

## Achieving success with small, translocated mammal populations

Kyle S. Van Houtan<sup>1,2</sup>, John M. Halley<sup>3</sup>, Rudi van Aarde<sup>4</sup>, & Stuart L. Pimm<sup>2,4</sup>

<sup>1</sup>Program in Science and Society, Emory University, Atlanta, GA 30322, USA

<sup>2</sup>Nicholas School of the Environment and Earth Sciences, Duke University, Durham, NC 27708, USA

<sup>3</sup>Department of Biological Applications and Technology, University of Ioannina, Greece

<sup>4</sup>Conservation Ecology Research Unit, University of Pretoria, South Africa

### Keywords

Density-dependence; protected areas; restocking; propagule pressure; ungulates.

### Correspondence

Kyle S. Van Houtan, Marine Turtle Assessment Program, Pacific Islands Fisheries Science Center, NOAA Fisheries, 2570 Dole Street, Honolulu, HI 96822, USA. Tel: +1 808 983 5300; fax: +1 808 983 2902. E-mail: kyle.vanhoutan@gmail.com

Received: 19 May 2009; accepted 15 October 2009

doi: 10.1111/j.1755-263X.2009.00081.x

### Abstract

Translocations are increasingly important tools for endangered species conservation, but their success is often uncertain. We analyzed 125 time series of grazing mammal translocations in South African protected areas. Some 94% of translocations succeeded (66% unambiguously) even though most populations began with <15 individuals and most of the species involved are of conservation concern. Adding new individuals to existing small populations increases per capita growth rates and seems to prevent translocations from failing. Growth of the translocated populations is both greater and less variable than wild mammal populations and appears less affected by the typically important ecological factors (e.g., initial propagule size, precipitation, reserve size, or presence within historical range). One-third of the populations showed robust signs of density dependence but we detect few examples of Allee effects. Our results, from empirical time series of small populations, offer new insights into achieving success for translocation programs limited to releasing few individuals.

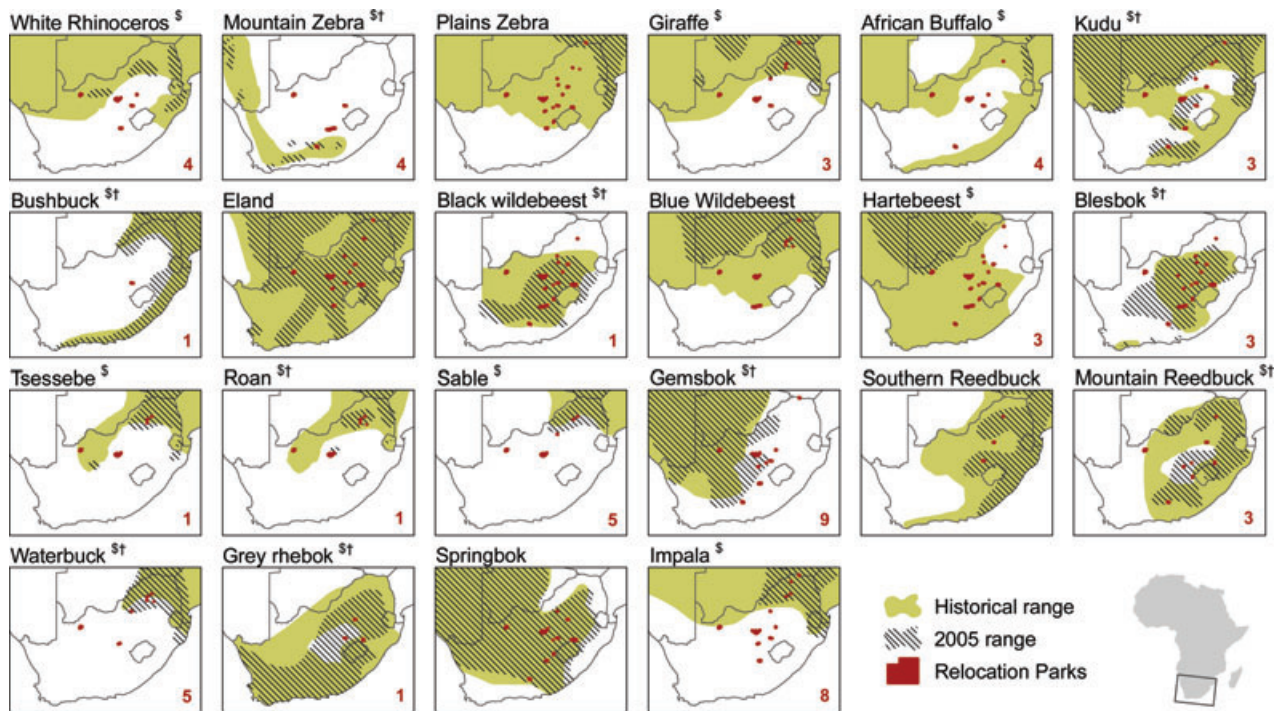
### Introduction

The success of animal translocations is a practical goal of biodiversity conservation and of interest for theoretical population biology. Many studies show translocations that begin with large founder populations are more successful (Griffith *et al.* 1989; Fischer & Lindenmayer 2000; Forsyth & Duncan 2001; Lockwood *et al.* 2005; Armstrong & Seddon 2008; Courchamp *et al.* 2008; Germano & Bishop 2009) as small populations of all kinds face greater extinction risks (Pimm 1991). But obtaining large numbers of rare or threatened species can be impractical and most translocations for these species fail (Griffith *et al.* 1989). How might translocations of small populations beat the odds of extinction? This study focuses on the growth rates of small populations, as well as their size, to understand translocation success.

