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Guidelines for large herbivore translocation simplified: black rhinoceros case study

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Summary

1. Most hypotheses for translocation success are elaborate, hierarchical, and untested combinations of socio-ecological predictors. Empirical support for those tested is vulnerable to spurious single-predictor relationships and does not account for the hierarchy amongst predictors and non-independence amongst individuals or cohorts. Testing hypotheses as *a priori* multi-level models promotes stronger inference.

2. We apply a 25-year (1981–2005) data base including 89 reintroduction and 102 restocking events that released 682 black rhinoceros *Diceros bicornis* into 81 reserves to test 24 hypotheses for translocation success, defined as survival to 1 year post-release. We made information-theoretic comparisons of hypotheses represented as hierarchical models incorporating random effects for reserve and release cohort predictors of death.

3. Mortality rates after restocking were higher than for reintroductions (13·4 cf. 7·9%, respectively) due largely to intraspecific fighting. No predictors strongly influenced reintroduction success, although cohorts consisting entirely of adult males were 8·2% of individuals but contributed 21·9% of deaths, and reserves with lowest carrying capacities (i.e. $<0{\cdot}1$ rhino km^{-2}) had a 16·3% mortality rate. Most models for restocking success were not supported. Only those including age class received substantial support. Age was the only predictor to strongly influence death rates. Predictors previously thought influential, like population density, reserve area and quality, and cohort size, were not supported.

4. *Synthesis and applications*. Simple rules succeeded where complex ecological and demographic hypotheses failed to predict survival after translocation of critically endangered black rhinoceros. Results support bold attempts by managers at translocations towards species recovery in most ways that they have historically occurred. Groups of rhinoceros of different size and composition can be successfully moved over large distances between different ecological contexts. Also, the release of cohorts into reserves that are relatively small, poorer habitat or already stocked need not be avoided so long as calves and all-male cohorts are not reintroduced, and only adults used for restocking. Our analysis demonstrates the importance of information-theoretic comparisons of *a priori* hierarchical models to test hypotheses for conservation management. We caution against interpreting simple correlations or regression amongst a large number of nested ecological and demographic variables.

Key-words: Bayesian inference, conservation management, DIC, *Diceros bicornis*, hierarchical model, MCMC, meta-population, post-release mortality, reintroduction, restocking

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Introduction

Translocation is an important tool for species recovery (IUCN 1987) to rescue individuals from threats (e.g. habitat destruction, hunting), reintroduce populations, and for genetic and demographic rescue by restocking. A consequence is the creation and management of an artificial meta-population towards species recovery. Reserves, populations and individuals vary in ways that may influence post-release survival, and the resources for translocation are limited. Managers must balance competing opportunities and risks when deciding between source and recipient reserves, and the composition of the cohort translocated.

Progress towards species recovery requires that we quickly discard incorrect hypotheses and find the simplest explanation for translocation success (Armstrong & Seddon 2008). Many hypotheses for translocation success are elaborate combinations of socio-ecological predictors based on their theoretical relationship with fitness. Cohort size (Griffith *et al.* 1989; Wolf, Garland & Griffith 1998; Fischer & Lindenmayer 2000), incorporating Allee and in- or out-breeding effects (Jamieson *et al.* 2007; Somers *et al.* 2008), density dependence (Linklater & Swaisgood 2008), competition (e.g. inter and intraspecific, Garrett *et al.* 2007) and habitat quality (Wolf, Garland & Griffith 1998), scale (e.g. body and range size, Bowman, Jaeger & Fahrig 2002), mating system (e.g. reproductive skew, Sigg, Goldizen & Pople 2005), social and ecological familiarity (Armstrong & Craig 1995; Stamps & Swaisgood 2007) and experience (e.g. of predators, Banks, Norrdahl & Korpimaki 2002; Frair *et al.* 2007) are all considered influential.

Most hypotheses have not been tested. The few tests reported have relied on correlations or regression (Griffith *et al.* 1989; Wolf, Garland & Griffith 1998; Fischer & Lindenmayer 2000) rather than comparisons of hypotheses as *a priori* models (Burnham & Anderson 2002; Johnson & Omland 2004; Whittingham *et al.* 2006). Moreover, their data sets include hierarchical data but tests have not incorporated the non-independence amongst levels (i.e. individual animal, release cohort and reserve). Such analyses are prone to under- or over-fitting and inflate the importance of higher level predictors (Gelman & Hill 2007; de Leeuw & Meijer 2008).

Although translocations are common, few data sets describing multiple translocations have been gathered and they tend to describe only a subset of successful translocations. Complete data sets including sufficient numbers of individuals, release cohorts, and sites for a robust analysis are rare but the critically endangered black rhinoceros *Diceros bicornis* Perissodactlya is an exception (Brett 1998). Post-release mortality rates amongst black rhinoceros vary and can be disastrously high (see Table S1, Supporting information). Correlations amongst 11 years of Kenyan data led Brett (1998) to identify conspecific resident and post-release density, and individuals' age and sex as the primary, and habitat quality as secondary, risk factors and to recommend moving '… rhinos to reserves with excellent habitat … at a relatively low rhino density, and in large groups; and, select adults for translocation, and adult females if available'. We applied an information-theoretic approach to compare hierarchical models as hypotheses for translocation success using a longer-term data set (1981–2005) from a wide bio-geographic range (Namibia and South Africa) as an advance on Brett's (1998) earlier work.

