

11 · *Rhino Management Challenges: Spatial and Social Ecology for Habitat and Population Management*

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11.1 Introduction

No other protected area has contributed as much to the conservation of Africa's white (*Ceratotherium simum* var. *simum*) and black (*Diceros bicornis* var. *minor*) rhinos as the Hluhluwe-iMfolozi Park (HiP). In 1895, when the Hluhluwe and Umfolozi Game Reserves (GR) were proclaimed, southern Africa's only remaining white rhinos were restricted to the Umfolozi GR and probably numbered fewer than 100 individuals (Owen-Smith, 1981). Black rhinos survived more widely in Zululand, but estimates of their numbers were not reported. By 1970, the white rhino population in HiP had grown to ~2000 animals (Owen-Smith, 1981; Figure 11.1A), while black rhino numbers exceeded 300 (Brooks and Macdonald, 1983; Figure 11.1B).

During the 1970s and 1980s, illegal hunting escalated across Africa due to growing demand for rhino horn for Eastern medicine and handles for Yemeni jambiya daggers (Western and Vigne, 1985). In 1976, both black and white rhinos (along with the three Asian species) were listed in Appendix I of the Convention on International Trade in Endangered Species, in an attempt to eliminate international trade in rhino products. Nevertheless, the continental black rhino population was reduced from ~65,000 individuals in 1970 to only ~2480 by 1992 (African Rhino Specialist Group, 1991, 1992). Within southern Africa, black rhinos were eliminated from Botswana and severely reduced in Zimbabwe (Milliken,

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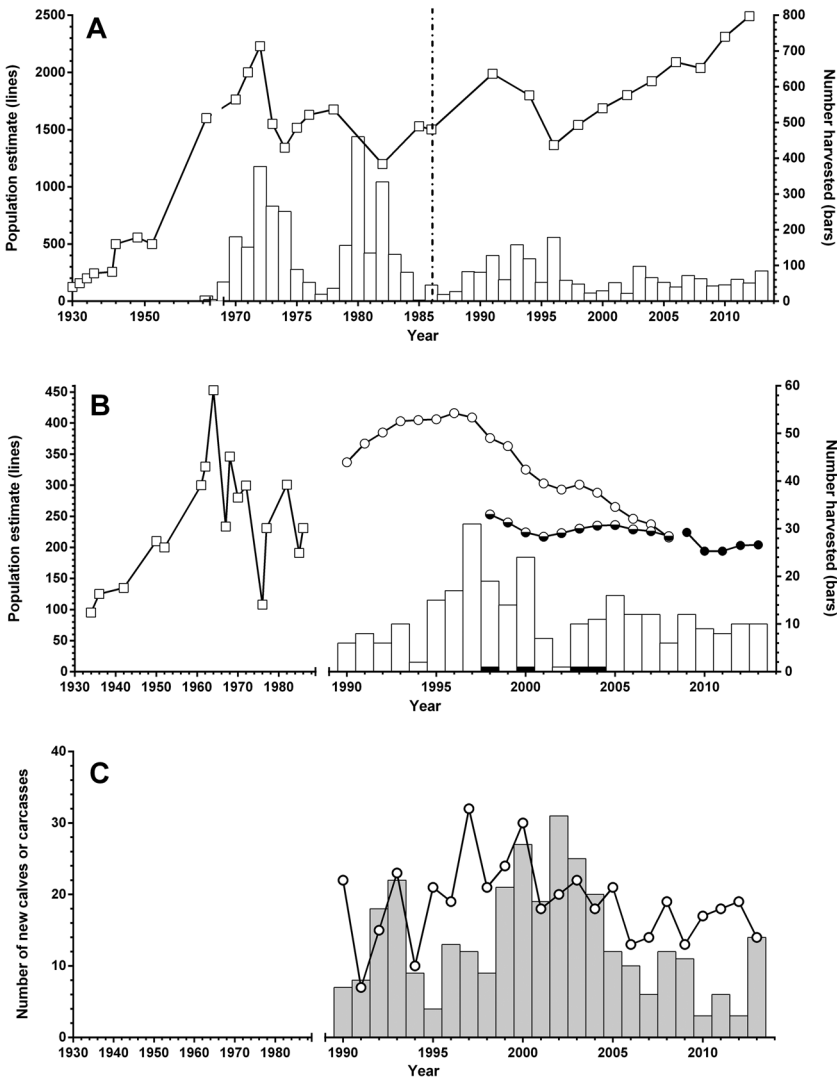