We present information on the dynamics of translocated mammal populations from an extensive empirical data set in South African nature preserves (Table S1). The

historical decline of grazing mammals across the southern African subregion from increasing human population numbers spurred widespread efforts in the mid 1900s to establish mammal populations within protected areas (du Plessis 1969; Skinner & Chimimba 2005). Many populations were reintroduced into reserves in areas where they were extirpated, i.e., within their historical range. Populations were also introduced in reserves where there was no historical documentation of their occurrence (Figure 1).

These nature preserves and their mammal populations are managed and this likely affects the dynamics of the translocated populations. First, and foremost, managers adopt strategies to prevent local extinction that is a natural feature of small populations (Van Houtan *et al.* 2007). Individual animals are expensive to purchase and relocate. Second, the most challenging features of the natural environment that regulate wild mammal populations were mitigated. Completely wild populations of these species are naturally limited in large part by resources



**Figure 1** Population relocations often took place in protected areas outside of the species historical distributions, inconsistent with IUCN policy (IUCN 2008). Seventeen of the 22 species in this study (\$) were introduced in reserves outside their historical range (red number below right is total number). Half of these species (†) now range freely outside of protected areas. See Methods for data sources.

and predators (Georgiadis *et al.* 2003; Owen-Smith 2003; Owen-Smith *et al.* 2005). Almost all of the reserves in this study contain water impoundments and none of the reserves maintained top predators such as lions (*Panthera leo*) or spotted hyenas (*Crocuta crocuta*). Though these management features might reduce the environmental stochasticity in the time series, some variability likely remains. For example, the demographic difficulties associated with sex ratio, genetic inbreeding, and the reproductive variability between individual females (Engen *et al.* 2003) are unavoidable and may still play an important role. As a result, study of translocations in these protected area settings—even though they are managed—might reveal important insights in terms of population dynamics and successful management strategies (Sarrazin & Barbault 1996).

Ecologists commonly use time series of natural populations to understand a variety of population features including growth rates, density dependence, and the time scales of population variability (Pimm & Redfearn 1988; Inchausti & Halley 2002; Saether *et al.* 2005; Brook & Bradshaw 2006). For understanding the survival of small populations, however, most research has been theoretical (Courchamp *et al.* 2008) and fewer studies concern the behavior of actual small populations that are of great interest to conservation practitioners (Sarrazin & Barbault

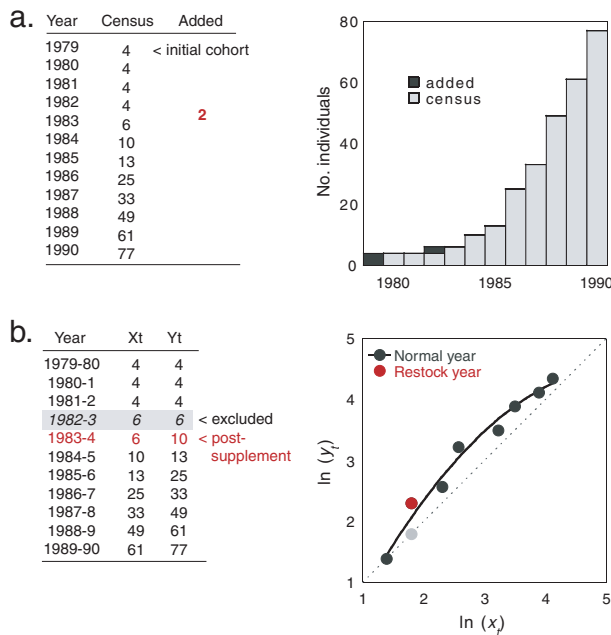
1996; Stephens & Sutherland 1999). Thus our data from exact population counts provide crucial information of the behavior of small populations of species of conservation concern.

These time series also allow us to investigate some important issues related to translocations. First, managers often weigh the initial propagule size as important, but is initial population size as important as commonly thought? Does failure rate depend on initial population size? Second, given that managers frequently restock small populations, do such additions affect population dynamics beyond simply increasing population size? Is growth rate affected by introductions of new animals? Third, to what extent does environmental variability continue to be an important factor in population growth? Do models incorporating environmental factors, such as precipitation, better predict growth rates? Finally, given a reduction of environmental stochasticity, it ought to be easier to observe density dependence. Do we observe density dependence including Allee effects?

## Methods

### Data

We use exact counts of grazing mammal populations translocated to South African protected areas obtained



**Figure 2** Modeled population growth from management records, example for Eland (*Taurotragus oryx*) at Soetdoring Nature Reserve, South Africa. Population time series from the raw census data with restocking years noted; b, we fit population growth models to log-transformed replacement data, excluding years (gray dot) when managers restocked populations (see Methods). Solid line is the best-fitting model (here a second-order growth model) the dotted line is equal replacement or zero growth.

