



Original article

Changes of population trends and mortality patterns in response to the reintroduction of large predators: The case study of African ungulates

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ABSTRACT

Large predators have been reintroduced to an increasing number of protected areas in South Africa. However, the conditions allowing both prey and predator populations to be sustained in enclosed areas are still unclear as there is a lack of understanding of the consequences of such reintroductions for ungulate population dynamics. Variation in lion numbers, two decades after their first release, offered a special opportunity to test the effects of predation pressure on the population dynamics of seven ungulate species in the 960 km² Hluhluwe-iMfolozi Park (HiP), South Africa. We used two different approaches to examine predator–prey relationships: the population response of ungulates to predation pressure after accounting for possible confounding factors, and the pattern of ungulate adult mortality observed from carcass records. Rainfall patterns affected observed mortalities of several ungulate species in HiP. Although lion predation accounted for most ungulate mortality, it still had no detectable influence on ungulate population trends and mortality patterns, with one possible exception. This evidence suggests that the lion population had not yet attained the maximum abundance potentially supported by their ungulate prey; but following recent increases in lion numbers it will probably occur soon. It remains uncertain whether a quasi-stable balance will be reached between prey and predator populations, or whether favoured prey species will be depressed towards levels potentially generating oscillatory dynamics in this complex large mammal assemblage. We specifically recommend a continuous monitoring of predator and prey populations in HiP since lions are likely to show more impacts on their prey species in the next years.

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1. Introduction

Large predators play an important role in natural ecosystems (Ale and Whelan, 2008) and their impact on ungulates can contribute towards maintaining prey diversity in complex multi-prey–multi-predator systems (Dalerum et al., 2008). In response to the local extirpation of carnivores (Woodroffe et al., 2007) and to the growing importance of maintaining a high biodiversity in the current context of conservation and eco-tourism (Hayward et al., 2009), large predators have been reintroduced to an increasing number of protected areas, especially in South Africa (Hayward et al., 2007a; Hayward and Somers, 2009). In some cases the aim has been specifically to restore the role of predation in limiting excessive herbivore populations and their associated impacts on

vegetation (Brooks and MacDonald, 1983). However, in certain situations the reintroduction of predators has led to progressive declines in the abundance of their main prey species, especially in small fenced reserves (Hunter, 1998; Power, 2002; Tambling and du Toit, 2005; Hayward et al., 2007b), thereby threatening the sustainability of the predator population unless prey numbers are periodically restored. This raises questions regarding the circumstances under which viable predator and prey populations can be maintained in relatively small, fenced protected areas. Addressing these questions requires knowledge of the effects of predators on the population dynamics of the ungulates forming their prey base.

Ideally, information is required not only on the population trends of potential prey species, but also on changing reproductive and mortality rates as well as on prey selection by the major carnivores. Studies encompassing these aspects have been undertaken in very large protected areas such as South Africa's Kruger National Park (Kruger hereafter; e.g., Owen-Smith and Mills,

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2008a). These have revealed how shifts in the distribution of the prime prey species of lions (*Panthera leo*) led to subsequent effects on other ungulates, including substantial declines in the abundance of several alternative prey species (Owen-Smith and Mills, 2006). In small fenced reserves where large predators have been reintroduced, research has focused on lion demography (Druce et al., 2004a) and its consequences for park management (Kettles and Slotow, 2009). Other studies have monitored the social behaviour of large predators (Kilian and Bothma, 2003) and their prey selection (Power, 2002; Hayward et al., 2007c). However, few insights regarding the conditions allowing both prey and predator populations to be sustained in enclosed areas of limited extent were provided by these studies (but see Druce et al., 2004b).

Hluhluwe-iMfolozi Park (HiP hereafter) in KwaZulu-Natal (South Africa) is a moderately small (960 km²) provincial reserve established in 1897 with remnant populations of leopards (*Panthera pardus*) and spotted hyenas (*Crocuta crocuta*), but no lions, cheetahs (*Acynomix jubatus*) or African wild dogs (*Lycaon pictus*). Due to the paucity of predators, ungulate populations were routinely culled to restrict numbers from the 1950s onwards (Brooks and MacDonald, 1983). Lions and cheetahs were reintroduced during the 1960s and wild dogs were initially reintroduced in 1980/1981 (Somers et al., 2008) to restore a full predator complement. Predator culling was later implemented to restrict the dispersal of lions beyond the porous park fence into adjoining communal land. Shrinkage of the lion population associated with inbreeding led to further lion reintroductions during the 1990s. Then, the cessation of further culling of these predators as well as curtailment of large-scale ungulate removals took place.

Prey populations have been regularly censused since 1986, supported by records of all animals found dead, and the apparent cause of death. This information provided the basis for our assessment of the effects of changing lion numbers on the population trends and observed mortalities of seven ungulate species over 1986–2010. We related variation in ungulate population growth rates to their abundance, annual rainfall total and lion numbers. Carcass records provided further information on the mechanisms governing population changes. Predation can impose additive mortality, but mortality can also be interactive, including the effects of malnutrition, indirectly induced by rainfall patterns (Owen-Smith, 1990). Moreover, between-sex differences in body size and habitat use in African ungulates are likely to lead to distinct sensitivities to predation between males and females (Owen-Smith, 2008). We therefore studied mortality patterns of ungulates through analyses of carcasses and relationships with lion numbers, rainfall and sex. We predicted that the principal prey species of lions would show a down-turn in population trend following a rise in the lion population, independent of any effect of rainfall, associated with an increased mortality largely through predation.

2. Material and methods

2.1. Study area

HiP is located in the KwaZulu-Natal province of South Africa and situated between 28°00' and 28°26' S, 31°43' and 32°09' E. Management units comprise the Hluhluwe section in the north (300 km²) and the iMfolozi section in the south (660 km²), both incorporating sections of the corridor that had separated the originally proclaimed game reserves. Topography ranges from 60 to 750 m above sea level, being hilly in the north and undulating in the south. Perennial surface water is available in the Black and White Umfolozi Rivers, and the Hluhluwe River, and no part of the park is more than 8 km from water in the dry season (Brooks and MacDonald, 1983). Mean annual rainfall over 1986–2010 ranged

from 1003 mm at Hilltop in Hluhluwe to 601 mm in the south-west of iMfolozi. Vegetation in the Hluhluwe section is predominantly a grassland–forest mosaic in the north, with extensive thickets, grading into thorn savanna towards the south of the iMfolozi section.

2.2. Ungulate populations

The major large ungulate species, based on 2006 population counts, include impala (*Aepyceros melampus*, $n = 23531$), nyala (*Tragelaphus angasi*, $n = 6531$), Burchell's zebra (*Equus quagga*, $n = 3717$), African buffalo (*Syncerus caffer*, $n = 3557$), blue wildebeest (*Connochaetes taurinus*, $n = 3508$), warthog (*Phacochoerus africanus*, $n = 2683$), white rhino (*Ceratotherium simum*, $n = 2068$), greater kudu (*Tragelaphus strepsiceros*, $n = 1146$), giraffe (*Giraffa camelopardalis*, $n = 798$), waterbuck (*Kobus ellipsyprimmus*, $n = 633$), African elephant (*Loxodonta africana*, $n = 370$ in 2007, H. Druce & T. Bodasing, pers. comm.) and black rhino (*Diceros bicornis*, $n = 230$ in 2003). Removals mainly through live capture and sales of these ungulates were curtailed following the severe 1982/3 drought when few animals died, because prior removals were deemed to have been excessive (Walker et al., 1987). Between 1986 and 2010, annual removals averaged less than 1% of the respective ungulate populations, except for nyala (1.5%).

Distance sampling (Buckland et al., 1993) has been employed since 1986 to monitor ungulate population densities, with ground counts conducted every two years since 1994. The 34 line transects cover the full extent of HiP (Fig. 1). For each sighting, the species, group size, GPS co-ordinates, distance to the animal, transect bearing and bearing to animal were recorded. DISTANCE (version 5.0, Thomas et al., 2006) was used to estimate population densities. Most transects were replicated at least 16 times during each census year to obtain a minimum of 60 sightings per species in order to provide a statistically robust estimate of the visibility fall-off per species around the transect lines (Buckland et al., 1993). Total population size estimates were then derived from censuses, which were conducted 11 times between 1986 and 2010.

In African ecosystems, lions favour prey species similar to or somewhat larger than their own body mass (>150 kg; Sinclair et al., 2003; Radloff and Du Toit, 2004; Hayward and Kerley, 2005; Owen-Smith and Mills, 2008b). The main prey species present in HiP are giraffe, buffalo, zebra, wildebeest, and kudu. Nyala and impala are the most abundant ungulates in this park (7 and 17 individuals/km² on average, respectively). Seven ungulate species were included in our analyses: three grazers, wildebeest, zebra and warthog; two browsers, giraffe and kudu; and two mixed-feeders, impala and nyala. However, buffalo was excluded from our analyses because heavy removals took place between 1994 and 2000 in an attempt to control bovine tuberculosis infection in this population (Jolles, 2007). Mortality records were obtained from animal carcasses found by park rangers during their patrols. Ungulate species, age-class and sex were identified where possible. The cause of death was interpreted from the presence of a predator nearby, spoor or other signs indicating the predator species responsible, or other evidence indicating poaching or an accidental cause of death. Preliminary analyses showed that patterns of ungulate population trends and mortalities tended to differ between sections. Considering ecological distinctions between Hluhluwe and iMfolozi, all analyses were performed separately for these sections.

