4 · *Temporal Changes in the Large Herbivore Fauna of Hluhluwe-iMfolozi Park*

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4.1 Introduction

This chapter is a reconstruction of the history of the large mammalian herbivore assemblage of Hluhluwe-iMfolozi Park (HiP) and the surrounding area. The region has had a long history of human occupation and human impacts on animal populations were considerable long before the park was proclaimed (Chapter 1). The rich and relatively well-documented history of the park spans ecologically informative time frames and transcends various political and economic agendas that drove past management policies. We focus on changes in large mammalian herbivores because they have formed a central part of the park's monitoring efforts (predators are covered in Chapter 12). Apart from being charismatic, important for ecotourism and highly valued in the wildlife industry, large mammalian herbivores are often central drivers of ecosystem structure and functioning (Chapin *et al.*, 1997; Paine, 2000). We use nearby archaeological deposits that represent mammal remains from the Late Pleistocene up to the Late Iron Age (eleventh to twelfth centuries) to provide information on the prehistoric and early historical faunal composition. Writings of European hunters and explorers and records of exported animal products sketch the situation during the 1800s, when impact intensified due to the arrival of these European hunters. Following park proclamation at the end of the nineteenth century, more regular and formal information on animal population trends becomes available

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in the form of unpublished management reports and some early published accounts on long-term ecological research. Regular surveys since 1986 enabled a rigorous analysis of the population trends of the last three decades. We present the herbivore dynamics within HiP in the context of strong human influence and natural regulation.

4.2 Early Records of Wildlife before the Game Reserves Were Proclaimed

Detailed records of vertebrate remains from Sibudu Cave, a Middle Stone Age human settlement approximately 150 km south of HiP, provide insight into mammalian assemblages since the Late Pleistocene in the vicinity of HiP. The main layers excavated contain faunal remains from the Middle Stone Age that date back to between 61,000 and 38,000 BP (Plug, 2004; Clark and Plug, 2008), while the upper layers extend into Iron Age times as recently as 800–900 BP. Although the species represented in the deposits include all extant species, the excavations suggest much richer large mammal diversity during the Late Pleistocene. The samples from the Middle Stone Age sequence are dominated by medium- to large-sized grazing bovids (Plug, 2004), mostly Burchell's zebra (*Equus quagga*), hartebeest (*Alcelaphus* sp.), and African buffalo (*Syncerus caffer*), although many large bovid bones remain unidentified. Older deposits of the Middle Stone Age sequence include the extinct Cape zebra (*Equus capensis*), long-horned African buffalo (*Pelorovis antiquus*), and a giant alcelaphine (*Megalotragus priscus*), all of which likely preferred predominantly open grassland habitats (Faith, 2014). While the abundance of these large grazers in the Middle Stone Age record may merely reflect a hunting preference of early humans, it does suggest that grassland habitat was widespread during the Late Pleistocene (Plug, 2004). Also present in the excavations are extant species not historically recorded from the region surrounding HiP: a hippotragine (*Hippotragus* sp.), giraffe (*Giraffa camelopardalis*), and impala (*Aepyceros melampus*). *Hippotragus* sp. and giraffe have also been recorded from archaeological sites further inland, in the midlands of KwaZulu-Natal, until around 4000 and 1000 BP, respectively (Plug and Badenhorst, 2001; Plug, 2004). Impala remains, although rare, have been found further to the north but also in the middle Thukela river basin (southward of the current park boundaries) until about 1200 BP (Plug and Badenhorst, 2001).

Early writings of hunters and explorers indicate that a remarkable abundance of wildlife persisted in the greater Zululand region alongside the Nguni people during the early 1800s. Henry Francis Fynn remarked on the 'tremendous abundance of game' seen during his visit to the Zulu king Shaka in 1824 (Fynn, 1950). Particular mention is made of the large numbers of elephant (*Loxodonta africana*), eland (*Taurotragus oryx*), and buffalo (Delegorgue, 1847), and other species regularly mentioned include white rhino (*Ceratotherium simum*), hippo (*Hippopotamus amphibius*), zebra, kudu (*Tragelaphus strepsiceros*), oribi (*Ourebia ourebi*), common and mountain reedbuck (*Redunca arundinum* and *R. fulvorufula*), bushbuck (*Tragelaphus scriptus*), and red duiker (*Cephalophus natalensis*) (Delegorgue, 1847; Drummond, 1875; Ward, 1896; Findlay, 1903; Lydekker, 1908). Delegorgue (1847) describes regular sightings of eland herds within the area later covered by the Umfolozi Game Reserve and downstream along the floodplain of the Mfolozi river (Delegorgue, 1847). Hippos were reported to occur in the Mfolozi and Hluhluwe rivers (Baldwin, 1894; Findlay, 1903) and reedbuck along the Hluhluwe and Manzibomvu rivers (Findlay, 1903).

None of the records of early European hunters and explorers make reference to giraffe in the Zululand area (Goodman and Tomkinson, 1987; McCracken, 2008). For this reason, giraffe are considered to be extralimital to the region (Goodman and Tomkinson, 1987). Historical records place the southern boundary of giraffe distribution north of Swaziland (Skinner and Chimimba, 2005). Similarly, mention of impala in these early records is very scarce and limited to coastal areas to the north-east of HiP (Drummond, 1875; Baldwin, 1894; Selous, 1908). However, the presence of both these species in archaeological remains further to the south and from inland areas is undisputed (Plug and Badenhorst, 2001; Plug, 2004) and the reasons for their disappearance 1000–1200 BP remain unclear (Rowe-Rowe, 1994; Cramer and Mazel, 2007). Whether impala and giraffe can be considered native to the HiP region is thus contentious.

Heavy exploitation of wildlife populations in Zululand by European and later also Zulu hunters continued through the late nineteenth century: 885 metric tonnes of ivory, 19,245 rhino horns, 2,015,246 unspecified animal skins, 22,154 buffalo hides, and 956 hippo hides were exported from Zululand between 1844 and 1904 (McCracken, 2008). Ivory exports dropped precipitously during the 1860s, indicating dwindling elephant numbers (McCracken, 2008). The last elephant within the current boundaries of HiP was shot on the banks of the Black Mfolozi by John Dunn in 1890 (Vincent, 1970). Similarly, the once-abundant eland had become locally extinct by 1880 (Foster, 1955; Vincent, 1970). By the beginning of the twentieth century, very few rhinos were said to remain (Findlay, 1903; Selous, 1908). The first 'official' estimate of 20–30 rhinos came from the first Zululand Game Conservator, Vaughan-Kirby, during the early 1920s, but in hindsight this underestimate was an attempt to foster the protection of the white rhino (Brooks, 2006). The early twentieth century population was likely much larger, because ground counts of white rhino conducted during the late 1920s indicated a minimum of 172 rhino in Umfolozi Game Reserve (Brooks, 2006), and counts in 1932 and 1936 recorded 220 and 226 rhino, respectively (Player and Feely, 1960; see also Chapter 11).

4.3 Early History of the Game Reserves: 1895–1952

The dwindling wildlife populations led to the proclamation of the Hluhluwe and Umfolozi Game Reserves in 1895 to preserve and maintain indigenous wildlife species, particularly white rhino (Brooks and Macdonald, 1983; Chapter 1). The reserves remained unfenced and were separated by the large stretch of land later referred to as the Corridor, which represented a functional corridor for animals to move between both reserves. Most of Umfolozi GR remained unfenced until the early 1950s, while the majority of the Hluhluwe GR boundaries were fenced off by 1941, leaving only a small section linking to the Corridor area to the south of the reserve unfenced (Brooks and Macdonald, 1983; see Chapter 1 for further details).