from game manager archives. Twenty-four reserves contained 178 relocated populations spanning 1949–2001. We present results from the 125 time series with at least five pairs of adjacent years over which to calculate population growth. Populations were monitored throughout the year and census records are true annual counts conducted at the same time each year. As the records are not samples, this avoids some of the difficulties of population inference associated with measurement error (Freckleton *et al.* 2006). Population counts are accompanied by management records of added and removed individuals. These data allow us to calculate a growth rate for each annual time step. If  $Y_t$  is the number of animals observed at the end of a year, the number at the start of the year, accounting for additions and removals, is  $X_t = Y_{t-1} - R + A$  (where  $A$  is the number of animals added and  $R$  those removed the year before). Thus the growth is assumed to occur *after* management each year. We log-transform population numbers so, if  $x_t$  and  $y_t$  are the natural logarithm of  $X_t$  and  $Y_t$ , respectively, the series of population changes due to growth alone (Figure 2) is

$$\{(x_{t_1}, y_{t_1}), (x_{t_2}, y_{t_2}), \dots, (x_{t_n}, y_{t_n})\},$$

where  $t_n > \dots > t_2 > t_1$ , though years are not necessarily consecutive. We exclude years where restocking occurred (Figure 2) as we suspect the time of the additions and the census counts were not synchronized. We did not exclude years with removals as they typically occurred when populations were already large (average  $N_{t-1} = 278$  for removals, average  $N_{t-1} = 23$  for additions). Tables S1 and S2 provides further details of populations used in this study.

We obtained ecological covariate data from a variety of sources. Rain gauges in each reserve provide local precipitation data for the study years. Precipitation is measured as the average total precipitation from all gauges (range = 1–15 gauges, average = 7), restricted to the dry season months of May–September (Owen-Smith *et al.* 2005). We obtained reserve attributes and shapefiles from the World Database on Protected Areas (IUCN & UNEP-WCMC 2007). Skinner & Chimimba (2005) contains current range maps, body mass, and taxonomy for all species. Du Plessis (1969) provides historical species distributions. We treat as conspecifics Cape mountain zebra (*Equus zebra zebra*) and Hartman’s mountain zebra (*E. zebra hartmannae*); also bontebok (*Damaliscus pygargus pygargus*) and blesbok (*D. pygargus phillipsi*).

### Population modeling

We characterize population growth through a model that varies in complexity:

$$N_t = r_0 (N_{t-1})^{\beta+c \ln N_{t-1}} \quad (1)$$

$$y = r_0 + \beta x + c x^2, \quad (2)$$

where the polynomial form of Equation 2 is the log-domain equivalent of Equation 1 when  $x_t = \ln N_{t-1}$  and  $y_t = \ln N_t$ . The log-transformation is natural for population time series as it reduces heteroskedasticity and leads to more Normal statistics (Williamson 1982, Morris & Doak 2002). We assume deviations from the model of log-transformed population data are Gaussian. Equation 2 can produce at least three different types of dynamics. When population growth is purely density-independent (zero-order) then  $\beta = 1$  and  $c = 0$ , and  $r_0$  is the linear growth rate. When  $c = 0$  and  $\beta$  is not necessarily equal to 1, this corresponds to a density-dependent growth model with a power law relating  $N_t$  and  $N_{t-1}$ . Given Gaussian perturbations of  $r$ , this leads to a lognormal population distribution at equilibrium (Engen 2001) and is consistent with what is often observed in wild populations (Halley & Inchausti 2002). In this (first-order) model, density dependence is negative when  $\beta < 1$ , and is positive (Allee type) when  $\beta > 1$ . Finally, when neither  $\beta$  nor  $c$  are constrained, the model (second-order) captures how density

dependence itself can vary with population size;  $c$  here represents the linear change of  $\beta$  with density.

For each population one of these models (zero, first or second-order) is selected based on the corrected Akaike Information Criterion for small samples ( $AIC_c$ ). The highest-ranking model is that with the lowest value of  $AIC_c$  where

$$AIC_c = n \left[ 2 \ln(D) + \frac{1 + (k-1)/n}{1 - (k+1)/n} \right], \quad (3)$$

where  $k$  is the number of parameters,  $n$  is the series length, and  $D$  is the root mean square (RMS) deviation between the data and the model (Hurvich & Tsai 1989). We extract the growth rate,  $r$ , from the highest-ranked model given at population size  $x$  using

$$r(x) = y(x) - x. \quad (4)$$

To investigate more closely the prevalence and type of density dependence in these populations, we estimate uncertainty about the first-order density dependence parameter,  $\beta$ , using a jackknife resampling procedure. We resample each time series, randomly removing one point from the set of log-transformed population sizes ( $x_t, y_t$ ). We then repeat the model-fitting procedure, choosing the model that gives the lowest value of the  $AIC_c$ . We perform this  $10^4$  times for each series, providing a range of  $\beta$  estimates from which we remove the upper and lower 2.5%. The remaining 95% of estimates serves as a measure of confidence of the model's estimate of  $\beta$ . If this entire jackknife interval is below the line  $\beta = 1$ , we conclude that the density dependence is negative (the replacement curve tends to level off with increasing population size). If it is above  $\beta = 1$  we conclude it is Allee type (the replacement curve steepens with increasing population size). For consistency with the lower limit of five records per time series, we perform the jackknife procedure only for the 124 series with 6 or more observations. When considering growth rates alone, we arrived at a 95% confidence interval (CI) using the formula  $r \pm t_{n-1, 1-\alpha/2} S/\sqrt{n}$  (Rosner 2000), where  $t$  is the statistic from the  $t$  distribution,  $n$  is the series length,  $\alpha$  is the significance level (in this case,  $\alpha = 0.05$ ) and  $S$  is the standard deviation of  $r$ .