2.3. Predator numbers

The first male lion entered the iMfolozi Game Reserve in 1958, followed by two females in 1965 (Anderson, 1981). Lion numbers had reached approximately 60 by the 1980s (Maddock et al., 1996). Between 1988 and 1992, all lions were eliminated from the

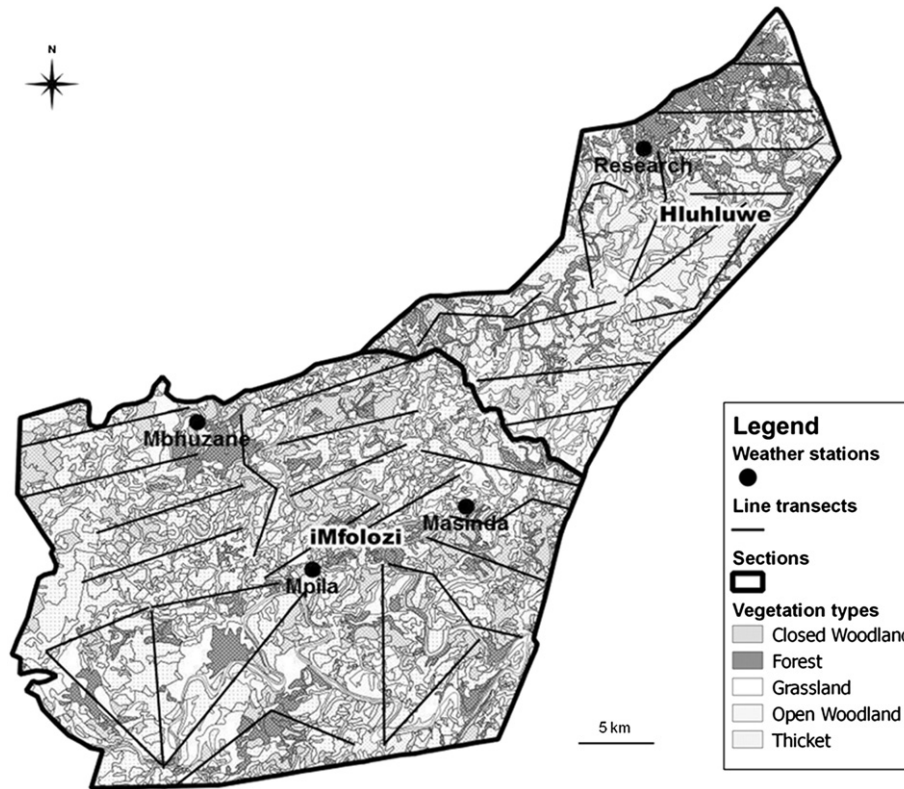


Fig. 1. Line transects and vegetation types at Hluhluwe and iMfolozi

northern part of the Hluhluwe section. Then, 13 female and 3 male lions were brought from Namibia between 1999 and 2001 (Trinkel et al., 2008) because of evidence of inbreeding. Between 2003 and 2004, the total lion population declined from 80 to 61 (Trinkel et al., 2008), but had rebounded to 114 by 2008 and reached an estimated 200 individuals in 2010. We used changing lion numbers between 1986 and 2010 derived from the above references, supported by technical reports lodged at the Hluhluwe Research Centre (Rob Slotow and Jan Graf, pers. comm.), separating estimates for the two sections of the park as best as we could (Table 1). Approximate numbers of other large predators were over 300 spotted hyenas in 2003–2004 (Graf et al., 2009) and around 50 wild dogs in 2004–2006 (Somers et al., 2008).

2.4. Ecological variables

We used monthly rainfall recorded at the Hluhluwe Research Centre in the Hluhluwe section and at Mbhuzane (North–West) in the iMfolozi section (Fig. 1). When no rainfall record was available at Mbhuzane (11 out of 300 monthly values), we used data from two other stations (Masinda in the North–East and Mpila in the centre): all three stations are located in the Northern half of the iMfolozi section and not in the wilderness area (Southern half of the iMfolozi section; Fig. 1). The dry season months extended from April to September. Annual rainfall was obtained from monthly totals summed over July–June and related to counts commenced in July (Fig. 2). To test the effect of rainfall patterns and lion numbers on ungulate population growth rates, we used mean values of these factors over the period between successive censuses. We did not consider rainfall over the period 1986–1991, as 5 years between two censuses was too long to measure potential impacts on annual growth rates. Since lion numbers only showed a slight increase between 1986 and 1991, we used mean values for this period in our analyses. To test the effect of

rainfall patterns and lion numbers on mortality records collected annually, we used rainfall data for each census year as well as the preceding year, and lion data for each census year. Rainfall (in mm) and lion numbers were log-transformed.

Ungulate population changes needed to be corrected for animal removals that had taken place between censuses, as well as for any reintroductions that had occurred. The net loss (L) was calculated as $L = R + D - I$, where R represents the number of live removals, D the number of dead removals and I the numbers of animals reintroduced. The mean annual population growth rate (r) can be calculated as follows: $r = \ln((N_t/N_0)^{1/t})$ where N_0 is the population at time “0” and N_t is the population at time “ t ”. We corrected our estimates for management losses: $rc = \ln(((N_t + \sum_0^{t-1} L)/N_0)^{1/t})$.

Without data on error measurement, we were not able to estimate variations in census errors over our study period. We therefore checked if the estimated population growth rates were biologically acceptable regarding each ungulate species. Some population estimates had obviously been largely overestimated and led to unrealistic annual growth rates. Thus, 1994 census estimates for warthog and wildebeest in Hluhluwe ($rc = 0.92$ and 0.48 respectively), 1998 census estimate for giraffe in iMfolozi ($rc = 0.43$), and 2006 census estimate for zebra in Hluhluwe ($rc = 0.44$) were removed from our analyses as recommended by Lango et al. (2008). Apart from these four overestimates, since ungulate censuses were performed using standardized procedures between 1986 and 2010, we assumed that the other estimates were unbiased.

In total 3537 carcasses were recorded for our seven ungulate species during our 11 census years. Among them, 75% were classified as adults ($n = 2668$; Table 2). As juvenile carcasses of medium-sized ungulates disappear very quickly in the field and are often entirely consumed by predators, we only considered the adult age-class in our analyses. Ungulate population growth rates are more sensitive to variation in adult survival (Gaillard et al., 2000),

Table 1

Annual estimates of lion numbers in Hluhluwe and iMfolozi between 1986 and 2010 (Note: the density ratio [iMfolozi/Hluhluwe = 2.6] was based on the 9 counts done within each section).

Year	Hluhluwe	iMfolozi	Total	Method	Source
1986	17	45	62	Total count only; use of ratio for each section	Maddock et al., 1996
1987	20	52	72	Mean value between 1986 and 1988; use of ratio for each section	Overestimate in Maddock et al., 1996
1988	23	59	82	Total count only; use of ratio for each section	Maddock et al., 1996
1989	20	60	80	Total population stable (around 80 lions)	Maddock et al., 1996
1990	20	60	80	Total population stable (around 80 lions)	Maddock et al., 1996
1991	20	60	80	Total population stable (around 80 lions)	Maddock et al., 1996
1992	20	60	80	Total population stable (around 80 lions)	Maddock et al., 1996
1993	0	60	60	60 lions in iMfolozi; lions eradicated in Hluhluwe	Maddock et al., 1996
1994	2	55	57	Total count only; very few lions in Hluhluwe	Maddock et al., 1996
1995	7	59	66	Total number derived from linear regression; use of ratio for each section	No available data
1996	11	62	73	Total number derived from linear regression; use of ratio for each section	No available data
1997	16	63	79	Minimum counts for each section	Lion Research Programme (report)
1998	19	66	85	Total number derived from linear regression; use of ratio for each section	No available data
1999	22	70	92	Total number derived from linear regression; use of ratio for each section	No available data
2000	25	73	98	Minimum counts for each section	Lion Research Programme (report)
2001	24	80	104	Minimum counts for each section	Lion Research Programme (report)
2002	21	68	89	Minimum counts for each section	Lion Research Programme (report)
2003	22	58	80	Minimum counts for each section	Lion Research Programme (report)
2004	21	40	61	Minimum counts for each section	Lion Research Programme (report)
2005	25	39	64	Minimum counts for each section	Lion Research Programme (report)
2006	27	47	74	Mean value between 2005 and 2007; use of ratio for each section	No report available for 2006
2007	29	55	84	Minimum counts for each section	Lion Research Programme (report)
2008	28	86	114	Minimum counts for each section	Lion Research Programme (report)
2009	42	108	150	Total count only; use of ratio for each section	Lion Research Programme (report)
2010	56	144	200	Total count only; use of ratio for each section	Lion Research Programme (report)

and neglecting juvenile mortality in our analyses would slightly underestimate the impact of predation on our ungulate populations. The amount of yearly variation in ungulate population density estimates between 1986 and 2010 was relatively high ($CV = 24\text{--}58\%$). These fluctuations are likely to be affected by sampling errors, inducing some noise in our population estimates; but they can also partly reflect variation in mortality and thereby the number of carcasses recovered. Consequently, we systematically included estimated population density as a covariate in our analyses of variation in mortality as represented by found carcasses. We also tested two-way interactions between the factors considered (species abundance, rainfall, sex and predation).

2.5. Carcass recovery and lion kills

We used available data on ranger numbers (i.e., observers) per year and per section for the last five censused years to test the impact of variations in sampling effort on carcass recovery. There was no significant increase in ranger numbers between 2002 and 2010 in Hluhluwe ($n = 5$; slope = 0.70; $p = 0.1291$); but a slight and significant increase was detected in iMfolozi ($n = 5$; slope = 1.15; $p = 0.0152$).

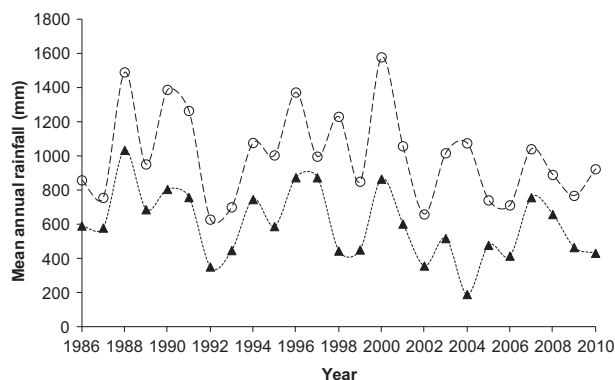


Fig. 2. Annual rainfall in Hluhluwe (circles; dashed line) and iMfolozi (black triangles; dotted line) between 1986 and 2010

However, when carcass numbers were corrected (carcasses/rangers), they showed the same trends as non-corrected carcass numbers, and were highly correlated with them in Hluhluwe ($n = 5$; $R^2 = 0.92$; $p = 0.0101$) and iMfolozi ($n = 5$; $R^2 = 0.99$; $p = 0.0001$). Consequently, variations in the numbers of rangers between 2002 and 2010 did not substantially affect the numbers of carcasses recovered every year. Moreover, for the period 1986–2001, the numbers of rangers varied little, and sampling guidelines provided to rangers did not vary over the whole study period (HiP staff, pers. comm.). We therefore assumed that the sampling method and effort for carcass recovery remained unchanged over our study period.

