

## Methodology

### Study areas

*Lake Nakuru NP.* Lake Nakuru NP ( $0^{\circ}50' \text{ S} - 1^{\circ}00' \text{ S}$  and  $36^{\circ}20' \text{ E} - 36^{\circ}25' \text{ E}$ ) was designated as a bird sanctuary in 1960, upgraded into a national park in 1968, established as a RAMSAR site in 1974 and became a rhino sanctuary in 1986. The completely fenced rhino sanctuary covers  $188 \text{ km}^2$  of which an area of  $44 \text{ km}^2$  is a shallow highly alkaline soda lake. Lake Nakuru NP ranges in altitude from 1200 to 1750 m and has an average annual rainfall of 850 mm. Its vegetation comprises a mixture of open grassland *Acacia*, *Tarchonanthus* bush land, deciduous and *Euphorbia* forests and riverine bush land (Mwasi, 2002; Adcock, Amin & Khayale, 2007).

*Nairobi NP.* Nairobi NP (2°18' S–2°20' S and 36°23' E–36°28' E) was established as the first national park in East Africa in 1945, and became a rhino sanctuary in 1963. It is partially fenced covering 117 km<sup>2</sup>. The unfenced 20 km stretching along the southern boundary is intended to allow wild ungulate migration. Nairobi NP ranges in altitude from 1,508 to 1,790 m and has an average annual rainfall of 800 mm. Its vegetation comprises deciduous forest, riverine thorn forests, shrubs and grasslands (Muya & Ogege, 2000; Adcock *et al.*, 2007).

*Ngulia RS.* Ngulia RS (3°01' S–3°06' S and 38°06' E–38°10' E) was established in 1985, and lies inside Tsavo West National Park. The completely fenced Ngulia RS was expanded twice before the study period, during which it covered 62 km<sup>2</sup>. Ngulia RS was expanded for a third time in 2007 to reach 88 km<sup>2</sup> (Okita-Ouma *et al.*, 2008a), and was conceived of as a way to re-establish a large free-ranging population within a much larger national park. This objective was initiated in 2008 when ten black rhinos were translocated out of Ngulia RS into the larger Tsavo West. Ngulia ranges in altitude from 600 to 1,800 m, and has an average annual rainfall of 600 mm. Its vegetation is composed of mixed species bushland thickets, grasslands, shrubs, low tree and herbs (Adcock *et al.*, 2007).

#### Data collection

Black rhino populations have been monitored using an individual ID-based approach in each of the sanctuaries since their establishment. Dedicated rhino-monitoring staff patrol each sanctuary on a daily basis, on foot or by vehicle, mainly in early morning and late afternoon hours as it is the best time to sight the mainly nocturnal black rhinos. Monitoring staff record a set of standardized parameters for each rhino sighting including identity (if known), location, group composition, behaviour, age and sex. Individual rhinos are recognized by a combination of features including ear notches, distinctive body marks, horn shapes, age and sex (e.g. Amin *et al.*, 2006). Rhinos that could not be recognized by any combination of these features were referred to as 'clean'. The ageing and sexing of rhinos followed standard categories established by the IUCN-SSC's African Rhino Specialist Group (AfRSG) (Adcock and Emslie, 2000, Unpublished Report). Birth and mortality data were also recorded using standardized data collection forms (Okita-Ouma *et al.*, 2008b, Unpublished

Report). To ensure good quality data, the Kenyan Rhino Programme has implemented data quality control procedures. The sighting information is checked by experienced accredited observers using 'ID' master files which contain details of potential identification features such as horn shape, ear tears, deformities, body scars or tail shape. The data are then stored and analysed using a comprehensive geographic information database management system (Amin, Okita-Ouma & Mulama, 2001) in each rhino area. Automatic retrieval of the data for further analysis was completed through computer scripting in MS-Access™ version 97 and Matlab™ version R12 software packages. These were also counter-checked by random manual calculations.

#### Data analysis

In order to better examine underlying population trends and to reduce the possible impact of year-to-year variations in the data, we based calculations of underlying growth rates on cumulative rhino numbers, which is the growth of a population after allowing for removals and introductions and man-induced deaths such as poaching. Data analysis was restricted to the period 1992 and 2003 because historical information was more readily available and analysable from 1992 onwards. Underlying growth rate was calculated for the sum of rhinos sighted in current year  $t$  and in the previous year  $t - 1$ .

