




Effects of age and sex ratios on offspring recruitment rates in translocated black rhinoceros

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Abstract: Success of animal translocations depends on improving postrelease demographic rates toward establishment and subsequent growth of released populations. Short-term metrics for evaluating translocation success and its drivers, like postrelease survival and fecundity, are unlikely to represent longer-term outcomes. We used information theory to investigate 25 years of data on black rhinoceros (*Diceros bicornis*) translocations. We used the offspring recruitment rate (ORR) of translocated females—a metric integrating survival, fecundity, and offspring recruitment at sexual maturity—to detect determinants of success. Our unambiguously best model ($AIC_w = 0.986$) predicted that ORR increases with female age at release as a function of lower postrelease adult rhinoceros sex ratio (males:females). Delay of first postrelease reproduction and failure of some females to recruit any calves to sexual maturity most influenced the pattern of ORRs, and the leading causes of recruitment failure were postrelease female death (23% of all females) and failure to calve (24% of surviving females). We recommend translocating older females (≥ 6 years old) because they do not exhibit the reproductive delay and low ORRs of juveniles (< 4 years old) or the higher rates of recruitment failure of juveniles and young adults (4–5.9 years old). Where translocation of juveniles is necessary, they should be released into female-biased populations, where they have higher ORRs. Our study offers the unique advantage of a long-term analysis across a large number of replicate populations—a science-by-management experiment as a proxy for a manipulative experiment, and a rare opportunity, particularly for a large, critically endangered taxon such as the black rhinoceros. Our findings differ from previous recommendations, reinforce the importance of long-term data sets and comprehensive metrics of translocation success, and suggest attention be shifted from ecological to social constraints on population growth and species recovery, particularly when translocating species with polygynous breeding systems.

Keywords: *Diceros bicornis*, mortality, offspring recruitment rate, recruitment failure, reproductive delay, translocation

Efectos de la Proporción de Edades y Sexos sobre las Tasas de Reclutamiento de Rinocerontes Negros Reubicados

Resumen: El éxito de la reubicación de animales depende del mejoramiento de las tasas demográficas después de la reubicación para establecer y hacer crecer a las poblaciones liberadas. No es probable que las medidas de corto plazo para evaluar el éxito de una reubicación y sus conductores, como la supervivencia y fecundidad post-liberación, representen resultados a largo plazo. Utilizamos teoría de la información para investigar 25 años de datos sobre reubicaciones del rinoceronte negro (*Diceros bicornis*). Usamos la tasa de reclutamiento de crías (TRC) de las hembras reubicadas - una medida que integra la supervivencia, la fecundidad y el reclutamiento de las crías en la madurez sexual - para detectar determinantes del éxito. Nuestro mejor modelo ($AIC_w = 0.986$) pronosticó que la TRC incrementa con la edad de las hembras al momento de la liberación como función de una proporción más baja de sexos en rinocerontes adultos después

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de la liberación (machos:bembras). El retraso de la primera reproducción post-reubicación y el fracaso de algunas hembras en reclutar mínimo a una cría hasta la madurez sexual influyeron más sobre el patrón de TRCs, y las principales causas del fracaso de reclutamiento fueron la muerte post-liberación de la hembra (23% de todas las hembras) y el fracaso de parto (24% de las hembras sobrevivientes). Recomendamos reubicar a las hembras más viejas (≥ 6 años) porque no exhiben el retraso reproductivo ni las TRCs bajas de las juveniles (< 4 años) o las tasas más altas de fracaso de reclutamiento de las juveniles y las adultas jóvenes (4 - 5.9 años). En donde sea necesaria la reubicación de juveniles, éstas deberían ser liberadas en poblaciones con mayoría de hembras disponibles sexualmente, en donde tienen mayores TRCs. Nuestro estudio ofrece la ventaja única de un análisis de largo plazo en un gran número de poblaciones replicadas - un experimento de ciencia-por-manejo como sustituto de un experimento manipulativo, y una rara oportunidad, particularmente para un taxón grande y en peligro crítico como es el rinoceronte negro. Nuestros resultados difieren de recomendaciones previas, refuerzan la importancia de los conjuntos de datos de largo plazo y de las medidas comprensivas del éxito de una reubicación, y sugieren que la atención se cambie de las limitaciones ecológicas a las limitaciones sociales que tienen el crecimiento poblacional y la recuperación de la especie, particularmente cuando se reubiquen especies con sistemas de reproducción poliginios.