The combined population totals of our seven ungulate species averaged 33,422 animals, representing about 25,000 adults (75% of these populations). Assuming an adult mortality rate of 5–10% per year, 1250–2500 adults would therefore die every year, which represented 13,750–27,500 carcasses of adult ungulates over 11 years. Hence our sample of 2668 adult carcasses over 11 years represented 10–20% of the potential adult mortality in this park. Accordingly, we assumed that this sample adequately represented year to year variation in mortality as well as the prey species contributing to it.

Between 1986 and 2010, 2317 carcasses of our studied ungulates were attributed to lion predation. The field rangers attributed a carcass to lions based on either seeing lion tracks (spoor) at the carcass, seeing lions feeding on the carcass or resting very close to the kill, or seeing lions making the kill. In order to assess which part of lion kills these carcasses represented, we predicted the annual number of kills per prey species per lion. First, we calculated the part of each prey in lion kills based on recovered carcasses between 1986 and 2010. A lion food intake of 4 kg/day/average individual (i.e. considering all age- and sex-classes; see Schaller, 1972, Bryden, 1978, Viljoen, 1993, Power, 2003) gives an annual prey consumption of 1460 kg/lion. For each prey, we estimated the annual number of items eaten per lion: we first estimated the total biomass eaten for each prey in multiplying 1460 kg by its proportion in lion kills. Then this biomass estimate was divided by the unit biomass of the prey species (adult female body weight corrected for edible mass; see Power, 2003). Using annual lion numbers (Table 1), we then estimated the predicted numbers of kills and compared them to the observed numbers of carcasses. Over our study period, recorded

Table 2
Adult carcasses (sex identified or not) of HiP ungulates recorded over 11 census years.

Species	1986	1991	1994	1996	1998	2000	2002	2004	2006	2008	2010	Total
a. Hluhluwe												
Giraffe	0	0	1	6	5	3	2	11	9	3	2	42
Kudu	0	1	4	4	10	5	4	6	7	2	0	43
Impala	10	2	11	6	32	16	23	36	22	13	16	187
Nyala	43	34	19	11	58	35	76	63	53	48	34	474
Warthog	4	0	4	0	10	5	14	6	14	7	1	65
Wilbebeest	2	1	10	14	23	26	11	14	16	21	9	147
Zebra	3	3	8	12	10	14	9	16	8	19	9	111
b. iMfolozi												
Giraffe	3	0	3	5	6	5	4	2	5	3	5	41
Kudu	13	8	26	9	11	14	23	9	19	9	3	144
Impala	10	10	41	30	37	53	125	41	68	34	36	485
Nyala	53	17	47	11	33	28	153	26	52	34	26	480
Warthog	0	3	7	2	1	19	25	13	9	5	0	84
Wilbebeest	29	23	32	15	19	11	29	13	14	28	9	222
Zebra	21	18	16	12	12	8	18	10	8	5	15	143

lion kills represented 12.5 and 6.4% of predicted kills in Hluhluwe and iMfolozi respectively, indicating that the number of found carcasses underestimates mortality due to lion predation in HiP.

Despite limited proportions of carcasses recovered, sample sizes collected over our 11 censused years highly varied within each prey species (CV = 39–94%). Since the detection probability of carcasses remained constant throughout our study period, fluctuations in carcass numbers were therefore likely to reflect fluctuations in ungulate mortalities. We therefore used the number of adult carcasses recorded during our 11 censused years ($n = 2668$) to investigate variations in observed ungulate mortalities.

2.6. Statistical analysis (Table 3)

We first fitted linear models including ungulate population growth rates between successive counts as the response variable and, as fixed effects, all combinations of the following factors (using their mean values between successive counts): predation pressure (measured as lion numbers), ungulate species abundance (total population estimates) and rainfall variation (annual or dry season). We then fitted log-linear models relating the number of carcasses as the response variable to all combinations of ungulate species abundance with lion predation pressure, sex of carcass and rainfall patterns (annual and dry season rainfall for the census year and the preceding year). The factor “sex” was not considered for warthog and zebra since the sex identification of adult carcasses was

Table 3
Symbol and description of variables used in models.

Variable	Description
Log N	Ungulate population size (number of individuals; log-transformed)
rc	Ungulate population growth rate (corrected for management losses)
Carcass	Number of carcasses
Log Mean Rain	Mean annual rainfall (mm; log-transformed) between successive game censuses
Log Rain	Annual rainfall (mm; log-transformed) in the census year
Log Rain b	Annual rainfall (mm; log-transformed) in the previous year
Log Mean Dry	Mean dry season rainfall (mm; log-transformed) between successive game censuses
Log Dry	Dry season rainfall (mm; log-transformed) in the census year
Log Dry b	Dry season rainfall (mm; log-transformed) in the previous year
Log Mean Lion	Mean lion numbers (mm; log-transformed) between successive game censuses
Log Lion	Lion numbers (log-transformed) used as a measure of predation pressure

unreliable for these two species (unknown sexes accounted for 27 and 30% in Hluhluwe, and 58 and 56% in iMfolozi, for warthog and zebra respectively). When evidence of over-dispersion occurred, we used a quasi-Poisson distribution with a corrected dispersion parameter. We used the Akaike Information Criterion corrected for small samples (AICc) to select the best models (Burnham and Anderson, 2002), and AICc weights (AICcW) to compare different models. All analyses were performed with R (version 2.11.1; R Development Core Team, 2010).

3. Results

3.1. Ungulate population growth rates (Fig. 3)

Although species abundance appeared as an important factor influencing ungulate population growth, usually included in the first or second best models (Appendix A), this factor was generally not retained, except for kudu in Hluhluwe (Table 4). In general, species abundance did not affect ungulate population growth in iMfolozi, apart from a negative effect for giraffe ($b = -0.4802 \pm 0.1983$; $R^2 = 0.46$; $p = 0.0460$; AICcW = 0.4511). In Hluhluwe, there was a negative effect of species abundance on the population growth rates of kudu ($b = -1.3637 \pm 0.3472$; $R^2 = 0.66$; $p = 0.0044$; AICcW = 0.7937), wilbebeest ($b = -0.5300 \pm 0.2197$; $R^2 = 0.45$; $p = 0.0466$; AICcW = 0.2056) and zebra ($b = -0.7983 \pm 0.3248$; $R^2 = 0.46$; $p = 0.0436$; AICcW = 0.4796), and this was supported by model averaging (AICcW).

The annual and dry season rainfall components did not have a significant influence on the population growth rates of ungulates in HiP (Appendix A). The effects of rainfall patterns were not retained in our best models (Table 4). There was only a negative effect of dry season rainfall on wilbebeest population growth rates in Hluhluwe ($b = -2.2620 \pm 0.8004$; $R^2 = 0.57$; $p = 0.0301$), and this was supported by model averaging (AICcW = 0.3507).

Models including lion predation were not selected (Appendix A), indicating that there was generally no detectable effect of changing lion numbers on ungulate population growth rates (Table 4). A negative effect of lion numbers was only found for zebra in iMfolozi ($b = -0.8271 \pm 0.3540$; $R^2 = 0.41$; $p = 0.0477$), and this was supported by model averaging (AICcW = 0.3730).

3.2. Mortality records

Species abundance was included as a covariate in all models for ungulate carcass records (Appendix B). This factor was positively related to adult mortalities of giraffe, impala and wilbebeest in