Figure 11.1 (A) White rhino population estimates (\square , 1930–) and live harvest (white bar, 1970–). The vertical dashed line indicates when the Sink Management Policy was initiated. (B) Black rhino population estimates (i) prior to 1990 (\square , running totals of sporadic separate estimates from Hluhluwe GR, Umfolozi GR and the Corridor), (ii) 1990–2008 (O) using ear-notched individuals and mark–resight techniques, (iii) 1998–2008 (\blacktriangledown) from revised mark–recapture estimates (Clining *et al.*, 2009), and (iv) the known entirely marked population 2009–2013 (\bullet), plus live harvest (white bar) and introduction numbers (black bar) (1990–2013). (C) Black rhinoceros calves (O) and carcasses (grey bar) reported each year (1990–2013).

1993). In contrast, rhinos within South Africa were less affected. From 1970 to 1994, poaching of both rhino species within HiP was restricted to fewer than five rhinos per year. Hence this park became the source of rhinos for establishing numerous small populations in captivity and for re-introduction and restocking across the continent.

Growing populations of both rhino species in HiP initially represented an international conservation success (Player, 1972; Emslie and Brooks, 1999). However, the strategic importance of HiP for rhino conservation brought more complex challenges. In this chapter, we contrast the population and management histories of the two rhino species in HiP, and consider the uncertainties for future management. As a framework, we provide hypotheses and predictions for adaptive management so that the role of density-dependent and density-independent influences on rhino vital rates and dispersal in HiP can be tested.

11.2 Population Success, Ecological Challenges

By the 1970s, concerns were being raised about the impact of the growing white rhino population on the grass cover and soils in HiP (Owen-Smith, 1973). White rhino grazing was responsible for a reduction in grass cover which exposed soils and stream banks to increased erosion. The completion of a rhino-proof fence around the park by 1966 threatened to compound this perceived problem (Owen-Smith, 1981; Chapter 5). The spectre grew of an overpopulation situation with adverse consequences for the environment and other animal species.

Black rhinos posed the opposite problem. After the discovery of 46 fresh black rhino carcasses in Hluhluwe GR in 1961 (Emslie, 1999) – a death-event for which reasons remain unknown – estimates of black rhino numbers continued to decline into the early 1970s (Figure 11.1B). Despite subsequent recovery, mainly through expansion in numbers in Umfolozi GR, an apparent further decline ensued during the late 1990s. This trend is now understood to have been an artefact of mark-resight estimates with certain assumptions violated (Clinning *et al.*, 2009). Nevertheless, concerns about the health of the black rhino population and the quality of its environment, especially its browse food resource, came to the fore.

Hence white and black rhinos pose different challenges requiring divergent management approaches. New strategies for both species were facilitated by technical advances in large animal capture.

11.3 Advances in Large Animal Capture

Collaboration between park managers and wildlife veterinarians during the late 1950s pioneered the use of chemical immobilization to capture animals as large as rhinos (Harthoorn, 1962a, 1962b; Player, 1972). This made it possible to redistribute rhinos not only in Africa but also internationally (King and Carter, 1965). Initially, rhinos were sent to zoos as an insurance against extinction in the wild (Player, 1972). Furthermore, the routine capture of large numbers of rhinos enabled HiP to become the source for the re-introduction and restocking of rhinos elsewhere.

Since the 1960s, > 4500 white rhinos and > 250 black rhinos have been transferred from HiP to various zoos, wildlife reserves, and private game ranches. For example, the white rhino population within Kruger National Park, which reached around 10,000 animals (Ferreira *et al.*, 2012), was derived from 336 white rhinos relocated from HiP between 1961 and 1972. The black rhino population there exceeds 600 animals (Ferreira *et al.*, 2011), founded when 20 black rhinos were relocated from HiP in 1971 (later augmented with others from Zimbabwe; Pienaar, 1970; Pienaar *et al.*, 1992; Emslie *et al.*, 2009). Twenty-eight black rhinos were brought from HiP to Malilangwe, Zimbabwe in 1998 (Emslie *et al.*, 2009). White rhinos have been re-introduced into protected areas in Botswana, Mozambique, Zimbabwe, and Namibia, and moved even as far as Kenya, although the species was historically absent there.

Currently, HiP is home to ~2500 white rhinos and ~200 black rhinos (Figure 11.1A,B), with populations of both species managed by live capture and translocation elsewhere. However, this approach has posed new challenges requiring a deeper understanding of rhino ecology and behaviour.

