Management and Conservation Article

Reserve Size, Conspecific Density, and Translocation Success for Black Rhinoceros

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ABSTRACT Fighting and accidental injury commonly cause black rhinoceros (rhino; *Diceros bicornis*) death after release. Smaller reserves and higher conspecific density after release (release density) might increase a rhino's encounter rate with hazards like fenced boundaries and conspecifics. We conducted a science-by-management experiment on the influence of reserve size and release density on rates of movement, association, and injury and death amongst 39 black rhinos during the first 100 days after their release into 4 Namibian and 8 South African reserves ranging in size from 670 ha to 45,000 ha. Association rates were negatively related to reserve size and positively correlated with release density. There was also a negative relationship between the proportion of the reserve traversed by individual rhinos and reserve size. In reserves $\geq$18,000 ha association rates were consistently zero but became elevated in reserves $\leq$11,500 ha and at release densities $\leq$9 km^2/rhino. Daily displacement did not increase with increasing reserve size >8,500 ha but in smaller reserves daily displacements indicated higher encounter rates by released rhinos with fenced boundaries. Three rhinos received fight-related injuries requiring intervention and 2 of 4 deaths were fight-related. All injuries and 3 deaths occurred in reserves $\leq$11,500 ha. Model selection based on Akaike's second-order Information Criterion indicated that the parameter release density alone best explained mortality risk. Traditionally considered risk factors, rhino sex, age, and presence of resident conspecifics, were superseded by the risk posed by releases into smaller reserves. Reserves $\leq$11,500 ha and release densities $\leq$9 km^2/rhino pose an increasing risk to rhino survivorship and so larger reserves and lower densities than these should be favored as release sites. (JOURNAL OF WILDLIFE MANAGEMENT 72(5):1059–1068; 2008)

Translocation of individuals for population reintroduction or supplementation is a necessary tool in meta-population expansion and management towards species recovery (International Union for the Conservation of Nature and Natural Resources 1998). Translocation is a strategy for spreading the risks of demographic and environmental stochasticity over many populations and managing their genetic health by exchanging potential breeders among them (Hastings and Harrison 1994, Hanski 1998). Translocations, however, are most often unsuccessful (e.g., % successful: 38–86%, Griffith et al. 1989; 19%, Dodd and Seigel 1991; 32%, Snyder et al. 1999; 26%, Fischer and Lindenmayer 2000).

Inter-individual familiarity, size, age structure, and sex ratio of release cohorts (Armstrong et al. 1994*a*, Linklater 2003*a*, Law and Linklater 2007), release timing, duration and technique (Bright and Morris 1994, Letty et al. 2000), prerelease husbandry or training (Biggins et al. 1998, McLean et al. 1999), and taxonomic and conservation status of the species (Wolf et al. 1998) influence translocation success. However, 2 closely related ecological factors have not figured prominently in previous analyses: size of the receiving reserve and conspecific density.

Reserve size can limit or facilitate postrelease movements, dispersal, social interactions, and conflict. A few studies of translocation have examined effects of reserve size (e.g.,

Matson et al. 2004) but none have included detailed postrelease monitoring to understand an animal's behavioral response to release in reserves of different size. Importantly, reserve size also determines conspecific density after a release (i.e., release density).

Recent reviews of translocations have suggested that releasing large numbers of animals is best but the possibility for social conflict, especially amongst relatively asocial species, may rise with increased density (Wolf et al. 1998, Fischer and Lindenmayer 2000). Aggression amongst released individuals or between residents and released animals may substantially compromise recovery programs (Kleiman 1989). Effects might range from minor, such as increased latency to settle and travel distances, to more major consequences such as fight-related injury and death. However, even increased travel is associated with higher mortality rates for many species (reviewed in Stamps and Swaisgood 2007).

That these 2 factors, size of the receiving reserve and conspecific density, have not been considered is surprising given the anecdotal importance attributed to them (Yalden 1993, Clarke and Schedvin 1997, Woodroffe and Ginsberg 2000) and the recent importance attributed to integration of behavior (e.g., postrelease movement and conspecific interaction) and ecology (i.e., reserve size and capacity) in conservation (e.g., Festa-Bianchet and Apollonio 2003). Thus, to improve translocation success it is important to understand effects of release density on rates of social conflict and how smaller reserves may increase exposure to a variety of risks. Gathering the knowledge towards this understanding, however, requires tracking fates of released

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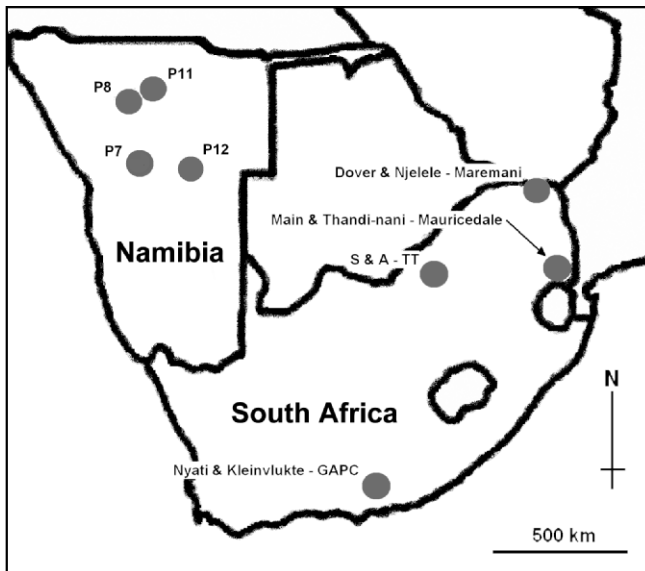
Figure 1. Map of southern Africa showing approximate locations of the 12 reserves into which black rhinoceros were released between March 2002 and August 2003. (For security reasons some reserves are represented by a code in place of the actual name. GAPC = Greater Addo Park Complex.)

animals and designing different releases as comparative experiments (Armstrong et al. 1994*b*). Such science-by-management efforts from translocations are unfortunately rarely achieved (Short et al. 1992).