Materials and methods

COMPILING PREDICTORS (FIXED EFFECTS)

The data set was compiled from reports on black rhinoceros translocations and post-release monitoring in Namibia and South Africa Rhino Management Group from 1981 to 2005 (1995–2005). It included 89 reintroduction and 102 restocking events that released 682 black rhinoceros of known age class (Hitchins 1978) and sex into 81 reserves on a known date (See Fig. S1, Supporting information). We pooled the three subspecies, *D. bicornis* var. *bicornis*, *minor* and *micheali*, because they are ecologically and morphologically equivalent and only subtly different genetically (Ashley, Melnick & Western 1990; O'Ryan, Flamand & Harley 1994; Swart & Ferguson 1997). All translocated rhinoceros (hereafter rhino) were individually identifiable. Receiving reserves were fenced and staff dedicated to monitoring so deaths after release were reliably detected.

Translocation reports also described the source and recipient reserves including reserve area and rhino population size. We supplemented this with information about the presence or absence of elephant *Loxodonta africana* and large predators (i.e. lion *Panthera leo* and spotted hyena *Crocuta crocuta*) capable of depredating rhino calves (Plotz & Linklater 2009); an ordinal value for nutrient geology (poor, moderate, and good); and estimate of reserves' carrying capacities (rhino km^{-2}) from Adcock (2001a,b). Information derived from these data included the distance between reserves; previous elephant, large predator, or translocation experience; release cohort adult sex ratio and its deviation from parity (0 = 45–55%, 1 = 25–45% or 55–80%, or 2 = 0–20% or 80–100% male); presence of conspecific residents (i.e. reintroduction vs. restocking); time since a reserve last received an introduction; sex and age structure, sex- and age-specific density, and proximity to carrying capacity of the resident and post-release population; and differences in nutrient geology, estimated carrying capacity, and size between source and recipient reserves. Introduction events were regarded as different if more than 1 month separated the release of individuals to the same reserve. Black rhino establish ranges within the first month post-release (Linklater & Swaisgood 2008).

All predictors were scaled to range between 0 and 1 prior to analyses to facilitate comparison of models' parameter estimates. Mortality rates were notably higher in the first year following translocation (Fig. 1, see also Brett 1998) and so we used a binary dependent variable for translocation success (i.e. survived the first year 0 or died 1). Individual survival (cf. population persistence, Griffith *et al.* 1989; Fischer & Lindenmayer 2000) is a more appropriate measure of translocation success for species, like black rhino, represented by few individuals of high economic value, and where the data set includes restocking events designed for genetic and demographic rescue by individuals.

COMPILING CANDIDATE MODELS

We began with the work of authors who have predicted or described factors contributing to higher post-release survival in black rhinoceros from smaller data sets or single translocations. Our first three models represent Brett's (1998) primary and secondary risk factors,

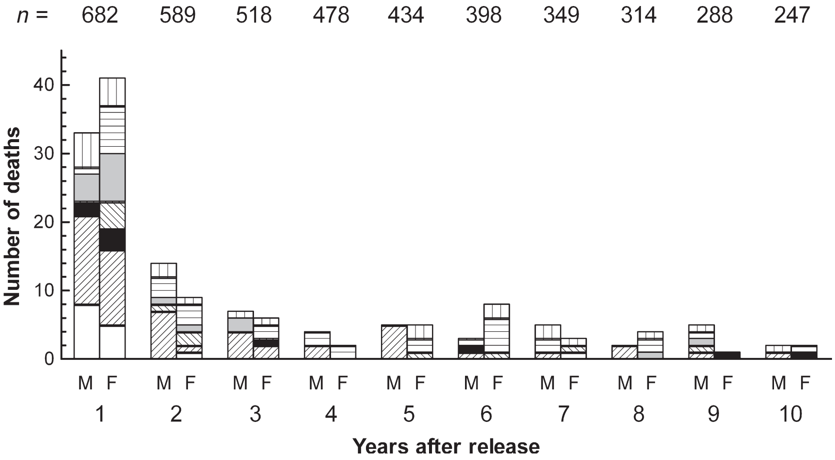

Fig. 1. Number of male (M) and female (F) deaths during the first ten years following translocation. Causes of death include translocation directly (□), intraspecific fighting (/), interspecific conflict, i.e. with elephant or predators (■), animal accident or misadventure (\), post-release stress (grey), unknown (–), and other (|). *n*, number of individuals translocated.

and recommendation (see Table S2, Supporting information). Various combinations of age, resident bull density, reserve size and conspecific density have also been identified as important (Adcock, Hansen & Lindemann 1998; Linklater & Swaisgood 2008; Hitchins & Anderson 1983) and so they constitute three more models. We added two models including cohort size alone (Fischer & Lindenmayer 2000) and combined with the carrying capacity of the recipient reserves (Griffith *et al.* 1989). These articles defined translocation success as population persistence, not the survival of individuals as we did. Nevertheless, we were interested in whether the positive influence of cohort size on population persistence that they describe might be counteracted by elevated competition and conflict. We then derived 14 other candidate models to investigate hypotheses about reserve capacity in terms of its resources or space, release cohort composition, individual rhino characteristics, translocation logistics, demographic and social disturbance, individual experience and source-recipient reserve and population similarity, and interspecific conflict (see Table S2, Supporting information).

We compared models for reintroduction and restocking separately because these are conducted to meet different conservation objectives and the success of restocking might be influenced by characters of the resident population not applicable to reintroductions.