Different models were evaluated to test for density dependence in Kenya's black rhino populations, following the approach of Cromsight *et al.* (2002). This approach assumes the following relationship between the modelled population number,  $N(t)$  and the observed census population number,  $P(t)$ , as

$$P(t) = N(t) + \varepsilon(t),$$

where  $\varepsilon(t)$  is an error term that shows the difference between  $N(t)$  and  $P(t)$ . The estimates for modelling  $N(t)$  are computed by minimizing the sum of squares of the error term. The models were evaluated based on the explained variance,  $R^2$ , as well as on the correlation between the predicted values and the observed values. This approach was applied to different models with a different structure of density dependence. We started with a simple exponential growth model, i.e. the black rhino population grows with a constant specific growth rate  $r$

$$N(t + 1) = N(t) + r \times N(t).$$

The ln-transformed version of this model was also applied to test for the density dependence feedback. The exponential model was used as null model against which to compare the logistic model and the so-called Fowler model (Fowler, 1981). This logistic model is formulated as:

$$N(t+1) = N(t) + N(t) \times r \times \left(1 - \frac{N(t)}{K}\right)$$

where  $K$  is the so-called carrying capacity. Whereas this logistic equation assumes a linear relationship between  $N(t)$  and the factor determines the strength of the density dependence,  $(1 - N(t)/K)$ . For large animals, Fowler (1981) suggested that it is more realistic to assume that density-dependent factors play a more important role closer to  $K$ . Using parameter  $n$ , the relation between  $N(t)$  and  $(1 - (N(t)/K)^n)$  is curvilinear and makes the contribution of this factor relatively large close to  $K$ .

Effective rhino density was expressed as numbers of rhinos per  $\text{km}^2$  of the entire sanctuary. In the case of the partially fenced Nairobi NP it was assumed that the number of rhinos straying out through the unfenced southern boundary was insignificant. This assumption was confirmed by the seasonal geographic locations of all rhinos as recorded in rhino information system. However, in the case of Lake Nakuru NP, the  $44 \text{ km}^2$  lake was excluded in density calculations. Adult sex ratio was derived by

dividing the number of adult females by the number of adult males in the population at the end of year  $t$ .

Linear and nonlinear regression analysis were used to investigate the density-dependence models and the correlations between the underlying growth rate and sex ratio by use of Microsoft Office Excel 2003 and spss packages.

## Results

The estimates of the regression coefficients for the different density dependence models are shown in Table 1. The results of the Fowler model are not reported as the standard errors of the estimates for the regression coefficients were much larger than the values of the estimates. We define the best fit as the model with the highest correlation coefficient ( $C$ ) and the lowest standard error. For Nakuru NP, exponential and logistic models performed more or less the same but exponential model was selected because logistic model had very large standard error. The same reasoning of large standard error led to selection exponential model over the better logistic model for Nairobi NP. For Ngulia sanctuary, the logistic model was the best in describing the density dependence but it gave unrealistic high values for the growth rate hence exponential model was selected over it. The results for the selected models in Table 1 are shown as predicted population numbers for each sanctuary in Fig. 1.

Lake Nakuru NP	$r$	$K$	$R^2$	$C$
<i>Exponential model</i>	<i>0.068 (0.024)</i>	–	<i>0.91</i>	<i>0.954 (P &lt; 0.001)</i>
Exponential model with ln	0.017 (0.006)	–	0.89	0.954 (P < 0.001)
Logistic model	0.118 (0.115)	122.4 (160.7)	0.91	0.955 (P < 0.001)
Nairobi NP				
<i>Exponential model</i>	<i>0.030 (0.026)</i>	–	<i>0.30</i>	<i>0.660 (P = 0.027)</i>
Exponential model with ln	0.008 (0.006)	–	0.26	0.657 (P = 0.028)
Logistic model	0.048 (0.392)	160.4 (2.094.6)	0.43	0.656 (P = 0.028)
Ngulia RS				
<i>Exponential model</i>	<i>0.086 (0.022)</i>	–	<i>0.943</i>	<i>0.986 (P &lt; 0.001)</i>
Exponential model with ln	0.030 (0.01)	–	0.859	0.963 (P < 0.001)
Logistic model	0.287 (0.084)	63.2 (8.7)	0.965	0.983 (P < 0.001)

**Table 1** Results for three density-dependence models for black rhino in each rhino sanctuary. The selected models are indicated in italic

The symbols are as follows:  $r$  is the estimated underlying growth rate (standard error between brackets),  $K$  the estimated carrying capacity (standard error between brackets),  $R^2$  is the explained variance by the model and  $C$  is the correlation coefficient between the observed and predicted population numbers.