Our initial calculations demonstrated that these time series typically have low variability. In order to assess this variability, an ideal comparison would be a set of purely wild populations growing exponentially after reintroduction or a bottleneck. However, such data are not readily available (see Introduction). A large set of time series is available from the Global Population Dynamics Database (GPDD, NERC 1999) though most of the series are for organisms close to equilibrium. In order to get a rough estimate of ecological variability, at least for or-

ganisms closer to equilibrium, we took a random sample of series of similar series lengths from the GPDD mammal database and estimated growth rates and variability after removing growth trend. Apart from the overall taxonomic grouping, no other ecological correlates (e.g., body size, latitude, trophic position) were used because series for comparable species types are not available in the GPDD. In addition, earlier studies (Halley & Inchausti 2002, Inchausti & Halley 2002) of the GPDD series found remarkably weak dependence of variability on taxonomic groupings.

Another measure of variability is demographic stochasticity. We compared the RMS deviation,  $D$ , from the fitted model as a function of population size with the value expected for purely demographic stochasticity due to births and deaths:

$$D_d = \sqrt{(b + \mu)N}, \quad (5)$$

where  $b$  is annual birth rate,  $\mu$  the annual death rate, and  $N$  the average population size. If we assume a characteristic lifetime of 10 years for individuals this means that the death rate is  $\mu = 0.1$ , which given the growth rate  $r_0$  can be used to estimate the birthrate  $b$ . Together with the average population size we used Equation 5 to derive an approximate value for deviation due to demographic stochasticity.

## Factors affecting population growth

To test whether the years immediately following restocking years have higher or lower growth rates, we normalized deviations from the highest-ranked models, dividing each model residual by the standard deviation for that series' residuals. A positive deviation of 1, for example, indicates a point one standard deviation above the fitted model. We group the deviates into six bins. The widths of bins were chosen to ensure approximately equal numbers of records in each bin while maximizing the resolution of the analysis. Observations in the resulting pool of 2,164 normalized deviates are grouped according to whether: (1) the observation followed a restocking year ( $n = 132$ ), (2) did not follow a restocking year but was from a population where restocking occurred ( $n = 1,368$ ), or (3) neither ( $n = 685$ ). Are the deviations more often positive (growth rate higher than model average) in these 132 instances and does this effect depend on population size? We focus on the differences restocking might have within populations where restocking occurred, or between groups (i) and (ii) (Figure S1 provides the full set of comparisons for all groups and growth models). To compare years that follow restocking with other years, we also repeated the above procedure  $10^5$  times for 132 randomly selected points from the entire set of 2,164

**Table 1** List of all species in population analysis with key attributes and statistics. IUCN Red list indicates 20 of 22 species in this study require conservation efforts for the species' survival during the study period (VU, vulnerable; LR/cd, conservation dependent; LR/lc, least concern). Seven of these species (denoted by †) have declining populations when last assessed by the IUCN. Growth rate,  $r$ , is determined from a density-independent growth model that averages annual rates of increase, averaged across populations within each species. Number of populations analyzed must have time series at least five records and growth parameters (total # of populations)

Species	Common name	Mass (kg)	Red list status	No. populations	First record	Series length ave (min–max)	$r$ ave (SD)
PERISSODACTYLA							
<i>Ceratotherium simum</i>	White rhinoceros	1900	VU	2 (4)	1962	21 (13–29)	0.08 (0.07)
<i>Equus zebra</i>	Mountain zebra	245	VU	3 (7)	1960	14 (9–22)	0.11 (0.03)
<i>Equus quagga</i>	Plains zebra	308	LR/lc	10 (14)	1956	17 (8–33)	0.14 (0.04)
RUMINANTIA							
<i>Giraffa camelopardalis</i>	Giraffe	1,010	LR/cd	4 (7)	1963	16 (7–30)	0.07 (0.13)
<i>Syncerus caffer</i>	African buffalo	552	LR/cd†	3 (6)	1967	16 (7–25)	0.2 (0.09)
<i>Tragelaphus strepsiceros</i>	Kudu	187	LR/cd	6 (9)	1961	17 (6–26)	0.13 (0.1)
<i>Tragelaphus scriptus</i>	Bushbuck	43	LR/lc	1 (1)	1966	27	–0.02
<i>Taurotragus oryx</i>	Eland	349	LR/cd	8 (13)	1950	20 (6–40)	0.16 (0.07)
<i>Connochaetes gnou</i>	Black wildebeest	145	VU	14 (17)	1950	17 (6–44)	0.16 (0.07)
<i>Connochaetes taurinus</i>	Blue wildebeest	233	LR/cd†	6 (9)	1971	12 (6–16)	0.2 (0.05)
<i>Alcelaphus buselaphus</i>	Hartebeest	135	LR/cd†	1 (17)	1949	19 (7–43)	0.13 (0.07)
<i>Damaliscus pygargus</i>	Blesbok	58	VU	13 (17)	1949	19 (7–46)	0.15 (0.08)
<i>Damaliscus lunatus</i>	Tsessebe	122	LR/cd†	3 (5)	1964	18 (12–23)	0.15 (0.1)
<i>Hippotragus equinas</i>	Roan	257	LR/cd†	3 (6)	1968	17 (7–24)	0.14 (0.02)
<i>Hippotragus niger</i>	Sable	219	LR/cd†	3 (5)	1964	17 (12–20)	0.14 (0.11)
<i>Oryx gazella</i>	Gemsbok	225	LR/cd	6 (7)	1953	18 (7–33)	0.13 (0.08)
<i>Redunca arundinum</i>	Southern reedbuck	57	LR/cd	2 (3)	1965	16 (12–19)	0.1 (0.08)
<i>Redunca fulvorufula</i>	Mountain reedbuck	30	LR/cd	3 (8)	1966	14 (10–21)	0.08 (0.17)
<i>Kobus ellipsiprymnus</i>	Waterbuck	247	LR/cd†	3 (6)	1966	19 (8–26)	0.16 (0.06)
<i>Pelea capreolus</i>	Gray rhebok	20	LR/cd	1 (3)	1978	20	–0.03
<i>Antidorcas marsupialis</i>	Springbok	39	LR/cd	10 (13)	1956	16 (8–32)	0.14 (0.11)
<i>Aepyceros melampus</i>	Impala	57	LR/cd	9 (12)	1950	20 (5–47)	0.19 (0.1)

in terms and calculated their average deviation and the slope of this deviation with respect to population size—a randomization test.