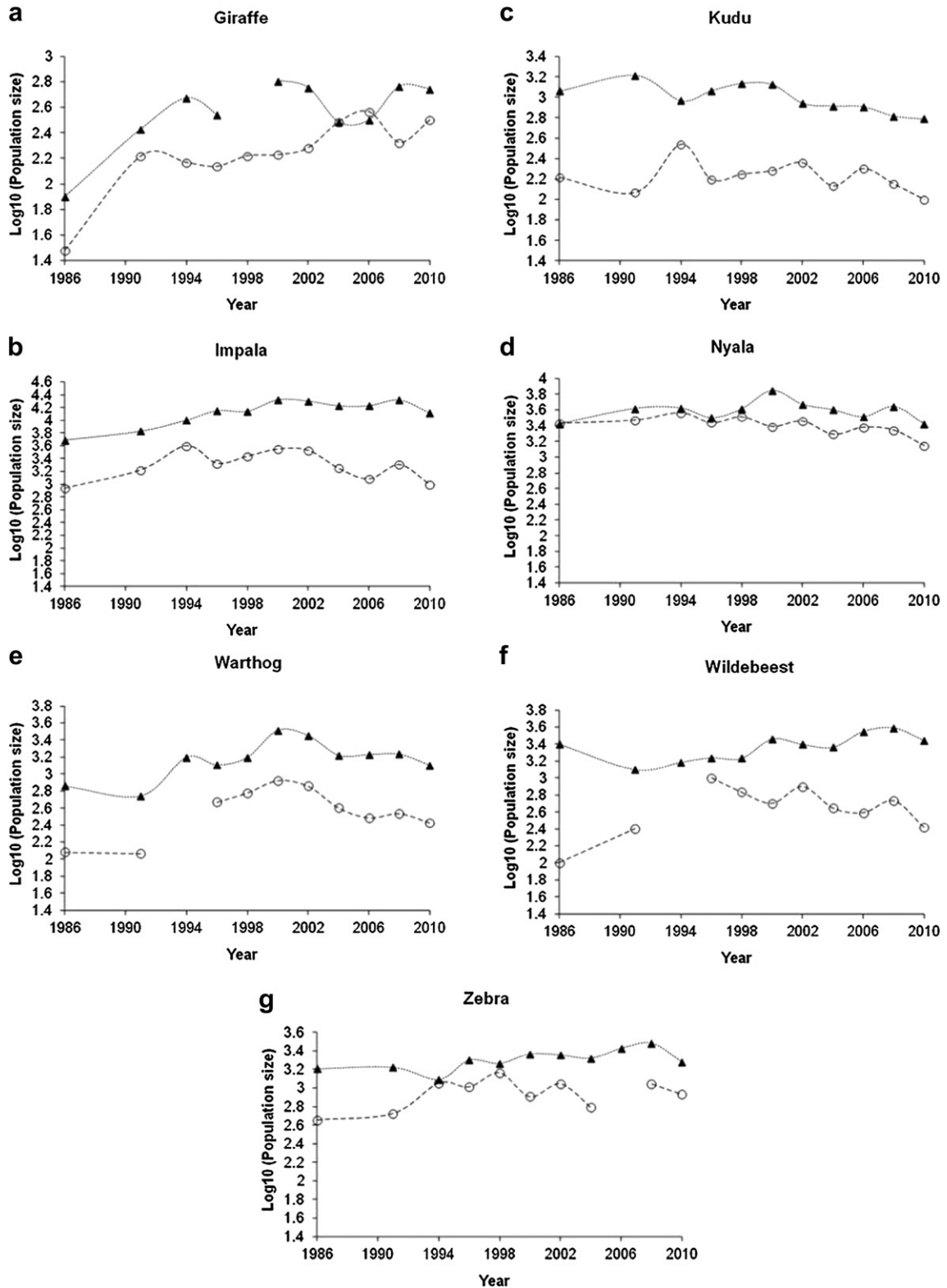


Fig. 3. Ungulate population estimates in Hluhluwe (circles; dashed line) and iMfolozi (black triangles; dotted line) between 1986 and 2010.

Hluhluwe, and impala and warthog in iMfolozi (Table 5). This result simply showed that more deaths were observed when these ungulates were more abundant. However, species abundance was negatively correlated to zebra adult mortalities in iMfolozi (Table 5).

Rainfall patterns affected carcass records of impala, nyala, warthog and wildebeest (Table 5; Appendix B). Annual rainfall had

a negative effect on nyala deaths in both sections, warthog in Hluhluwe and impala in iMfolozi. Annual rainfall in the preceding year affected nyala positively and wildebeest negatively in Hluhluwe. Dry season rainfall positively affected impala and wildebeest carcasses in Hluhluwe. Dry season rainfall in the previous year had

Table 4

Selected models of ungulate population 1 growth rates in Hluhluwe and iMfolozi (Codes for significance: ***<0.0001; **<0.001; *<0.01).

Species	n	Factors	Estimate	SE	P
a. Hluhluwe ungulates					
Giraffe	10	Intercept	0.0703	0.0538	0.2230
Kudu	10	Intercept	3.0365	0.7821	0.0047**
		Log N	-1.3637	0.3472	0.0044**
Impala	10	Intercept	-0.0238	0.0781	0.7680
Nyala	10	Intercept	-0.0012	0.0410	0.9770
Warthog	9	Intercept	0.0238	0.0546	0.6750
Wildebeest	9	Intercept	-0.0192	0.0783	0.8120
Zebra	9	Intercept	0.0003	0.0679	0.9970
b. iMfolozi ungulates					
Giraffe	9	Intercept	0.0501	0.0653	0.4650
Kudu	10	Intercept	-0.0285	0.0342	0.4260
Impala	10	Intercept	0.0403	0.0421	0.3630
Nyala	10	Intercept	-0.0055	0.0531	0.9200
Warthog	10	Intercept	0.0246	0.0637	0.7090
Wildebeest	10	Intercept	0.0238	0.0436	0.5980
Zebra	10	Intercept	0.0143	0.0418	0.7410

a positive effect on nyala records in both sections and impala carcasses in iMfolozi (Table 5).

Lion abundance did not directly affect carcass records for adult ungulates in either section of HiP (Appendix B; Table 5).

There were no between-sex difference in adult mortality in Hluhluwe. In iMfolozi, adult mortality was relatively greater for males in giraffe and impala. A similar, but marginally non-significant effect was observed for kudu and wildebeest (Table 5).

The most commonly identified cause of adult mortality among ungulates in HiP was predation; unknown causes represented the second most important category (Table 6). Predation was the most common cause of adult mortality for all studied ungulates, except for giraffe in iMfolozi where unknown causes represented 50% ($n = 70$) of observed mortalities. Poaching was the second most common cause of mortality after predation for warthogs in iMfolozi. Lion was the most common predator identified for giraffe, kudu, wildebeest, zebra and warthog. Adult mortality of impala was attributed equally to lion, leopard and wild dog predation. These three predators also accounted for a large part of nyala adult mortality.

4. Discussion

Our analysis of population growth rates showed that HiP ungulates were affected little by both rainfall variation and changes in lion numbers between 1986 and 2010. However, when dry season rainfall decreased, the wildebeest population in Hluhluwe declined, suggesting that this grazer was sensitive to dry season resource deficiencies, supporting previous findings by Ogotu and Owen-Smith (2003) for Kruger. The only prey species showing a detectable effect of increased lion numbers on its population growth rate was zebra, and only in iMfolozi. Within this section of the park, zebra was the third prey species in lion kills, after buffalo and wildebeest. This result is therefore in accordance with our prediction and suggests a potential higher impact of lion on their most preferred prey species (based on lion kill records) at HiP. In iMfolozi, important increases in lion numbers between 2008 and 2010 could have caused a higher predation pressure on zebra, one of their preferred prey. This observation is likely to be supported by the decline observed in zebra numbers during the last two years. In iMfolozi, ungulate populations did not appear to be influenced by species abundance (except for giraffe), whereas it seemed to affect the population growth rates of several species in Hluhluwe, especially kudu. However, because sampling errors can induce spurious density-dependent effects (Shenk et al., 1998; Freckleton et al., 2006) and stochastic environmental variations can contribute to increase

Table 5

Selected models of ungulate adult mortalities ($n =$ number of sexed carcasses, $\phi =$ dispersion parameter, codes for significance: ***<0.0001; **<0.001; *<0.01). ϕ All carcasses (sex identified or not) were analysed for warthog and zebra.

Species	n	Factors	Estimate	SE	p	ϕ
a. Hluhluwe ungulates						
Giraffe	32	Intercept	-7.2660	3.2980	0.0394*	1.66
		Log N	3.2900	1.3810	0.0272*	
Kudu	42	Intercept	-4.1510	3.2300	0.2130	1.90
		Log N	2.1340	1.4190	0.1480	
Impala	172	Intercept	3.2128	5.4646	0.5639	3.10
		Log N	1.7455	0.8521	0.0486*	
		Log Rain b	-4.7437	2.5560	0.0799	
		Log Dry	3.2092	1.1696	0.0133*	
Nyala	458	Intercept	4.2301	3.6327	0.2603	2.87
		Log N	-0.7867	0.8533	0.3695	
		Log Rain	-3.3173	0.7857	0.0006***	
		Log Rain b	2.2829	0.9343	0.0258*	
Warthog ^s	65	Log Dry b	1.9992	0.7690	0.0187*	
		Intercept	9.7653	5.4339	0.1154	2.51
		Log N	1.6963	0.8774	0.0945	
		Log Rain	-4.1459	1.6189	0.0375*	
Wildebeest	124	Intercept	-4.2964	6.7048	0.5313	1.16
		Log N	2.8310	0.7832	0.0026**	
		Log Rain	3.7511	1.2075	0.0072**	
		Log Rain b	-7.1627	2.4814	0.0113*	
Zebra ^s	111	Log Dry	3.7381	1.4313	0.0196*	
		Intercept	-5.3721	3.4531	0.1640	1.95
		Log N	1.4539	0.9599	0.1740	
		Log Dry b	1.5521	0.8640	0.1160	
b. iMfolozi ungulates						
Giraffe	34	Intercept	-1.1526	2.1925	0.6059	1.18
		Log N	0.2498	0.8334	0.7680	
		Sex	1.3437	0.4976	0.0152*	
Kudu	138	Intercept	8.8273	5.8779	0.1505	2.97
		Log N	-1.5367	1.5297	0.3284	
		Log Dry	-1.4293	0.9236	0.1392	
Impala (1)	439	Sex	0.6286	0.3079	0.0562	
		Intercept	-4.4405	3.0927	0.1703	2.27
		Log N	3.4008	0.6397	<0.0001***	
		Log Rain	-2.4512	0.6646	0.0020**	
Impala (2)	439	Log Dry	-1.2593	0.7559	0.1152	
		Log Dry b	0.9841	0.3626	0.0153*	
		Sex	0.4878	0.1482	0.0046**	
		Intercept	-6.5505	2.6316	0.0242*	2.35
Nyala	471	Log N	2.9633	0.5463	<0.0001***	
		Log Rain	-1.5922	0.4808	0.0044**	
		Log Dry b	1.4325	0.3699	0.0014**	
		Log Lion	-0.9951	0.6506	0.1457	
Warthog ^s	84	Sex	0.4878	0.1505	0.0051**	
		Intercept	8.4089	5.5433	0.1488	9.81
		Log N	1.3372	1.2851	0.3135	
		Log Rain	-3.5033	1.1433	0.0074**	
Wildebeest	188	Log Rain b	-2.0434	1.4311	0.1726	
		Log Dry b	2.2020	0.8326	0.0177*	
		Sex	0.4002	0.2945	0.1930	
		Intercept	-8.9810	4.1800	0.0639	3.04
Zebra ^s	143	Log N	5.6020	1.4240	0.0043**	
		Log Lion	-4.0420	2.1730	0.0999	
		Intercept	4.2624	2.4696	0.1006	2.21
		Log N	-0.6953	0.7370	0.3573	
Zebra ^s	143	Sex	0.3878	0.2209	0.0952	
		Intercept	10.9377	2.8763	0.0037**	1.18
		Log N	-2.5480	0.8603	0.0159*	

fluctuations in population estimates, it is difficult to assess the importance of density dependence on ungulate populations in HiP.