**Table 2** Results of the regression analysis with underlying growth rate as the dependent variable and sex ratio as the independent variable

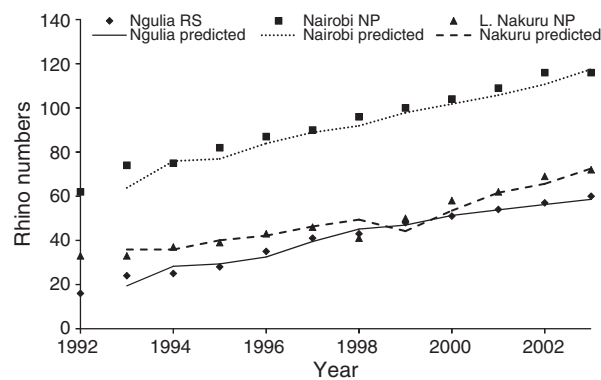
	$b_1$	$t$	$P$	$R^2$
Lake Nakuru NP	10.290 (3.303)	3.116	0.011	0.49
Nairobi NP	4.329 (1.255)	3.449	0.006	0.54
Ngulia RS	7.750 (2.755)	2.813	0.018	0.39

The symbols are as follows:  $b_1$  is the estimated regression coefficient for the growth rate (standard error between brackets),  $t$  is the  $t$ -value of the regression coefficient,  $P$  is the corresponding  $P$ -value and  $R^2$  is the explained variance by the model

## Discussion

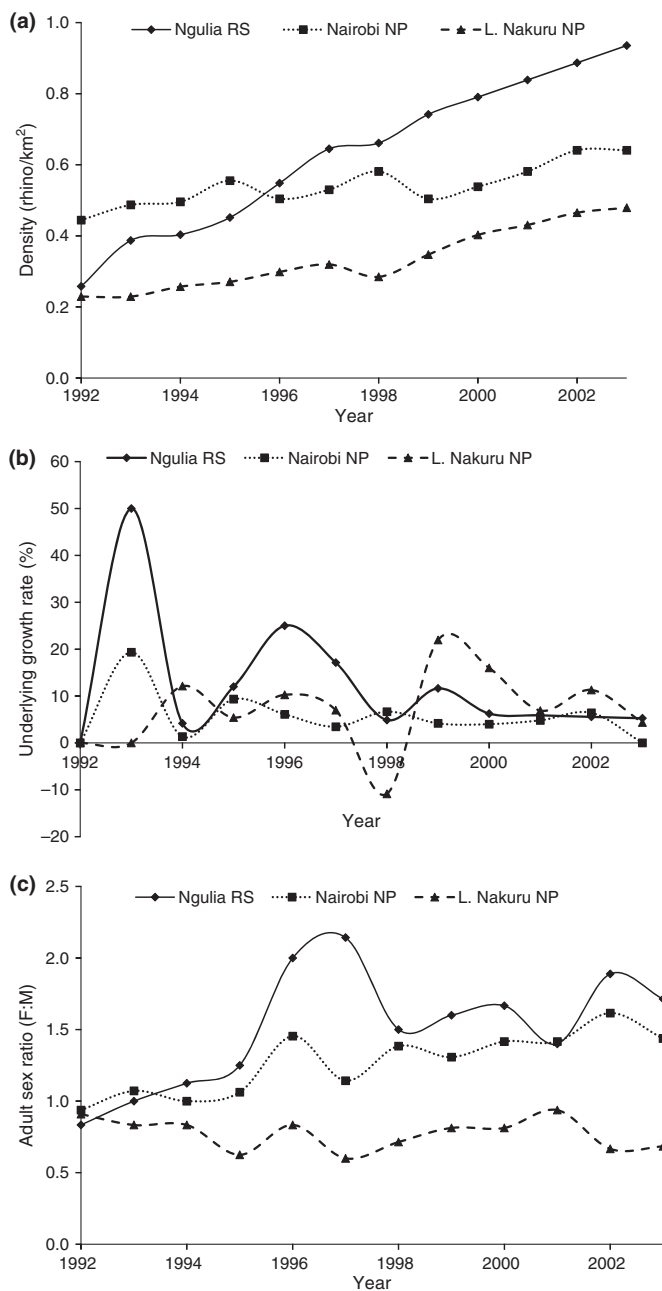
### Density dependence models

Even though the logistic model provided the best fit to describing the trends in black rhino numbers in the three sanctuaries it provided large standard errors and unrealistic values for  $r$  and  $K$  in some populations. For these reasons the exponential model which assumes black rhino grows endlessly at a constant  $r$ , was selected since it gave