To see whether other factors affect growth, we extracted the growth rate at  $n = 20$  from the highest-ranked model. We ran analyses of covariance with  $r(20)$  as a response variable using as covariates the initial population size, average dry-season rainfall, reserve location with respect to historical distribution, and reserve size. Twenty is of practical interest for managers as evidenced in that the average population where restocking occurred in this study was  $n = 23$ . For this analysis we use only those reserves and species with at least three representative populations. Both factors and covariates were considered in combinations and ranked using the  $AIC_c$  (3), further details are available in Table S3.

We digitized, georeferenced, and mapped species distributions with ArcGIS 9.2 (ESRI 2008). We transformed range maps with a quadratic model, limiting the RMS error to  $<0.1$ . Because of known resolution issues with range maps (Hurlbert & Jetz 2007), we conservatively consider protected areas  $>75$  km outside a species histori-

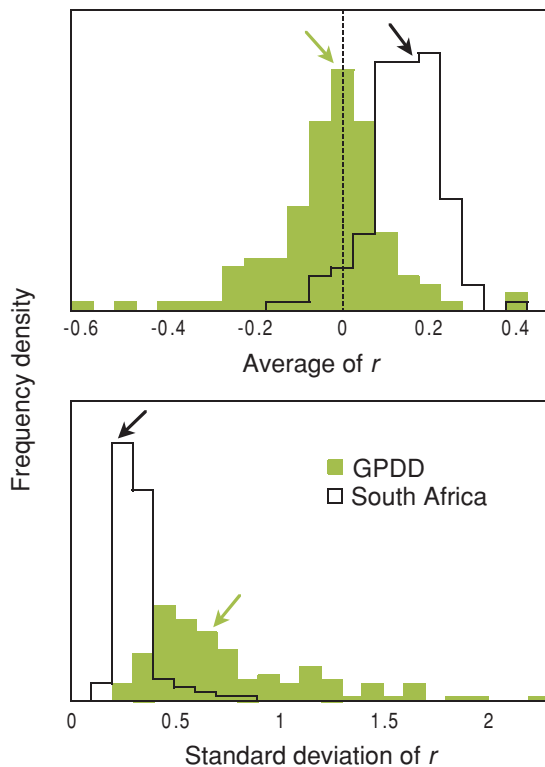
cal range to be outside the range, using the same distance to distinguish current and historical ranges.

## Results

If we consider populations where the linear rate of increase is positive ( $r > 0$ ) to be a proxy of successful establishment, then 116 translocations (94%) were successful. In 82 cases (66%), the entire 95% CI for growth-rate was situated above zero. In the remaining 43 populations, the CI lay on either side of zero. The CI was never entirely below zero and therefore we do not identify any populations as surely failing. Table 1 presents the full set of species in the South African translocations with key characteristics, conservation status, and linear growth rates. The high rate of translocation success is particularly relevant as 17 of the 22 species here are categorized by the IUCN (2008) as requiring conservation efforts for their global survival (Table 1).

The translocated populations we analyzed typically had high growth rates and low variability in growth rate

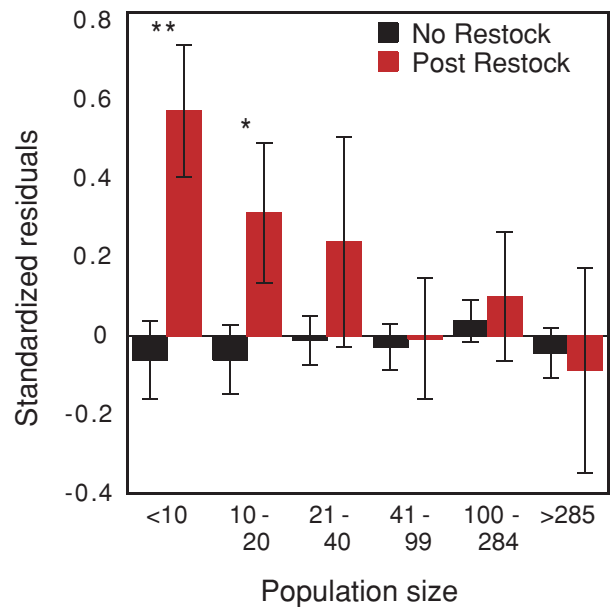




**Figure 3** Growth, variability, and density dependence (DD) in 124 re-located populations of grazing mammals. (a) Managed South African populations grow more rapidly ( $r_{\text{average}} = 0.14$ ) and show less variability ( $\sigma_{\text{average}} = 0.21$ ) when compared to randomly selected “wild” mammal populations from the Global Population Dynamics Database ( $r_{\text{average}} = -0.03$ ,  $\sigma_{\text{average}} = 0.67$ ). Growth rate,  $r$ , determined from a zero-order model that assumes no DD. Arrow indicates series average value. (b) Distribution of  $\beta$ , the DD coefficient shown as a red line, in the first-order growth model for all populations, ranked by ascending value. Pink shaded area about the line is the 95% CI of jackknife estimations that omit series observations. Considering the uncertainty from the jackknife, we observe Allee effects in four series (3%) and saturation effects in 13 (10%). Insets are growth plots under different DD conditions. Dashed lines separate the data about  $\beta = 1$ .