In 1897 a continent-wide outbreak of rinderpest reached what we now know as KwaZulu-Natal (Ballard, 1983) and decimated wildlife and livestock populations (Brooks and Macdonald, 1983). Cattle losses of almost 70% were reported (Ballard, 1983). According to Foster (1955), the Zululand buffalo populations suffered particularly heavy losses, while kudu, reedbuck, and bushbuck were also affected although 'in no way as serious as buffalo'. By 1905, substantive recovery of wild ungulates following the rinderpest epizootic had occurred (Foster, 1955; Brooks and Macdonald, 1983). This led to a resurgence of tsetse flies (*Glossina* spp.) and hence the incidence of another major livestock disease for which the tsetse fly acts as a vector: nagana or African trypanosomiasis (caused by *Trypanosoma* spp. parasites; Henkel, 1937; Brown, 2008). Farmers attributed increased nagana prevalence to the recovery of wildlife populations (Brown, 2008) and considered the game reserves as sources of infection (Minnaar, 1989). Dissatisfaction from local residents eventually led the provincial administration to organize a concerted campaign from May 1929 to the end of 1930. The aim was to eradicate all ungulate species, except white rhino, from the buffer zones surrounding Umfolozi GR and to drive those that remained into the game reserve. This resulted in the slaughter of >25,000 ungulates in these designated buffer zones, and 377 individuals from inside the boundaries of Umfolozi GR (Mentis, 1970; Minnaar, 1989; Table 4.1). During the same campaign, >5000 animals were killed in buffer zones around Hluhluwe GR, and >2000 inside the current reserve boundaries (Bourquin and Hitchins, 1979). Because Hluhluwe GR was strictly protected during this time, the latter number likely reflects animals shot in the area south of the Hluhluwe river, which was not then part of the proclaimed reserve. Despite this effort, prevailing drought conditions drove wildlife to move beyond the yet unfenced reserves. Authorities thus concluded that alleviating the threat demanded the eradication of ungulates from inside the reserve boundaries. Consequently, between 1932 and 1954, administrative responsibility of Umfolozi GR was officially assigned to the Division of Veterinary Services to undertake this (Vincent, 1970; Brooks and Macdonald, 1983). Between the late 1930s and the early 1950s, more than 70,000 animals were killed in Umfolozi and surrounding buffer zones (Mentis, 1970; Table 4.1). During this second campaign, Hluhluwe GR remained protected, although ~5400 animals were shot in the buffer zone around this reserve (Bourquin and Hitchins, 1979).

Throughout the first and second shooting campaigns, bushbuck and grey duiker (*Sylvicapra grimmia*) represented ~50% of all animals shot (~25,000 individuals of each, Table 4.1). Despite these massive kills, both these species maintained large populations until the early 1950s (Mentis, 1970). Using actual numbers of animals killed and estimates of reproductive rates, Mentis (1970) back-calculated population sizes of various species in 1942 early during the second campaign. The Umfolozi GR bushbuck population was estimated to have been larger than 12,000 individuals in 1942 and described as still 'very numerous' 10 years later (Mentis, 1970), while the Hluhluwe population remained at around 1000 individuals throughout the campaigns (1936 estimate: Henkel, 1937; 1950 estimate: Anon., 1952). Similarly, grey duiker populations in Umfolozi GR were also referred to as still 'very numerous' by 1952 (Mentis, 1970), and the Hluhluwe grey duiker population apparently doubled between 1936 and the early 1950s (Henkel, 1937; Anon., 1952). While these two species seemed to survive

Table 4.1 *Numbers of various large herbivore species shot during the game eradication campaign of 1929–1930 and while the management of Umfolozi Game Reserve (UGR) and surrounding regions was under the control of the veterinary authority during 1942–1954. Few animals were shot within UGR during 1929–1930 because it had protected status and the animals reported shot in Hluhluwe Game Reserve (HGR) then were probably in the region south of the Hluhluwe river that was not part of the proclaimed game reserve at that time. In 1929–1930, UGR and its buffer zones covered 1400 km^2 and in 1942–1950 1150 km^2. The extent of the other sections was not recorded. UGR buffer zones encompassed regions subsequently included in the game reserve, but extended beyond the present-day boundaries in the south and west (extracted from Mentis (1970) and Bourquin and Hitchins (1979))*

	1929–1930					1942–1950			
Species	UGR	UGR buffer zones	HGR	HGR buffer zones	Total	UGR	UGR buffer zones	HGR buffer zone	Total
Buffalo	5	120	7	13	145	13	19	6	38
Bushbuck	22	2173	453	1337	4185	7540	14,692	1138	23,370
Bushpig	0	22	16	39	77	98	299	14	412
Duiker, grey	10	2987	2	383	3382	4728	15,733	1024	21,485
Duiker, red	0	0	0	19	19	0	9	59	68
Impala	0	0	0	0	0	16	3	14	33
Klipspringer	0	5	0	0	5	47	50	2	99
Kudu	2	286	0	15	303	759	679	72	1510
Nyala	0	0	0	0	0	23	16	228	267
Reedbuck, common	0	390	2	449	841	396	2952	198	3546
Reedbuck, mountain	0	12	0	19	31	334	3173	157	3664
Steenbok	1	306	0	17	324	558	1437	50	2045
Warthog	216	3456	524	1109	5305	7661	5173	2225	15,059
Waterbuck	26	504	0	173	703	535	474	157	1166
Wildebeest	26	664	996	1906	3592	721	304	130	1155
Zebra	69	15130	158	666	16023	917	845	78	1840
Grand total	377	26162	2158	5645	34,342	24,346	45,858	5430	75,634

the anti-nagana campaigns well, this could not be said for populations of most of the larger species. By the middle of the century, wildebeest and zebra had been eliminated from Umfolozi GR. Similarly, based on the population estimates reported in Mentis (1970), the Umfolozi GR reedbuck population (including both the common and the mountain reedbuck species) dropped by 96% between 1942 and 1952 (Mentis, 1970) and waterbuck (*Kobus ellipsiprymnus*) dropped to 15% of its former abundance (Mentis, 1970). By 1952, steenbok (*Raphicerus campestris*) numbers were a mere 5% of what they were calculated to have been 10 years prior (Mentis, 1970). Interestingly, only approximately 3% of the estimated population of buffalo was culled in Umfolozi GR and the population was still estimated at approximately 1000 individuals in 1942 (Mentis, 1970). However, following the massive culling of other species during the 1940s, the Umfolozi GR buffalo population was believed to have migrated out of the park to the north (Foster, 1955), leaving only a handful of individuals during the early 1950s (Mentis, 1970; Brooks and Macdonald, 1983). These massive drops in population numbers need to be interpreted with caution as the 1942 estimates were derived from a calculation based on kill numbers and assumed reproductive rates and not from direct counts. As such, it does not take into account surviving animals or migrations to and from the area. Regardless, at the start of the 1950s, populations of most large ungulate species were either entirely eliminated or nearly so in Umfolozi GR.

Hluhluwe GR was less affected, particularly during the second campaign, and by the start of the 1950s the reserve had maintained large populations of ungulates, including many wildebeest and zebra (Bourquin and Hitchins, 1979). Likewise, the buffalo population in Hluhluwe at the end of the nagana campaigns was estimated to be in the region of 700. However, several smaller antelope species experienced severe population collapses in Hluhluwe GR as well. The Hluhluwe populations of both species of reedbuck were halved between 1936 and 1950 (Bourquin and Hitchins, 1979). Foster (1955) refers to 'countless numbers [of reedbuck] on either side of the road' throughout the Corridor in 1906, but they had become a 'vanishing population' by the 1950s. Deane (1966) mentions that reedbuck was the most frequently seen animal in the Corridor during the early twentieth century, but were noticeably rare by 1954. Similarly, steenbok numbers in Hluhluwe estimated at approximately 100 in 1936 had become 'very few' (Bourquin and Hitchins, 1979). Waterbuck numbers in Hluhluwe were low (300) in 1936, but remained unchanged in 1950 (Bourquin and Hitchins, 1979).