11.4 Density Dependence and Compensatory Population Growth

The recovery of both African rhinos globally depends on remaining populations functioning as sources of animals for re-introduction and restocking. According to the theory underlying sustainable harvesting, reductions in population density should promote compensatory increases in reproduction and survival because food or other resource limitations are alleviated (Rosenberg *et al.*, 1993). Hence, source populations should be able to provide a sustained supply of 'surplus' animals for relocation elsewhere. Being initially stocked at low density, the relocated animals

should show higher rates of reproduction and better survival, particularly of young animals, than the more crowded source population.

Logistic harvest models assume immediate demographic responses as soon as the population density is reduced. However, the spatial and social processes that underlie the population trend are more complex. Individual animals differ not only in age and sex, but also in their social relationships and hence ability to move freely in response to density reductions. The effects of removals are not experienced by individuals living remote from the place from which animals were taken. There may also be delays before the effects of reduced competition for food become manifested in survival and reproductive rates. Over some range in density, vital rates may remain uninfluenced by density reductions (Fowler, 1981). Limitations of current behavioural and ecological knowledge are recognized impediments to the sustainable harvest of exploited species (Reynolds *et al.*, 2001).

Following animal removals, density-dependent responses in population growth rate might not take place, or be delayed, if any of the following circumstances apply.

1. More productive individuals are preferentially removed.
2. The availability of food resources is not improved.
3. The space made vacant is not immediately utilized by the remaining animals.
4. Remaining animals experience greater pressure from predators responding to higher densities of other prey species (Courchamp *et al.*, 2000).

Rates of recolonization following harvesting are rarely documented. Recolonization can be rapid for highly mobile species, particularly where the population surrounding the harvested area includes many young, non-breeding animals. However, species with slow life histories, like rhinos (Owen-Smith, 1988), are generally slow to disperse into vacant habitat. Population redistribution may be delayed by spatially loyal behaviours (territoriality or home range fidelity; Stamps and Swaisgood, 2007). Where recolonization is slow, the size and spatial arrangement of harvested areas become important considerations (Novaro *et al.*, 2005). Larger harvested areas are recolonized more slowly and recolonization rates are reduced if they are in close proximity to other harvested areas. Moreover, higher-quality habitats support higher animal densities, and if these localities are repeatedly harvested (e.g. density-dependent capture bias) a greater proportion of the population will be left in poorer

habitat. Thus, for species that do not respond spatially to harvest by rapid recolonization, a poor recruitment response overall might result.

The effects of consumption on food quality have been demonstrated for large grazers, like white rhinos, which can maintain ‘grazing lawns’ providing low-fibre and hence relatively nutritious forage (Waldram, 2005; Chapter 6). The concept has been extended to browsers that maintain ‘hedgcs’ of low-growing shrubs (Makhabu and Skarpe, 2006; Fornara and du Toit, 2007; Croomsigt and Kuijper, 2011). Grasses and shrubs can grow taller and hence more fibrous, or beyond the reach of herbivores, if grazing or browsing pressure is reduced by removals.

Lastly, smaller species able to respond more rapidly might benefit from the food made available by rhino removals, and pre-empt gains by the larger competitor. For black rhinos, these include kudu (*Tragelaphus strepsiceros*), nyala (*T. angasi*), and impala (*Aepyceros melampus*), which also browse the low-growing shrubs favoured by black rhinos.

11.5 Live Harvest of Rhinos

The initial motivation for live removals of white rhinos was to alleviate a threatened overpopulation situation associated with the risk of a population crash and adverse consequences for other species. However, an important aim was also to distribute the species more widely as insurance against a possible disaster in HiP, such as a lethal disease outbreak. For black rhinos, population management was more narrowly aimed at establishing viable populations outside HiP. Hence the contexts for managing the two rhino species within HiP were quite different – white rhinos were numerous and growing rapidly while black rhino numbers were much lower and the population seemed to be shrinking.

11.5.1 Dispersal Sink Management of White Rhinos

The growth rate of the white rhino population up until 1971, incorporating animals removed after 1962, was a constant 9.5% per year (Owen-Smith, 1981). Assuming logistic growth, maximum sustainable yields are obtained by reducing the population towards half of the ultimate carrying capacity and harvesting at half of the maximum growth rate. However, judging from the habitat changes occurring, the total of 2000 white rhinos present in HiP in 1970 was not far below the maximum number that could be supported despite the lack of any density-dependent reduction in the population growth rate. This is consistent with Fowler’s

(1981) finding that large mammal populations do not show demographic responses to food shortfalls until their abundance is close to carrying capacity (see Chapter 5). Simply counteracting the annual population growth in this situation would require the removal of almost 200 rhinos every year. Removals could be reduced by about one-third if concentrated selectively on subadults approaching maturity, which have a high future reproductive value. However, this high rate of harvest would be difficult to maintain and disruptive.