HIERARCHICAL MODELLING WITH RANDOM EFFECTS

We used Bayesian inference to construct hierarchical binary response logistic regression models in WinBUGS 3·0·2 (Spiegelhalter *et al.* 2007) for each of the 24 hypotheses (see Table S2, Supporting information). Release cohorts ranged from 1 to 30 individuals and some reserves received up to five restocking events. Individuals, therefore, are nested within release cohorts that in turn are nested within reserves. Thus, comparison of models for restocking success required random effects at two levels (release cohort and reserve), but reintroduction models required only one level (reserve) because only the first cohort released into a reserve is a reintroduction. Survival was modelled as a linear function on a logit scale, and thus, we assigned a $N(0, 10^3)$ prior to the regression coefficients and a $N(0, \sigma)$ prior to the random effects, where σ was drawn from $U(0, 100)$.

Parameters (estimated values of the regression coefficients and their posterior distributions or credible intervals) were estimated using Markov chain Monte Carlo (MCMC) methods (Spiegelhalter *et al.* 2002). Model convergence was evaluated in WinBUGS using the Brooks-Gelman-Rubin diagnostic tool (Gelman & Rubin 1992; Brooks & Gelman 1998) after simultaneously running two Markov chains with markedly different initial values (i.e. 0 and 1) and examining the autocorrelation and trace plots. Models were run for 250 000 iterations, the first 30 000 iterations discarded, and posterior distributions of the parameters examined. Competing models were ranked by their deviance information criterion (DIC, Spiegelhalter *et al.* 2002) – a measure of the fit of the model to the data, where additional parameters are penalized. DIC is a technique for comparing complex hierarchical models. Discussion indicates some concerns about the stability of the parameter penalty term (see also Gelman & Hill 2007, p. 525). Further research and discussion (Celeux *et al.* 2006) suggests that DIC currently lacks proper theoretical derivation. Thus, its application should be regarded as a plausible and developing, rather than a well-established approach to model selection. We used the general rule that models with DIC within two units of the lowest model's value are considered to have compelling support, four to seven DIC units greater than the minimum value have considerably less support, and greater than ten, no support (Spiegelhalter *et al.* 2002; see also, Burnham & Anderson 2002).

We examined the credible intervals of predictors in the leading models (ΔDIC ≤ 2) for overlap with zero and compared their absolute scaled coefficients to identify predictors with largest effect sizes. Given the absence of interaction terms we scaled continuous coefficients by multiplying each by two standard deviations of the predictor and comparing their absolute values as measures of effect size (Gelman & Hill 2007).

Results

The most common causes of death during the first year (attributed by field rangers) were intraspecific conflict (i.e. fighting, 32%), injury during transport and release (18%), and post-release stress (15%), but for many (11%) the cause was unknown (Fig. 1). Deaths attributed to accident or conflict with predators or elephants were less common. Translocation to restock had almost twice the mortality rate of reintroductions (13·4 cf. 7·9% mortality, respectively, Fig. 2). Intraspecific fighting and post-release stress causing death were 2·4 and 1·9 times higher, respectively, after restocking cf. reintroduction.

REINTRODUCTION

It was not possible to distinguish between the value of most hypotheses for reintroduction success because all hypotheses were at least weakly supported (i.e. ΔDIC < 7, Table 1).

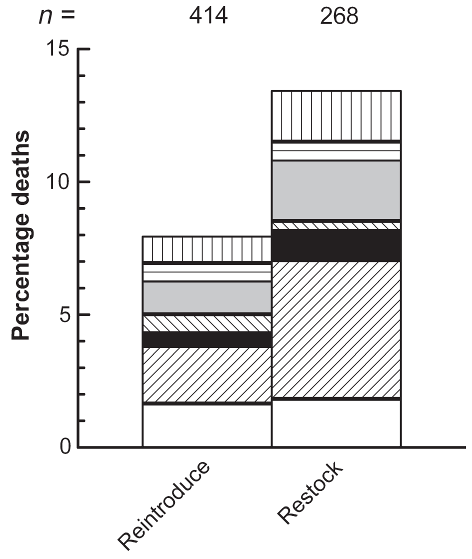

Fig. 2. Mortality (%) during the first year after reintroduction and restocking. Causes of death include translocation directly (□), intraspecific fighting (/), interspecific conflict, i.e. with elephant or predators (■), animal accident or misadventure (\), post-release stress (grey), unknown (–), and other (|). *n*, number of individuals translocated.

We are able, however, to demonstrate that some should not be considered important because other models substantially exceed their influence. In particular, the complex ecological and demographic hypotheses represented by Brett's (1998) recommendation performed substantially worse than four other models (Table 1).

All predictors' parameter estimates, even in models receiving substantial support (i.e. ΔDIC < 2), had credible intervals overlapping zero and so the magnitude and direction of predictors' influence on survival probability is uncertain (Fig. 3). Nevertheless, the influence of some predictors can be dismissed because their parameters were relatively small (e.g. recipient reserve area and the difference between source and recipient reserve carrying capacity and size) or suggested a relationship counter to that expected from theory (e.g. post-release adult density, the difference between source and recipient reserves habitat quality in terms of carrying capacity or nutrient geology, and translocation distance). Counter-intuitive associations between higher post-release density, longer distance translocation, release into poorer habitat, and improved post-release survival are unlikely to be evidence of a causative relationship. Greater success (survival) with lower conspecific densities, larger reserves, improved habitat, and reduced translocation distance was not supported. The possibility remains that these predictors influence survival rates, but clearly not in the way or magnitude expected. Nevertheless, weak, albeit ambiguous, support was indicated for some parameters and they warrant consideration, particularly those which describe a cohort's vulnerable or dangerous age–sex classes. In particular, the proportion of bulls and calves in the release cohort, and reserve carrying capacity featured in the leading models (Table 1) and had the largest effect sizes (Fig. 3).

