

Black rhinoceros are slow to colonize a harvested neighbour's range

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Live-harvests from source populations for translocation are key to rapid recovery for many species. Contrary to common assumption, however, reduced density might not immediately improve vital rates because animal recolonization is slow – creating management uncertainty about harvest adequacy or sustainability. Reports measuring animal recolonization are rare. We measured the response of the 19 same- or opposite-sex neighbours of 11 live-harvested black rhinoceros (*Diceros bicornis minor*) in Hluhluwe-iMfolozi Park, South Africa, by comparing the size and location of their activity areas for an average two years before and after harvest. The only significant change was a decolonization response by opposite-sex neighbours, especially males after the harvest of a female neighbour. Recolonization of habitat after harvest, at least by neighbours, might not just be slow but also further delayed by the disruption of long-standing breeding relationships with important implications for the spatial pattern and frequency of harvest.

Key words: decolonization, density-independence, *Diceros bicornis*, harvest, source population, translocation, ungulate.

INTRODUCTION

Density-independent (exogenous), as well as dependent, factors influence population growth but are rarely demonstrated or incorporated in population management. Exogenous influences might be especially influential in the populations of large animals with slow life-histories and ramp-like (McCullough 1992) or density-vague (Strong 1986) growth rates. The relationship between changes in density and individuals' investment in survival and reproduction (fitness) is mediated by social and breeding relationships. Density vagueness, therefore, may be caused by behaviour-induced time-lags between changes in density and consequences for fitness that retard population regulation or growth.

Knowing the causes and duration of the time-lag to a density-dependent response is important for harvesting sustainably, especially for endangered species particularly susceptible to over-exploitation (Purvis 2001). The absence of an immediate compensatory response after harvest might be misinterpreted as evidence that the population still exceeds carrying capacity or lives in deterio-

rating habitat, and requires repeated harvest. As the interval between harvests decreases relative to the time-lag to a population response, the risk of local extinction from repeated harvest increases.

Harvesting the critically endangered (IUCN 2006) black rhinoceros (*Diceros bicornis minor*: Rhinocerotidae L.) for translocation from surviving endemic populations has been key to the species' recovery. South African populations increased from two containing 110 individuals in 1960, to more than 25 including 1100 individuals (Emslie 2004). Harvesting is also increasingly motivated by the need to maintain source population productivity and health by reducing density (Emslie 2001). An immediate and positive response by the source population to harvesting, however, is assumed but not tested. Nor is our understanding of black rhinoceros social and spatial organization sufficient to make this assumption confidently (Linklater 2003).

Recolonization of harvested habitat may occur by emigration or recruitment. Immigrants could be dispersers (most often juveniles) arriving from distant areas or neighbours. Neighbours are more likely to have had a relationship (affiliative or

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agonistic) with the harvested animal. They will also, therefore, be amongst the first to recognize and benefit from the habitat made available by being its early immigrants. Immigration by neighbours is also more likely to contribute rapid post-harvest recruitment because they are breeders with established local relationships and familiar with local habitat. Other immigrants will not have these advantages and are more likely to be sub- or young adults slower to breed after arrival.

Neighbours might differ in their response, however, depending on whether an opposite- or same-sex conspecific was harvested. Rhinoceros populations, like many large polygynous ungulates, are structured by intra-sexual competition for mates or space, particularly between males, affiliative relationships amongst some females (*i.e.* friendships or kinships), and inter-sexual associations (*i.e.* breeding relationships). Black rhinoceros are comparatively solitary living and so we make two predictions about how conspecifics could respond to the harvest of neighbours: 1) males and females, but especially males, should respond to the harvest of a same-sex conspecific neighbour by colonizing its historical range, but 2) they should respond by moving away from the area after the harvest of an opposite-sex conspecific because they were likely to have been an established or potential mate.

We predict that not only will black rhinoceros neighbours be slow to recolonize a harvested neighbour's range but that even decolonization by opposite-sex individuals might occur, with profound implications for managing and harvesting strategic source populations.