It would be more effective to allow the population to approach closer to carrying capacity so that density-related influences on birth intervals, calf survival, and age at first reproduction would come into play, but the ultimate carrying capacity was not known, and changes in these vital rates might be too slow to avoid an over-shoot of the carrying capacity. The only regulatory mechanism that could be sufficiently quick-acting is dispersal, i.e. movements of animals out of densely settled areas. Estimates of dispersal rates could be obtained from changes in the regional distribution of white rhinos recorded in successive aerial censuses, particularly in the numbers of white rhinos moving beyond the protected area before the fence was completed. Between 1953 and 1970, the difference between the overall population growth rate and the rate of increase within the highest-density region between the two Mfolozi rivers amounted to about 3% per year (Owen-Smith, 1988). Dispersal movements were mostly by subadult animals of both sexes, plus some adult males. For the subadult segment, the specific dispersal rate was estimated to be 7.5% per year. This dispersal rate could potentially stabilize the population if coupled ultimately with modest density-dependent reductions in fecundity and offspring survival as well as delayed maturity. However, changes in rates of reproduction and survival would need to be more drastic to halt population growth in the absence of dispersal.

The biggest question, however, was how dispersal could take place after the park became completely fenced. The proposed solution was to establish sink zones within the fenced area from which most rhinos settling would be removed (Owen-Smith, 1973, 1981, 1988). No removals should take place in the remainder of HiP, where white rhinos would be allowed to establish the carrying capacity naturally through dispersing into the sinks when food ran short. Positive intrinsic growth within the core area would be counterbalanced by negative growth within the sink zones (Pulliam, 1988), maintained by live removals. Other species threatened by the grassland changes induced by high densities of white rhinos in the core area could persist in the sink zones.

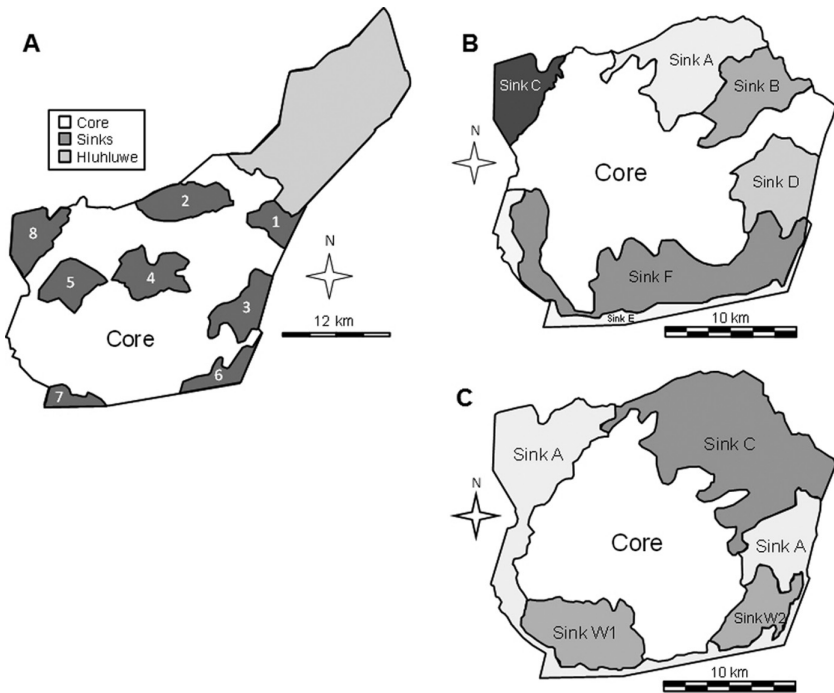


Figure 11.2 Changing locations of designated dispersal sinks for white rhinos within the Hluhluwe-iMfolozi Park. (A) Sinks initially established in 1986. (B) Sinks maintained from 1992 to 1996. (C) Current location of sinks established in 1997.