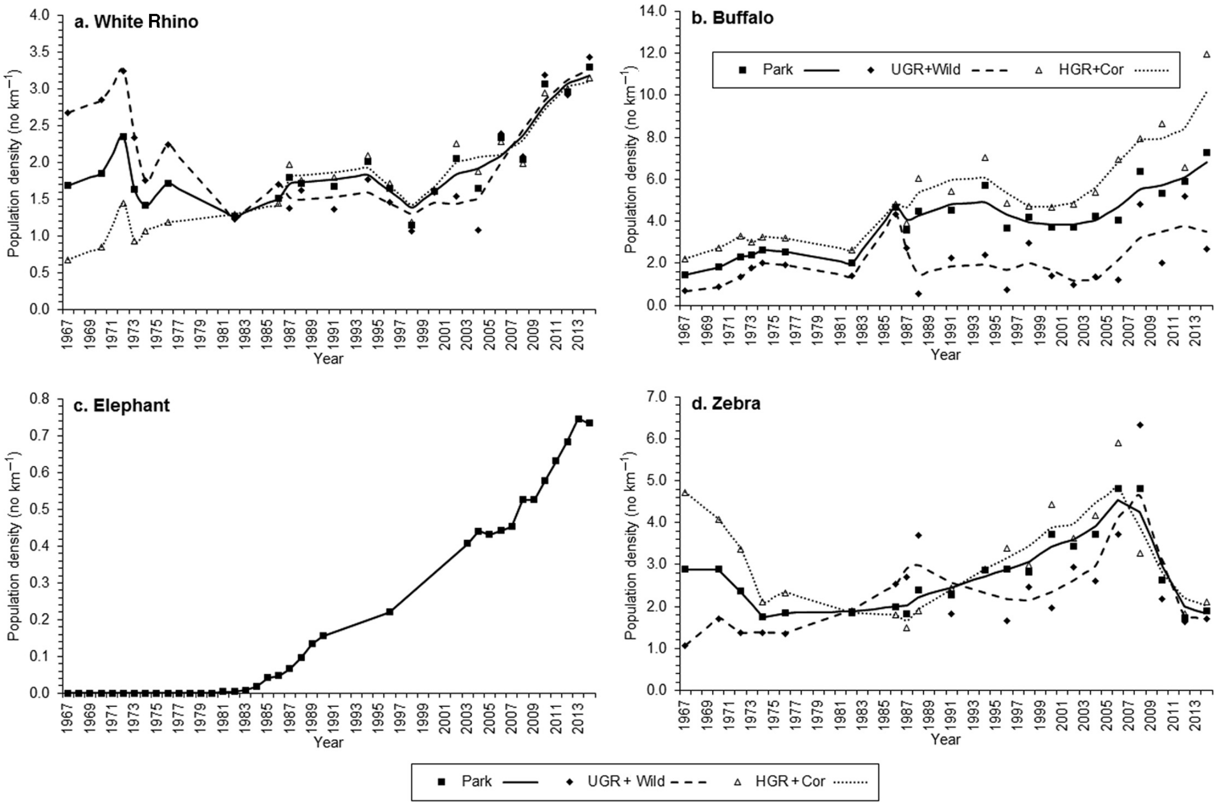
Rhinos of both species remained protected throughout the 1929–1952 game eradication campaigns (Minnaar, 1989). By the early 1950s, around 500 white rhinos occurred in Umfolozi GR (Foster, 1955) and they had recolonized the area north of Umfolozi. In 1950, an estimated 20 occurred in Hluhluwe (Bourquin and Hitchins, 1979), while approximately 70 were present in the Corridor in 1958 (Deane, 1966). Black rhino (*Diceros bicornis*) numbers were estimated at 10 individuals in Umfolozi GR and 190 in Hluhluwe during the early 1950s (Foster, 1955; Bourquin and Hitchins, 1979; see Chapter 11).

4.4 Herbivore Population Trends after 1952

4.4.1 A Time of Faunal Restoration – Population Recovery and (Re)Introductions

In 1952 the responsibility of reserve management was assumed by the newly established Natal Parks, Game and Fish Preservation Board (Vincent, 1970). At this time, fencing of Umfolozi GR commenced at a large scale but was only completed by 1965 (Vincent, 1970). As ungulate populations within Hluhluwe GR had been little affected by the anti-nagana campaigns, wildebeest, warthog (*Phacochoerus africanus*), and zebra began dispersing southwards, crossing the Corridor to repopulate Umfolozi GR (Deane, 1966; Vincent, 1970). Dispersal into Umfolozi GR was facilitated following a flood in July 1963 which deposited sand, making the Black Mfolozi river shallower and hence easier to cross for a longer portion of the year (Vincent, 1970). White rhino followed the opposite dispersal route and gradually dispersed northwards into Hluhluwe (Vincent, 1969).

This period also saw several successful and unsuccessful attempts to (re)introduce species. Impala and nyala (*Tragelaphus angasi*) were introduced in Hluhluwe GR in 1936, although a few nyala may have been present in the Hluhluwe river thicket (Hitchins and Vincent, 1972). By the 1940s impala had entered Umfolozi, as 16 of them were shot during the 1942–1950 nagana campaign (Mentis, 1970). Still only about 10 impala were estimated to occur in Umfolozi GR by 1952 (Foster, 1955; Mentis, 1970). Following its initial re-introduction in Hluhluwe, nyala had colonized Umfolozi GR by 1937 (Foster, 1955), and in 1952 a minimum of 50 individuals occurred in Umfolozi GR (Foster, 1955). Foot counts in 1967 came to a minimum of 550 and 850 impala and nyala in Umfolozi GR, respectively (Bourquin, 1968) and both species have increased rapidly since (Figure 4.1). Further introductions included


a. White Rhino
b. Buffalo
c. Elephant
d. Zebra
Population density (no km^{-1})
Year
Park
UGR+Wild
HGR+Cor
Park
UGR + Wild
HGR + Cor