METHODS

Hluhluwe-iMfolozi Park (HiP), South Africa (S 28.00–28.43, E31.716–32.015), includes approximately 90 000 hectares. Park topography of lowland flood plains and rolling hills in the south, to steep hill country in the north, ranges from 20 to 580 m above sea level (a.s.l.). The sub-tropical vegetation varies from grasslands to *Acacia* sp. woodlands and denser thickets dominated by broadleaf species like *Euclea* and *Maytenus* (Whateley & Porter 1983). HiP contained around 220–250 black rhinoceros (1998–2008, Clinning *et al.* 2009), the largest surviving endemic population of only two in southern Africa (Brooks & Macdonald 1983) and so a strategic source population (Emslie 2004). The population has been live-harvested since the late-1970s but more intensely after 1990, with an average of 12

and up to 27 individuals harvested annually.

Records by field rangers of black rhinoceros sightings during patrols, January 1991 to February 2002, described their identity (ear notched), sex and age class (Hitchins 1978), and location. We searched this dataset for individuals harvested in the years 1994–98 to ensure at least three years of data on conspecific neighbours before and after the individual rhinoceros' harvest. We used a minimum three-year period because others have found it sufficient to detect resident rhinoceros at the relatively low observation rates obtained (Emslie 2001; Walpole *et al.* 2001). We also limited our selection to those sighted at least 10 times prior to harvest and which had one female or male adult conspecific neighbour whose ranges overlapped theirs (*i.e.* a same- and opposite-sex neighbour) prior to harvest. These neighbours were also required to have a pre- and post-harvest sightings record including 10 observations each.

The activity areas of harvested rhinoceros and their male and female neighbours were defined by their mean centre, area, and minimum convex polygon (MCP, Burgman & Fox 2003) boundaries using Hawth's tools extension (Beyer 2004), in the geospatial software package ArcGIS 9.1 (ESRI Inc. 2005). We use the MCPs derived here only to describe activity areas for comparison amongst individual rhinoceros, not as an absolute measure of home range. Neighbours could colonize harvested habitat by increasing their activity area to incorporate the newly available habitat, or move their activity area towards the harvested activity area, thus increasing overlap and reducing distance with the harvested neighbour's historical range. Therefore, the sizes of male and female activity areas, and the distance between the mean centre of the harvested rhinoceros and its conspecific male and female neighbour's activity area, and their overlapping area, were compared before and after harvest of a neighbour.

We used a multivariate ANOVA to test for the influence of harvested rhinoceros' sex and whether the neighbour was of the same- or opposite-sex on changes in activity area, and distance and overlap between their activity areas, before and after harvest. We used natural logarithmic transformations to address inequality of variance between subjects. The procedure was conducted in SPSS (SPSS Inc. 2005). For all statistical tests we regarded the critical value (α) of ≤ 0.05 as statistically significant and considered $P < 0.1$ as a statistical trend important to discuss given the small