Lower rainfall can increase ungulate mortality directly through lessened vegetation growth and hence forage production. Higher amounts of rainfall also increase the density of vegetation, facilitating lion hunting success (Funston et al., 2001). Giraffe, kudu and zebra mortality was apparently unaffected by rainfall variation, in contrast to the pattern for kudu documented in Kruger (Owen-Smith, 1990; Owen-Smith and Mills, 2006). In Hluhluwe, warthog mortality decreased with increasing annual rainfall, indicating that

Table 6

Different causes of observed adult mortalities (%) in HiP ungulates (The part of lion predation in carcasses attributed to predators is specified in the last column. The most common cause is indicated in bold.).

Species	n	Unknown	Accident	Natural	Poaching	Predators	Lion predation
a. Hluhluwe ungulates							
Giraffe	80	38.8	3.8	12.5	1.3	43.8	97.1
Impala	346	19.9	1.7	6.1	0.9	71.4	30.8
Kudu	104	24.0	2.9	4.8	1.0	67.3	88.6
Nyala	978	21.1	2.0	8.1	1.1	67.7	31.6
Warthog	121	19.0	0.8	12.4	10.7	57.0	59.4
Wildebeest	282	16.7	1.1	5.0	0.4	77.0	96.8
Zebra	224	14.7	1.8	4.0	0.9	78.6	94.9
b. iMfolozo ungulates							
Giraffe	70	50.0	8.6	11.4	0.0	30.0	81.0
Impala	1029	24.5	4.7	5.2	1.7	63.8	23.3
Kudu	285	22.8	2.1	1.8	1.1	72.3	82.5
Nyala	873	26.8	2.2	7.0	1.3	62.8	47.3
Warthog	184	21.7	2.7	1.6	33.7	40.2	67.6
Wildebeest	457	17.3	1.5	2.0	0.4	78.8	96.1
Zebra	306	15.4	2.9	1.6	0.0	80.1	94.7

this grazer is sensitive to diminished grass growth. Adult mortality of the two mixed-feeders was both positively and negatively affected by rainfall patterns, suggesting that impala and nyala were probably sensitive to declines in forage production during dry periods, but also to a potential higher hunting success related to dense vegetation during wet periods. Finally our analysis on ungulate carcasses showed that the vulnerability to lion predation of several ungulate species was male-biased, particularly for giraffe and impala, as had been found in Kruger (Owen-Smith, 2008). This analysis did not show any detectable impact of variations in lion numbers on ungulate mortalities. The relative small sample size of annual mortalities in several ungulate populations probably limited the power of our statistical analysis and reduced the probability of detecting interannual variations in mortalities.

In HiP, predation was the main agent of recorded deaths among adult ungulates. Lion accounted for more than 80% of observed mortality among adult giraffe, kudu, wildebeest and zebra. Nevertheless, lion predation had no detectable impact on the growth of giraffe and kudu populations in HiP, in contrast to findings for kudu in Kruger (Owen-Smith et al., 2005; Owen-Smith and Mills, 2006). Impala and nyala were preyed upon by a wide range of predators, as previously found in other African ecosystems (Hayward and Kerley, 2008; Owen-Smith and Mills, 2008b). Despite wildebeest ranking second (19%) in lion kills in HiP, no independent effect of variation in lion numbers on their recorded mortality was detected. However, the positive effect of rainfall variation indicated a potential interactive effect of predation pressure on this species. Zebra was the third most important prey in lion kills in HiP (15%), and appeared to be more vulnerable to direct effects from changing lion numbers than wildebeest.

The general lack of influence of changes in lion numbers on medium-sized ungulates in HiP could have resulted from the relatively limited density of this large predator population. Lion numbers in HiP fluctuated in response to management interventions (shooting and reintroductions) and to the effects of inbreeding (Trinkel et al., 2008), and increased progressively only after 2006. In small protected areas, lion populations can also be regulated by diseases, since it has been showed that inbreeding depression increases susceptibility to bovine tuberculosis in lions (Trinkel et al., 2011), or by density-dependent mechanisms related to territory vacancies or food limitation (Trinkel et al., 2010). To establish the conditions required to allow both prey and predator populations to be sustained in enclosed areas, two indices have been proposed: large predator carrying capacity and prey/predator ratios (Hayward et al., 2007b). Using the formula proposed by

Hayward et al. (2007b), lion carrying capacity for HiP, based on the abundance of their preferred prey species, was estimated to be 160 individuals in 2008, when there were only 114 lions present. By 2010, the carrying capacity supported by prey availability had dropped to 146 lions, whereas around 200 lions were present, indicating that lions had by then potentially exceeded their estimated carrying capacity.

We compared prey/lion ratios in HiP (this study) with data for six other protected areas of different sizes in Southern Africa, representing prey by ungulates within the size range 15–850 kg, following Hayward et al. (2007b; Table 7). In Pilanesberg and Madjuma, declines in ungulate populations were attributed to lion predation (Power, 2002; Tambling and du Toit, 2005), when prey/lion ratios were below 100. In other parks where prey/lion ratios were >150, no substantial prey declines were noted. The prey/lion ratio remained well above 200 in HiP, except in 2010, but this overall measure may mask the impacts incurred by specific prey populations. The abundance and diversity of medium-sized ungulate species contribute to sustaining predator populations, and may affect the vulnerability of larger species with correspondingly lower population growth potentials (Ogutu and Owen-Smith, 2003). In very large protected areas, such as Hwange and Kruger, the preferred prey species of lion did not show much change in abundance in response to changing lion numbers (Owen-Smith and Mills, 2006). However, in Kruger the management of water points in the 1980s affected the distribution of ungulates, and subsequently lion; which contributed to increase predation pressure on alternative prey species, such as roan antelope (Harrington et al., 1999). We expect that the high lion abundance reached in HiP in 2010 will shortly be reflected by declines in populations of other principal prey species besides zebra, perhaps followed by diminishing numbers of alternative prey species like kudu.

5. Management implications

Whether diminishing populations of the principal prey species will lead to quasi-stable coexistence between predator and prey populations, or persistent oscillatory dynamics – as generally projected by simple models of predator–prey interactions – remain to be established. Hence it is essential that detailed monitoring of both lion and ungulate numbers in HiP be continued with sufficient intensity to detect the trajectories followed by the interacting populations, in particular with regard to the populations of alternative prey species that may be threatened by prey switching.

Table 7
Prey/lion ratios estimated in 7 Southern African protected 1 areas.

	HiP (this study)	Shamwari	Kalahari	Kruger	Hwange	Pilanesberg	Madjuma
Years	1986–2010	2004	80s	60s	1974	1997	1998
Area (km ²)	960	187.46	9591	19,000	15,000	500	15
Prey declines (lion)	No	No	No	No	No	Yes	Yes
Prey density (ind/km ²)	39.3	27.03	2.04	11.72	4.84	6.06	24.58
Lion density (ind/km ²)	0.09	0.08	0.01	0.06	0.03	0.1	0.53
Prey/lion ratio	437	338	204	195	161	61	46

Data source: Hayward et al., 2007b.

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Appendix A. Models of population growth rates (10 first models presented here; selected models in bold).

Table A.1
Hluhluwe.

	df	AIC	AICc	ΔAICc	AICcW
<i>Giraffe models</i>					
<i>rc</i> ~ Log <i>N</i>	3	−6.9207	−2.9207	0.0000	0.3470
<i>rc</i> ~ Intercept	2	−4.1160	−2.4017	0.5190	0.2677
<i>rc</i> ~ Log mean Dry	3	−6.3722	−1.5722	1.3485	0.1768
<i>rc</i> ~ Log <i>N</i> + Log mean Lion	4	−7.6858	0.3142	3.2349	0.0688
<i>rc</i> ~ Log mean Rain	3	−3.7770	1.0230	3.9437	0.0483
<i>rc</i> ~ Log mean Lion	3	−2.8389	1.1611	4.0818	0.0451
<i>rc</i> ~ Log mean Dry + Log <i>N</i>	4	−6.7725	3.2275	6.1482	0.0160
<i>rc</i> ~ Log mean Dry + Log mean Lion	4	−6.3431	3.6569	6.5776	0.0129
<i>rc</i> ~ Log mean Dry * Log <i>N</i>	5	−16.2229	3.7771	6.6978	0.0122
<i>rc</i> ~ Log mean Rain + Log mean Dry	4	−4.4803	5.5197	8.4404	0.0051
<i>Kudu models</i>					
<i>rc</i> ~ Log <i>N</i>	3	−7.4959	−3.4959	0.0000	0.7937
<i>rc</i> ~ Log <i>N</i> + Log mean Lion	4	−7.7260	0.2740	3.7699	0.1205
<i>rc</i> ~ Log mean Rain + Log <i>N</i>	4	−7.1949	2.8051	6.3010	0.0340
<i>rc</i> ~ Intercept	2	1.2497	2.9640	6.4599	0.0314
<i>rc</i> ~ Log mean Dry + Log <i>N</i>	4	−4.7875	5.2125	8.7084	0.0102
<i>rc</i> ~ Log mean Lion	3	3.2423	7.2423	10.7382	0.0037
<i>rc</i> ~ Log <i>N</i> * Log mean Lion	5	−7.5320	7.4680	10.9640	0.0033
<i>rc</i> ~ Log mean Rain	3	4.3553	9.1553	12.6512	0.0014
<i>rc</i> ~ Log mean Dry	3	4.3808	9.1808	12.6767	0.0014
<i>rc</i> ~ Log mean Rain + Log mean Dry + Log <i>N</i>	5	−8.2397	11.7603	15.2562	0.0004
<i>Impala models</i>					
<i>rc</i> ~ Intercept	2	3.3475	5.0618	0.0000	0.4658
<i>rc</i> ~ Log <i>N</i>	3	1.5491	5.5491	0.4874	0.3651
<i>rc</i> ~ Log mean Lion	3	5.3255	9.3255	4.2637	0.0553
<i>rc</i> ~ Log mean Rain	3	5.7577	10.5577	5.4960	0.0298
<i>rc</i> ~ Log mean Dry	3	5.8481	10.6481	5.5864	0.0285
<i>rc</i> ~ Log <i>N</i> + Log mean Lion	4	2.8452	10.8452	5.7834	0.0258
<i>rc</i> ~ Log mean Rain + Log <i>N</i>	4	1.0728	11.0728	6.0111	0.0231
<i>rc</i> ~ Log mean Dry + Log <i>N</i>	4	4.3236	14.3236	9.2619	0.0045
<i>rc</i> ~ Log <i>N</i> * Log mean Lion	5	2.1047	17.1047	12.0429	0.0011
<i>rc</i> ~ Log mean Rain + Log mean Dry	4	7.6820	17.6820	12.6203	0.0008
<i>Nyala models</i>					
<i>rc</i> ~ Intercept	2	−9.5532	−7.8389	0.0000	0.6760
<i>rc</i> ~ Log <i>N</i>	3	−8.7703	−4.7703	3.0686	0.1457
<i>rc</i> ~ Log mean Lion	3	−7.5665	−3.5665	4.2724	0.0798
<i>rc</i> ~ Log mean Rain	3	−7.4848	−2.6848	5.1541	0.0514
<i>rc</i> ~ Log <i>N</i> + Log mean Lion	4	−8.8623	−0.8623	6.9766	0.0207
<i>rc</i> ~ Log mean Dry	3	−5.3117	−0.5117	7.3272	0.0173
<i>rc</i> ~ Log mean Rain + Log <i>N</i>	4	−8.0598	1.9402	9.7791	0.0051
<i>rc</i> ~ Log mean Rain + Log mean Dry	4	−5.5686	4.4314	12.2703	0.0015
<i>rc</i> ~ Log mean Rain + Log mean Lion	4	−5.4883	4.5117	12.3506	0.0014
<i>rc</i> ~ Log mean Dry + Log <i>N</i>	4	−5.1010	4.8990	12.7379	0.0012
<i>Warthog models</i>					
<i>rc</i> ~ Log mean Lion	3	−6.8356	−2.8356	0.0000	0.4524
<i>rc</i> ~ Intercept	2	−4.0701	−2.3558	0.4798	0.3559