( $\sigma_{\text{average}} = 0.2$ ). This is much lower than typical data from the GPDD mammal populations at least at equilibrium (Figure 3) for which the standard deviation in annual growth is over three times higher ( $\sigma_{\text{average}} = 0.7$ ). However, the variability was still considerably higher than the level of pure demographic stochasticity (Figure 5) suggesting that environmental variability is still playing a role in the population dynamics. This result is not sensitive to other reasonable estimates of mortality ( $0.05 < \mu < 0.2$ ).

Based on the  $AIC_c$ , 81 populations (65%) are best described by a density-independent model, while the first-order model was highest-ranked in 19 cases (15%) and the second-order in 25 (20%). Using the jackknife analysis to investigate the parameter  $\beta$  of the 124 populations,



**Figure 4** Small populations show an increase in per capita growth rates after new individuals are added, or restocked, offsetting the potentially negative effects of small initial cohort populations. Years immediately following restocking events perform above the growth model when population size is <20 individuals (t-test:  $**p = 0.001$ ,  $*p = 0.01$ ) though there are differences lacking statistical evidence when population size is 21–40. Columns represent the average normalized residual value within each bin. Bin widths are selected for equal samples of the smaller (post restock) treatment. Samples in each bin for the restocking and control treatment are (left to right): 22, 23, 22, 24, 20, 21; and 118, 148, 220, 280, 331, 271; respectively. Error bars represent the standard error of the mean.

13 (10%) show negative density dependence ( $\beta < 1$ ) and we find positive density dependence ( $\beta > 1$ ) or Allee effects in 4 (3%). No dependence of this parameter on series length was observed.

When populations are small, in years immediately following restocking they grow faster than would be expected from the highest-ranked model of population growth (Figure 4). Restocking boosts growth when populations are <20 individuals and measure a similar (though lacking statistical evidence) difference when populations measure 21–40 individuals (Figure 4). Comparable differences were found in only 1.02% of the  $10^5$  randomly chosen sets showing that this effect is unlikely to have arisen by chance. The increase in growth following restocking may play an important role in improving the success of translocated populations, especially those with Allee dynamics. All four populations where we observe Allee affects were also restocked and subsequently successfully established.

We found no evidence that the ecological correlates had any appreciable effect on growth  $r(20)$ . All models

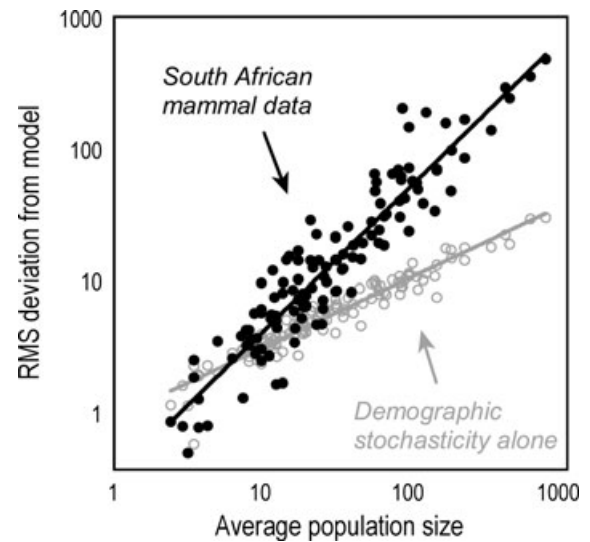
involving correlates had a larger  $AIC_c$  than the null model in which  $r(20)$  has a constant plus noise (details in Table S2). Neither the effects of average dry season rainfall, initial cohort size, nor reserve size predict population growth rates. Translocations inside a species' historic range fare no better than those outside their range. Though it is against international guidelines (IUCN-SSC 1998), most species were introduced in reserves outside their historic distributions (Figure 1). The  $AIC_c$  tended to increase with added parameters, so we did not examine all possible higher order effects.

## Discussion

Our analyses of translocated populations gives four results: (i) high rates of success for translocations of species of conservation concern (ii) high growth rates and low variance in growth with no statistical evidence for relationship between ecological factors and growth, (iii) relatively weak density dependence, and (iv) a boost in growth rates of small populations following restocking with new individuals.

Why the translocations were successful requires some explanation. Even though most populations begin with <15 individuals, out of the 125 populations examined, 94% of translocations succeeded ( $r > 0$ ). Although 66% of the populations are unambiguously growing, based on the 95% CI being entirely above zero, none of the populations declined unambiguously. This is somewhat at variance with the widespread belief that initial size dominates considerations of translocation. Instead, these populations' success reflects the strong role being played by management to eliminate dependence on environmental factors. It is clear that these translocated populations are much less influenced by the environmental stochasticity that influences wild populations of African grazing mammals (McNaughton & Georgiadis 1986). Our detailed comparison of growth with ecological correlates reveals no influence from the various possible factors that we expect to exert an effect upon growth rate. Neither precipitation, nor inclusion in the historical geographic range, appears to influence growth. It is likely that the presence of reservoirs combined with the absence of top predators in these reserves plays a major role in buffering against seasonality and drought, perhaps by increasing juvenile survival (Owen-Smith *et al.* 2005). This is also seen in the fact that growth rates on average are high and the variability about of growth rate is low. That the translocated populations show low variability (Figure 3) indicates that annual vagaries of the environment are not dominant.