Palabras Clave: *Diceros bicornis*, fracaso de reclutamiento, mortalidad, retraso reproductivo, reubicación, tasa de reclutamiento de crías

摘要: 动物放归行动的成功取决于放归后种群统计参数的提高, 以促进放归种群的成功建群和随后的种群增长。评估放归成功与否及其驱动力的短期指标, 如放归后的存活率和繁殖力, 不太可能反映长期的后果。我们用信息论的方法分析了黑犀牛 (*Diceros bicornis*) 25 年的放归数据, 并用放归雌性的后代补充率 (ORR) — 一个整合了存活率、繁殖力及性成熟时后代补充情况的指标, 来探讨放归成功的决定因素。我们确定的最优模型 ($AIC_w = 0.986$) 预测在较低的成年犀牛性比 (雄性: 雌性) 情况下, ORR 随着放归时雌性年龄的增加而增加。放归后第一次繁殖的延迟以及一些雌性没有获得达到性成熟年龄的后代对 ORR 的模式影响最大, 种群补充失败最主要的原因是放归后雌性的死亡 (占有雌性的 23%) 以及产仔失败 (占有存活雌性的 24%)。我们建议放归时选择年龄较大 (≥ 6 岁) 的雌性, 因为它们没有表现出延迟繁殖, 而亚成体 (< 4 岁) 具有低的 ORR, 或亚成体及年轻成年雌性 (4-5.9 岁) 具有较高的后代补充失败率。当必须放归亚成体时, 应将它们释放到偏雌性的种群中, 这样它们会有更高的 ORR。我们的研究为大量放归种群的长期分析提供了独特的优势—即基于管理的科学实验作为操纵实验的替代, 以及难得的研究机会, 特别是对于像黑犀牛这样大型极度濒危的类群。我们的结果有别于前人的建议, 强调了建立长期数据集和衡量放归成功的综合指标的重要性, 同时建议将注意力从种群增长和物种恢复的生态限制因素转移到社会限制因素上, 特别是当放归一夫多妻婚配制度的物种时。【翻译: 胡怡思; 审校: 魏辅文】

关键词: 黑犀牛 (*Diceros bicornis*), 死亡率, 后代补充率, 种群补充失败, 繁殖延迟, 放归

Introduction

Animal translocations to expand and manage metapopulations can serve as remarkable in situ experiments of species evolutionary capacity (Dawson et al. 2011; Linklater et al. 2017), inform ecological understanding (Sarrazin & Barbault 1996), and improve a vital tool in biodiversity conservation (Armstrong & Seddon 2008). Successful species recovery requires improved demographic rates (e.g., survival, fecundity, and offspring recruitment) for the establishment and growth of translocated populations. Variations in conservation practices aside, the success or failure of animal translocations at individual and population scales should be predicted by theoretical relationships between socioecological influences and evolutionary fitness (e.g., number of founders, rate of population increase, or effect of competition) (MacArthur & Wilson 1967; Griffith et al. 1989).

Documented failure rates (e.g., Griffith et al. 1989; Fischer & Lindenmayer 2000; Komers & Curman 2000) indicate that translocations can be high-risk endeavors.

More recent analyses, however, point to success, particularly for ungulates (Van Houtan et al. 2009; Linklater et al. 2012). Contrary to theory (e.g., Griffith et al. 1989; Wolf et al. 1996; Fischer & Lindenmayer 2000), successes have been reported for small populations and across a wide range of demographic and environmental contexts. Departures from theory may occur because most studies of translocations use a single short-term metric to evaluate success, for example, postrelease survival (e.g., Maran et al. 2009; Hamilton et al. 2010; Linklater et al. 2011) or fecundity (e.g., Maillard et al. 2002; Dalbeck & Heg 2006; Ismail et al. 2011). Survival and fecundity following release are only initial indicators of success. Although they provide valuable information for predicting the establishment of a translocated population, exploring the combined effects of these vital rates and subsequent generational recruitment is likely to provide greater insight into the drivers of animal fitness and postrelease population dynamics (Baxter et al. 2008; King et al. 2012; Gedir et al. 2013; Law et al. 2013). Thus, the collection and analysis of longer-term, multigeneration data sets that

integrate survival, fecundity, and recruitment success by released individuals are necessary but rarely achieved, especially for long-lived species.

Analyses of long-term translocation data sets that include multiple demographic rates must also transcend the historical reliance on correlations or multiple regressions (Griffith et al. 1989; Wolf et al. 1996; Fischer & Lindenmayer 2000) that do not also consider the hierarchical structure of data typical of translocations (i.e., several individuals may be released into reserves that receive several cohorts over time). Therefore, many factors previously identified as important, like release cohort size or habitat quality (Griffith et al. 1989; Wolf et al. 1996; Fischer & Lindenmayer 2000), may be spurious (Johnson & Omland 2004; Whittingham et al. 2006). Instead, analyses should test among models of alternative hypotheses that incorporate the nested dependence of individuals within and among the cohorts released at the same sites (e.g., reserves).

The black rhinoceros (*Diceros bicornis*) (hereafter rhinoceros) is a polygynous, sexually dimorphic mega-herbivore and is relatively asocial compared with most large ungulates. Key strategies for promoting the long-term recovery of this critically endangered species are protection coupled with translocation programs for population reestablishment, range expansion, and maintaining genetic diversity (Emslie et al. 2009). Rhinoceros translocations are the primary tool for managing the demographic and genetic structure of populations and the metapopulation (Emslie et al. 2009) and mitigating multiple conservation threats, including resurgent illegal hunting for the international trade in rhinoceros horns (Biggs et al. 2013). Previously published evaluations of rhinoceros translocation success have identified predictors such as rhinoceros age at translocation, release cohort size, adult rhinoceros sex ratio and density, habitat quality, and reserve area; however, these covariates have explained only short-term metrics of success, such as survival (e.g., Brett 1998; Linklater & Swaisgood 2008; Linklater et al. 2011). An advanced understanding of the factors that interact to impact postrelease vital rates and influence longer-term population dynamics is lacking.