Table 1. Outcomes of 20 candidate models for reintroduction mortality

Model no.†	Candidate model, hypothesis	pD	DIC	ΔDIC$_i$
8	Fischer & Lindenmayer (2000)	23·4	227·3	0·0
4*	Adcock, Hansen & Lindemann (1998)	22·4	228·0	0·7
13	Cohort composition – bulls	22·9	228·1	0·8
1*	Brett's (1998) primary risk factors	25·2	228·3	1·0
15	Cohort composition – dependent calves	22·9	228·5	1·2
9	Griffith *et al.* (1989)	23·2	228·6	1·3
19	Ecological similarity of source and recipient reserves	27·4	228·7	1·4
14	Cohort composition – juveniles	23·7	228·8	1·5
7* (also 11‡)	Reserve capacity (space) (also Linklater & Swaisgood 2008)	24·4	228·9	1·6
5	Linklater & Swaisgood (2008)/Hitchins & Anderson (1983)	21·9	228·9	1·6
20	Experience of translocation and fenced confinement	24·8	228·9	1·6
6*	Walker (1994)	26·1	229·0	1·7
16	Cohort composition – adult sex ratio	21·6	229·4	2·1
21	Experience of elephant and predators	25·7	229·7	2·4
17	Individual rhino characteristics	23·5	229·7	2·4
2	Brett's (1998) secondary risk factors	22·3	229·8	2·5
24	Interspecific conflict	23·9	229·9	2·6
10	Reserve capacity (resources)	26·8	230·2	2·9
3*	Brett's (1998) recommendation	28·4	230·3	3·0
12	Cohort composition – all predictors	27·8	234·1	6·8

Models are in descending order from the most to least supported based on deviance information criteria (DIC).
pD, estimated number of parameters.
*Models include data at multiple levels.
†See Table S2 (Supporting information) for predictors in models.
‡Models are the same for reintroductions where there was no resident population. Models 18, 22 and 23 are missing because they included predictors relevant only to restocking.

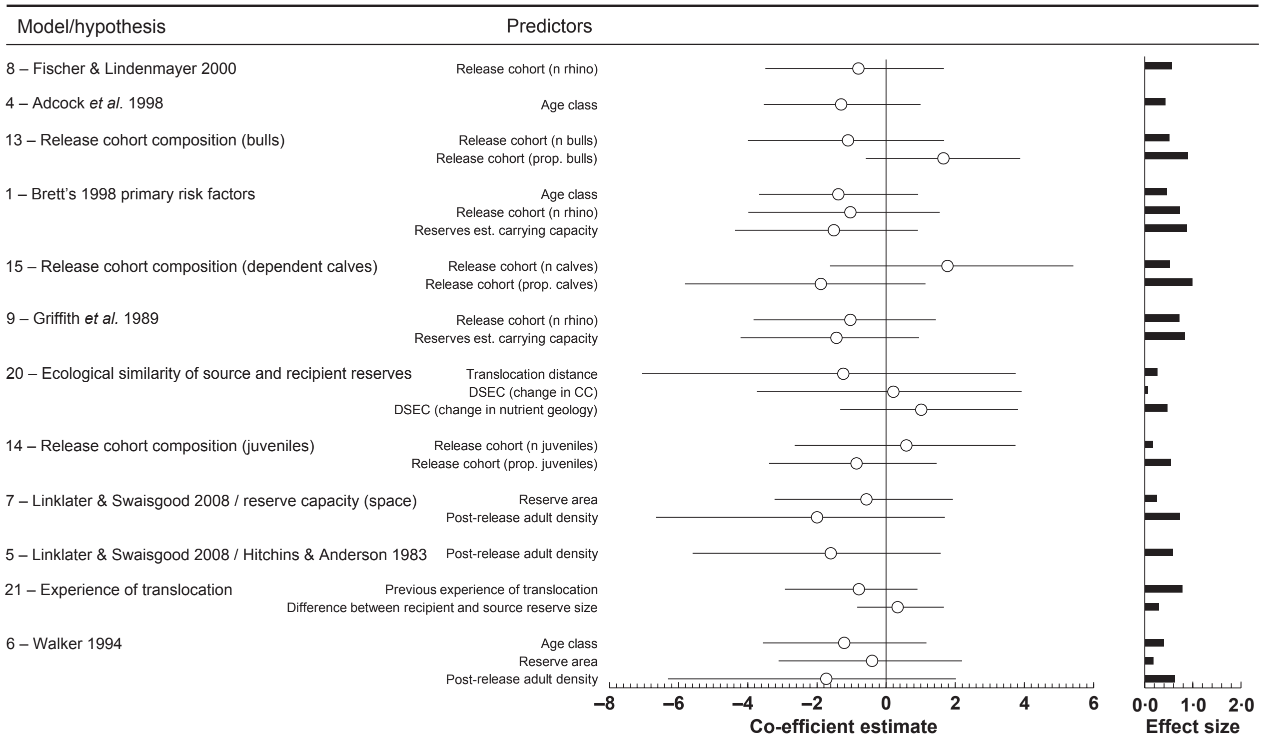

Fig. 3. Parameter estimates from posterior densities and scaled effect size of coefficients for each predictor (see Table S2, Supporting information) in the 12 hypotheses for reintroduction success (survival to one year post-release) that received substantial support (i.e. ΔDIC ≤ 2; Table 1). Open circles (○) represents mean parameter (coefficient) estimates and horizontal lines represent their credible intervals. A value of zero indicates that the predictor had no influence on post-release survival, while a positive value indicates a positive relationship between the predictor and mortality. Effect sizes are derived by multiplying each coefficient by two standard deviations of the corresponding predictor and converting to absolute values.