We describe behavior, injury, and death amongst 39 black rhinoceros (rhino[s]; *Diceros bicornis*) released into 12 reserves of varying size and ecological and social contexts across southern Africa. Black rhinoceros home-range size varies markedly with ecological conditions (e.g., 1.2–133 km^2; Frame 1980, Lent and Fike 2003) and most reserves are small by comparison. Our objective was to begin building an empirical understanding of black rhino post-release behavioral ecology that might be used to assist

population managers in better treating the problem of black rhino mortality after release (e.g., Brett 1998). We hypothesized that larger reserves and lower conspecific densities would reduce frequent and forced encounters with other rhinos and other hazards such as fenced boundaries. We predicted that somewhere on the continuum between the largest and smallest reserves currently receiving rhinos, postrelease movements and associations of released rhinos would reveal the minimum ideal release density and size of reserves to receive them.

STUDY AREA

The study included releases into 12 fenced reserves that varied in size from 670 ha to 45,000 ha (Fig. 1; Table 1). To ensure rhino population security we have assigned some reserves a code and not revealed their exact locations. All reserves receiving black rhinos had historically been livestock farms and their climates dominated by a cold–dry winter and warm–wet summer. Rainfall was strongly seasonal in southern Africa with most falling between early spring (Sep) and mid-autumn (Apr). Nevertheless, the geographical spread of reserve locations from northern and central Namibia through to southeastern South Africa meant their climate and vegetation differed within this general pattern. Reserves in Namibia and northern South Africa were arid and semiarid landscapes with savannah vegetation, tending to denser and larger stature woody species at lower altitudes and in the higher rainfall regions of eastern South Africa, and giving way to succulent thicket vegetation in the wetter southeast.

METHODS

We used the existing meta-population management programs of 2 government conservation agencies in South Africa (i.e., Ezemvelo KwaZulu-Natal Wildlife [EKZNW] and South Africa National Parks [SANP]) and another in

Table 1. The sizes (ha), vegetation types, and elevation (m) and rainfall (mm) ranges of the 12 Namibian or South African reserves into which 39 black rhinos were released between March 2002 and August 2003, the size, sex, and age composition of the release cohort and resident population, and overall conspecific density after release (release density, rhinos/km^2).

Subspecies of *D. bicornis*	Reserve name or code[a]	Reserve size (ha)	Vegetation type	Elevation[b] (m)	Rainfall (mm)	Resident ad population size	Rhinos released	Release density (rhinos/km^2)
minor	Thandi Nani-Mauricedale GR	670	Lowveld forest	268–458	750–1,000	1 M[c]	1 M, 3 F, 1 calf	0.75
bicornis	Kleinvlakte-GAPC	744	Valley thicket	162–271	500–750	none	1 M, 2 F	0.40
minor	Main-Mauricedale GR	2,500	Lowveld forest	269–505	750–1,000	1 M, 3 F[c]	2 M	0.24
michaeli	S-TT	3,600	Arid savannah	971–996	500–750	10 M	1 M	0.31
bicornis	P12	5,600	Arid savannah	1,640–1,709	250–500	none	3 F, 3 M	0.11
bicornis	P11	11,500	Arid savannah	1,083–1,106	250–500	1 M	3 F, 2 M	0.05
minor	Dover-Maremani GR	18,000	Arid savannah	428–571	250–500	none	2 F, 2 M	0.02
minor	Njelele-Maremani GR	20,000	Arid savannah	454–559	250–500	2 M, 3 F	2 F	0.035
michaeli	A-TT	30,000	Arid savannah	906–1014	500–750	2 M, 6 F[c]	2 F, 2 calves	0.03
bicornis	P8	35,000	Arid savannah	1,119–1,245	250–500	5 M, 5 F	1 F, 1 calf	0.03
bicornis	Nyati-GAPC	40,855	Valley thicket	174–562	500–750	1 M, 4 F	3 M	0.02
bicornis	P7	45,000	Arid savannah	1,360–1,539	250–500	4 M, 5 F	1 F	0.02

[a] For security reasons some reserves are represented by a code in place of the actual name. Abbreviations: GR = Game Ranch or Reserve; GAPC = Greater Addo Park Complex.

[b] Altitudinal range over which we observed rhinos during monitoring.

[c] Resident ad M were removed from the population before release of additional rhinos and some were released back into the population 1–4 months later.