We used information theory to investigate a long-term data set documenting female rhinoceros survival and reproduction following translocations among a large number of reserves across southern Africa to test hypotheses predicting long-term generational reproductive success. Concurrent examination of multiple translocations offered a unique opportunity for a natural experiment whereby populations can be treated as replicates. Our aim was to test previous hypotheses found to influence short-term translocation success with a new metric more relevant to longer-term population dynamics, offspring recruitment rate (ORR) by each released female, which combines postrelease female survival, fecundity, and offspring recruitment at sexual

maturity. We sought to improve understanding of how populations are affected by translocations and provide insight into the offspring recruitment contribution of released females, as well as inform policy making and the conservation and management of threatened species.

Methods

We used covariates related to translocation characteristics, release cohorts, and source and recipient reserves and their rhinoceros populations to analyze postrelease survival and reproduction for female black rhinoceros translocated among reserves in Namibia and South Africa from 1981 to 2005 (Supporting Information). Rhinoceros establish ranges within 1 month of release (Linklater & Swaisgood 2008), so translocations to the same reserve separated by >1 month were considered different releases. Every translocated rhinoceros was individually identifiable and monitored such that births and deaths were detected with accuracy.

To study the potential for growth of translocated rhinoceros populations, our metric for translocation success was postrelease ORR for each released female (i.e., number of calves recruited per female per year), where a recruit is a calf that survives to earliest potential sexual maturity (4 years old) (Goddard 1970; Okita-Ouma 2004; Law et al. 2013). Although it is uncommon for large mammals to successfully birth from conceptions during their first few years following onset of sexual maturity, it is possible, particularly under favorable conditions. Thus, we selected 4 years old (i.e., age of earliest physiological capability for reproduction in a female rhinoceros) as time of first possible conception because at this age they could be recruited into the sexually reproductive population. The ORR metric combines adult female survival, calf production, and calf survival at sexual maturity in a single variable. These elements have the potential to significantly influence long-term population viability and growth. The modeled response variable was ORR for each translocated female whose total number of postrelease recruited calves was known. This included females that calved during their ORR calculation period, but confirmation of a calf's fate (i.e., recruitment or death before reaching sexual maturity) occurred beyond the mother's ORR period. Only a female's potentially reproductive years were considered when calculating ORR, by accounting for the prereproductive period for females that had not yet reached sexual maturity when released and assuming onset of reproductive senescence at 35 years (Ochs 2001). Thus, the period for ORR calculation commenced at time of release or postrelease sexual maturity and terminated at the end of the study (31 December 2005), female death, or expected time of reproductive senescence. Only females translocated for the first time were included in analyses and then only if they

spent a minimum of 4 potentially reproductively viable postrelease years in that reserve (i.e., our data showed that rhinoceros fecundity variance reached an asymptote 4 years after translocation). The exception was reproductively viable females that died within 4 years of release; each of their ORRs was confirmed as zero.

We took an information-theoretic approach to evaluate hypotheses for translocation success by fitting linear mixed-effects regression models in R 3.2.3 (R Core Team 2015) with the lme4 package (Bates et al. 2015). We created an a priori model set to test our new metric for translocation success (ORR) by building on previous analyses of rhinoceros establishment success (Linklater et al. 2011), including testing for interactions between environmental, demographic, and individual characters (Linklater et al. 2012). These previous analyses consolidated the work of authors who, using relatively small data sets or single translocations, identified variables that appeared to contribute to postrelease survival, including release cohort size (Brett 1998), age of released rhinoceros (Walker 1994; Adcock et al. 1998; Brett 1998), resident bull density (Adcock et al. 1998), reserve size (Walker 1994; Linklater & Swaisgood 2008), habitat quality (Brett 1998), and postrelease conspecific density (Walker 1994; Adcock et al. 1998; Brett 1998; Linklater & Swaisgood 2008). We also included models to evaluate previous hypotheses for translocation success in general, which included covariates such as release cohort size and habitat quality (Griffith et al. 1989; Wolf et al. 1996; Fischer & Lindenmayer 2000) (see Table 1 & Supporting Information for model covariates and definitions). Although rhinoceros translocation techniques (e.g., pre- and post-transport time in captivity and enclosure design) sometimes varied among years and regions, they did not influence establishment success (survival), the shorter term vital rate most likely to be affected (Linklater et al. 2011); thus, differences in techniques were not considered in our modeling of longer-term consequences. We used second-order AIC (AIC_c) for model evaluation (Burnham & Anderson 2002). Female ages were classified as <1, 1-1.9, 2-3.9, 4-5.9, and ≥ 6 years. All models included random effects to account for variation among reserves and translocation cohorts nested within reserves. We tested for collinearity among covariates with Spearman rank correlations (Lehmann & D'Abrera 1998) and all comparisons had $|\rho| < 0.70$. Prior to analyses, we scaled continuous predictors by subtracting the mean and dividing by 2 SD (Gelman 2008).