Younger age classes and the release of several calves in larger cohorts, even when they were a small proportion of the cohort, were weakly associated with higher mortality rates. Calf survival, even though calves were translocated with their mothers, was poor overall but better when they and their mothers were the majority of the release cohort. Mothers with calves were part of four reintroductions including 40 individuals that incurred a 15% mortality cf. 7·5% for reintroductions that did not include calves (Fig. 6a). Mortality rates amongst calves were lower where the cohort consisted only of mothers and their dependent calves (i.e. 3·8% deaths in six translocations including 13 mother–calf pairs).

Cohorts consisting entirely of large dominant bulls, even if they were released singly, had higher mortality rates (Fig. 4a). Translocations of only adult males accounted for 21·9% of deaths but represented only 8·2% of released individuals. It is not the case, however, that incremental increases in the proportion of bulls, as potential aggressors, corresponded to elevated risk because mortality rates were low and similar in other cohort sex-ratio categories, at least until bulls constituted as much as 60% of the released cohort. Examples where bulls were the majority of the cohort are too few to compare (Fig. 4a). After the cohort's composition of bulls and calves, carrying capacity of the recipient reserve also received weak support. The poorest habitats estimated as capable of supporting $<0{\cdot}1$ rhino km^{-2} were associated with higher mortality rates (Fig. 4b).

RESTOCKING

In contrast to reintroduction, most hypotheses for survival after restocking were not supported (Table 2). In particular, the release cohort's composition (e.g. size and age and sex structure); ecological difference between recipient and source reserve; presence of elephants or large predators and individual's previous experience with them; magnitude of demographic change imposed by the release; previous translocation experience; and Brett's (1998) secondary risk factors were not influential (i.e. ΔDIC > 10). Brett's (1998) primary risk factors and overall recommendation, Adcock, Hansen & Lindemann (1998) and Walker's (1994) hypotheses, and individual characters (e.g. age, sex) were the only models supported (i.e. ΔDIC < 2, Table 2).

The release of young rhino had a particularly strong influence on restocking success. Age featured in all five models receiving substantial support (Table 2), and was the only predictor whose parameter estimate's credible interval did not include zero (Fig. 5). Juvenile females (2–4 years old), young adult males (4–6 years old) and especially dependent calves had elevated post-release mortality rates when used to restock

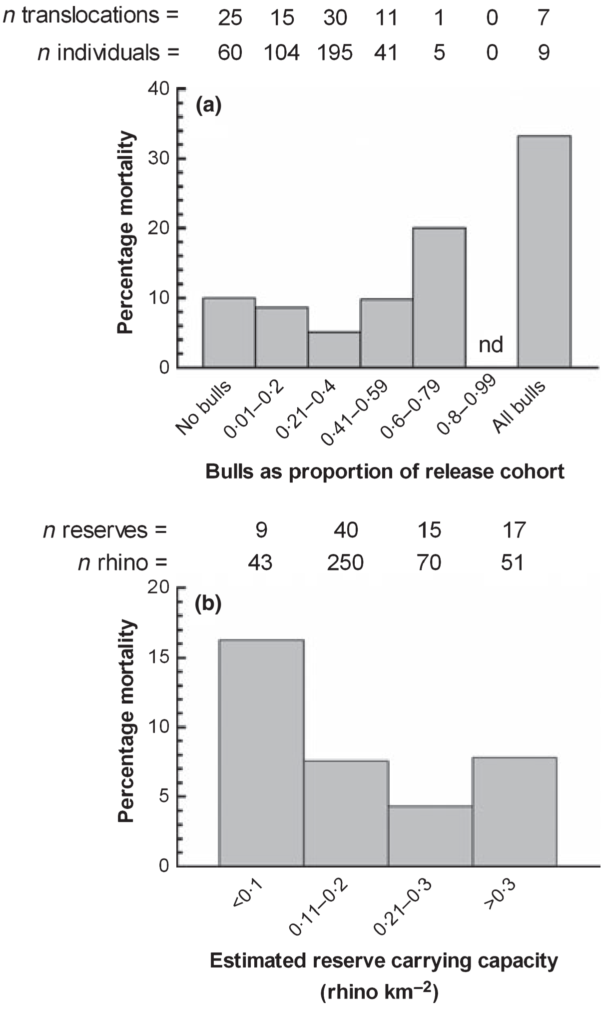

Fig. 4. Mortality (%) in the first year after reintroduction amongst (a) cohorts composed of different proportions of bulls and (b) recipient reserves with different carrying capacity estimates. All-bull reintroductions, particularly as singletons, resulted in higher mortality. Reserves with the poorest habitats had elevated mortality rates. The number (*n*) of translocation cohorts or reserves, and rhino translocated are shown for each category.

populations (Fig. 6b). Most calves (59%), particularly males, died in the first year after release. Comparisons of effect sizes indicate that all other predictors in supported models had a relatively small or no influence on survival probability (Fig. 5). Some can be dismissed because they feature in unsupported models without age (e.g. release cohort size in model 8, resident adult male density in model 23, and reserve size and post-release adult density in model 7, see Table 2), were positive in some models and negative in others (e.g. post-release adult density), their coefficients were very small (e.g. post-release adult density, and reserve area and carrying capacity), or suggested a relationship contrary to that expected from theory. For example, releases into reserves with higher habitat quality (carrying capacity) and lower resident male densities had more deaths. These counter-intuitive outcomes raise doubts about the importance of conspecific density and habitat quality to restocking success. The leading models do not perform better than a model including only age.