Namibia (Ministry of Environment and Tourism [MET]) during 2002 and 2003 as an experiment in the relationship between reserve size, release density, and black rhino sociality and movement after release. Translocations involved the sale or donation for custodianship of black rhinos from large government-owned reserves like Etosha National Park, Namibia, and Hluhluwe-iMfolozi Park, South Africa, to private farms or conservancies or the transfer of rhinos from one conservation agency's reserve to another (i.e., MET to SANP). Two reserves received black rhinos of the eastern (*D. b. micheali*), 4 of the southeastern (*D. b. minor*), and 6 of the southwestern (*D. b. bicornis*) subspecies (Table 1).

Capture, transportation, veterinary care, and husbandry of black rhinos varied somewhat between sites but conformed to standard procedures (Rogers and McKenzie 2001) previously applied widely (Hofmeyr et al. 1975, Hitchins 1984, Geldenhuys 1991, Kock 1992, Morkel 1994, Linklater et al. 2006). We aged individuals at capture using Hitchen's (1978) size-class criteria. We installed MOD-80 or the larger MOD-125 horn-implant transmitter (Telonics, Inc., Mesa, AZ) in adults depending on the size of their horn. Installation of horn-implant transmitters occurred either while the rhino was already immobilized at capture or while it was in boma (i.e., on-site prerelease enclosures) and conformed to procedures described previously (Pienaar and Hall-Martin 1991, Shrader and Beauchamp 2001). Releases were conducted at dusk with one rhino released/day over consecutive days by simply opening the door of their boma. We applied appropriate animal care and use (Institutional Animal Care and Use Committee approval no. 169).

We monitored the postrelease movements and social behavior of 39 (34 ad) black rhinoceros released (Table 2). Black rhinos are crepuscular, most active around dawn and dusk, tending to sleep during the middle of the day when it is hottest, and move most overnight between early evening and late morning (Joubert and Eloff 1971). Thus, to quantify and compare amounts of movement between different rhinos on different reserves, we designed a sampling regime to measure animal displacement between 2 locations on consecutive days, which we called daily displacement.

To ensure comparable information between rhinos, we selected individuals at random without replacement until each rhino released into a reserve had been located before selecting again from the population of released rhinos. If a search failed to find a rhino then that rhino became a priority for subsequent days until we found it. We determined rhino locations using radio signal strength and direction to obtain a visual sighting or by triangulation. For triangulation we took ≥ 2 and more often 3 or 4 and up to 6 bearings from recorded locations to estimate the rhino's position without a visual sighting. We estimated rhinos' locations from triangulation using Locate II software (2000; Pacer Ltd., Truro, Nova Scotia, Canada). Triangulation has the advantage of minimizing observer disturbance. To maximize the frequency with which measures of daily displacement were made, we located each randomly selected rhino every day for 3–6 consecutive days, providing a sequence of visual sightings and triangulated locations.

We used the data to generate 2 metrics of rhino movement: 1) distance traveled on the first day after release, and 2) largest daily displacement recorded during several time intervals in the first 100 days after release. When interpreting daily displacement relative to reserve size it is important to know that a distance between 2 locations on consecutive days provides a minimum estimate of the distance traveled by a rhino between those 2 consecutive points and, therefore, is only an index of how much the individual might have encountered potential hazards. Actual movements are probably larger, particularly in small reserves where a rhino found at opposite ends of the reserve on consecutive days may have traveled across that reserve and met the fenced boundary more than once.

The probability of a newly released rhino having an aggressive interaction with a conspecific is determined by the rate at which it encounters and associates with other rhinos. We estimated rates of association between rhinos released into reserves of different size as the proportion of occasions that we observed each rhino with another rhino in proximity. The rule-of-thumb adopted for the definition of proximity was that if the observer could see another rhino while observing the focal rhino then those rhinos were regarded as proximal to each other. This rule-of-thumb worked well because dense vegetation prevented long-distance visibility on most occasions. When 2 rhinos were proximal, we estimated the distance between them and categorized it into 0–1, 1–3, 3–6, 6–10 or >10 rhino body-length intervals. On rare occasions when visibility was better, we sometimes observed other rhinos at greater distances such that we placed the distance between the individuals into a <200-m or 200–300-m category. We used distance categories and rhino body-lengths as units of measure to reduce errors associated with estimating distance on a continuous scale of primary units. On other rare occasions vegetation was so dense that we could not see one of the rhinos and so we could not estimate the distance between them. Nevertheless, we knew that another rhino was proximal to the visible rhino because we were receiving a radio signal with strength ≥ 5.0 Gain from the unseen rhino. Correlations between radio signal strength and actual distance to the rhino for those whose location was known indicate that a radio signal strength of ≥ 5.0 equates to a distance <234 m or, on average, 86 m ($n = 9$; W. L. Linklater, Victoria University of Wellington, unpublished data).

We tested the nonlinear negative relationship between reserve size and association rate using logarithmic regression. We used Pearson correlations to test relationships between release density and inter-individual association and between the largest distance possible to travel across each reserve and the proportion of that distance actually achieved by each rhino, because they are continuous variables. We grouped daily displacements into periods of time (days) on

Table 2. Reserve name and sex, age, and release date of the 39 black rhinos monitored after release into 12 reserves in Namibia and South Africa, between March 2002 and August 2003.