Results

Offspring Recruitment Rates

We analyzed ORR for 203 female rhinoceros released into 51 reserves among 80 separate translocations. Among

females that survived 4 years postrelease ($n = 156$), the mean (SD) period from which ORR was calculated was 9.0 (4.7) years and ranged from 4 to 22 years. The model including covariates for the interaction between female age at release and postrelease adult sex ratio (ASR) was unambiguously the best model for predicting ORR ($AIC_w = 0.986$) (Table 1). The model predicted that ORR increases with age as a function of decreasing postrelease ASR (males:females); postrelease ASR had the largest effect size (scaled regression β coefficients, mean [SE]: postrelease ASR, -0.092 [0.023]; age, 0.050 [0.018]; age \times postrelease ASR interaction, -0.083 [0.030]). The interaction between age and ASR indicated that ORR was suppressed more for older females than for younger females as populations became more male biased. The top model performed substantially better when random effects were included (with random effects, $AIC_c = -274.6$; without random effects, $AIC_c = -262.3$). Reserve and release cohort random effects accounted for 18% and 35% of residual variation, respectively.

Mean (SE) ORR of females in female-biased populations (0.166 [0.017], $n = 89$) was double that of those in populations at ASR parity (0.080 [0.011], $n = 84$) and male-biased populations (0.076 [0.016], $n = 30$; $F_{2,194} = 12.05$; $p < 0.001$) (Fig. 1). Mean ORRs of translocated young adult (4–5.9 years old: 0.119 [0.021] [calves recruited per year], $n = 56$) and adult (≥ 6 years old: 0.139 [0.013], $n = 102$) females were twice that of females released as juveniles (<4 years old: 0.064 [0.013], $n = 45$; $F_{2,194} = 5.68$; $p = 0.004$) (Fig. 1). Although there were sometimes significant differences between ORRs among other covariates, all other models including covariates describing release cohorts, population demography and density, and reserve habitat were relatively poor predictors of ORR (i.e., $\Delta AIC_c > 11$) (Table 1). For example, females had significantly higher ORRs following releases into reserves that did not contain conspecifics (i.e., reintroduction: 0.137 [0.012], $n = 121$) than those that were released into reserves that had resident rhinoceros (i.e., restocking: 0.087 [0.015], $n = 82$; independent samples t test: $t = 2.70$; $p = 0.008$), but the presence of rhinoceros in reserves prior to translocation was not predictive of ORR ($\Delta AIC_c = 19.9$; $AIC_w = 0$) (Table 1).

The influence of ASR and its interaction with age on ORR appeared to be acting through its influence on females' reproduction (calving) rate. The pattern of calving matched that for ORR; it decreased (mean [SE] calves per year) as the population became more male biased (female biased: 0.23 [0.02], $n = 78$; parity: 0.15 [0.02], $n = 54$; male biased: 0.10 [0.02], $n = 78$; $F_{2,153} = 11.91$; $p < 0.001$). Calving was, similar to ORR, also significantly higher in females released as adults relative to juveniles (juveniles: 0.11 [0.02], $n = 32$; young adults: 0.17 [0.02], $n = 39$; adults: 0.21 [0.02], $n = 85$; $F_{2,153} = 6.52$; $p = 0.002$). Thus, there was significant variation in calving among age classes with different ASRs. Juveniles

Table 1. Comparison of a priori models predicting postrelease offspring recruitment rate (i.e., calves recruited per female per year) of translocated female black rhinoceros ($n = 203$) in southern Africa 1981–2005.