Table A.1 (continued)

	df	AIC	AICc	Δ AICc	AICcW
<i>rc</i> ~ Log mean Dry	3	−4.1002	0.6998	3.5354	0.0772
<i>rc</i> ~ Log N	3	−4.0611	0.7389	3.5746	0.0757
<i>rc</i> ~ Log mean Rain	3	−0.4211	4.3789	7.2145	0.0123
<i>rc</i> ~ Log N + Log mean Lion	4	−5.2360	4.7640	7.5997	0.0101
<i>rc</i> ~ Log mean Rain + Log N	4	−7.2932	6.0401	8.8757	0.0053
<i>rc</i> ~ Log mean Rain + Log mean Dry	4	−3.5920	6.4080	9.2437	0.0044
<i>rc</i> ~ Log mean Dry + Log mean Lion	4	−3.1826	6.8174	9.6530	0.0036
<i>rc</i> ~ Log mean Rain + Log mean Lion	4	−2.7976	7.2024	10.0380	0.0030
<i>Wildebeest models</i>					
<i>rc</i> ~ Log mean Dry	3	−2.1072	2.6928	0.0000	0.3507
<i>rc</i> ~ Log N	3	−1.0394	3.7606	1.0678	0.2056
<i>rc</i> ~ Intercept	2	2.4048	4.1191	1.4263	0.1719
<i>rc</i> ~ Log mean Rain + Log N	4	−8.3126	5.0207	2.3279	0.1095
<i>rc</i> ~ Log mean Rain + Log mean Dry	4	−4.2817	5.7183	3.0255	0.0773
<i>rc</i> ~ Log mean Lion	3	3.0616	7.0616	4.3688	0.0395
<i>rc</i> ~ Log mean Dry + Log mean Lion	4	−1.1642	8.8358	6.1430	0.0163
<i>rc</i> ~ Log mean Rain	3	4.3891	9.1891	6.4963	0.0136
<i>rc</i> ~ Log N + Log mean Lion	4	−0.3027	9.6973	7.0045	0.0106
<i>rc</i> ~ Log mean Rain + Log mean Dry + Log mean Lion	5	−8.9030	11.0970	8.4042	0.0052
<i>Zebra models</i>					
<i>rc</i> ~ Log N	3	−3.7603	1.0397	0.0000	0.4796
<i>rc</i> ~ Intercept	2	−0.1599	1.5544	0.5147	0.3708
<i>rc</i> ~ Log mean Lion	3	1.0599	5.0599	4.0202	0.0643
<i>rc</i> ~ Log mean Dry	3	1.9326	6.7326	5.6929	0.0278
<i>rc</i> ~ Log N + Log mean Lion	4	−2.8489	7.1511	6.1113	0.0226
<i>rc</i> ~ Log mean Rain	3	2.5199	7.3199	6.2801	0.0208
<i>rc</i> ~ Log mean Dry + Log N	4	−3.6335	9.6998	8.6601	0.0063
<i>rc</i> ~ Log mean Rain + Log N + Log mean Lion	5	−10.1083	9.8917	8.8520	0.0057
<i>rc</i> ~ Log mean Rain + Log mean Dry	4	3.0035	13.0035	11.9637	0.0012
<i>rc</i> ~ Log mean Dry + Log mean Lion	4	3.6707	13.6707	12.6309	0.0009

Table A.2

iMfolozi.

	df	AIC	AICc	Δ AICc	AICcW
<i>Giraffe models</i>					
<i>rc</i> ~ Log N	3	−4.3294	0.4706	0.0000	0.4511
<i>rc</i> ~ Intercept	2	−0.8537	0.8606	0.3900	0.3712
<i>rc</i> ~ Log mean Lion	3	0.2622	4.2622	3.7916	0.0678
<i>rc</i> ~ Log mean Dry	3	0.4543	5.2543	4.7837	0.0413
<i>rc</i> ~ Log mean Rain	3	1.2626	6.0626	5.5920	0.0275
<i>rc</i> ~ Log mean Rain + Log N	4	−6.6267	6.7067	6.2361	0.0200
<i>rc</i> ~ Log N + Log mean Lion	4	−2.3328	7.6672	7.1967	0.0123
<i>rc</i> ~ Log mean Dry + Log mean Lion	4	−0.9285	9.0715	8.6009	0.0061
<i>rc</i> ~ Log mean Rain + Log mean Lion	4	1.7819	11.7819	11.3114	0.0016
<i>rc</i> ~ Log mean Rain + Log mean Dry	4	2.4313	12.4313	11.9607	0.0011
<i>Kudu models</i>					
<i>rc</i> ~ Intercept	2	−13.1711	−11.4568	0.0000	0.6823
<i>rc</i> ~ Log N	3	−12.2235	−8.2235	3.2333	0.1355
<i>rc</i> ~ Log mean Lion	3	−11.7031	−7.7031	3.7537	0.1044
<i>rc</i> ~ Log mean Dry	3	−10.5063	−5.7063	5.7505	0.0385
<i>rc</i> ~ Log mean Rain	3	−9.5562	−4.7562	6.7007	0.0239
<i>rc</i> ~ Log N + Log mean Lion	4	−10.7932	−2.7932	8.6636	0.0090
<i>rc</i> ~ Log mean Dry + Log N	4	−10.3989	−0.3989	11.0579	0.0027
<i>rc</i> ~ Log mean Rain + Log N	4	−9.1874	0.8126	12.2694	0.0015
<i>rc</i> ~ Log mean Rain + Log mean Dry	4	−8.7869	1.2131	12.6699	0.0012
<i>rc</i> ~ Log mean Dry + Log mean Lion	4	−8.5069	1.4931	12.9499	0.0011
<i>Impala models</i>					
<i>rc</i> ~ Intercept	2	−9.0226	−7.3083	0.0000	0.4488
<i>rc</i> ~ Log N	3	−10.1230	−6.1230	1.1853	0.2481
<i>rc</i> ~ Log mean Lion	3	−9.6438	−5.6438	1.6645	0.1953
<i>rc</i> ~ Log mean Dry	3	−7.5563	−2.7563	4.5520	0.0461
<i>rc</i> ~ Log N + Log mean Lion	4	−9.8598	−1.8598	5.4485	0.0294
<i>rc</i> ~ Log mean Rain	3	−4.8186	−0.0186	7.2896	0.0117
<i>rc</i> ~ Log N * Log mean Lion	5	−14.4461	0.5539	7.8622	0.0088
<i>rc</i> ~ Log mean Dry + Log N	4	−8.5766	1.4234	8.7316	0.0057
<i>rc</i> ~ Log mean Rain + Log N	4	−8.0194	1.9806	9.2889	0.0043
<i>rc</i> ~ Log mean Dry + Log mean Lion	4	−6.2257	3.7743	11.0826	0.0018
<i>Nyala models</i>					
<i>rc</i> ~ Log N	3	−6.9880	−2.9880	0.0000	0.4628
<i>rc</i> ~ Intercept	2	−4.3774	−2.6631	0.3249	0.3934

(continued on next page)