Dispersal sink management of the white rhino population was eventually initiated in 1986 (Conway *et al.*, 2001). The aim was to maintain white rhino density within the sinks at around one rhino/km², with the number of animals exceeding this density being removed annually. However, some of the sink zones seemed too small to be effective and two of the sink zones were inappropriately located centrally within Mfolozi (Figure 11.2A). Therefore, in 1992 the designated sinks were enlarged and shifted so that all lay on the periphery of Mfolozi (Figure 11.2B; Maddock, 1992). In Mfolozi, the resulting central core area covered 302 km² and was surrounded by sink zones totalling 433 km². Within Hluhluwe, merely a fixed upper limit of 500 white rhinos was set because of its narrow confines. A benefit of the peripheral arrangement was that white rhino densities were lowered near park boundaries where poaching risks were highest (Maddock, 1992; Balfour, 1999). In 1997, minor adjustments were made to the sink boundaries so that they ran around

the entire periphery of the park (Figure 11.2C). For Hluhluwe, the fixed upper limit was raised to 700 animals because the white rhino population there had remained relatively stable at ~ 500 individuals since the late 1980s despite removals amounting to only 2% of the local population per year. The limit was then removed in 2005 as the white rhino density within Hluhluwe was thought to be too low to maintain grazing lawns in that high-rainfall section of the park. As shown in Figure 11.1A, removals overall have generally remained at fewer than 100 white rhinos per year over the past two decades. Nevertheless, the white rhino population has continued to grow.

Sinks within the current configuration (Figure 11.2C) are managed differently. In the two sinks labelled A (144 km^2), all animals found within them, except for females with calves < 1 year old, are removed annually. In the Corridor Sink C (114 km^2), white rhinos are removed only once the density in the core reaches 2.5 rhinos/km^2 , as a safety valve to prevent the white rhinos in the core from potentially exceeding what available resources can support. Sinks W1 and W2 (30 and 20 km^2 , respectively) lie within the wilderness section of Mfolozi where roads are excluded. Hence, capture vehicles are not allowed to enter, making removing rhinos from these areas logistically difficult. To overcome this restriction, helicopters have been used to transport rhinos out of the sink (Cooke, 1998), meaning that capture is more costly. Accordingly, white rhinos are removed from the wilderness sinks only after the white rhino density in the core area of the park exceeds three rhinos/ km^2 .

11.5.2 Metapopulation Management of Black Rhinos

In contrast to the sink management policy for white rhinos, the conservation strategy for black rhinos in HiP is outwardly focused towards metapopulation expansion to overcome the isolation and relatively small size of the HiP population. However, much dissension exists about the magnitude of the removals of black rhinos that the park can sustain. Between 1990 and 2013, 2–31 black rhinos were harvested from HiP each year (Figure 11.1B), totalling 276 animals. The failure of the population to compensate has been interpreted as evidence for underharvesting (Emslie, 2001). Based on the logistic model, reducing the population density to 75% or less of ecological carrying capacity would be required to generate compensatory increases in rates of survival and reproduction and hence much higher population growth. Others have suggested that the population has been reduced beyond its capacity to compensate given

current habitat conditions (Balfour, 2001). More recently, it has been recommended that a constant proportional harvest of 5% should be removed each year (Goodman, 2001; Cromsigt *et al.*, 2002).

Uncertainties in estimates of the black rhino population by different methods may have contributed to overharvesting (Clinning *et al.*, 2009). Historical highs and the subsequent declines were not as large as formerly believed (Figure 11.1B). Taking into account animals removed, the black rhino population is estimated to have increased intrinsically at 3.4% per annum between 1998 and 2008. However, removals during this period averaged $5.2 \pm 0.8\%$ of the population per year, and have been opportunistically and patchily distributed over the park (Figure 11.3). Whether the population growth rate would increase if the density were to be reduced further is debatable, particularly following Fowler's (1981) suggestion that density dependence only kicks in close to carrying capacity.

Choices of the black rhinos to be removed were influenced both by HiP section rangers and the expectations or requirements of those receiving the rhinos. Only females without calves were captured, potentially including a high proportion of young animals contributing most to future population growth (Clinning *et al.*, 2009). Rangers tended to favour removing old males that might already have contributed genes to the population, or subadults yet to reproduce, rather than prime-aged animals. Buyers wanted young or prime-aged adults with high reproductive potential.