Model ^a	Model fixed effects ^b	K^c	AIC_c^d	ΔAIC_c^e	AIC_w^f
Ind-TLC interaction 1	age x PR ASR	6	-274.6	0.0	0.986
Ind characters 1	age	4	-263.2	11.4	0.003
Ind-TLC interaction 2	age x TLC ASR	6	-262.9	11.7	0.003
Brett 1998 recommendation	age + TLC size + PR density + hab	7	-262.6	12.0	0.002
Brett 1998 primary risks	age + TLC size + resident density + hab	7	-261.5	13.1	0.001
Walker 1994	age + qrea + PR density	6	-260.7	13.9	0.001
Ind-hab interaction 1	age x PR density	6	-260.6	14.0	0.001
Adcock et al. (1998)	age x resident male density	6	-259.9	14.7	0.001
Ind-hab interaction 2	age x resident density	6	-259.6	15.0	0.001
TLC character 1	PR ASR	4	-259.4	15.2	0.000
Reserve hab quality 1	hab + release season + nutrient geology	6	-258.6	16.0	0.000
Intraspecific conflict 1	resident density + resident proximity to CC	5	-254.8	19.8	0.000
Translocation type	reintroduction or restocking	4	-254.7	19.9	0.000
TLC character 2	TLC ASR	4	-253.6	21.0	0.000
Fischer and Lindenmayer 2000	TLC size	4	-252.5	22.1	0.000
Ecological change	R-S hab + R-S nutrient geology + TL distance	6	-252.5	22.1	0.000
Null model ^g	no fixed effects	3	-251.9	22.7	0.000
TLC composition 1	TLC size + TLC proportion of bulls	5	-251.3	23.3	0.000
TLC composition 2	TLC size + TLC proportion of juveniles	5	-251.1	23.5	0.000
Interspecific conflict 1	resident predators present	4	-250.8	23.8	0.000
Griffith et al. (1989)	TLC size + Hab	5	-250.7	23.9	0.000
TLC composition 3	TLC size + TLC proportion of calves	5	-250.7	23.9	0.000
Ind experience	R-S area	4	-250.3	24.3	0.000
Linklater and Swaisgood 2008	PR density	4	-250.2	24.4	0.000
TLC-Hab interaction 1	TLC ASR x PR density	6	-250.2	24.4	0.000
Sociodemographic change 1	density change + TLC size cf. resident population	5	-250.1	24.5	0.000
Intraspecific conflict 2	resident density	4	-249.8	24.8	0.000
Reserve hab quality 2	hab	4	-249.8	24.8	0.000
Interspecific conflict 2	resident elephants present	4	-249.8	24.8	0.000
TLC-hab interaction 2	TLC ASR x Hab	6	-249.3	25.3	0.000
Sociodemographic change 2	ASR change + ASR more/less extreme	5	-249.3	25.3	0.000
Intracohort interaction	TLC size x TLC proportion of juveniles	6	-249.0	25.6	0.000
TLC-hab interaction 3	TLC size x hab	6	-248.7	25.9	0.000
Brett 1998 secondary risks	PR density + PR proximity to CC	5	-248.3	26.3	0.000
Ind-TLC-hab interaction	TLC size x TLC proportion of bulls x hab	10	-241.2	33.5	0.000
TLC-hab interaction 4	TLC size x TLC proportion of juveniles x hab	10	-241.2	33.5	0.000

^aModels represent previous hypotheses for general and rhinoceros-specific translocation success; ind, individual; TLC, translocation cohort; hab, habitat.

^bModels with interaction terms also include each individual predictor variable additively (e.g., $a \times b$ refers to model including $a + b + a \times b$ as fixed effects). Abbreviations: PR, postrelease; age, $<1/1-1.9/2-3.9/4-5.9/\geq 6$ years; ASR, adult sex ratio (males/females); TLC, translocation cohort; density, adult rhinoceros density (rhinoceros per square kilometer); hab, habitat quality (reserve ecological carrying capacity [CC] [Adcock 2001]); area, reserve area (hectares); nutrient geology (poor, moderate, or good); reintroduction, reserve contains no rhinoceros prior to release; restocking, reserve contains resident rhinoceros prior to release; R-S, difference between recipient and source reserve; TL distance, translocation distance (kilometers); calves, dependent calves.

^cNumber of parameters.

^dSecond-order Akaike information criterion.

^eDifference in AIC_c between current model and best model.

^f AIC weight.

^gModel includes only random effects and no fixed effects.

in male-biased populations had the lowest calving rate (0.05 [0.02]), whereas adults in female-biased populations exhibited a 5-fold higher calving rate (0.26 [0.02]).

Postrelease Reproductive Delay

The pattern in fecundity with ASR among age classes may have been strongly influenced by delays to first reproduction after a female's release, especially because we expected the greatest impacts of a translocation to occur soon after release and because reproductive delays were

common in younger, especially primiparous, mothers. We examined time to first reproduction by females after release (for all adults) or postrelease sexual maturity (for juveniles) to explain variation among ORRs. This postrelease reproductive delay decreased as age increased at all ASRs (time to first calf in years [SE] across ASRs: juveniles, 4.58 [0.33], $n = 18$; young adults, 3.79 [0.43], $n = 31$; adults, 2.98 [0.16], $n = 48$; $F_{2,94} = 6.56$; $p < 0.001$) (Fig. 2a) in the same way ORRs did, although delay in juveniles may be partly due to a naturally occurring delay in reproduction following onset of sexual maturity.