Reserve name or code[a]	Rhino identification no.[b]	Sex	Age[c]	Release date	Fate
Thandi Nani-Mauricedale GR	8	F	F	21 Nov 2002	Injured Jan 2003
Thandi Nani-Mauricedale GR	12	F	F	19 Nov 2002	Injured Dec 2002
Thandi Nani-Mauricedale GR	15	F	F	19 Nov 2002	
Thandi Nani-Mauricedale GR	44	F	F	20 Nov 2002	
Thandi Nani-Mauricedale GR	10	M	F	11 Dec 2002	
Thandi Nani-Mauricedale GR	00[d]	M	B	20 Nov 2002	Died 14 Feb 2003
Kleinvlakte-GAPC	60	F	F	20 May 2003	
Kleinvlakte-GAPC	40	M	F	20 May 2003	
Kleinvlakte-GAPC	11	F	D	20 May 2003	
Main-Mauricedale GR	1	M	E	19 Nov 2002	
Main-Mauricedale GR	8	M	F	20 Nov 2002	
S-TT	33	M	4	10 Jun 2003	Injured Jul 2003
P12	2	F	3	23 Mar 2003	
P12	10	F	3	3 Apr 2003	
P12	15	F	4	31 Mar 2003	
P12	1	M	2.5	21 Mar 2003	
P12	36	M	12	30 Mar 2003	Died 7 Oct 2003
P12	50	M	3	25 Mar 2003	
P11	0	F	D	Apr 2002	Died 28 Apr 2002
P11	1	F	F	24 Apr 2002	
P11	2	F	F	24 Apr 2002	
P11	31	F	F	23 Apr 2002	
P11	0	M	F	Apr 2002	
Dover-Maremani GR	56	F	F	6 Aug 2003	
Dover-Maremani GR	72	F	E	6 Aug 2003	
Dover-Maremani GR	0	M	F	6 Aug 2003	
Dover-Maremani GR	10	M	F	6 Aug 2003	
Njelele-Maremani GR	6	F	F	6 Aug 2003	
Njelele-Maremani GR	21	F	F	6 Aug 2003	
A-TT	50	F	12	10 Jun 2003	
A-TT	4	F	9	15 Jun 2003	
A-TT	33	F	1.5	15 Jun 2003	
A-TT	11	F	1	10 Jun 2003	
P8	12	F	F	18 Apr 2002	
P8	13	F	C	18 Apr 2002	Died 8 Apr 2002
Inyati-GAPC	60	M	F	20 May 2003	
Inyati-GAPC	12	M	F	30 Jun 2003	
Inyati-GAPC	01[e]	M	3	8 Jun 2003	
P7	40	F	E	27 Apr 2002	

[a] For security reasons some reserves are represented by a code in place of their actual name. Abbreviations GR = Game Ranch or Reserve; GAPC = Greater Addo Park Complex.

[b] Ear notch no.

[c] We estimated age either in yr as of 1 Jan 2003 or age class (A is <6 months, B is 6–12 months, C is 1–2 yr, D is 2–4 yr, E is 4–6 yr, and F is >6 yr old, after Hitchins 1978).

[d] Calf of 44; Thandeka, born in the boma and released with its mother.

[e] This young male was confined to a smaller part of the Inyati reserve. His release into the larger reserve occurred when fences were removed. His release date is when he was first observed to cross the historical boundary.

an ordinal scale (1–5, 6–15, 16–25, 26–40, 41–70, and 71–100) after release to examine the relationship between minimum, average, and maximum daily displacement and time since release using a Spearman rank correlation.

We adopted an information-theoretic approach to testing hypotheses about the cause of injuries and mortalities after release (Whittingham et al. 2006). In compiling our candidate models we began with the understanding that sex, age, and presence of resident conspecifics have previously been strongly implicated in mortalities after release and we adopted all three as our starting model (Brett 1998). Secondly, we considered whether the new variables of reserve size and release density, together or alone, performed better than our starting model. Lastly, we considered whether reserve size and release density, singularly or together, improved the fit of the starting model. These hypotheses are numbered in sequence and listed as candidate models (Table 3). We conducted all procedures using SPSS version 14.0.0 (SPSS, Inc., Chicago, IL) to generate log-likelihood ratios and calculate Akaike Information Criterion for each model in the way described by Burnham and Anderson (2002). We used a second-order Akaike's Information Criterion (AIC_c) as our information-theoretic statistic because model and sample size were small (i.e., $n = 39$ rhinos with from 1 to 5 explanatory variables [K] such that $n/K < 40$; Burnham and Anderson 2002). We judged the relative power of candidate models by comparing their AIC_c and ratios of Akaike weights (w_i). Models with lowest

Table 3. The 7 candidate models for mortality risk amongst 39 black rhinos released into 12 southern African reserves between March 2002 and August 2003. The rationale sequence for candidate models is indicated by the model number but the models are in descending order based on the second-order Akaike's Information Criterion (AIC$_c$).

Model no.	Candidate models[a]	K[b]	AIC$_c$	ΔAIC$_c$	Akaike wt
2a	release density	1	34.713	0	0.430
3a	sex, age, resident conspecifics, and release density	4	36.453	1.740	0.180
2b	reserve size	1	36.662	1.949	0.162
2c	reserve size and release density	2	36.922	2.209	0.142
3c	sex, age, resident conspecifics, release density, and reserve size	5	38.970	4.257	0.051
1	sex, age, and resident conspecifics	3	41.043	6.330	0.018
3b	sex, age, resident conspecifics, and reserve size	4	41.309	6.596	0.016

[a] Sex was the categorical variable M or F. Age class was the categorical variable juv (<5 yr age or classes A, B, C, or D) or breeding age (≥5 yr old or age class E or F). Age classes: A is <6 months, B is 6–12 months, C is 1–2 yr, D is 2–4 yr, E is 4–6 yr, and F is >6 yr old, after Hitchins (1978). Residents present was the categorical variable as to whether conspecifics were already resident in the reserve before release. Reserve size was in ha. Release density was black rhinos/km^2 after release including both released and resident conspecifics.
[b] No. of estimating parameters in candidate model.