We also find that demographic stochasticity appears to be mitigated through active management. Most pop-



**Figure 5** Scatter plot showing the RMS deviation,  $D$ , from the fitted model as a function of population size for both the real data and as expected for demographic stochasticity. Black circles represent the RMS deviation from the best model for all points in the series. The abscissa is the geometric mean of population size for all points in the series. Open gray circles represent the corresponding RMS deviation according to Equation (5) ( $b$  is annual birth rate,  $\mu$  is annual death rate, and  $N$  is average population size) expected if the variability is due to simple demographics alone. Here stochasticity is due to births and deaths, assuming a characteristic lifetime of 10 years for individuals.

ulations began with a few individuals and this might limit growth from simple imbalances in sex ratios, age structure, or from inbreeding. Managers in the South African protected areas often restocked small populations by adding individuals in subsequent years. This produced two interesting effects. The first is that the years immediately following these supplemental introductions show an increase in growth rates, displayed as these years consistently performed above the highest-ranked growth models (Figure 4). The second indication is that the restocking kept populations with signs of Allee dynamics from failing. These results are akin to those from wild butterfly metapopulations (Kuusaari *et al.* 1998) and exotic species invasions (Lockwood *et al.* 2005) indicating this may be a general phenomena in the success of small populations. Together, this suggests that continued propagule pressure more so than large initial propagules may be an important strategy in protected species translocations.

Though the effects of environmental stochasticity on growth are reduced (Figure 3), they are not eliminated. In Figure 5 where the actual variability of series is compared to that expected from simple demographic stochasticity alone, we see that not only is the variability larger than that explained by demographic factors, but the rate of increase of variability with population size ( $SD \sim N$ ) is characteristic of environmental rather than demographic

stochasticity ( $SD \sim \sqrt{n}$ ) (Lande 1998, Engen *et al.* 2003). This indicates that environmental stochasticity is still an important factor in these populations, even in the managed South African nature preserves analyzed in this study.

Species recovery plans that involve translocations might become even more commonplace, for example to combat climate change (Hoegh-Guldberg *et al.* 2008). Although the populations in this study enjoyed a degree of intensive management that may not always be neither possible nor desired for some populations, the results from our study offer practical insights for managers by presenting proven success stories in an adaptive management framework (Sarrazin & Barbault 1996; Sutherland *et al.* 2004). How applicable the results from this study of translocated mammals will be to other taxa remains to be seen. Several species in this study have declined dramatically in the modern era (Figure 1) making their conservation especially urgent.

## Acknowledgments

We are grateful to M. Alford, T. Iwamura, R. Guldemon, T. Wassenar, and J. Wilson. KSVH was supported by the Strategic Initiative in Science and Religion at Emory University and by the Dean's Office of the Nicholas School of the Environment at Duke University. C Bradshaw and three anonymous reviewers improved an earlier version of this manuscript.

## Supporting Information

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

**Figure S1** Comparison of the years immediately following restocking events to years without restocking, given a greater range of growth models. In the main text, we only presented the results of the normalized deviates from the highest ranked model, and only of the two treatments within populations that received additions (see Methods). Here we include the results from each of the three growth models, and then the highest ranked model. Additionally, we show the deviates from the populations that were never restocked. In all model scenarios, small populations have a greater per capita growth rate following restocking events.

**Figure S2** Scatter plot of boost in per capita rate of increase at low population numbers. Populations at low number show a per capita growth increase following the addition of new individuals. Scatter plots of normalized deviates from the best fitting growth models for post-supplement and years without population additions.

**Table S1** Twenty four South African protected areas in the population relocation database. World Database of Protected Areas (WPDA) category by management purpose: II, ecosystem conservation and recreation; IV, conservation through management intervention; and V, landscape conservation and recreation. The number of populations represents the data usable in our analyses, though there are more. None of the reserves contained any species of top predators roaming freely in the same areas with grazing mammals. Messina Proefplas is an experimental farm and while it is a fenced, protected area like the other sites, it is not considered a "nature reserve" by the WPDA. Karoo Nature Reserve was redesignated Camdeboo National Park in 2005. Asterisk (\*) indicates protected areas had populations with discontinuous records or insufficient data, but appear in the analyses of geographic range (Figure 1).

**Table S2** (see attached text file) Further details of each population examined in this article, including the number of observations ( $x, y$ ) pairs ("Obs."), and the results of the population growth model statistics. The parameters and AICc values for the three models fitted to each of the 125 populations that we examined. The error term is assumed to be Gaussian, given the log-transformation of the raw population counts. See Methods for details of the population growth model and the DD parameters.

**Table S3** Model structure and correlates used to examine growth rate  $r(20)$ .  $D$  is the RMS deviation of the model from the data.  $N$  is the number of points in the analysis. The error term is assumed to be Gaussian. The highest ranking model of covariates is model of population growth without any ecological covariates. This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1755-263X.2008.00002.x>

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

## References

- Armstrong, D.P., Seddon P.J. (2008). Directions in reintroduction biology. *Trends Ecol Evol* **23**, 20–25.
- Brook, B.W., Bradshaw C.J.A. (2006). Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology* **87**, 1445–1451.
- Courchamp, F., Berec L., Gascoigne J. (2008). *Allee effects in ecology and conservation*. Oxford University Press, Oxford.
- du Plessis, S.F. (1969). *The past and present geographical distribution of the Perissodactyla and Artiodactyla in southern Africa*. University of Pretoria, Pretoria, South Africa.