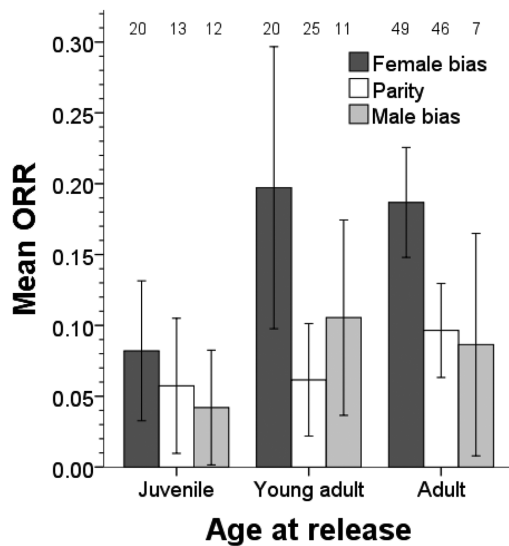


Figure 1. Mean postrelease offspring recruitment rate (ORR) (i.e., calves recruited per female per year) and 95% CI (n = 203) by age at release (juvenile, <4 years; young adult, 4–5.9 years; adult, ≥6 years) and postrelease population adult sex ratio (males:females; female bias, <0.40; parity, 0.40–0.60; and male bias, >0.60) of translocated female black rhinoceros in southern Africa 1981–2005 (numbers above bars, number of translocated females in each category). The 3 youngest age classes have been amalgamated into 1 category representing females that had not reached sexual maturity at time of translocation.

Thus, among females that eventually calved, mean ORRs of those released as juveniles and young adults were over twice that for all females in these age classes (juvenile, 0.169 [0.012]; young adult, 0.255 [0.029]), whereas the mean for older adults was 58% higher (0.220 [0.011]) than for all older adult females. Time to first postrelease calf did not vary strongly with postrelease ASR. Age class was a strong determinant of reproductive delay and, therefore, ORR after release.

Reproductive Failure

The pattern in fecundity rates with ASRs among age classes was strongly influenced when many females experienced complete calf recruitment failure. This occurred for nearly half (47%) of translocated females, and those failures occurred less commonly with adults in female-biased populations and disproportionately in younger age classes (Fig. 2b). Across ASRs, recruitment failure decreased with increases in female age at release (i.e., 62%, 54%, and 36% for juveniles, young adults, and adults, respectively) (Fig. 2b). The length of individual postrelease reproductive periods examined was similar among age

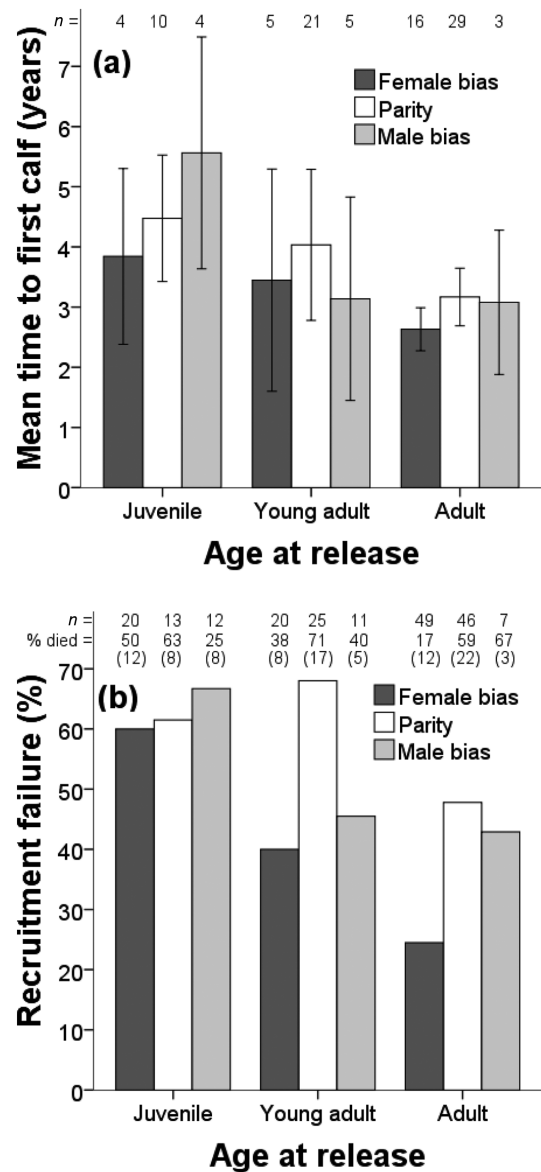


Figure 2. Translocated female black rhinoceros (a) mean time to first calf (95% CI; n = 97) from release (all adults) or from postrelease sexual maturity (juveniles) and (b) rates of recruitment failure (no calves surviving to sexual maturity) (n = 203) by age at release (juvenile, <4 years; young adult, 4–5.9 years; adult, ≥6 years) and postrelease population adult sex ratio (males:females; female bias, <0.40; parity, 0.40–0.60; male bias, >0.60) in southern Africa 1981–2005 (n, total number of translocated females in each category; % died, proportion of females with recruitment failure due to mortality within 4 years postrelease; in parentheses, number of females experiencing recruitment failure). The 3 youngest age classes have been amalgamated into 1 category representing females that had not reached sexual maturity at time of translocation.

classes (mean [SD], range in years: juveniles, 7.7 [4.1], 4–20; young adults, 8.9 [5.0], 4–22; adults, 9.4 [5.0], 4–22), so females within each age class had a similar opportunity to produce a calf, although one might expect naturally lower reproduction in females that have more recently reached sexual maturity. The pattern of recruitment failure, therefore, was not explained by differences in the lengths of the data record among age classes.