11.6 Evaluating Rhino Population Responses

11.6.1 White Rhino

Between 1962 and 1974, white rhino removals were aimed at reducing the population to alleviate 'overgrazing'. Thereafter until 1985 the number of white rhinos harvested was adjusted annually to maintain numbers within some crudely estimated carrying capacity, with more individuals being removed during dry years (Brooks and Macdonald, 1983). The annual off-take between 1974 and 1985 averaged 146 animals (range 3–460) and amounted to 10.5% of the population. This effectively suppressed population increase. When surprisingly few herbivores died during the severe 1982/3 drought (Walker *et al.*, 1987), it became apparent that removals of white rhinos and other grazers had been excessive. From 1986 onwards the sink management policy was applied and the number

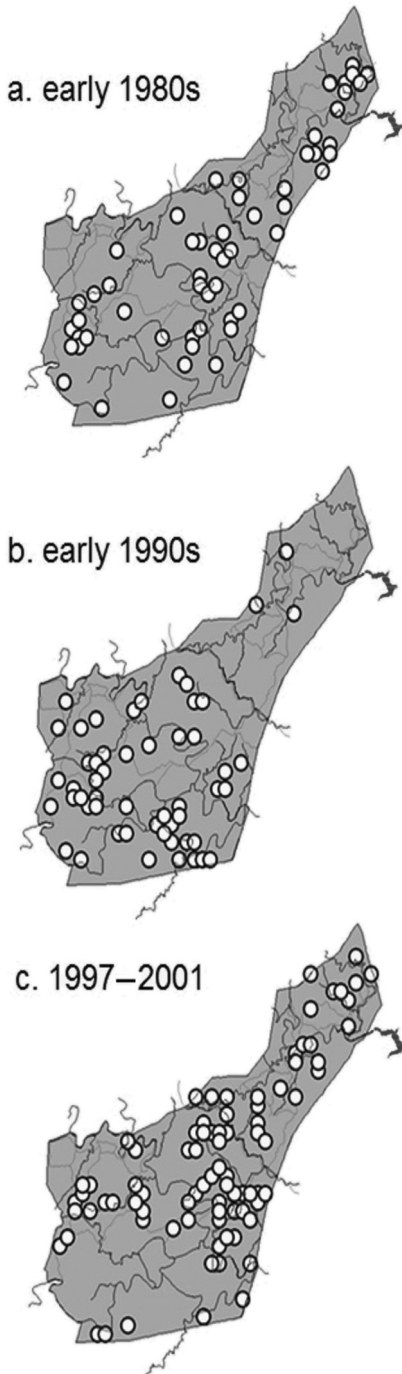


Figure 11.3 Changing locations of the places where black rhino removals took place from 1980 to 2001.

of white rhinos harvested annually was reduced to a mean of 66 animals (range 19–179), representing on average 3.6% of the population. This slowed the net growth of the white rhino population between 1986 and 2012 to an annual average of 1.8%, indicating an intrinsic growth rate of 5.4% per year. This is substantially lower than the annual rate of increase of 9.5% prior to 1971 (Owen-Smith, 1981). Hence, density-dependent feedbacks on reproduction and survival evidently became increasingly effective. However, the number of rhinos dispersing into the sinks and consequently removed has shown no change since the policy was implemented, despite a strong increase in rhino numbers. Nevertheless, overgrazing within the core region has no longer been raised as a concern.

There are practical problems in applying the sink removal strategy, apart from the barrier to motor vehicles entering into the wilderness sinks. The number of rhinos counted in the sinks, which is used to set the annual removal quotas, can fluctuate unpredictably from year to year, affecting the number that can be offered to potential buyers. This complicates planning and logistics for both management and game capture staff, and may not match the demand (market) for white rhinos. Despite such concerns, dispersal sink management of white rhinos has been retained over the past 28 years, and is consistent with the policy of process-based management adopted by the conservation agency (Chapter 1).

11.6.2 Black Rhinos

The maximum growth rate of a black rhino population should be similar to that of white rhinos, i.e. around 9% per year (Knight, 2001). However, with allowance for removals, the black rhino population in HiP has grown by only 3.6% per year over 1998–2013 (Figure 11.1B). The population total within the park has actually declined because live harvests during this period averaged 5.0% per year during this period. Surprisingly, there has been no compensation for the progressively reduced density. Records supplied by field rangers show no changes in numbers of new calves and found carcasses recorded annually.

Of 22 fully adult female black rhinos captured for translocation between 2004 and 2006, just seven (32%) were pregnant (EKZN Wildlife, unpublished data). Estimates of reproductive performance based on captured animals are probably larger than the overall population-wide rate because cows with young calves are less likely to be pregnant and are avoided by the capture team. Hence the average birth interval probably exceeds 3 years, which is somewhat longer than the mean calving

interval of 2.5 years recorded for white rhinos in HiP (Owen-Smith, 1981). Predation on young calves may further reduce the population performance of black rhinos in HiP (Plotz and Linklater, 2009). The filarial nematodes and associated lesions typical of black rhinos in HiP may also debilitate animals there (Plotz, 2014). All in all, however, drivers of the poor growth rate of HiP's black rhino population remain poorly understood.