Discussion

Intraspecific conflict was commonly associated with post-release death amongst black rhinoceros, consistent with observations of others, e.g. at least 8 of 18 (44%, Adcock, Hansen & Lindemann 1998) and 53% (Brett 1998) of post-release mortalities from intraspecific fighting. Even in source populations, wounds from horns feature in a large proportion of deaths (i.e. 23 of 87 fresh carcasses, Hitchins & Anderson 1983). Moreover, these values do not betray sub-fatal impacts of aggression on body condition, which would explain the increase in deaths attributed to post-release stress after restocking cf. reintroductions (Fig. 2). Conspecific conflict is an important consideration in black rhinoceros population management.

High rates of fight-related death have led others to attribute importance to factors like resident and post-release density (Walker 1994; Brett 1998; Linklater & Swaisgood 2008), especially of bulls (Adcock, Hansen & Lindemann 1998), and reserve size (Walker 1994; Linklater & Swaisgood 2008) and habitat quality (Brett 1998). Survival might be enhanced by translocations to larger, higher quality reserves at lower densities to reduce rates of conspecific encounter, conflict and competition (Walker 1994; Linklater & Swaisgood 2008). Moreover, restocking reserves in which the residents were only recently introduced or that have unoccupied habitat as refuge from dominant and aggressive conspecifics might be favoured because subsequent introductions are met with less aggressive defence of space (Adcock, Hansen & Lindemann 1998). In arriving at these suggestions, however, authors have not differentiated between translocations for reintroduction cf. restocking, although the risks of conflict and competition are particularly associated with restocking (Fig. 2). It is also possible that fight-related deaths are not the primary cause, but a symptom, of translocation failure for other reasons (e.g. poorest habitats or cohorts of vulnerable or dangerous individuals). Conflict might also be unavoidable and difficult to manage directly, but its potential to result in death might be reduced by managing other characters of the release cohort, introduction, or reserve. Discriminating between these possibilities requires the separate treatment of reintroduction and restocking and comparison of representative *a priori* models.

SUPPORTED AND UNSUPPORTED HYPOTHESES

All models for reintroduction success received some support and most substantial support, although the influence of their individual predictors was weak such that no one hypothesis predominated. Most models for restocking success, however, received no support, and the explanatory power of the few leading hypotheses was accounted for by the contribution of a single predictor: age class. Although authors have recommended large release cohorts (Griffith *et al.* 1989; Brett 1998; Wolf, Garland & Griffith 1998; Fischer & Lindenmayer 2000) including individuals that are not predator-, competitor-, or translocation-naïve (Banks, Norrdahl & Korpimaki 2002; Frair *et al.* 2007), and favouring large reserves with low conspecific density (Linklater & Swaisgood 2008) and high-quality

Table 2. Outcomes of 24 candidate models for restocking mortality

Model no.†	Candidate model, hypothesis	pD	DIC	ΔDIC_i
1*	Brett's (1998) primary risk factors	31·4	200·4	0·0
4*	Adcock, Hansen & Lindemann (1998)	27·5	200·5	0·1
6*	Walker (1994)	29·9	200·7	0·3
17	Individual rhino characteristics	27·1	201·0	0·6
3*	Brett's (1998) recommendation	33·7	202·3	1·9
12	Cohort composition – all predictors	41·4	210·5	10·1
10*	Reserve capacity: resources	36·9	213·1	12·7
14	Cohort composition – juveniles	27·4	213·2	12·8
22*	Degree of demographic/social disturbance	36·5	213·3	12·9
19	Ecological similarity of source and recipient reserves	32·4	214·4	14·0
8	Fischer & Lindenmayer (2000)	29·5	215·4	15·0
9*	Griffith *et al.* (1989)	31·1	215·9	15·5
5	Linklater & Swaisgood (2008)/Hitchins & Anderson (1983)	29·1	216·3	15·9
20	Experience of translocation and fenced confinement	30·3	216·3	15·9
15	Cohort composition – dependent calves	31·2	216·4	16·0
7*	Linklater & Swaisgood (2008)	31·3	216·4	16·0
23	Intra-sexual conflict (resident bulls)	29·1	216·5	16·1
13	Cohort composition – bulls	30·4	216·5	16·1
11*	Reserve capacity: space	33·4	216·8	16·4
18	Time since last release	28·1	216·9	16·5
2*	Brett's (1998) secondary risk factors	30·6	216·9	16·5
24	Interspecific conflict	29·2	217·0	16·6
21	Experience of elephant and predators	33·3	217·4	17·0
16	Cohort composition – adult sex ratio	31·1	217·4	17·0

Models are in descending order from most to least supported based on deviance information criteria (DIC).
pD, estimated number of parameters.
*Models include data at multiple levels.
†See Table S2 (Supporting information) for predictors in models.

(Griffith *et al.* 1989; Brett 1998; Wolf, Garland & Griffith 1998) or familiar (Stamps & Swaisgood 2007) habitat, these appeared to be relatively unimportant to black rhinoceros survival after reintroduction and restocking. The potential benefits of large release cohorts for population persistence (Griffith *et al.* 1989; Fischer & Lindenmayer 2000) was also not counteracted by increased competition amongst released individuals.

The unimportance or small effect sizes of most, and especially the more complex models of translocation success, at least in black rhinoceros of Namibia and South Africa, indicates that ecological and demographic factors have weaker influence on post-release survival than previously suggested. This raises the possibility that others have mistakenly attributed importance to complexes of ecological and demographic influences, albeit for strong theoretical reasons, more simply explained by unusual release cohorts (e.g. all male reintroductions and several calves in large cohorts) or single predictors of vulnerability like age. For example, our model comparison indicates that the explanatory power of Brett's (1998) hypotheses and recommendation in Kenya might be largely accounted for by rhino age without recourse to the other predictors. Post-release mortalities are more likely in younger age classes (Brett 1998; Linklater & Swaisgood 2008) less able to defend themselves or escape, and less adept at finding food, water, and cover after release (Adcock, Hansen & Lindemann 1998).