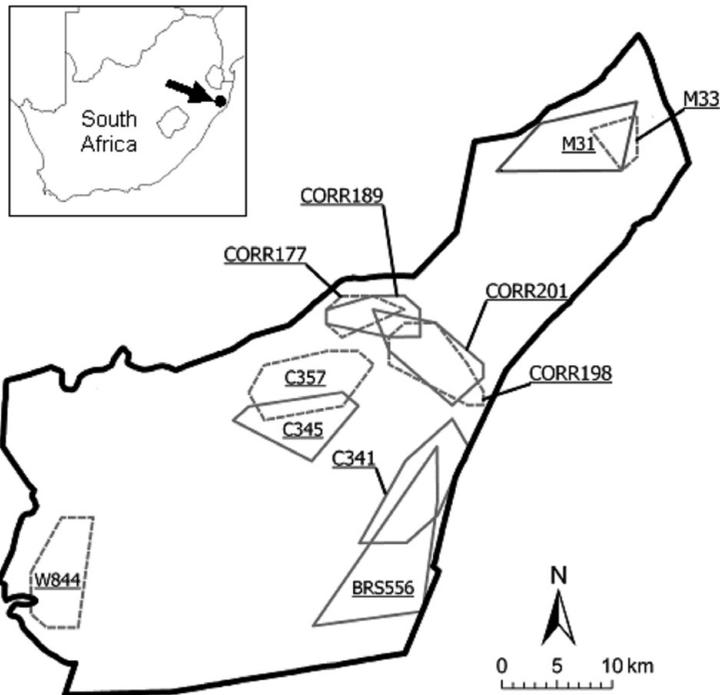


Fig. 1. Map of Hluhluwe-iMfolozi Park, KwaZulu-Natal Province, South Africa, showing the locations of focal harvested rhinoceros activity areas as minimum convex polygons.

sample of harvested-neighbour same- and opposite-sex pairs available.

RESULTS

Eleven adult (*i.e.* >E size-age class, Hitchins 1978) harvested rhinoceros: five females and six males, were identified that met our criteria. Their activity areas were constructed from 11 to 54 locations over 2.2 to 6.5 years prior to their harvest (Fig. 1). The time before and after harvest over which the 10 locations of neighbouring adult male and female were made averaged 2.2 and 1.8 years, respectively (range 0.3 to 4.6 years) and were not statistically different (paired *t*-test, $t = 1.629$, d.f. = 18, $P = 0.121$). This indicates that the population of rhinoceros were sighted at similar rates before and after their neighbour was harvested and their activity areas constructed from observations over a similar period.

There were no significant effects of harvested rhinoceros sex, the neighbour's sex (same- or opposite-sex), or their interaction on activity area, and distance and overlap in activity areas, before and after harvest, although the influence of harvested rhinoceros' sex was approaching significance (MANOVA: Harvested rhinoceros' sex,

$F_{3,13} = 2.67$, $P = 0.091$; Neighbour's sex, $F_{3,13} = 0.245$, $P = 0.864$; Harvested \times Neighbour rhinoceros' sex, $F_{3,13} = 1.36$, $P = 0.299$). The reason for the latter statistical trend is revealed by between-subject tests. There was a significant effect of a rhinoceros' sex on change in overlap of its range by a neighbour after its harvest (ANOVA: Activity area overlap, $F_{1,15} = 8.93$, $P = 0.009$) and statistical trend for changes in activity area before and after harvest (ANOVA: Activity area, $F_{1,15} = 3.46$, $P = 0.082$).

Both sexes tended to reduce overlap with a harvested female's historical range but respond differently if the harvested neighbour was male. If the harvested rhinoceros was male, male neighbours increased overlap and reduced distance (change in: distance, -1.1 ± 1.3 km; overlap: $9.0 \pm 7.2\%$ overlap) and female neighbours decreased overlap and increased distance (change in: distance, 0.76 ± 1.0 km; overlap: $-21.7 \pm 5.5\%$ overlap) (paired *t* males, $t_3 = 3.939$, $P = 0.029$; females, $t_4 = 2.43$, $P = 0.072$; Fig. 2C–F). The different response by males depending on the sex of the harvested neighbour appeared to be partly achieved by reductions in the size of their activity areas if the harvested neighbour was female, but