11.7 Social Ecology of Dispersal Movements

For both rhino species, the challenge to improving harvest strategies for population and habitat management is the same – a better understanding of the behaviour and ecology of individuals and resources under a harvest regime. In particular, understanding dispersal movements and habitat colonization is crucial to testing hypotheses about how their populations might respond to removals. Simple harvest models assume that resources released by the population reduction will be taken up by the remaining animals. Vacant home ranges could become reoccupied by the expansion of neighbouring home ranges or by recolonization from elsewhere. The source for recolonization could be either socially or spatially displaced adults, or settlement by dispersing subadults. Larger body size is generally associated with slower life histories and, therefore, slow dispersal rates (Owen-Smith, 1988). Rhinos and equids (Linklater and Cameron, 2009) are unusual among ungulates because natal dispersal movements are made by both sexes. More is known about such movements for white rhinos than for black rhinos.

For white rhinos, natal dispersal following the breaking of maternal bonds is a slow process extending over several years. Mothers drive away their previous offspring following the birth of a new infant typically when the older calf is ~2.5 years of age. Former calves, now termed subadults, form associations (i.e. become 'buddies') with other subadults and/or with adult females that have calves > 3 months of age (Owen-Smith, 1975). Subadult-only groups may explore and travel extensively, but at some stage they may join and move with adult females lacking a small calf (Owen-Smith, 1975; Shrader and Owen-Smith, 2002). By doing this, subadults gain experience of the locations of grazing areas, distribution of water, and of presence of other white rhinos in a wide area (Shrader and Owen-Smith, 2002). These associations last from a single day to several years. As a result, individuals can move between a number of different 'buddies' before settling into a home range (females)

or territory (males). As females only settle into home ranges at around 7 years of age after giving birth (Owen-Smith, 1975), their dispersal phase lasts about 4.5 years. Males first occupy territories when they are around 10 years of age, so dispersal can last for around 8 years.

The physical features that defined the boundaries of dispersal sinks (rivers, roads, streams) do not inhibit the movements of white rhinos. The sink zones are large enough to enclose the home ranges and territories of resident adults. However, some of the animals removed from the sinks may have been neighbouring residents with territories or home ranges extending across the core-sink boundary. The removal of these adult females could reduce the availability of dispersal opportunities for subadults into the sinks. Among adults dispersal movements are mainly made by males, but adult females can also shift their home ranges. This is evident from the continuing harvests of pregnant females as well as adult males from the sink zones. Nevertheless, the origins of these colonists are unknown.

Natal dispersal by black rhinos has not been studied. We expect longer times and distances of dispersal for males, as among white rhinos, but this has not yet been documented. Nevertheless, we expect dispersal to be a slow process as in white rhinos. Observations on black rhinos following their release into new reserves (Linklater *et al.*, 2006) suggest that their dispersal and settlement may likewise be socially mediated. Sighting records of individual black rhinos within HiP before and after the removal of neighbouring rhinos indicate that black rhinos do not shift their ranges into unoccupied habitat during the first 2 years after the harvest. Black rhinos of opposite sex to the animal removed actually shifted their ranges away from the vacated habitat (Linklater and Hutcheson, 2010). Reproductively mature individuals seem slow to colonize uninhabited or under-utilized space (Lent and Fike, 2003).

11.8 Uncertainties as Hypotheses for Rhino Responses to Harvest

Based on the above findings, we formulated four hypotheses to explain why rhinos of both species have not responded to live harvests as expected. These hypotheses are distinguished by at least one of their predictions about (1) the abundance and feeding pressure of rhino, (2) rhino competitors, and (3) rhino fecundity and recruitment after harvest (Table 11.1). Also pertinent are dispersal rates by rhino and competing species, the responses of key food species, and predator diets after a

Table 11.1. The predictions of increases (↑), decreases (↓) or 'no change' that four hypotheses for a poor response by rhino to harvest make about abundance and feeding pressure of (1) rhino and (2) rhino competitors, and (3) rhino fecundity and recruitment after its harvest in the area harvested

Hypothesis	Rhino feeding and density (1)	Competitor density and feeding (2)	Rhino fecundity and recruitment (3)
Social constraints	↓	No change	No change
Depredation constraints	No change	No change	↓
Competitor substitution	↓	↑	No change
Ecological constraints	↑	No change	↓

harvest, but these are more difficult to measure without recourse to individual animal studies or intensive and extensive vegetation sampling. The three predictions of our framework, however, are comparatively easy to measure, with most rhino monitoring programmes and supporting infrastructures, and are the minimum necessary for a differential diagnosis of the problem.