Table A.2 (continued)

	df	AIC	AICc	Δ AICc	AICcW
<i>rc</i> ~ Log mean Lion	3	-3.5004	0.4996	3.4876	0.0809
<i>rc</i> ~ Log <i>N</i> + Log mean Lion	4	-5.0540	2.9460	5.9340	0.0238
<i>rc</i> ~ Log mean Dry	3	-0.9990	3.8010	6.7889	0.0155
<i>rc</i> ~ Log mean Rain	3	-0.9763	3.8237	6.8116	0.0154
<i>rc</i> ~ Log mean Dry + Log <i>N</i>	4	-3.1384	6.8616	9.8495	0.0034
<i>rc</i> ~ Log mean Rain + Log <i>N</i>	4	-3.1308	6.8692	9.8572	0.0033
<i>rc</i> ~ Log mean Rain + Log mean Lion	4	-0.0725	9.9275	12.9155	0.0007
<i>rc</i> ~ Log mean Dry + Log mean Lion	4	-0.0461	9.9539	12.9418	0.0007
<i>Warthog models</i>					
<i>rc</i> ~ Intercept	2	-0.7253	0.9889	0.0000	0.4572
<i>rc</i> ~ Log <i>N</i>	3	-2.3596	1.6404	0.6514	0.3301
<i>rc</i> ~ Log mean Lion	3	1.1192	5.1192	4.1303	0.0580
<i>rc</i> ~ Log mean Dry + Log <i>N</i>	4	-2.2980	5.7020	4.7130	0.0433
<i>rc</i> ~ Log mean Rain + Log <i>N</i>	4	-1.7595	6.2405	5.2516	0.0331
<i>rc</i> ~ Log mean Rain	3	2.4649	6.4649	5.4760	0.0296
<i>rc</i> ~ Log mean Dry	3	2.5057	6.5057	5.5168	0.0290
<i>rc</i> ~ Log <i>N</i> + Log mean Lion	4	-0.3610	7.6390	6.6500	0.0164
<i>rc</i> ~ Log mean Dry + Log mean Lion	4	4.0711	12.0711	11.0821	0.0018
<i>rc</i> ~ Log mean Rain + Log mean Lion	4	4.3272	12.3272	11.3383	0.0016
<i>Wildebeest models</i>					
<i>rc</i> ~ Intercept	2	-8.3170	-6.6027	0.0000	0.3525
<i>rc</i> ~ Log mean Lion	3	-9.6694	-5.6694	0.9334	0.2210
<i>rc</i> ~ Log <i>N</i>	3	-9.3532	-5.3532	1.2495	0.1887
<i>rc</i> ~ Log mean Rain	3	-8.9256	-4.1256	2.4771	0.1021
<i>rc</i> ~ Log mean Dry	3	-7.2069	-2.4069	4.1958	0.0433
<i>rc</i> ~ Log <i>N</i> + Log mean Lion	4	-10.0169	-2.0169	4.5859	0.0356
<i>rc</i> ~ Log mean Rain + Log <i>N</i>	4	-11.6087	-1.6087	4.9940	0.0290
<i>rc</i> ~ Log mean Rain + Log mean Lion	4	-10.2974	-0.2974	6.3053	0.0151
<i>rc</i> ~ Log mean Dry + Log mean Lion	4	-9.1658	0.8342	7.4370	0.0086
<i>rc</i> ~ Log mean Rain + Log mean Dry	4	-7.7379	2.2621	8.8649	0.0042
<i>Zebra models</i>					
<i>rc</i> ~ Log mean Lion	3	-12.3383	-8.3383	0.0000	0.3730
<i>rc</i> ~ Log <i>N</i>	3	-11.7617	-7.7617	0.5766	0.2796
<i>rc</i> ~ Intercept	2	-9.1361	-7.4218	0.9165	0.2359
<i>rc</i> ~ Log <i>N</i> + Log mean Lion	4	-13.5375	-5.5375	2.8008	0.0920
<i>rc</i> ~ Log mean Rain	3	-5.0982	-0.2982	8.0401	0.0067
<i>rc</i> ~ Log mean Dry + Log mean Lion	4	-9.2535	0.7465	9.0848	0.0040
<i>rc</i> ~ Log mean Rain + Log <i>N</i>	4	-8.3962	1.6038	9.9421	0.0026
<i>rc</i> ~ Log mean Dry + Log <i>N</i>	4	-8.2524	1.7476	10.0858	0.0024
<i>rc</i> ~ Log mean Rain + Log mean Lion	4	-8.2371	1.7629	10.1012	0.0024
<i>rc</i> ~ Log <i>N</i> * Log mean Lion	5	-12.2454	2.7546	11.0929	0.0015

Appendix B. Models of ungulate carcasses (10 firs models presented here; selected models in bold).

Table B.1

Hluhluwe.

	<i>k</i>	AIC	AICc	Δ AICc	AICcW
<i>Giraffe models</i>					
Carcass ~ Log <i>N</i> + Log Rain + Log Dry b + Log Lion + Sex	6	66.3944	71.9944	0.0000	0.1793
Carcass ~ Log <i>N</i> + Log Dry b + Log Lion	4	70.2621	72.6150	0.6206	0.1315
Carcass ~ Log <i>N</i> + Log Dry b + Log Lion + Sex	5	69.0841	72.8341	0.8397	0.1179
Carcass ~ Log <i>N</i> + Sex	3	71.8028	73.1361	1.1417	0.1013
Carcass ~ Log <i>N</i> + Log Rain + Log Dry b	4	70.9748	73.3277	1.3333	0.0921
Carcass ~ Log <i>N</i> + Log Lion + Sex	4	71.2015	73.5544	1.5600	0.0822
Carcass ~ Log <i>N</i>	2	72.9808	73.6123	1.6179	0.0799
Carcass ~ Log <i>N</i> + Log Lion	3	72.3794	73.7128	1.7183	0.0760
Carcass ~ Log <i>N</i> + Log Rain + Log Lion	4	71.4871	73.8400	1.8456	0.0713
Carcass ~ Log <i>N</i> + Log Dry b + Sex	4	71.5645	73.9175	1.9230	0.0686
<i>Kudu models</i>					
Carcass ~ Log <i>N</i> + Log Rain + Log Rain b + Log Dry	5	79.3930	83.1430	0.0000	0.2819
Carcass ~ Log <i>N</i> + Log Dry	3	83.3761	84.7094	1.5664	0.1288
Carcass ~ Log <i>N</i>	2	84.3993	85.0309	1.8879	0.1097
Carcass ~ Log <i>N</i> + Log Dry + Log Dry b	4	83.0111	85.3640	2.2210	0.0929
Carcass ~ Log <i>N</i> + Log Lion	3	84.5560	85.8893	2.7464	0.0714
Carcass ~ Log <i>N</i> + Log Rain b * Log Dry	5	82.1553	85.9053	2.7623	0.0708
Carcass ~ Log <i>N</i> + Log Rain + Log Lion	4	83.7546	86.1076	2.9646	0.0640
Carcass ~ Log <i>N</i> + Log Dry * Log Dry b	5	82.4294	86.1794	3.0364	0.0618
Carcass ~ Log <i>N</i> + Log Dry b	3	84.9242	86.2576	3.1146	0.0594
Carcass ~ Log <i>N</i> + Log Rain b	3	84.9320	86.2653	3.1223	0.0592
<i>Impala models</i>					
Carcass ~ Log <i>N</i> + Log Rain b + Log Dry	4	139.9908	142.3437	0.0000	0.2076
Carcass ~ Log <i>N</i> + Log Rain + Log Rain b + Log Dry + Log Dry b	6	137.3445	142.9445	0.6008	0.1537
Carcass ~ Log <i>N</i> + Log Rain + Log Rain b + Log Dry + Log Dry b + Log Lion	7	135.1330	143.1330	0.7893	0.1399

Table B.1 (continued)