We suggest that respecting the hierarchical structure of the data and employing an information-theoretic approach to *a priori* model selection when data is probably highly inter-correlated and non-independent underlies the simpler conclusions we obtained in comparison with previous efforts. Most release cohort or reserve characters appear to have received erroneous support in conventional analyses relative to individual animal influences (Brett 1998) as expected when the hierarchical structure of the data is not explicitly modelled (de Leeuw & Meijer 2008). Unless hypotheses are compared as *a priori* models, it is not possible to differentiate between biologically real relationships and Type I errors amongst the many correlations that result (Aitkin 1974; Johnson & Omland 2004). Many variables identified as influential by correlation or regression proved spurious (i.e. reserve area, cohort size, adult and adult male resident density, and post-release adult density) or uncertain and, at best, weak (i.e. habitat quality). We expect many currently strongly held opinions about the importance of particular factors in translocation success originate from biologically irrelevant correlations. Complex ecological and demographic models are not necessary to predict black rhinoceros translocation success, at least as measured by post-release survival to 1 year.

PREDICTORS OF TRANSLOCATION FAILURE

Translocation of mothers with dependent calves is ill-advised, especially when restocking. Interestingly, there was a sex-differential risk when using juvenile and young adults to restock populations. These may have important

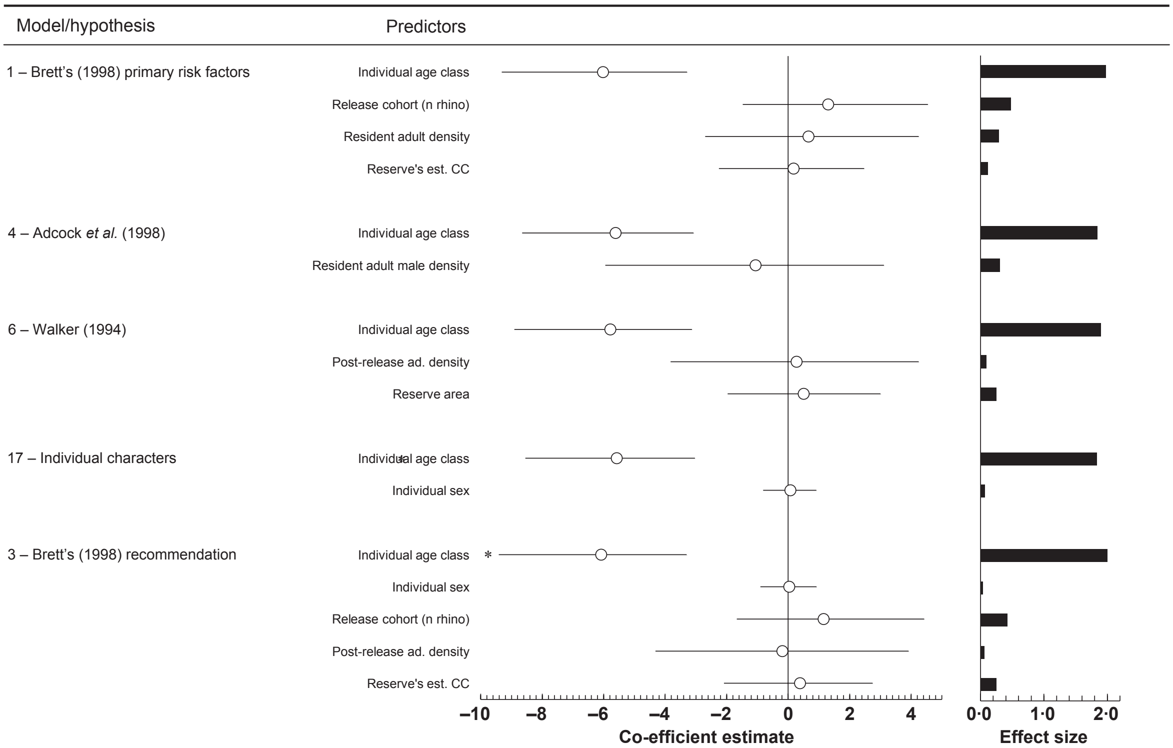

Fig. 5. Parameter estimates from posterior densities and scaled effect size of coefficients for each predictor (see Table S2, Supporting information) in the five hypotheses for restocking success (survival to one year post-release) that received substantial support (i.e. ΔDIC ≤ 2, Table 2). Open circle (○) represents mean parameter (coefficient) estimate and horizontal lines represent their credible intervals. A value of zero indicates that the predictor had no influence on post-release survival, while a positive value indicates a positive relationship between the predictor and mortality. *Only predictor, age, whose credible interval does not include zero. Effect sizes are derived by multiplying each coefficient by two standard deviations of the corresponding predictor and converting to absolute values.

implications for sex- or age-biased translocation strategies designed to reduce the impact of harvest on the source population or maximize productivity after release. Juvenile, but not young adult, females had high post-release mortality. The reverse was true for males where juvenile males did not feature in mortality statistics but were a large portion of young adult deaths.