The *social constraint hypothesis* suggests that when harvests depress local rhino densities, recolonization is slow such that habitat and resources remain under-utilized. Thus, distributed harvests result in a patchwork of low- and high-density areas rather than freeing resources more generally through the population. Accordingly, resource recovery in depressed-density areas does not influence the wider population performance, meaning that in high-density areas resource limitations remain effective. In particular, the social constraints hypothesis predicts that the density of animals in the harvested area will remain depressed for a prolonged period.

The *depredation constraint hypothesis* suggests that the compensatory recruitment response of rhinos to reduced density is prevented or limited by predation. Where densities are reduced, but predator densities remain the same, the proportional predation rate on the harvested species might increase. This hypothesis predicts that there is reduced recruitment into the breeding population, which slows the population increase despite

occupation of the vacated home range by other rhinos. It is relevant only for black rhinos where predation on calves could be great enough to be demographically important (Brain *et al.*, 1999; Plotz and Linklater, 2009). Predation on white rhino calves appears to be rare (Owen-Smith, 1973, 1988).

The *competitor substitution hypothesis* suggests that rhinos are slower than their competitors at recolonizing areas from which rhinos have been harvested. This hypothesis predicts that the removal of rhinos is followed by an increase in the local abundance and feeding activity of other browsers (e.g. kudu for black rhino and wildebeest for white rhino). The ongoing and increased impact of competitors prevents the recovery of food resources and thus may inhibit recolonization of vacant home ranges by rhinos.

The *ecological constraint hypothesis* suggests that historical harvesting has not reduced densities sufficiently to free food resources, particularly for black rhinos. This hypothesis predicts that the feeding pressure of rhinos will be only briefly depressed in areas from which rhinos have been removed because recolonization is rapid. This hypothesis best matches the expectations of simple harvest models.

We do know that neighbouring black rhinos appear reluctant to colonize the ranges of harvested rhino, partly because reproductive relationships are disrupted (Linklater and Hutcheson, 2010). We also know that home range sizes of black rhinos have not changed appreciably over the past 50 years (Linklater *et al.*, 2010; Plotz *et al.*, 2016) since first measured (Hitchins, 1969, 1971). Thus, there is no firm evidence that black rhino in HiP are expanding their ranges in response to deteriorating habitat conditions (contrary to the conclusions of Reid *et al.*, 2007; Slotow *et al.*, 2010). We know that lions and spotted hyenas are responsible for some level of predation on black rhino calves (Plotz and Linklater, 2009), although the impact on population performance needs to be assessed. Taken together, observations of slow recolonization, range size stasis, and predation on calves could indicate that social and depredation constraints are playing a role in reducing the response of the black rhino population to removals. How potential competitors respond to the resources released has yet to be investigated.

Harvesting models based on simple density-dependent functions continue to be used as a guide to optimal sustainable harvests in fisheries management (Punt and Smith, 2001). However, recent experience has emphasized the importance of animal behaviour and spatial ecology for the reliability of harvest quotas (Milner-Gulland, 2001; Sutherland and

Gill, 2001). We have presented a realistic hypothetical framework for the role of density-dependent and density-independent influences on rhino vital rates and dispersal in HiP, which is testable even where detailed, individual-based data are lacking. Our hope is that this framework will help design variations in rhino harvest regimes in order to evaluate these hypotheses.

11.9 Final Considerations

HiP has been a laboratory of innovation and enlightened conservation management for both white and black rhinos. Collaborative relationships and an outward focus have meant that what has happened in HiP has been influential for international rhino conservation over half a century. The overall success in rhino conservation will ultimately be judged by the diminishing importance of HiP as a source for metapopulation management. However, as we write, escalating illegal hunting is once more threatening the gains achieved in rhino conservation in South Africa. During 2008–2015, official figures show that 5048 rhinos were killed, with the largest proportion being white rhinos from Kruger Park (www.stoprhinopoaching.com/, accessed 16 February 2016). Since 2013, the poaching rate has escalated to over 1000 rhino killed nationally per year. Fortress protection is again becoming the primary conservation activity.

Appropriately, a small museum in HiP emphasizes the critical role of this protected area in the conservation of all of the world's rhinos through innovative advances in technology, science, and adaptive management. In the spirit of that tradition, we hope that our framework provides the foundation for the next advance in the management of rhinos.

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