AIC$_c$ have most support from the data. Relative support between candidate models was the difference between each model's AIC$_c$ and the minimum value from all models (ΔAIC$_c$). We considered models with ΔAIC$_c \leq 2$ to have compelling support from the data and models with ΔAIC$_c > 10$ to have no support (Burnham and Anderson 2002).

RESULTS

We obtained from 1 to 40 measures of daily displacement ($\bar{x} = 15$/rhino) from 31 of the 34 adult rhinos through sequential visual sightings or triangulation during the first 100 days after their release. We obtained from 4 to 66 visual observations ($\bar{x} = 22$/rhino) from 27 of the 34 adult rhinos to measure conspecific proximity and association rates during the first 100 days after release. Records for individual rhinos varied for the 2 measures of daily displacement and association for several reasons, including the early failure of the radiotransmitter (e.g., F 11 of Kleinvlakte-Greater Addo Park Complex [GAPC], M 00 of P11, and M 00 of Dover-Maremani; Table 2), dense vegetation (e.g., thicket valley–bushveld vegetation in Kleinvlakte and Nyati of the GAPC; Table 1), simultaneous translocations on distant reserves (e.g., to P7, 8 and 11; Table 1), and, in one case, unexpected restrictions on researcher activity (e.g., P12; Table 1). We excluded individuals from association analyses if we sighted them on <5 occasions.
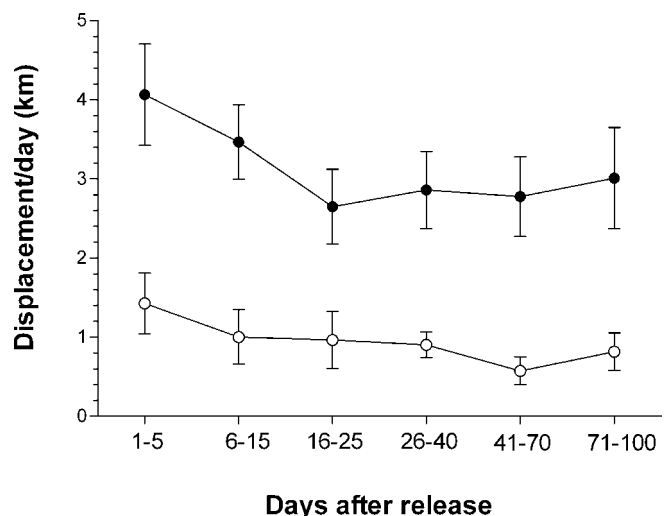
Daily Displacement

Average minimum and maximum daily displacement by released rhinos was highest during the first 5 days (min. 1.4 ± 0.38 km/day, max. 4.1 ± 0.64 km/day) and declined thereafter (Fig. 2). Movements appeared to stabilize at a lower level after 15 days but variance remained high with values of daily displacement ranging from 0.0 km to 15.1 km. Thus, the decline in daily displacement was weak (Spearman's rank correlation of average daily displacement, $r = -0.15$, $n = 116$, $P = 0.105$). Twenty-five days after release variability in the values of minimum daily displacement had declined, perhaps indicating that most rhinos had settled into a routine or established a relationship with a particular site by that time. Maximum values of daily
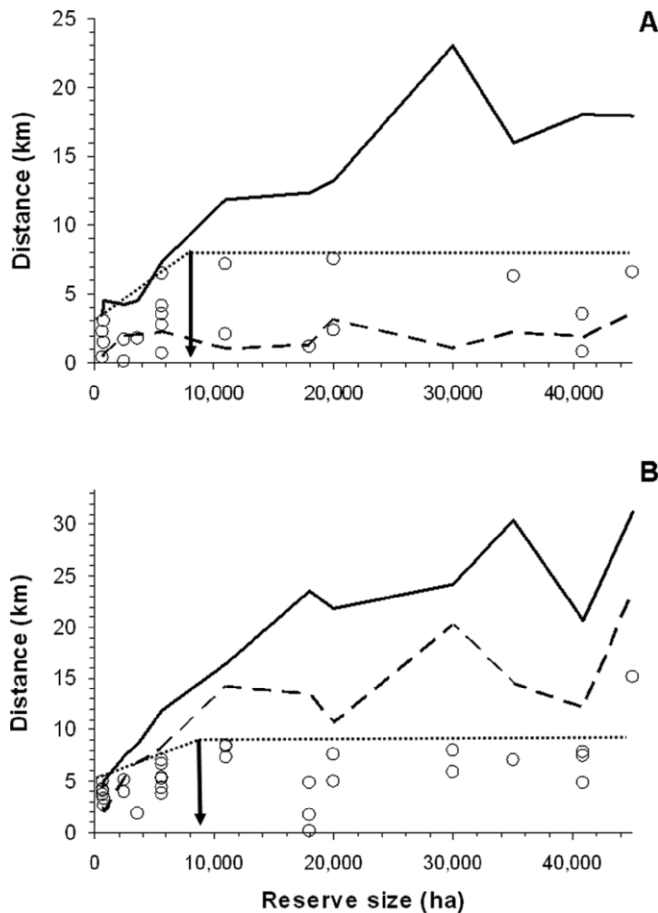
displacement were more variable and consistently variable throughout the first 100 days after release.