Recruitment failure can result from a female dying within 4 years of release, failing to calve, or her calves failing to survive to sexual maturity. Female deaths (23% of all translocated females), followed by failure to calve (24% of surviving translocated females), were the leading causes of recruitment failure. Among females that calved, only 11% did not have any survive to sexual maturity, and this did not vary with age or postrelease ASR. Thus, calf death was only a minor contributor to the pattern of recruitment failure. Postrelease death of females itself was not strongly associated with age class (although it was more common among younger females as a percentage of females in each age class across ASRs: juveniles, 29%; young adults, 30%; adults, 17%), and recruitment failure due to postrelease female death was also similar among age classes (as a percentage of recruitment failure in each age class across ASRs: juveniles, 46%; young adults, 57%; adults, 45%) (Fig. 2b). Among surviving translocated females, failure to calve (i.e., excluding females that had calves that did not survive to sexual maturity) was highest in juveniles (as a percentage of females in each age class across ASRs: juveniles, 41%; young adults, 21%; adults, 19%) but varied little among ASRs (as a percentage of females in each ASR category across age classes: female bias, 21%; parity, 26%; male bias, 29%). Among surviving females, there was also a clear association of recruitment failure with ASR (as a percentage of females in each ASR category across age classes: female bias, 27%; parity, 32%; male bias, 42%) and with age (as a percentage of females in each age class across ASRs: juveniles, 47%; young adults, 44%; adults, 36%). Therefore, recruitment failure due to reproductive failure most drove the pattern of reproductive performance.

Discussion

Our translocation study offers the unique advantage of a long-term analysis across a large number of replicate populations—a science-by-management experiment as a proxy for a manipulative experiment, and a rare opportunity, particularly for a large, critically endangered taxon such as black rhinoceros. Examining the survival of released individuals is only the first consideration when determining drivers of translocated-population dynamics. Investigating released animal fecundity is also misleading if offspring do not survive to breeding age. Therefore, by employing a metric such as ORR,

which integrates the survival of translocated females, their postrelease reproductive performance, and the recruitment of their offspring to sexual maturity, we have provided a more relevant measure of translocated-population success and potential for growth and recovery of the species metapopulation.

A Simple Model from Apparent Complexity

Many factors working in concert—density dependent and independent, extrinsic and intrinsic to individuals and populations—may influence the dynamics of animal populations. Animal translocations to establish new or supplement existing populations may seem to demand a large set of potential influences and their complex interactions to model the reproductive performance of the postrelease population. However, our results showed that the potential for long-term translocation success is explained by a remarkably simple model—the interaction of age and postrelease ASR. Optimizing age of translocated individuals and the ASR of the population after release may be key to more rapid success for the protection and recovery of threatened species, and specific strategies will depend on the behavior and social dynamics of individual species. Moreover, we found that conditions created in the postrelease population are as important as characteristics of the translocations and released cohorts, and both should be considered when determining predictors of translocation success.

Sex Ratios, Age, and Sexual Conflict

Sex ratios determine levels of intra- and intersexual competition (Cureton et al. 2010; Eldakar et al. 2010), which can have profound implications for female fitness (Linklater et al. 1999) and population growth (Gerber et al. 2010). However, disentangling the effects of male-male competition and harassment of females to breed and female mate choice is problematic and rarely possible (Tobler et al. 2011). Females released as young adults and adults exhibited higher ORRs in female-biased populations, which may reflect reduced sexual harassment from competing males or their resilience to intrasexual competition for breeding opportunities, but most likely the former. Increasing rates of sexual harassment of females where male-male competition for mates is more intense affect female survival and reproductive success in other Perissodactyls (e.g., horses [Linklater et al. 1999] and zebras [Sundaresan et al. 2007]). In our study, postrelease female mortality was strongly influenced by their age at release as a function of postrelease population ASR. The low ORRs of translocated juveniles regardless of population ASR may be a result of their inexperience with older conspecifics, making them vulnerable to both intra- and intersexual competition. Perhaps when newly reproductively active females (i.e., those released

as juveniles) make their initial forays to seek mates, their inexperience interacting with aggressive males or more competent females results in missed breeding opportunities or imposes an energetic cost for which they are unable to compensate. If such possibilities underlie naturally occurring delays in reproduction following the onset of sexual maturity, interactions between age and ASR may exaggerate their effect in certain translocation contexts. Previous rhinoceros-translocation studies have found differences in predictors of rhinoceros survival between reintroduction and restocking events (Linklater et al. 2011, 2012). Considering the apparent importance of intra- and intersexual interactions in influencing ORR and the higher ORRs of females when reintroduced versus restocked, the model representing the presence of conspecifics prior to translocation ranked surprisingly low (Table 1). Most likely, this is a release effect which is superseded by the longer term importance of other influences when ORR is considered.