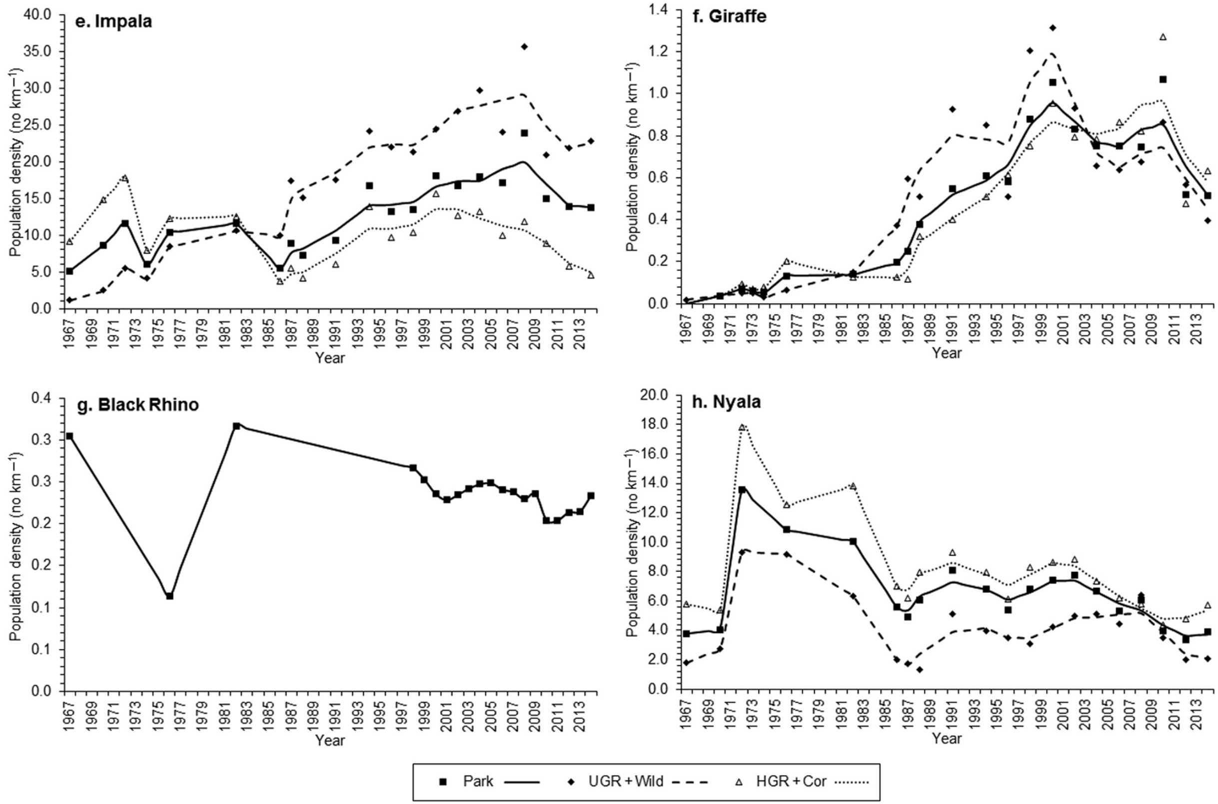


Figure 4.1 Long-term population trends of the more common ungulate species from 1967 onwards in order of decreasing current population biomass. Population density is presented for Hluhluwe and the Corridor sections combined and for Mfolozi and the Wilderness sections combined. No density estimates are available for the Wilderness section between 1986 and 2006 and the density displayed for this period represents only the Mfolozi section. (A) white rhino; (B) buffalo; (C) elephant; (D) zebra; (E) impala; (F) giraffe; (G) black rhino; (h) nyala, (I) wildebeest; (J) kudu; (K) warthog; (L) waterbuck.

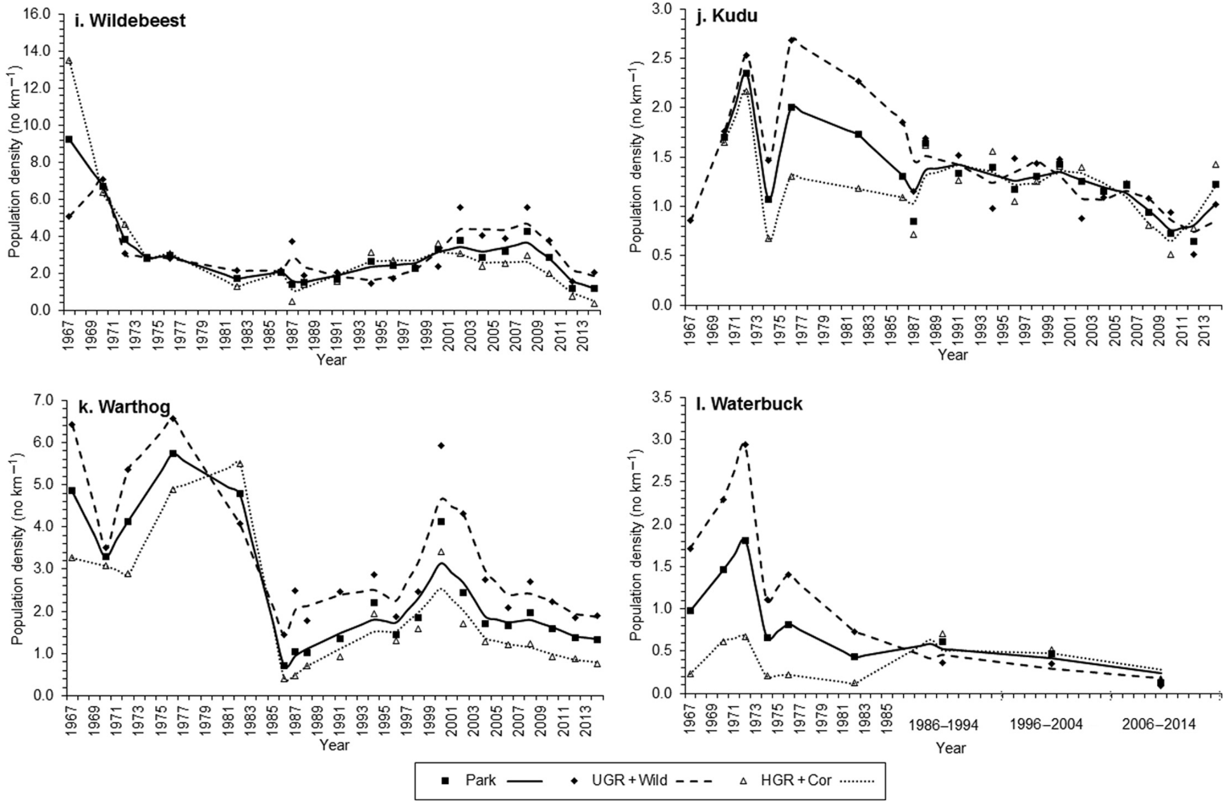


Figure 4.1 (continued)

four surviving giraffe brought into Hluhluwe GR south of the Hluhluwe river between 1949 and 1957 (Bourquin *et al.*, 1971) and nine into Umfolozi GR in 1965/66 (Vincent, 1970; Brooks and Macdonald, 1983). Less successful was the re-introduction of 14 eland from the Drakensberg into Umfolozi in 1964 (Vincent, 1970). All except for a single male died within a few years, apparently due to tick infestations. During the mid-1990s over 20 eland were again released in Mfolozi, but all died of heart-water, a disease spread by ticks, or fell prey to lion (Craig Reid, personal communication). No eland currently remain in HiP. The final herbivore restoration was the re-introduction of elephants in Hluhluwe GR in 1981 (Brooks and Macdonald, 1983) and into Umfolozi GR in 1985 (Wills, 1986; see Chapter 14). Carnivore populations were also re-established during this period with the arrival of the first lion (*Panthera leo*) in 1958 followed by the introduction of more lions in 1965, and re-introductions of cheetahs (*Acinonyx jubatus*) in 1966 and wild dogs (*Lycaon pictus*) in 1980/81 (see Chapter 12).

4.4.2 The Era of Population Management and Concerns about Overgrazing: Late 1950s–1980

The 1960s saw the effective inclusion of the Corridor as part of the game reserve complex through fencing of its eastern and western boundaries. Fencing of the entire reserve complex was completed by the start of the 1970s (Brooks and Macdonald, 1983). The perception at the time was that the restriction on animal movement and lack of predators had led to excessive grazing impacts on the grasslands. Concerns about over-utilization were further fuelled by drought conditions prevailing during the mid-1950s, worsening grass cover losses, soil erosion and shrub encroachment in Hluhluwe GR (Ward, 1958). Consequently, culling was initiated in Hluhluwe GR and the northern Corridor in 1954 directed particularly at wildebeest, zebra, and warthog and extended to Umfolozi GR and the southern Corridor in 1960 (Table 4.2; Brooks and Macdonald, 1983). In 1969, 'Operation Rhino' was instigated to capture white rhinos and distribute the local subspecies more widely through other wildlife areas to reduce the risk that the entire world population, confined at that time mostly within Umfolozi GR, could be wiped out by a disaster such as a disease outbreak. White rhino removals were expanded during the early 1970s because of concern about widening 'overgrazing' during a sequence of low rainfall years, and other species that might

Table 4.2 *Numbers of various large herbivore species removed (live removal as well as shot animals) per decade since 1954. Data from the 1950s to the 1970s were extracted from Brooks and Macdonald (1983) and Bourquin and Hitchins (1979). 1: UGR + corridor south of Hlabisa road, 2: HGR + corridor north of Hlabisa road. Data from the later decades were extracted from the park's animal removal database (EKZNW, unpublished data)*