**Fig 1** Observed (*dots*) and predicted (*lines*) population numbers of black rhino in each rhino sanctuary. The predicted population numbers are based on the selected models given in Table 1. Densities of black rhinos increased in each sanctuary between 1992 and 2003. Densities rose from 0.23 to 0.48 rhinos  $\text{km}^{-2}$  in Lake Nakuru NP; from 0.44 to 0.64 rhinos  $\text{km}^{-2}$  in Nairobi NP and from 0.26 to 0.94 rhinos  $\text{km}^{-2}$  in Ngulia RS (Fig. 2a). The underlying growth rates over the same period increased in Lake Nakuru NP but decreased in Nairobi NP and Ngulia RS (Fig. 2b). Adult sex ratio in Lake Nakuru NP remained in favour of males while in Nairobi NP and Ngulia RS it remained in favour of females (Fig. 2c)

realistic  $r$  but with similar significance levels as logistic model (Table 1; Fig. 1). Since the logistic model failed to give realistic  $r$  and  $K$  its assumption that black rhino populations will become limited at high densities by a lack of resources and that populations will possibly stabilize near an equilibrium density yet did not hold for these populations. This implied that there were no density-dependent effects on  $r$  in any population. For the selected exponential model, we found maximum  $r$  to be between 0.6% and 10.8%. Other studies on rhinoceros found comparable growth rates varying between 4.7% and 11% (Hitchins & Anderson, 1983; Moehlman, Amato & Runyoro, 1996; Loon & Polakow, 1997; Cromsight *et al.*, 2002). The reason exponential models gave the best fit compared with other models could have several explanations (i) overall, the degrees of freedom were only eleven per population hence the possibility of masking the occurrence of density dependence; (ii) In Lake Nakuru NP, the results could have actually confirmed that indeed the population had not reached its maximum stocking density for density dependence effects to start playing important role. Recent studies (e.g. Adcock *et al.*, 2007) estimated highest stocking density for Lake Nakuru NP as 0.51 rhino  $\text{km}^{-2}$  (74 animals) while the actual population size at the end of the study period was 69 animals; (iii) In Nairobi NP, the translocation of 41 animals out of the national park over the study period could have resulted in the maintenance of exponential growth but which ranged between 3.0% ( $\pm 2.6\%$ ). Given the very low  $r$  value and the fact that the average density, 0.54 rhinos  $\text{km}^{-2}$  (63 animals) remained above the expert maximum estimated stocking density of 0.34 rhinos  $\text{km}^{-2}$  (40 animals) (Adcock *et al.*, 2007) despite translocations, we can not rule out effects of density dependence on this population. Translocations therefore may not have fully achieved the primary objective of improving  $r$  and (iv) In Ngulia NP, even though the exponential model gave the best fit, the relatively high  $r$  could be misleading partly because of the few degrees of freedom and the initial high growth rates recorded as a result of small population size. The reality on the ground was a declining  $r$  that was attributed to deteriorating habitat due to high density of other browsers (Okita-Ouma *et al.*, 2008a). Because of the highly degraded habitat, Ngulia's maximum stocking densities reduced from estimated 0.81 rhino  $\text{km}^{-2}$  (50 animals) (Foose *et al.*, 1991) to 0.41 rhino  $\text{km}^{-2}$  (25 animals) (Adcock *et al.*, 2007). Black rhino density itself may have been playing an important role on  $r$ . It is thus important to



**Fig 2** A comparison of annual trends in black rhino (a) density, (b) underlying growth rate and (c) sex ratio in the three sanctuaries between 1992 and 2003. All the three sanctuaries showed a positive relationship between underlying growth rate and sex ratio. In all cases, the intercept was not significant (Table 2; Fig. 3)

ground-truth results of any density dependent model especially for long lived slow growing herbivores as their density dependence effects can be masked by other factors. We suggest that a possible way of solving the need for ground truthing would be to first relate densities with expert estimates that take into account biotic and abiotic factors (Adcock, 2001) before evaluating a density dependence model.