Our results confirm the fundamental and, now, longitudinal role age can play in translocation success, demonstrating increased postrelease population success when translocating adults versus juveniles (e.g., Sarrazin & Legendre 2000; Linklater et al. 2011; Lewis et al. 2012; but see Robert et al. 2004). But, our study also revealed a role for sexual conflict that replaces other hypotheses previously thought to be important for translocation success, particularly extrinsic factors and density dependencies (e.g., number of animals released or habitat quality) (e.g., Griffith et al. 1989; Fischer & Lindenmayer 2000; Komers & Curman 2000). More specifically, release cohort size (Brett 1998; Linklater et al. 2012), rhinoceros density (Walker 1994; Adcock et al. 1998; Brett 1998; Linklater & Swaisgood 2008), habitat quality (Brett 1998), familiarity with release site ecology (Stamps & Swaisgood 2007), and reserve size (Walker 1994; Linklater & Swaisgood 2008) have all been considered influential when translocating rhinoceroses but were not supported by our larger, longer-term data (but see Brett [1998] and Linklater et al. [2011]). This result suggests that attention should be shifted from ecological to social constraints on population growth and species recovery for this critically endangered mammal. Moreover, our results promote the importance of social structure in the postrelease population, and, as such, intraspecific competition and sexual conflict should be considered when translocating species, in particular those with a polygynous breeding system.

Recruitment Failure

Although maternal death, offspring mortality, and failure to conceive or complete gestation can all contribute to recruitment failure, the generally high variability among ASR categories suggests that sexual conflict may have the greatest impact on reproductive success, followed by maternal survival, although the latter is exacerbated

for females translocated as juveniles and young adults. The high rate of recruitment failure, especially among females released as juveniles and young adults, is problematic because the intent of translocations is also to maintain genetic diversity. In a polygynous species such as rhinoceros for which effective population size is already reduced by male reproductive skew (Garnier et al. 2001), the large component of females failing to recruit calves (47%) imposes an extreme female reproductive skew after release and exacerbates the genetic bottleneck. Minimizing recruitment failure is of particular importance for large, longer lived species that tend to have high rates of adult and offspring survival and low reproductive rates. The evidence suggests that translocating mature females into, or the creation of, populations with female-biased sex ratios would reduce rates of recruitment failure following translocations.

Recommendations and Future Work

As is typical with threatened species, particularly large mammals, their translocated populations are inherently small and, thus, more likely to experience significant variability in ASR (Linklater et al. 2017). Extremes of sex ratio are often imposed by released cohorts, which can lead to heightened sexual conflict among released individuals. We recommend avoiding extremely male-biased sex ratios or, more directly, harnessing favorable female-biased sex ratios for improved translocation success. Greater population growth and genetic representation by the founders is also more likely to be achieved by translocating older females that do not have the reproductive delay and low ORRs of juveniles or the higher recruitment failure rates of juveniles and young adults. If translocation of juveniles is necessary, it may be preferable to release them into female-biased populations, where they have slightly higher ORRs. Of course, in addition to released populations, the long-term productivity of source populations must also be considered, in that longer-term success of the metapopulation will be achieved when there is a balance among subpopulations. Our recommendations from real-world outcomes are congruent with the straight-forward hypothetical guidelines set out by Hearne and Swart (1991) for translocating to optimize the growth of the metapopulation. Rhinoceros translocation experience has reinforced the usefulness of theory.

A considerable amount of black rhinoceros data have been collected over decades; however, much of these data are not made widely available for independent analyses and evaluation, particularly during times of conservation crisis (e.g., periods of heightened illegal rhinoceros hunting and trade). Substantial black rhinoceros translocation and demographic data have been summarized in various gray literatures (Linklater 2003), but few people have had access to these documents, and, thus, they are not widely open to independent review.

Improving management toward conservation depends on new information being subject to independent quality control and made readily available to a diverse audience of potential contributors (Linklater 2003) because the process of peer review and critique is essential for advancing the quality of conservation science (Calver & King 2000; Armstrong & Seddon 2008). This paper is intended to subject the data to wider access and scrutiny.

In this study, we responded to calls for new metrics of translocation success that better reflect long-term population viability. Our findings demonstrate that recruitment failure or postrelease reproductive delay or both are preventing young female rhinoceros from realizing their reproductive potential, and future research should include intensive postrelease behavioral and spatiotemporal monitoring to elucidate how interactions between females and conspecifics of both sexes may be limiting breeding opportunities and, to a lesser extent, calf survival. In addition, analyses of temporal changes in populations are necessary to determine whether higher ORRs translate into improved population growth for rhinoceros. Nonetheless, adult survivorship is typically high for large herbivores such as rhinoceros (i.e., >95%). Where our recommendations can be followed, achieving the higher average ORRs described (i.e., approximately 0.12 calves recruited per female per year) for a greater number of translocated females could translate into population growth rates exceeding 8% per annum (assuming ASR parity). Achieving high growth rates in black rhinoceros populations is essential to increasing the metapopulation to viable long-term levels for species rescue, as well as helping populations withstand periodic poaching crises like the one currently occurring.

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Supporting Information

Definitions, means, and ranges of continuous covariates included in models (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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