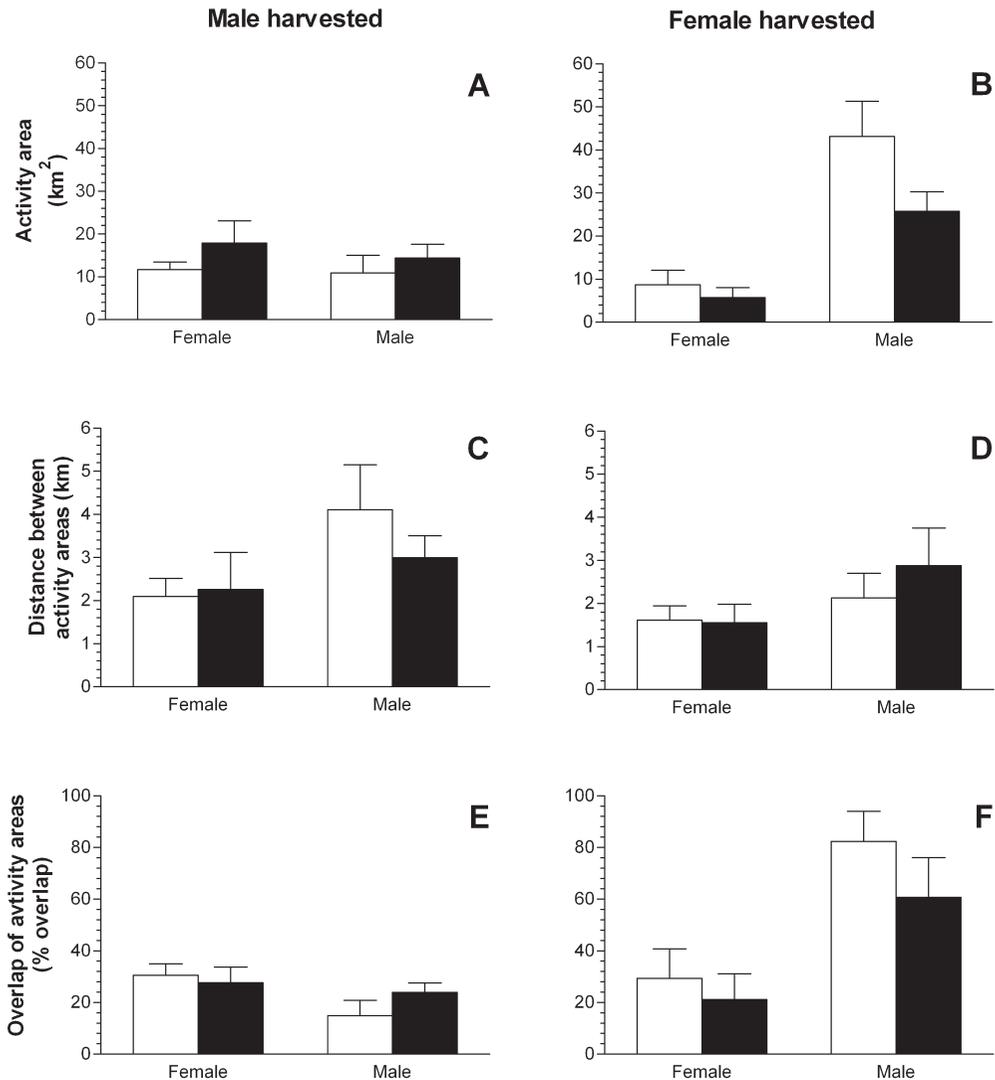


Fig. 2. Mean (± 1 S.E.) size (km^2) (A, B), and distance (km) between (C, D) and percentage (%) overlap (E, F), of individual male and female black rhinoceros's (*Diceros bicornis* var. *minor*) activity areas before (\square) and after (\blacksquare) the harvest of a male (A, C, E) or female (B, D, F) conspecific neighbour.

by increasing area used if the harvested neighbour was male (Fig. 2A–B). In comparison, there were no differences in how females' activity areas changed in size or location with the harvest of a male compared with female conspecific neighbour.

The interaction between the harvested rhinoceros' sex and sex of the neighbour was approaching significance for change in the overlap of their ranges after harvest. Same-sex neighbours demonstrated a weak recolonization response and opposite-sex neighbours a decolonization response to harvest (ANOVA, harvested rhinoceros'

sex \times neighbour's sex: Activity area overlap, $F_{1,15} = 3.89$, $P = 0.067$). No other between-subject effects were significant or approaching significance.