	1954–1959		1960s		1970s		1980s	1990s	2000s	2010–2014	
Species	UGR[1]	HGR[2]	UGR[1]	HGR[2]	UGR[1]	HGR[2]	HiP	HiP	HiP	HiP	Total
Buffalo	1	0	5	0	193	130	891	2347	1568	172	5307
Bushbuck	2	0	78	0	0	0	0	0	0	0	80
Bushpig	–	0	–	0	0	0	0	0	0	0	0
Duiker, grey	–	0	–	0	0	0	0	0	0	0	0
Duiker, red	–	0	–	0	0	0	0	0	0	0	0
Elephant	0	0	0	0	0	0	0	1	34	7	42
Giraffe	0	0	0	0	0	0	0	99	156	26	281
Impala	1	1599	771	6800	4522	7787	9613	3524	4013	981	39,611
Klipspringer	–	0	–	0	0	0	0	0	0	0	0
Kudu	0	0	7	21	88	4	106	132	60	0	418
Nyala	0	538	78	718	2038	2155	4633	1626	2528	165	14,479
Reedbuck, common	–	0	–	0	0	0	0	0	0	0	0
Reedbuck, mountain	–	0	–	0	0	0	0	0	0	0	0
Rhino, black	0	6	0	0	2	38	44	132	106	37	365
Rhino, white	0	0	74	0	1526	53	1318	896	459	318	4634
Steenbok	–	0	–	0	0	0	0	0	0	0	0
Warthog	302	4670	13,823	4724	3275	2869	997	151	388	32	31,231
Waterbuck	0	0	75	0	48	72	20	87	28	0	330
Wildebeest	25	2537	5038	3806	2027	1896	1366	0	146	115	16,809
Zebra	19	1052	870	684	148	641	651	71	135	58	4329
Grand total	350	10,402	20,819	16,753	13,867	15,645	19,639	8919	9621	1911	117,916

be competing with white rhinos for forage, especially wildebeest and warthog, were heavily culled within Umfolozi GR as well as in Hluhluwe GR (Brooks and Macdonald, 1983). Culling of all of the more common herbivores then became aimed at counteracting the influence of rainfall patterns on veld condition, with more animals being removed in dry years when veld conditions were considered to be vulnerable to overgrazing and fewer removals in wet years when veld conditions improved. During the 1960s, 1970s, and part of the 1980s, very large numbers of warthog, wildebeest, zebra, and nyala were culled in both Umfolozi and Hluhluwe (Table 4.2; Brooks and Macdonald, 1983). Impala were subject to especially heavy culling because they were perceived to be extra-limital (Table 4.2). Few pure browsers, represented by black rhino, kudu, and giraffe, were removed, mainly directed at live sales. The heavy removals resulted in very few herbivores dying of malnutrition during the severe 1982/83 drought, and low wildlife sightings by tourists when conditions improved after the drought (Walker *et al.*, 1987).

4.4.3 Towards Process-Based Management: 1980s

At the start of the 1980s the severity of the culling programme and the appropriateness of the agriculturally based approach to setting carrying capacities were called into question (Walker *et al.*, 1987). A reassessment of management policies led to the implementation of a process-based management approach, curtailing removals and allowing for natural population variation (see Chapter 1 for further details). Herbivore management changed to the manipulation of herbivore landscape use through strategic burning practices (Brooks and Macdonald, 1983). Moreover, culling increasingly included live capture and sale of wildlife to restock other protected areas. Finally, biennially repeated ground surveys using distance sampling (Burnham *et al.*, 1980) were implemented to provide less-biased estimates of total populations than provided by the aerial counts that were used in the late 1960s and 1970s (Knott, 1986; specific details on implementation are provided in Appendix 4.1). The strong reductions in annual animal removals led to population increases in several of the ungulate species from the 1980s until the early 2000s, particularly by wildebeest, zebra, and warthog (Figure 4.1; see Box 4.1 for an overview of the different counting methods and Box 4.2 for a description of population trends). Annual removals were strongly reduced by the mid-1980s for these species, but continued into the 2000s for impala, nyala and buffalo (Table 4.2).

Box 4.1 *Interpreting Results from Different Counting Methods*

Interpreting long-term population trends is particularly problematic due to the changes in estimation techniques. When comparing density estimates between periods, the differing biases in the different methods used must be taken into account. The population trends described in this chapter can be divided into three main periods according to the counting methods used: pre-1960s, 1960s to early 1980s, 1986 to present.

Pre-1960s: Early twentieth-century estimates resulted from foot counts or through expert-based guestimates at the time. For this reason, the early foot count estimates are excluded from the trends represented in the graphs in Figure 4.1.

1960s–1985: The first aerial count covering Hluhluwe GR, Umfolozi GR, and the Corridor was conducted in 1967 by fixed-wing aircraft. Further aerial counts were carried out using a helicopter annually from 1970–1976 (Melton, 1978a). Further aerial counts were done during 1981 (Brooks, 1982) and 1983 (Brooks *et al.*, 1983); a combination of fixed-wing, helicopter, and foot counts in 1981, and by helicopter in 1983. Because aerial counts incorporate an inherent undercount bias depending on the size and behaviour of the species (Melton, 1978b), aerial count totals have been compared with animals counted on the ground in local areas (Melton, 1978b; Bothma *et al.*, 1990; van Hensbergen *et al.*, 1996). This indicated that 70% or more of larger species like wildebeest and zebra are tallied by helicopter but only 33–50% of smaller species like impala and warthog, with more animals missed from a fixed-wing aircraft. The estimates from 1967 onwards presented in this chapter were extracted from Brooks and Macdonald (1983) and have been corrected for this undercount bias using specific correction factors per species reported in Brooks (1978).

1986–present: The dense woody cover over much of HiP, and the continuing uncertainty over the reliability of the aerial counts, led to the decision to move away from aerial counts. Accordingly, after initial trials (Knott and Venter, 1987, 1990) a switch was made starting in 1986 to carry out distance-sampling based ground counts using a set of transects representing most of HiP (see Appendix Figure A4.1 for a map and detailed methods). Since 1994, these ground surveys have been undertaken biennially using volunteers supported by park staff. Because of difficulties in access and restrictions on clearing transects, the wilderness section of Mfolozi was only effectively incorporated from 2006 onwards. These distance sampling estimates are inherently unbiased, but subject to greater sampling error, and therefore have been smoothed in the plots (Figure 4.1).

For consistency, the population trends shown by the more common ungulate species in HiP are plotted as density estimates separately for the Mfolozi section and for Hluhluwe plus the Corridor, as well as for the entire complex combined (Figure 4.1). Furthermore, the animals removed for population control (Table 4.2) must also be considered in interpreting the trends shown.

Box 4.2 *Noteworthy Features of the Population Trends Shown by Various Ungulate Species in Rough Order of their Body Size*

Elephant

Elephant numbers in HiP have increased exponentially following their re-introduction in the early 1980s. There is little sign as yet of any reduction in population growth rate.

White rhino

White rhinos were initially concentrated mostly in Umfolozi GR, but heavy removals substantially reduced the Umfolozi GR subpopulation while numbers were allowed to grow in the Corridor and Hluhluwe GR. Following recent reductions in animals removed, the Umfolozi subpopulation has reached similar density levels to those exhibited around 1970, and very similar densities also now prevail over the rest of HiP.

Black rhino

Pre-1960, the Hluhluwe black rhino population approached the highest density for the species recorded anywhere in Africa. After 1960, this population crashed following deaths from unknown causes. There was some compensation from increasing numbers in Umfolozi, but overall fewer black rhinos currently persist within HiP than the park had originally supported.