Sex differential mortality amongst juvenile and young adult age classes might be due to sex differences in age at first reproduction because it is a high-risk period in a large polygynous vertebrate's life. Female black rhinoceros attract the sexual interest of bulls at their first oestrous around 3·5 years of age (first parturition between 4·8 and 5·3 years, Schenkel & Schenkel-Hulliger 1969; and a 1·3-year gestation, Linklater 2007), but males begin challenging bulls as they approach adult size (i.e. 6 years). Thus, a post-release age–sex differential mortality might be the amplification of an existing risk amongst first-time breeders. Age will, therefore, be an additional consideration in attempts at genetic and demographic rescue of small populations by differential sex allocation (Linklater 2003; Law & Linklater 2007), and will diminish the value of harvesting strategies that target younger age-classes (Hearne & Swart 1991).

Age *per se* was not a leading factor in reintroduction success, but calf deaths were higher if several of them were translocated as part of a large cohort, such that dependent calves had subtly poorer survival overall (Fig. 6a). Reintroduced adult males (released mostly as singletons, but also with one or two other males, Fig. 4a) were highly likely to die. Interestingly, this may explain why a role for release cohort size was not supported by our analysis, although others have recommended large cohorts because of an apparently high death rate amongst smaller releases of black rhino, particularly singletons (Brett 1998). Cohorts consisting entirely of males were the most common small reintroductions and so, when the distinction between all-male and mixed-sex reintroductions is not made, small release cohorts appear high risk.

All-male reintroductions have largely been conducted to remove males 'excess' to breeding requirements (e.g. for hunting) and to reduce competition in source reserves, rather than as a strategy for meta-population expansion. Indeed, if managers do introduce one sex first it is usually females to confer resident-advantage over males introduced later – a way of reducing the impact on females of intersexual conflict. All-female reintroductions had low mortality rates, although not lower than reintroductions with a balanced sex ratio. Thus, managers might be better advised to use 'excess' males in restocking for genetic rescue of other small populations. While conflict occurs during restocking using bulls, their survival rates are comparatively high and certainly higher than when moved into small, unoccupied reserves alone or with one or two other bulls.

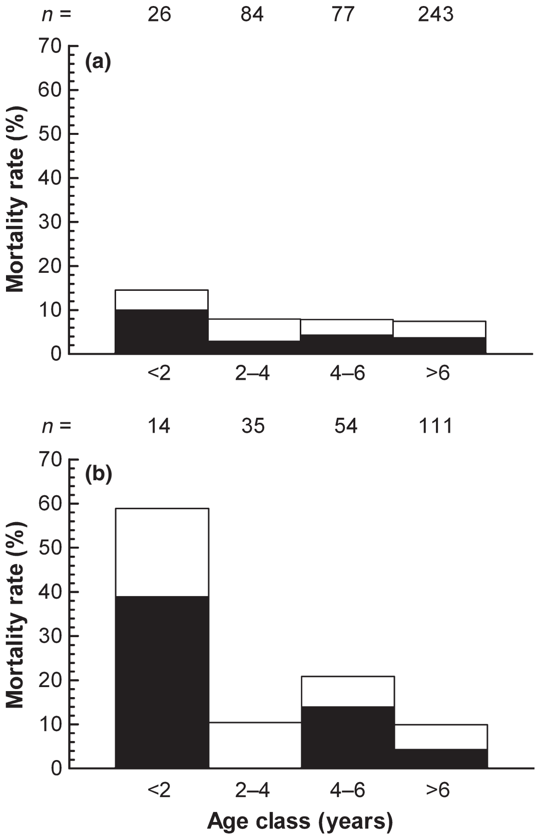

Fig. 6. Male (■) and female (□) mortality (%) in the first year post-release by age classes after (a) reintroduction and (b) restocking. *n*, number of rhino translocated.

No other factors had an influence on reintroduction and restocking success. Nevertheless, a precautionary interest in some weak, albeit inconclusive, predictors may be worth retaining for closer future examination. In particular, a case for greater caution when reintroducing populations to the poorest habitats received ambiguous support. No such ambiguities were associated with the outcomes of the restocking analysis.

This remarkable record of black rhinoceros translocations provides practical insights to biodiversity managers. Achieving high survival in translocations of many species might not be as complicated as the literature leads us to believe. Importantly, our findings should reassure managers planning bold attempts at reintroduction and restocking, at least in the way they have occurred historically. For example, the movement of groups of rhinoceros of different size and composition over varying distance distances between different ecological contexts were similarly successful. The release of cohorts into reserves that are relatively small, poor habitat, or already stocked, need not be avoided so long as the young and all-male cohorts are not released. Nevertheless, post-release survival does not necessarily translate into population growth, particularly for large mammals in which poor conditions are more likely to limit fecundity before survivorship. We would expect different results if translocation success was defined by post-release breeding or population growth and other longer-term metrics of success that involve reproductive investment. Moreover, in this work we confined ourselves to testing existing hypotheses because there were many, rather than explicitly examining for interactions amongst individual predictors. While some predictors might have negligible or weak influence alone, their interaction with another predictor could be important. The next stage should examine predictors for important relationships in a longer-term assessment of translocation success. Lastly, while intraspecific conflict is associated with many post-release deaths it is almost impossible to manage directly. It is probable that conflict cannot be avoided, especially during restocking. Nevertheless, the vulnerability of released animals can be managed to reduce conflict-related deaths. High mortality amongst younger animals, especially calves, and cohorts of adult males after reintroduction, mean that such translocations are ill-advised.

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Supporting Information

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

Fig. S1. Numbers of black rhinoceros *Diceros bicornis* translocated from Namibian and South African reserves, 1981–2005.

Table S1. Previous reports of average post-release mortality rates after multiple translocations of black rhinoceros *Diceros bicornis*.

Table S2. The predictors featuring in each of 24 models representing hypotheses for establishment success (survival to 1 year) after reintroduction and restocking of black rhinoceros *Diceros bicornis*.