- Engen, S. (2001). A dynamic and spatial model with migration generating the log-Gaussian field of population densities. *Math Biosci* **173**, 85–102.
- Engen, S., Lande, R., Sæther, B.-E. (2003). Demographic stochasticity and Allee effects in populations with two sexes. *Ecology* **84**, 2378–2386.
- ESRI (2008). title. Environmental Systems Research Institute, Inc., Redlands, CA.
- Fischer, J., Lindenmayer D.B. (2000). An assessment of the published results of animal relocations. *Biol Conserv* **96**, 1–11.
- Forsyth, D.M., Duncan R.P. (2001). Propagule size and the relative success of exotic ungulate and bird introductions to New Zealand. *Am Nat* **157**, 583–595.
- Freckleton, R.P., Watkinson A.R., Green R.E., Sutherland W.J. (2006). Census error and the detection of density dependence. *J Anim Ecol* **75**, 837–851.
- Georgiadis, N.J., Hack M., Turpin K. (2003). The influence of rainfall on zebra population dynamics: implications for management. *J Appl Ecol* **40**, 125–136.
- Germano, J., Bishop P. (2009). Suitability of amphibians and reptiles for translocation. *Conserv Biol* **23**, 7–15.
- Griffith, B., Scott J.M., Carpenter J.W., Reed C. (1989). Translocation as a species conservation tool: status and strategy. *Science* **245**, 477–480.
- Halley, J.M., Inchausti P. (2002). Lognormality in ecological time series. *Oikos* **99**, 518–530.
- Hoegh-Guldberg, O., Hughes L., McIntyre, S., *et al.* (2008). Assisted colonization and rapid climate change. *Science* **321**, 345–346.
- Hurlbert, A., Jetz W. (2007). Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proc Nat Acad Sci USA* **104**, 13384–13389.
- Hurvich, C., Tsai C.-L. (1989). Regression and time series model selection in small samples. *Biometrika* **76**, 297–307.
- Inchausti, P., Halley J. (2002). The long-term temporal variability and spectral colour of animal populations. *Evol Ecol Res* **4**, 1033–1048.
- IUCN (1998). Guidelines for re-introductions. IUCN/SSC Re-Introduction Specialist Group, Gland, Switzerland, pp. 10.
- IUCN (2008) *The IUCN red list of threatened species*. Available from: <http://www.iucnredlist.org/>. Accessed June 2009.
- IUCN & UNEP-WCMC (2007) *World Database on Protected Areas* [WWW document]. Available from: <http://www.wdpa.org/>. Accessed June 2009.
- Kuusaari, M., Saccheri I., Camara M., Hanski I. (1998). Allee effect and population dynamics in the Glanville fritillary butterfly. *Oikos* **82**, 384–392.
- Lande, R. (1998). Demographic stochasticity and Allee effect on a scale with isotropic noise. *Oikos* **83**, 353–358.
- Lockwood, J., Cassey P., Blackburn T. (2005). The role of propagule pressure in explaining species invasions. *Trends Ecol Evol* **20**, 223–228.
- McNaughton, S.J., Georgiadis N.J. (1986). Ecology of African grazing and browsing mammals. *Annu Rev Ecol Syst* **17**, 39–65.
- Morris, W., Doak D. (2002). *Quantitative conservation biology: theory and practice of population viability analysis*. Sinauer Associates, Sunderland, MA.
- NERC (1999) *Global population dynamics database*. Available from: <http://www.sw.ic.ac.uk/cpb/cpb/gpdd.html>. Accessed June 2009.
- Owen-Smith, N. (2003). Page 93–109 in M. Festa-Bianchet, M. Apollonio, editors. *Animal behavior and wildlife conservation*. Island Press, Washington, D.C.
- Owen-Smith, N., Mason D.R., Ogotu J.O. (2005). Correlates of survival rates for 10 African ungulate populations: density, rainfall and predation. *J Anim Ecol* **74**, 774–788.
- Pimm, S.L. (1991). *The balance of nature? Ecological issues in the conservation of species and communities*. University of Chicago Press, Chicago.
- Pimm, S.L., Redfearn A. (1988). The variability of population densities. *Nature* **334**, 613–614.
- Rosner, B. (2000). *Fundamentals of Biostatistics*. Thomson Learning, Duxbury, MA.
- Sæther, B.-E., Lande R., Engen S. *et al.* (2005). Generation time and temporal scaling of bird population dynamics. *Nature* **436**, 99–102.
- Sarrazin, F., Barbault R. (1996). Re-introductions: challenges and lessons for basic ecology. *Trends Ecol Evol* **11**, 474–478.
- Skinner, J.D., Chimimba C.T. (2005). *The mammals of the southern African subregion*. 3rd edn. Cambridge University Press, Cambridge, UK.
- Stephens, P., Sutherland W.J. (1999). Consequences of the Allee effect for behaviour, ecology and conservation. *Trends Ecol Evol* **14**, 401–405.
- Sutherland, W.J., Pullin A.S., Dolman P.M., Knight T.M. (2004). The need for evidence-based conservation. *Trends Ecol Evol* **19**, 305–308.
- Van Houtan, K.S., Pimm S.L., Halley J.M., Bierregaard R.O., Lovejoy T.E. (2007). Dispersal of Amazonian birds in continuous and fragmented forest. *Ecol Lett* **10**, 219–229.
- Williamson, M. (1982). *The analysis of biological populations*. Edward Arnold, London.

**Editor:** Dr. Corey Bradshaw