The largest displacement during the first night after release was 7.54 km by female 21 on Njelele (Maremani: 20,000 ha). In the largest reserves maximum displacements on the first day were intermediate between the release site and the greatest distance to the opposite fence. In smaller reserves the first day's displacement was similar to the distance between the release site and the opposite fence (Fig. 3A). First-night movements were restricted by the fenced boundary in reserves smaller than approximately 8,000 ha. In reserves >8,000 ha rhinos' displacement on the first day was less than the distance to the furthest fence-line and, therefore, it is much less likely that rhinos encountered the fence during the first night after release.

The largest daily displacement recorded during the first 100 days after release was 15.1 km for female 40 on P7. However, her single overnight movement on that particularly large reserve (45,000 ha) was exceptional. At other
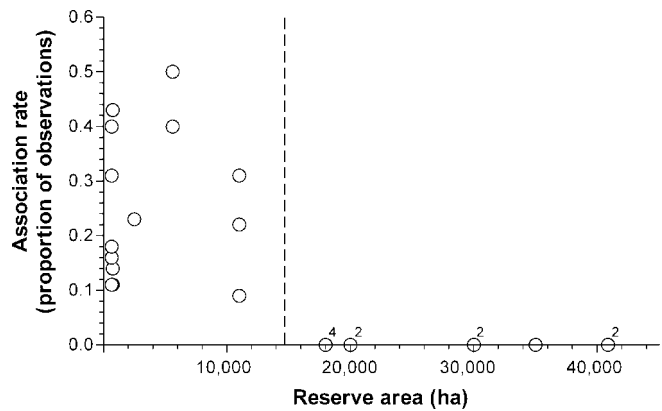

Figure 2. Average minimum (○) and maximum (●) values of daily displacement (km/day ±1 SE) by 39 black rhinoceros during subsequent periods of time up to 100 days after release into 12 reserves across southern Africa between March 2002 and August 2003.

Figure 4. The association rate (portion of observations proximal to another conspecific) by 39 black rhinoceros during the first 100 days after release between March 2002 and August 2003 into reserves of different size (ha). Numbers adjacent to some data points denote the number of individuals that each point represents where data points exactly overlap.

Figure 3. Postrelease movements of 39 black rhinoceros relative to the boundaries of 12 southern African reserves of different size (ha) between March 2002 and August 2003: (A) distance (km) traveled on the first night after release, and (B) largest daily displacement (km) by individual black rhinos during the first 100 days after release. The solid line in A represents the greatest distance between the release site and reserve boundary and in B the greatest distance across each reserve. The dashed line in A represents the shortest distance between the release site and the reserve boundary and in B the shortest distance across the reserve perpendicular to its longest axis. The dotted line indicates the largest movements across reserves of different size and the arrows the reserve size above which movement appears no longer to be limited by fenced boundaries.

times she and other rhinos did not exceed around 8 km/day (Fig. 3B). There was a negative relationship between the greatest distance that it was possible to travel across each reserve and the largest proportion of that distance actually achieved in a day by each rhino during the first 100 days after release (Pearson correlation, $r = -0.71$, $n = 29$, $P < 0.001$). In the largest reserves maximum daily displacement did not approach the greatest distance that it was possible to travel across the reserve between fenced boundaries. Moreover, maximum daily displacements did not exceed the shortest distance across the reserve. In comparison, maximum daily displacements in smaller reserves (<8,500 ha) approached, and in very small reserves (<3,000 ha) exceeded, those distances or metrics of reserve size. Reserves smaller than approximately 8,500 ha constrained rhino movements, whereas on larger reserves movements appeared to be constrained less by fenced boundaries.

Conspecific Association

Proximity on most occasions (72 of 94 measures of inter-individual distance; i.e., 77%) meant that rhinos were within 10 body lengths (approx. 30 m) of each other. We saw some ($n = 14$) at a greater distance (<300 m) and we could not estimate 8 inter-individual distances due to poor visibility in thick vegetation. Nevertheless, due to the strength of the nearby but unseen rhino's signal we can be certain that it was within 234 m and on average approximately 86 m from the position of the observers and, therefore, the visible rhino.

Rates of association by individual rhinos with others in the population ranged from zero to 0.50 associations per observation. That is, for up to half of the occasions that we visually sighted a rhino, ≥1 other rhino was proximal to it (Fig. 4). All associations observed between rhinos were temporary (i.e., we did not observe a rhino more than twice with the same other rhino in a sequence of observations) with one exception. We observed female 40 with male 30 on 11 consecutive sightings over 37 days, a period that culminated in a mating. Because this high rate of association was clearly associated with reproductive activity, we removed this outlier from the analysis.