DISCUSSION

Black rhinoceros do not immediately recolonize the range of a harvested neighbour. There was only a weak recolonization response amongst neighbours as measured by an increase in their activity area and movement towards the harvested neighbour's historical range. Importantly, the only significant responses actually involved a reduction

in activity area and its movement away from the harvested neighbour's historical range. In this way, decolonization by neighbours of a harvested rhinoceros' range was more evident than recolonization, at least for the first one to two years after the harvest.

Recolonization after animal harvesting is rarely described (Conover 2002). Recolonization can be rapid for highly mobile species (e.g. foxes, *Pseudalopex culpaeus*, Novaro *et al.* 2005), particularly where the surrounding population includes younger, non-breeding animals that are mobile in their quest for breeding opportunities (e.g. recolonization by eagles, *Aquila chrysaetos*, after the removal of individuals preying on lambs, Phillips *et al.* 1991). However, it may also be extremely slow for many species. For example, neighbouring white-tailed deer (*Odocoileus virginianus*) can be slow to shift their ranges to include areas where density has been reduced by harvest such that immigration rates into harvested habitat can be negligible for up to two years (McNulty *et al.* 1997). In badgers (*Meles meles*) complete removal of groups did not result in shifts by neighbouring group territories into the vacant habitat (Cheeseman *et al.* 1993). Recent work with juvenile dispersal by white rhinoceros (*Ceratotherium simum* var. *simum*, Shrader & Owen-Smith 2002) and black rhinoceros after release into new reserves (Linklater *et al.* 2006) suggests that dispersal and settlement may be socially facilitated. New populations are slow to colonize uninhabited reserve space (Lent & Fike 2003). Clearly, the constraints imposed on density-dependent emigration-immigration by social and spatial relationships require greater investigation in this and many other species.

The pattern we observed indicates that a black rhinoceros' response to the harvest of a neighbour is mediated by intra- and inter-sexual relationships. The relative magnitude and direction of the response for males compared with females after the harvest of a same- or opposite-sex neighbour were consistent with what is known about black rhinoceros social and spatial organization. There was a weak, non-significant and, therefore, probably slow, recolonization response by same-sex neighbours, but a significant decolonization response by opposite-sex neighbours, with the responses in both cases being strongest by males. Where male-male relationships are largely competitive, the strongest recolonization response should be recorded by males after the removal of a male

neighbour. It is not surprising that female responses were less marked because female-female relationships with neighbours are likely to be both affiliative (e.g. philopatric kin), and agonistic (e.g. spacing): *i.e.* on average neutral. Where a breeding relationship is part of the reason for individuals occupying habitat, then the harvest of one appears to cause the other to reduce their use of the area, and even move their activities away, perhaps in search of a new relationship. Overall, these results indicate that re-colonization of habitat after harvest, at least by neighbours, might not just be slow, but delayed by the disruption of long-standing inter-sexual, perhaps breeding, relationships. It might be unrealistic, therefore, to expect breeding-age black rhinoceros to re-colonize harvested habitat quickly, and certainly not faster than annual harvest regimes. Our results might explain, therefore, why the HiP black rhinoceros population has performed poorly under the current harvest regime (Clinning *et al.* 2009), even though it was considered a low to moderate, and insufficient, off-take by many (Emslie 2001). Re-colonization by breeding age adults may be primarily influenced, at least in the short-term, by endogenous, not exogenous, influences. Harvesting of individuals should probably not be concentrated on the landscape to avoid generating persistent areas of under-utilized habitat.

Stronger conclusions from these analyses are limited by the small sample and retrospective analysis of a dataset not designed for this purpose. Nevertheless, reports that describe recolonization are rare and increasingly important. We hope, therefore, that these tentative data encourage greater effort towards understanding how the population dynamics of endangered species subject to harvest might be retarded by behaviour. Until behavioural responses to harvest are better understood, managers should not assume that the absence of a compensatory response is evidence for habitat deterioration or a population still at or exceeding carrying capacity. Rather, it may just be a consequence of a behaviourally mediated time-lag between harvest and habitat re-colonization, and therefore a delay in utilization towards compensatory fecundity and recruitment.

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