Giraffe

Giraffe grew rapidly in numbers following introductions and currently fluctuate around an overall density of 0.7 animals/km^2.

Buffalo

The buffalo population has grown progressively despite quite heavy removals during the late 1990s when culling was aimed at eliminating animals infected with bovine tuberculosis (see Chapter 13).

Zebra

Following the cessation of heavy culling after 1982, zebra initially increased towards the density levels that they had attained in the 1960s. However, since 2008 there has been a downturn in their numbers over the whole park.

Wildebeest

Despite removals being greatly reduced after 1982, wildebeest did not regain the numbers that they had attained in the late 1960s. Wildebeest numbers went into steep decline after 2008 and hardly any wildebeest remained in Hluhluwe by 2014.

Waterbuck

Waterbuck have been a source of concern because of the progressive decline in their numbers (currently estimated at roughly 120 animals in total). Very few waterbuck were removed.

Kudu

As for waterbuck, kudu have also incurred little culling. Nevertheless, their population density has also declined progressively since the late 1970s.

Nyala

Heavy culling during the 1970s and early 1980s reduced nyala densities considerably below their peak levels attained around the early 1970s. From the mid-1980s their numbers were stabilized by continuing removals. However, their density declined after 2008, particularly in Mfolozi, despite the curtailment of culling since the late 2000s.

Impala

Heavy culling kept impala density at or below 10 animals/km^2 during the 1970s and 1980s. With reduced removals after 1982, the impala population grew towards a density approaching 30 animals/km^2 within Mfolozi. A decline in impala density became evident in Hluhluwe after 2002 and in Umfolozi after 2008.

Warthog

The high density of warthogs that occurred prior to the 1980s was greatly reduced by culling. The population recovered until 2001, but has declined strongly during the 2000s without massive culling.

Less-Common Ungulate Species

Several ungulate species are currently too uncommon or localized to be counted reliably, so that only broad decadal trends can be described (Table 4.3). Among these species, grey duiker, red duiker, and bushpig (*Potamochoerus larvatus*) seem to be maintaining their abundance during recent decades. However, grey duiker had been far more numerous prior to the 1970s when their local density in western Umfolozi GR was estimated to be four to five animals/km^2 (Owen-Smith, 1973). Common reedbuck, mountain reedbuck, bushbuck, blue duiker, and steenbok have declined to critically low numbers.

4.4.4 Population Declines by Several Small- to Medium-Sized Antelope Species

Despite an increase in populations of many species since the early 1980s, several small- to medium-sized antelopes continued their declines to numbers that can hardly be regarded as viable. While more than 1700 waterbuck were reported in 1972 (Brooks and Macdonald, 1983), the current estimates show a mere 120 remaining park-wide (Figure 4.1). Similarly, common and mountain reedbuck populations that were estimated to still number 623 and 152 individuals, respectively, during 1972 (Brooks and Macdonald, 1983) have now almost disappeared

Table 4.3 *Population estimates for species that currently occur in low numbers within Hluhluwe-iMfofozi Park. The 1982 estimate is from Brooks and Macdonald (1983). From 1986 onwards estimates are based on distance sampling records aggregated over 10 years to ensure a robust approximation*

Period	Bushpig	Grey duiker	Red duiker	Blue duiker	Bushbuck	Common reedbuck	Mountain reedbuck	Steenbok
1982	346	1410	455	?	479	165	136	235
1986–1994	106	794	343	6	73	56	40	93
1995–2004	100	398	232	6	58	13	16	9
2005–2014	97	442	329	5	25	10	21	3

(Table 4.3). Other smaller antelope species that have shown drastic declines are bushbuck, steenbok, and blue duiker (*Philantomba monticola*), all with population sizes of < 50. While bushbuck were still numerous at the end of the anti-nagana campaigns in 1952 (1000s), the current population estimate is 25 for the entire park.

Several factors could have been responsible for the population declines by these species. For reedbuck (Deane, 1966; Anderson, 1979), and steenbok (Anderson, 1979; Brooks and Macdonald, 1983), deterioration of grasslands due to ongoing encroachment by woody plants since the early 1950s has been invoked (Ward, 1958; see also Chapter 3). Competition with other grazers has been suggested for reedbuck (Deane, 1966) and waterbuck (Melton, 1987). Declines in bushbuck, and perhaps blue duiker, have been attributed to competition with the increasing nyala population (Anderson, 1979; Brooks and Macdonald, 1983). On a local scale within Hluhluwe, wetland drainage brought about by the construction of roads may have altered grassland quality, possibly further isolating subpopulations of specialist feeders such as reedbuck and waterbuck and contributing to their population crashes (Tony Whateley, personal comments). All in all, there is no conclusive evidence for any of the mentioned drivers of population decline, and a combination of drivers likely played a role.

4.4.5 Effects of Increasing Predator Populations: 2000s

During the past few decades, predator populations have recovered following successful re-introductions (see Chapter 12). Since 2004 the lion population has increased about twofold whereas the wild dog population increased three- or fourfold between 2002 and 2010 (although it has shrunk again since). This increase in predators coincides with drops in the numbers of zebra, wildebeest, nyala, and impala (specifically since 2008; Figure 4.1). All of these species have been shown to be the preferred prey species of predators (Chapter 12). In contrast, buffalo showed a slight increase over the past several decades (Figure 4.1B) despite their vulnerability to lion predation. However, over the past 15 years the buffalo population has been affected by a bovine tuberculosis (*Mycobacterium bovis*) control programme (Chapter 13). This programme has dramatically reduced the prevalence of this disease in the HiP buffalo population, which may have boosted the population growth rate through lowered mortality rates and enhanced fecundity. Such positive effects on growth rate may be counteracting any effects of possible increases in predation pressure.

Interestingly, the decline in numbers for species such as impala and wildebeest started earlier and has been much steeper in Hluhluwe than in other regions of the park (Figure 4.1E,I), which may indicate an exacerbated effect of predation due to the woody plant encroachment within Hluhluwe (Chapter 3).

4.4.6 Changes in Functional Composition

HiP has experienced some consistent trends in the functional composition of its ungulate assemblage during the last 40–50 years. Following the 1960s' and 1970s' culling removals, overall herbivore biomass increased substantially (Figure 4.2). However, while mixed feeders and, to a lesser extent, browsers have increased park-wide, increase among grazers has been restricted to the Corridor. White rhino and buffalo currently contribute equally to more than 90% of the grazer biomass and growth in grazer biomass can be mostly attributed to these two species. Perhaps even more striking is the mounting influence of the largest herbivores (body mass > 400 kg) during the last 40–50 years, specifically elephant, giraffe, black and white rhino, and buffalo (Figure 4.3). Hippos also still occur in the park, but numbers are very low and fluctuate quite strongly driven by variation in water levels in perennial water sources in the park. Species in this size range contribute more than three times as much to total herbivore biomass than they did in 1980, whereas species the size of zebra and smaller have decreased in aggregate biomass by a third in the same period. The strong increase in large-bodied species is mostly due to the expansion of numbers of white rhino within the Corridor and Hluhluwe plus the recovery of their numbers within Mfolozi towards earlier peak densities, combined with the growth in the elephant, and to some extent buffalo, populations. This has led to a situation where the total biomass of large herbivores within HiP currently exceeds 10,000 kg/km^2, rivalling that in the Serengeti ecosystem and double that in Kruger National Park (see Figure 5.1 in Chapter 5). Another striking pattern is the drastic decline of the small body-size category (dominated by impala and nyala) during the early 1980s, particularly in Hluhluwe GR. The early 1980s were characterized by a severe drought, a final phase of heavy culling of impala and nyala and the introduction of a main predator of impala and nyala – wild dogs – into Hluhluwe GR. The combination of these three factors could have driven the drastic decline of small-bodied ungulates in Hluhluwe GR during the early 1980s.