There was not a simple linear relationship between reserve size or release density and association rates. Rather, we never observed rhinos released in reserves ≥18,000 ha and at densities >20 km²/rhino or <0.05 rhino/km² associating with other rhinos during the first 100 days after release (Fig. 4), but in smaller reserves (≤11,500 ha) association rates were elevated (logarithmic regression, $F_{1,23} = 12.3$, $r^2 = 0.35$, $P = 0.002$). Thus, there was also a positive relationship between the density of rhinos after release (range 0.02–0.75 rhinos/km²) and association rates on each reserve (Pearson correlation, $r = 0.78$, $n = 10$, $P = 0.008$).

Injury and Death

Injuries and mortalities from fighting were more common in the smaller reserves (Table 2). Reserve managers intervened

successfully in 3 cases of fight-related injury to young male 33 on S-TT and females 12 and 15 on Thanda Nani (Mauricedale; Tables 1 and 2). The calf of the female released on P8 was also killed, 5 days after they were released together, during conflict with another rhino. One male was killed by another on P12 133 days after their release. Almost all (6 of 7) injuries requiring intervention or deaths occurred in reserves ≤11,500 ha. Of the 5 mortalities or interventions to rescue animals with fight-related wounds 4 occurred on reserves ≤5,600 ha that had postrelease densities ≥0.11 rhino/km^2 (or ≤9.1 km^2/rhino) compared with 0.02–0.05 rhino/km^2 (or 20–50 km^2/rhino) in larger reserves (≥11,500 ha). We could not reliably attribute to conflict 2 other mortalities. One female drowned in a swimming pool 4 nights after release (F 00, P11) and a calf with an infected injury, perhaps from thorns or wire, drowned in a pond (M 00, Thanda Nani). Of the 4 mortalities, 3 were juveniles or calves still with their mothers when translocated. Overall, reserves ≤11,500 ha had a 27% injury or mortality rate (6 of 22 rhinos) compared with a 6.3% rate (1 of 16) for reserves ≥18 000 ha.

Both reserve size and release density individually provide more parsimonious and superior inference than our starting model that included rhino sex, age, and resident conspecifics as explanatory variables (Table 3). However, the model including only the parameter release density provided strong inference having both substantial levels of empirical support (i.e., Δ_i AIC$_c$ < 2) and greatest parsimony (i.e., $K = 1$; Table 3). Mortality risk was not better predicted by the combination of release density with reserve size, indicating that these variables are strongly correlated. There was also empirical support for a larger model incorporating the traditionally considered variables: sex, age, and presence of resident conspecifics in combination with release density (i.e., Δ_i AIC$_c$ <2; Table 3).

DISCUSSION

Postrelease Behavior and Settlement Time
Daily distances traveled after releases were highly variable; this appears to be a consequence of 2 contrasting responses by rhinos to release. Rhinos responded to release by secreting themselves in dense vegetation for several days during which time they moved very little from day to day, in what is best described as hiding. At other times rhinos traveled widely in what may function as searching, avoidance, or flight behavior. This finding is consistent with the bimodal nature of the stress response and previous observations about individual variability in the reclusiveness of black rhinos. Animals may demonstrate a fight–flight response or engage in a passive conservation–withdrawal response to stress with implications for survival (Moberg and Mench 2000, Banks et al. 2002) and black rhinos are variously sedentary or wide-ranging in their movements after release (Hamilton and King 1969). Differences between rhinos in which mode forms their initial response to release suggests that temperament may play a role in responses to the stress of novel environments.

Nevertheless, the average, although weak, decline in minimum distances traveled indicates that rhinos generally began showing signs of settlement within 15 days after release and that the initial settlement process was complete within 25 days. Ongoing variability in maximal movements might indicate, however, that other components of the settlement process were not complete after 100 days or that the variability in movements observed is typical of black rhinos. For example, rhinos may spend several days doing little traveling while they use and perhaps exhaust a resource patch, but then undertake sporadic lengthy travels to locate a new resource patch. Observations of movements by endemic or locally born rhinos compared to newly released rhinos will be required to understand when postrelease movement behavior converges with a rhino's behavior in less managed contexts.

Reserve Size and Release Density
Given enough physical and social space black rhinos will establish themselves in new reserves without accident or conflict with conspecifics. At least for the first 100 days after release and with the exception of new breeding relationships, rhinos appear to actively avoid other rhinos—probably a behavioral response to minimize conspecific encounters and conflict. The tendency for rhinos released into lower densities and larger reserves to avoid being with other rhinos suggests that the high rates of association in smaller reserves are forced upon the rhinos by smaller reserve size and higher conspecific density. Rather than a simple linear relationship of decreasing association rates with increasing reserve size or lower population density, there appears to be a threshold somewhere between reserves 11,500 ha to 18,000 ha in size and population densities between 0.05 and 0.11 rhinos/km^2 (or 9.1 to 20 km^2/rhino) when association rates become elevated.

Importantly, we also observed a reserve size threshold around 8,500 ha for rhino movements relative to the reserves' boundaries. In reserves <8,500 ha daily displacements indicate that released rhinos were probably regularly encountering the fenced boundary and modifying their movements accordingly. Rhino daily displacement did not increase with increases in reserve sizes >11,500 ha where the size of the reserves ensured that the distance across the reserve and from the release site to the reserve's furthest boundary were ≥10 km. Thus, such large reserves appear not to constrain rhinos' postrelease movements. There appears to be a self-imposed limit to how far a rhino will travel after release when movements are unconstrained. Conservative movement behavior by rhinos when released into large reserves, particularly without resident conspecifics, might explain why rhinos tend to establish ranges adjacent to the release site and are comparatively slow to expand or shift those ranges and so colonize new habitat in some reserves (Hamilton and King 1969, Lent and Fike 2003).