#### *Sex ratio and underlying growth rates*

Based on our hypothesis we cautiously deduce from the model results that female biased sex ratios can contribute to the increase in  $r$ . The  $r$  in Lake Nakuru NP increased despite a male biased sex ratio, in Nairobi NP the  $r$  remained very low despite the high female biased sex ratio, whereas in Ngulia RS ground-truthing indicated a declining  $r$  despite female biased sex ratio. Three factors,

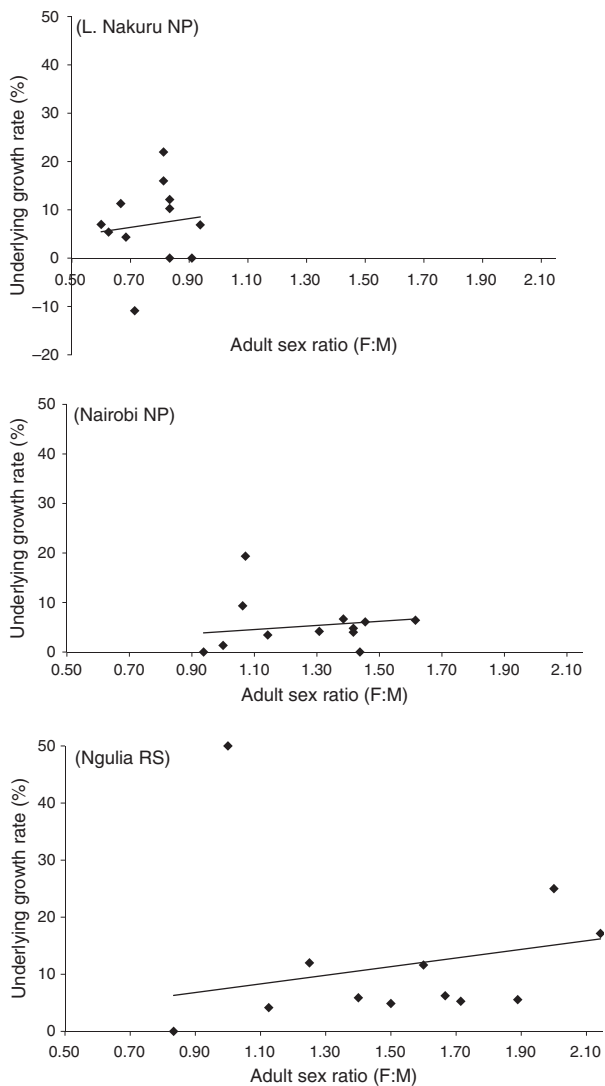


Fig 3 Relationship between underlying growth rate and sex ratio at zero intercept in the three sanctuaries (dots) and predicted underlying growth rates (line) from 1992 to 2003

including low  $R^2$ , translocation strategies and density dependent effects underpin our cautionary deduction and also help in explaining these counter-intuitive predictions. The positive correlation between  $r$  and sex ratio in Lake Nakuru NP could have meant that other factors for example females' ages at first calving and inter-calving intervals were excellent. The phenomenon of male-biased adult sex ratios has been observed in some enclosed black rhino populations in South Africa (Adcock, 2000, Unpublished Report) and in other wildlife species such as

the re-introduced Asiatic wild ass (*Equus hemionus*) in Negev Desert, Israel (Saltz & Rubenstein, 1995). The phenomenon arises from unexplained phenotypic or genotypic factors or through chance in small populations (Clutton-Brock, Albon & Guinness, 1984). Whatever the underlying explanation of male-biased sex ratios in small populations of medium to large body sized herbivores, it is imperative to adopt translocation strategies that enhance  $r$ . In Nairobi NP, translocation records showed that translocation strategies targeted sub-adults, leaving behind females with calves, and very old or reproductively immature males unable to immediately continue with breeding. Previous discussion on the density dependent models reveal that Nairobi NP and Ngulia RS were mostly above their recommended maximum stocking densities hence the possibility of density dependence factors as opposed to sex ratio playing important role in limiting  $r$ . We therefore recommend that surplus males should be removed when the population is increasing in size. In addition, when the population approaches maximum stocking density, it is important that females with calves at >2 years old constitute the priority candidates for translocation (Brett *et al.*, 2001, Unpublished Report). This mixed translocation strategy ensures a balanced sex and age structure for both the donor and recipient populations as successfully practiced in Zimbabwe (Brett *et al.*, 2001, Unpublished Report) and currently being tried in Kenya.

## Conclusion

We conclude by recommending that in evaluating density dependent models, it is important to interpret results alongside ground truthing observations. We suggest that future density dependence studies should relate animal densities using the expert derived stocking densities that take into account biotic and abiotic factors rather than using absolute density of animals per unit area. We recommend that sex ratios must be continuously monitored and manipulated to achieve maximum productivity in intensively managed populations, such as those in Kenya's rhino sanctuaries. We also recommend timely translocations and strategies that take into account age and sex structures of donor population. When carefully managed, Kenya's rhino sanctuaries have great potential to provide a substantial and continuous surplus of rhinos for re-stocking other areas. Our results have important implications for future management of black rhinos, both in Kenya and elsewhere.

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