Changes in functional composition of herbivores could have far-reaching consequences for the structure and composition of HiP's savanna

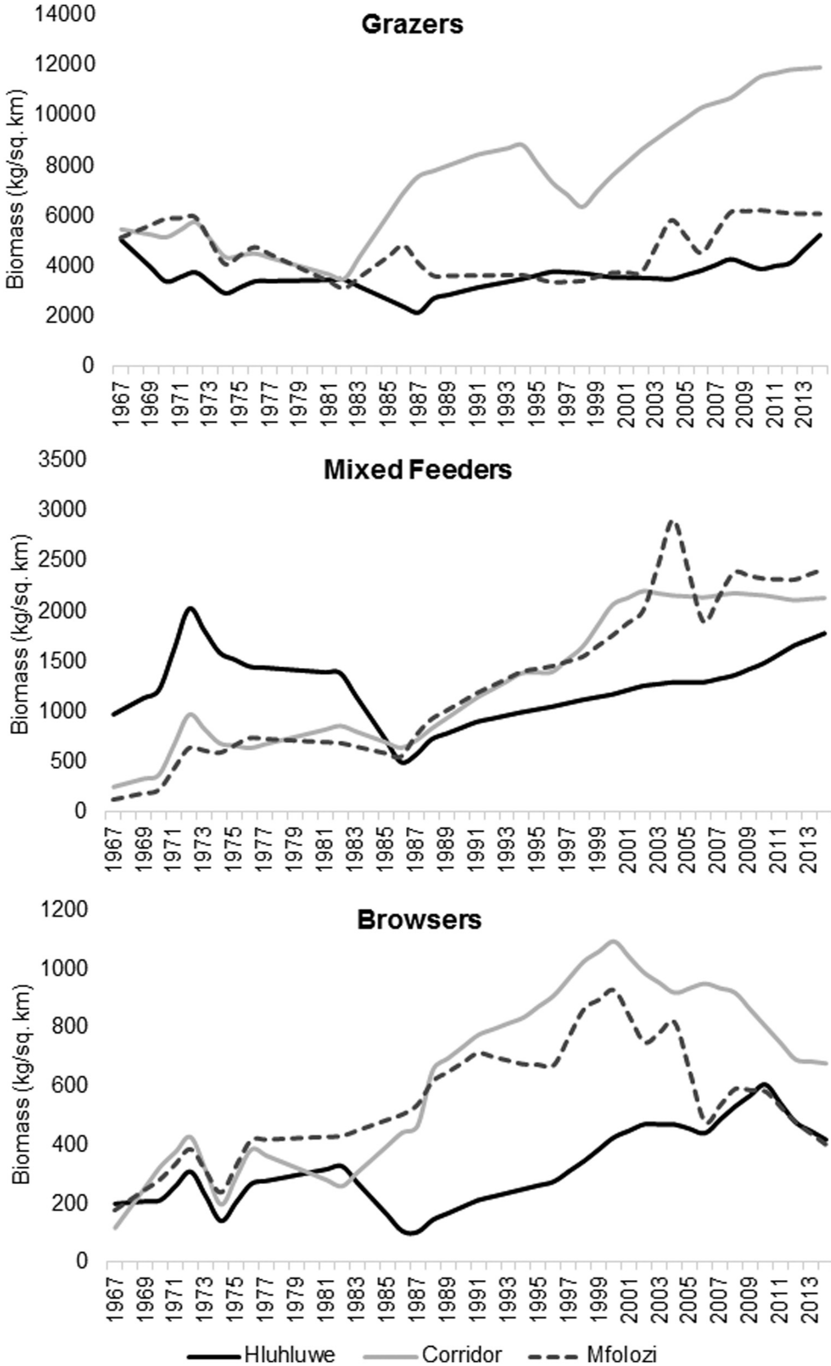


Figure 4.2 Changes in biomass density for herbivores of different functional groups between the years 1967 and 2014. Functional groups are categorized as follows:

grasslands and woodlands (refer to Chapters 5 and 6 for white rhino, and Chapter 14 for elephant). Competitive and facilitative relationships between the expanding white rhino population and other grazers are considered in Chapter 5.

4.5 Concluding Remarks

HiP's ungulate populations showed wide fluctuations and varying trends prior to 1982, driven mainly by human influences. Following the curtailment of animal removals, densities of the main grazers increased, until recent downturns especially in wildebeest, zebra, and warthog. Even the two browsers least affected by culling, i.e. giraffe and kudu, showed little indication of a persistent 'carrying capacity'. While studies elsewhere have demonstrated how rainfall variation controls population trends of savanna herbivores (Ogutu and Owen-Smith, 2003), such a relationship is not evident in the HiP data. Rainfall in HiP tended to be above average through the 1990s and below average after 2000 (Chapter 2). Density estimates from distance sampling are subject to quite wide confidence limits, and are obtained only biennially, possibly obscuring the short-term effects of annual or seasonal rainfall on population growth.

The most recent trends in population patterns, particularly of grazers such as zebra and wildebeest, raise intriguing questions about predator–prey dynamics in small fenced reserves. Theory suggests that the growing abundance of predators will lead to coupled oscillations in predator–prey abundance. Will this happen in HiP, or will populations of herbivores stabilize at some lower abundance by becoming confined to habitats where they are relatively more secure from predation? Although we currently lack the answer to this question, it seems clear that we are

Figure 4.2 (*caption continued*) grazers (white rhino, buffalo, zebra, wildebeest, waterbuck, warthog, common reedbuck, and mountain reedbuck); browsers (black rhino, giraffe, kudu, bushbuck, grey duiker, red duiker, steenbok, and blue duiker); and mixed feeders (elephant, nyala, and impala). Separate estimates are presented for Hluhluwe, the Corridor, and Mfolozi. Mfolozi biomass estimates prior to 1986 and after 2006 are calculated for an area including the Wilderness. Elephant numbers were not available per section as they roam across the entire park. For the purpose of this figure we assumed that elephants were distributed evenly across the park and therefore added the total biomass contribution of elephants to each section weighted by section area. Three-quarters average female body-weight estimates, obtained from Owen-Smith (1988), were used in biomass calculations.