The greatest risks are indicated for reserves <11,500 ha because released rhinos appear unable to avoid each other, and particularly for reserves <8,500 ha because their movements after release inevitably challenge the reserves'

most distant boundaries. That the candidate model including only release density provided strongest and most parsimonious inference for mortality risk supports this conclusion. Moreover, the difference between this simple model and the starting model (i.e., sex, age, and presence of resident conspecifics) was substantial (i.e., ratio $w_i \geq 23.9$).

Importantly, reserve size and release density models performed better individually than the starting model based on the previous expectation that the interaction of sex and age, and presence of resident conspecifics were the greatest risk factors in postrelease death (Brett 1998). Although young female rhinos, and reserves with resident, particularly mature male, conspecifics also contributed disproportionately to our injury and mortality statistics, mortality risk was better explained by release density. This does not contradict Brett's (1998) conclusion that young rhinos are more vulnerable, particularly if released into reserves that already have a resident population, but it does indicate that these risk factors are secondary and exacerbated by being confined in smaller reserves at higher density. The preponderance of juveniles amongst the deaths is a reminder that translocating juveniles or mothers with calves is also ill-advised (Emslie and Brooks 1999). Translocations into small reserves, particularly if they introduced juveniles, were less successful.

Although private properties that have received black rhinos in the past averaged 16,333 ha, 5 of the 13 properties (38%) reported by Hall-Martin and Castley (2003) were <10,000 ha. A few particularly large reserves can make the average reserve size receiving black rhinos look better than the actual distribution of participating reserves. Reserve size averaged 17,789 ha in our study, which appears a reasonable size for minimizing risk, but half ($n = 6$) of the contributing reserves were <12,000 ha and 4 (33%) were <5,000 ha. Hall-Martin and Castley (2003) and Brett (1998) report large differences in the longer term performance of the 13 and 9 populations they describe, respectively, which they attributed primarily to the reserves' different ecological carrying capacities. Ecological carrying capacity is a function of vegetation suitability and productivity and reserve size, and resource availability to rhinos is a function of conspecific density. Measuring ecological carrying capacity requires expertise, is time-consuming and expensive and, therefore, more often than not crudely estimated, if at all (Emslie and Adcock 1994). Moreover, even if carrying capacity estimates are realistically achievable they may not be useful in the dynamic semiarid habitats of southern Africa (McLeod 1997). Reserve size and release density for recently reintroduced populations, however, are always known. Thus, it would have been interesting, and potentially useful, to know whether and to what degree the performance of historically reintroduced populations could be explained by reserve size and release density. Determining the influence that these variables have on longer term population performance is an important next step to choosing wisely between reserves for receiving black rhinos. At least for the first 2 years after release when casualties from fighting and accident are elevated, reserve size and conspecific density may have greater pragmatic value than the empirically elusive concept of ecological carrying capacity for predicting population performance.

Source populations of black rhinos are sustained at higher densities than those we monitored after release (i.e., up to 0.7–1.6 black rhinos/km²; Goddard 1969, Hitchins and Anderson 1983, Conway and Goodman 1989) but without such high rates of fight-related death. The behavioral system for social spacing and avoiding escalated conflict in rhinos takes time to establish after release and so the rate of injurious aggression and conspecific-inflicted mortalities are much higher among newly translocated individuals (see also Brett 1998). The critical factor contributing to the high levels of conflict appears to be lack of familiarity with the environment including its conspecifics. We speculate that larger less-populated reserves enable reintroduced rhinos to initially avoid one another and gradually become familiar with the environment and conspecific neighbors until they have established social and spatial relationships more similar to those found in stable rhino populations.

Ours is the first published report of a comparative behavioral study of multiple translocation and releases of varying success that includes 3 of the 4 black rhino subspecies as subjects. There has been an absence of such geographically wide-ranging and taxonomically encompassing studies of black rhino behavior, ecology, and management (Linklater 2003b). Although, our sample size (12 sites and 39 black rhinos) is statistically small where a multitude of factors influence postrelease behavior and mortality, our study is nonetheless the largest study of its type to date by an order of magnitude. Previously only single-site or anecdotal (Raath and Hall-Martin 1989), rather than experimental or comparative, studies have been conducted, or studies comparing different populations have been limited to data gathered through retrospective and remote questionnaires (Hall-Martin and Castley 2003).

MANAGEMENT IMPLICATIONS

Traditionally considered risks to survival posed by rhino age, sex, and already resident conspecifics can be ameliorated by favoring translocations to large reserves. Reserves ≤11,500 ha pose an increased risk to rhino survivorship due to increasing rates of encounter by the rhino with the key hazards associated with postrelease mortality—artificial hazards like fences and other rhinos. Reserves >11,500 ha and densities after release <0.11 rhino/km² (>9 km²/rhino) should be favored for black rhino introductions. For best results, encounter rates with other rhinos or the reserve's boundary can be reduced to lowest possible levels if the receiving reserves are ≥18,000 ha and there is, on average, <0.05 rhino/km² (>20 km² available/rhino). Intensive postrelease monitoring, of the type described here, and intervention strategies should be planned in advance of a release, particularly for small and densely populated reserves to quickly identify fight-related injuries and enable immediate intervention.

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