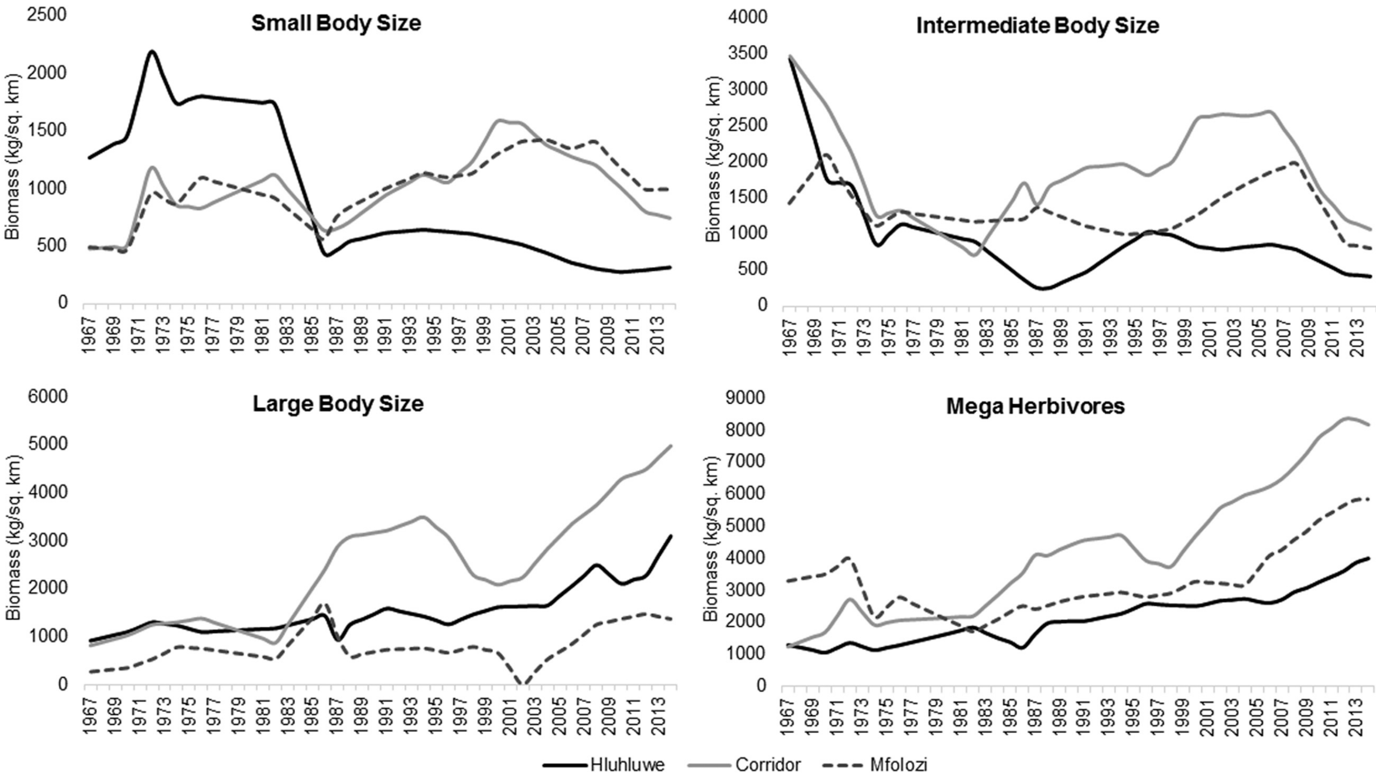


Figure 4.3 Changes in biomass density for herbivores of different size classes between the years 1967 and 2014, derived as in Figure 4.2. For the rare species for which small sample size only allowed park-wide estimates to be calculated, we assumed that the proportional distribution across sections remained the same as it was in 1982. Size classes were distinguished as small (adult male weight less than 150 kg, including blue duiker, steenbok, red duiker, grey duiker, mountain reedbuck, bushbuck, impala, common reedbuck, warthog, and nyala); intermediate (adult male weight 150–400 kg, including kudu, waterbuck, wildebeest, and zebra); large (adult male weight 400–1000 kg, including buffalo only); and megaherbivores (adult male weight > 1000 kg, including giraffe, black rhino, white rhino, and elephant).

currently experiencing a re-establishment of the predator–prey dynamics in HiP. One of the key current concerns and questions for the conservation management of HiP is what trajectory the carnivore–prey dynamics will follow (see Chapter 12).

The herbivore species that have declined to numbers threatening their survival in the park are certain of the smaller ungulate species. They appear unable to cope with habitat changes, increased competition with expanding populations of other ungulate species or higher predator numbers. This is contrary to general assumptions about the kinds of species most vulnerable to extinction. It is widely assumed that very large species are most in danger because of their slow population growth rates (see e.g. Cardillo *et al.*, 2005). On the contrary, observations in HiP show that it is some of the smaller species that are more vulnerable, because of their narrower habitat requirements and vulnerability to predation. This situation can be drastically altered when humans become predators on the very largest species, albeit merely for parts such as tusks and horns (Chapter 11). Regrettably, the current rhino and elephant poaching crisis spreading across Africa could soon alter the upwards trends of even these megaherbivores.

Appendix 4.1. Details on Methods for Estimating Population Abundances from the Distance-Sampling Transects

From 1986 onwards, the estimation technique was a ground census technique using line transects with visibility bias corrected using distance sampling protocols developed by Burnham *et al.* (1980) and refined by Buckland *et al.* (1993). Since 1994, these surveys have been undertaken biennially.

The transect network consists of 34 transects (Figure A4.1) ranging in length from 3.88 to 12.94 km and totalling approximately 281 km. Transects are evenly distributed across the park and cover roughly 30% of the area. All except the eight transects situated in the Wilderness section are cut prior to each census. In an attempt to adhere to the management policy of minimal interference in the wilderness, population surveys in this section were initially performed using point transects. However, by 2006, the point transect method was abandoned as unsuccessful and the line transect method was extended to the wilderness, although the transect lines remained uncut. For this reason only the Wilderness estimates from 2006 onwards are incorporated in the trends discussed in this chapter.

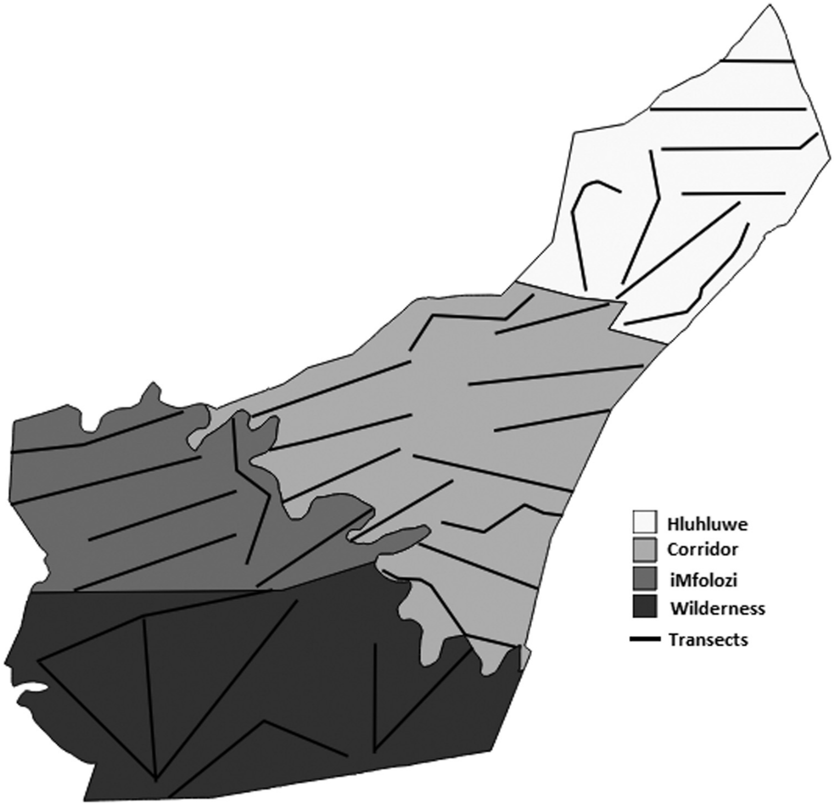


Figure A4.1 Map of Hluhluwe-iMfolozi Park showing line transect positions in each of the four sections (shaded).

Each transect is walked approximately 14 times on a three-day rotation. Surveys are completed in the late dry season between July and October.

Census-derived density estimates were calculated using distance sampling methods and the software DISTANCE (version 6.2, Thomas *et al.*, 2010). By using information on the position of each animal relative to the position of the observer, this technique takes into account the decreasing possibility of detecting animals that are further from the observer (Buckland *et al.*, 1993). Depending on sighting frequency, a survey-specific detection function was calculated either separately per section or a park-wide detection function was used to calculate section-specific densities.

For the purposes of this chapter, census derived density estimates were calculated separately per section. For a few rare species, notably blue duiker, red duiker, waterbuck, bushbuck, common reedbuck, mountain reedbuck, steenbok, and bushpig, observations were amalgamated over a 10-year period to ensure a statistically robust density estimate.

While suitable for most large mammalian species, ground counts are inappropriate for species with shy habits such as black rhino or dangerous species such as elephant. In this instance, these species were surveyed through a combination of aerial counts aimed specifically at quantifying these populations and mark–recapture techniques using trap cameras and ad hoc staff sightings.

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