	<i>k</i>	AIC	AICc	ΔAICc	AICcW
Carcass~Log <i>N</i> + Log Rain b + Log Dry + Log Dry b + Log Lion + Sex	7	135.1345	143.1345	0.7908	0.1398
Carcass~Log <i>N</i> + Log Rain b + Log Dry + Log Dry b + Sex	6	137.7391	143.3391	0.9954	0.1262
Carcass~Log <i>N</i> + Log Rain b + Log Dry + Log Lion	5	141.3332	145.0832	2.7395	0.0528
Carcass~Log <i>N</i> + Log Dry + Log Dry b + Log Lion	5	141.4743	145.2243	2.8806	0.0492
Carcass~Log <i>N</i> + Log Rain + Log Rain b + Log Dry	5	141.5616	145.3116	2.9679	0.0471
Carcass~Log <i>N</i> + Log Dry + Log Dry b	4	143.0135	145.3664	3.0227	0.0458
Carcass~Log <i>N</i> + Log Rain b + Log Dry + Sex	5	141.9908	145.7408	3.3971	0.0380
<i>Nyala models</i>					
Carcass~Log <i>N</i> + Log Rain + Log Rain + Log Dry b	5	163.7738	167.5238	0.0000	0.4044
Carcass~Log <i>N</i> + Log Rain + Log Rain b + Log Dry b + Log Lion	6	161.9445	167.5445	0.0207	0.4002
Carcass~Log <i>N</i> + Log Rain + Log Rain b + Log Dry b + Sex	6	165.0662	170.6662	3.1424	0.0840
Carcass~Log <i>N</i> * Log Lion + Log Rain	5	167.4593	171.2093	3.6855	0.0641
Carcass~Log <i>N</i> + Log Rain + Log Dry b + Log Lion + Sex	6	167.2769	172.8769	5.3531	0.0278
Carcass~Log <i>N</i> * Log Rain b + Log Lion	5	170.7109	174.4609	6.9371	0.0126
Carcass~Log <i>N</i> + Log Rain + Log Lion	4	174.6047	176.9576	9.4338	0.0036
Carcass~Log <i>N</i> + Log Rain + Log Rain b + Log Lion	5	174.7821	178.5321	11.0083	0.0016
Carcass~Log <i>N</i> * Log Dry b + Log Rain	5	175.4886	179.2386	11.7148	0.0012
Carcass~Log <i>N</i> + Log Rain + Log Dry b	4	178.9394	181.2923	13.7685	0.0004
<i>Warthog models (without sex)</i>					
Carcass~Log <i>N</i> + Log Rain	3	58.13798	62.1380	0.0000	0.7231
Carcass~Log <i>N</i> + Log Rain + Log Rain b	4	57.59541	65.5954	3.4574	0.1284
Carcass~Log <i>N</i> + Log Rain + Log Dry b	4	59.86403	67.8640	5.7261	0.0413
Carcass~Log <i>N</i> + Log Rain + Log Dry	4	60.03397	68.0340	5.8960	0.0379
Carcass~Log <i>N</i> + Log Rain + Log Lion	4	60.10435	68.1044	5.9664	0.0366
Carcass~Log <i>N</i> + Log Rain b + Log Dry b	4	61.83618	69.8362	7.6982	0.0154
Carcass~Log <i>N</i> + Log Dry b	3	67.06105	71.0611	8.9231	0.0083
Carcass~Log <i>N</i> + Log Rain + Log Rain b + Log Dry	5	57.73099	72.7310	10.5930	0.0036
Carcass~Log <i>N</i> + Log Rain + Log Rain b + Log Dry b	5	57.97194	72.9719	10.8340	0.0032
Carcass~Log <i>N</i> + Log Rain + Log Rain b + Log Lion	5	58.83594	73.8359	11.6980	0.0021
<i>Wildebeest models</i>					
Carcass~Log <i>N</i> + Log Rain + Log Rain b + Log Dry	5	91.6084	95.8941	0.0000	0.3006
Carcass~Log <i>N</i> + Log Rain + Log Rain b + Log Dry + Sex	6	90.0814	96.5429	0.6488	0.2173
Carcass~Log <i>N</i> + Log Rain + Log Rain b + Log Dry + Log Dry b	6	92.2277	98.6892	2.7951	0.0743
Carcass~Log <i>N</i> * Log Lion + Log Rain	5	94.5163	98.8020	2.9079	0.0702
Carcass~Log <i>N</i> + Log Rain + Log Lion	4	96.3074	98.9741	3.0800	0.0644
Carcass~Log <i>N</i> + Log Rain b + Log Dry b	4	96.4949	99.1616	3.2675	0.0587
Carcass~Log <i>N</i> + Log Rain + Log Rain b + Log Lion	5	94.9198	99.2055	3.3114	0.0574
Carcass~Log <i>N</i> + Log Rain b * Log Lion	5	94.9374	99.2232	3.3291	0.0569
Carcass~Log <i>N</i> + Log Rain + Log Rain b + Log Dry + Log Lion	6	92.9172	99.3788	3.4847	0.0526
Carcass~Log <i>N</i> + Log Rain * Log Dry b	5	95.3000	99.5858	3.6917	0.0475
<i>Zebra models (without sex)</i>					
Carcass~Log <i>N</i> + Log Dry b	3	60.53507	64.5351	0.0000	0.4768
Carcass~Log <i>N</i> + Log Rain + Log Dry b	4	58.63102	66.6310	2.0960	0.1672
Carcass~Log <i>N</i>	2	65.30871	67.0230	2.4879	0.1374
Carcass~Log <i>N</i> + Log Lion	3	65.26656	69.2666	4.7315	0.0448
Carcass~Log <i>N</i> + Log Rain b + Log Dry b	4	61.38937	69.3894	4.8543	0.0421
Carcass~Log <i>N</i> + Log Dry	3	65.73814	69.7381	5.2031	0.0354
Carcass~Log <i>N</i> + Log Dry b + Log Lion	4	61.8055	69.8055	5.2704	0.0342
Carcass~Log <i>N</i> + Log Dry + Log Dry b	4	62.53505	70.5351	6.0000	0.0237
Carcass~Log <i>N</i> + Log Rain	3	66.91473	70.9147	6.3797	0.0196
Carcass~Log <i>N</i> + Log Rain b	3	67.00257	71.0026	6.4675	0.0188

Table B.2

iMfolozi.

	<i>k</i>	AIC	AICc	ΔAICc	AICcW
<i>Giraffe models</i>					
CarcassGIF~Log <i>N</i> + Sex	3	63.1226	64.6226	0.0000	0.3233
CarcassGIF~Log <i>N</i> + Log Rain b + Sex	4	62.9718	65.6385	1.0159	0.1946
CarcassGIF~Log <i>N</i> + Log Lion + Sex	4	64.8351	67.5017	2.8792	0.0766
CarcassGIF~Log <i>N</i> * Sex	4	65.0084	67.6750	3.0525	0.0703
CarcassGIF~Log <i>N</i> + Log Dry b + Sex	4	65.0142	67.6808	3.0583	0.0701
CarcassGIF~Log <i>N</i> + Log Dry + Sex	4	65.0665	67.7332	3.1106	0.0683
CarcassGIF~Log <i>N</i> + Log Rain + Sex	4	65.1224	67.7890	3.1665	0.0664
CarcassGIF~Log <i>N</i> + Log Rain b * Sex	5	63.7953	68.0810	3.4585	0.0574
CarcassGIF~Log <i>N</i> + Log Rain b + Log Dry + Sex	5	64.5544	68.8401	4.2175	0.0393
CarcassGIF~Log <i>N</i> * Log Rain b + Sex	5	64.8511	69.1369	4.5143	0.0338
<i>Kudu models</i>					
Carcass~Log <i>N</i> + Log Dry + Sex	4	138.0052	140.3581	0.0000	0.2581
Carcass~Log <i>N</i> + Log Lion + Sex	4	138.3733	140.7262	0.3681	0.2147

(continued on next page)

Table B.2 (continued)

	<i>k</i>	AIC	AICc	ΔAICc	AICcW
Carcass ~ Log <i>N</i> + Log Rain + Log Dry + Log Dry + Sex	6	136.1990	141.7990	1.4409	0.1256
Carcass ~ Log <i>N</i> + Log Dry * Sex	5	138.8246	142.5746	2.2165	0.0852
Carcass ~ Log <i>N</i> + Log Rain + Log Rain b + Log Dry + Sex	6	137.2404	142.8404	2.4823	0.0746
Carcass ~ Log <i>N</i> + Log Dry + Log Dry b + Sex	5	139.3131	143.0631	2.7050	0.0667
Carcass ~ Log <i>N</i> + Log Rain b + Log Dry + Sex	5	139.8849	143.6349	3.2768	0.0502
Carcass ~ Log <i>N</i> * Sex + Log Dry	5	139.9938	143.7438	3.3857	0.0475
Carcass ~ Log <i>N</i> * Sex + Log Lion	5	140.3609	144.1109	3.7528	0.0395
Carcass ~ Log <i>N</i> + Log Rain b + Sex	4	141.8472	144.2001	3.8420	0.0378
<i>Impala models</i>					
Carcass ~ Log <i>N</i> + Log Rain + Log Dry + Log Dry b + Sex	6	149.9081	155.5081	0.0000	0.4357
Carcass ~ Log <i>N</i> + Log Rain + Log Dry b + Log Lion + Sex	6	150.6069	156.2069	0.6988	0.3072
Carcass ~ Log <i>N</i> + Log Rain + Log Rain b + Log Dry b + Sex	6	152.4500	158.0500	2.5419	0.1222
Carcass ~ Log <i>N</i> + Log Rain + Log Rain b + Log Dry + Log Dry b + Sex	7	150.3702	158.3702	2.8621	0.1042
Carcass ~ Log <i>N</i> + Log Rain + Log Rain b + Log Dry + Log Dry b + Log Lion + Sex	8	151.2875	162.3644	6.8563	0.0141
Carcass ~ Log <i>N</i> + Log Rain b + Log Dry + Log Dry b + Log Lion + Sex	7	154.4330	162.4330	6.9249	0.0137
Carcass ~ Log <i>N</i> + Log Dry + Log Dry b + Log Lion + Sex	6	160.0003	165.6003	10.0922	0.0028
Carcass ~ Log <i>N</i> + Log Rain + Log Rain b + Log Dry + Sex	6	167.3557	172.9557	17.4476	0.0001
Carcass ~ Log <i>N</i> + Log Rain + Log Rain b + Log Dry b + Log Lion	6	172.6483	178.2483	22.7402	0.0000
Carcass ~ Log <i>N</i> + Log Dry b + Log Lion + Sex	5	175.5041	179.2541	23.7460	0.0000
<i>Nyala models</i>					
Carcass ~ Log <i>N</i> + Log Rain + Log Rain b + Log Dry b + Sex	6	262.5169	268.1169	0.0000	0.8710
Carcass ~ Log <i>N</i> + Log Rain + Log Rain b + Log Dry + Log Dry b + Sex	7	264.1845	272.1845	4.0676	0.1140
Carcass ~ Log <i>N</i> + Log Rain + Log Rain b + Log Dry b + Log Lion	6	271.3292	276.9292	8.8123	0.0106
Carcass ~ Log <i>N</i> + Log Rain + Log Dry b + Log Lion + Sex	6	273.4353	279.0353	10.9184	0.0037
Carcass ~ Log <i>N</i> + Log Rain + Log Rain b + Log Dry b	5	279.0011	282.7511	14.6342	0.0006
Carcass ~ Log <i>N</i> + Log Rain + Log Rain b + Log Dry + Log Dry b	6	280.6688	286.2688	18.1519	0.0001
Carcass ~ Log <i>N</i> + Log Rain + Log Dry + Log Dry b + Sex	6	283.7820	289.3820	21.2651	0.0000
Carcass ~ Log <i>N</i> + Log Rain + Log Dry b	4	298.3512	300.7041	32.5872	0.0000
Carcass ~ Log <i>N</i> + Log Rain b + Log Dry + Log Dry b + Sex	6	308.7717	314.3717	46.2548	0.0000
Carcass ~ Log <i>N</i> + Log Rain b + Log Dry + Log Dry b	5	325.2559	329.0059	60.8890	0.0000
<i>Warthog models (without sex)</i>					
Carcass ~ Log <i>N</i> + Log Lion	3	58.03807	61.4666	0.0000	0.4151
Carcass ~ Log <i>N</i> + Log Dry + Log Lion	4	55.28895	61.9556	0.4890	0.3250
Carcass ~ Log <i>N</i> + Log Rain b + Log Lion	4	58.80604	65.4727	4.0061	0.0560
Carcass ~ Log <i>N</i> + Log Dry b + Log Lion	4	58.84514	65.5118	4.0452	0.0549
Carcass ~ Log <i>N</i> + Log Dry	3	62.28531	65.7139	4.2472	0.0496
Carcass ~ Log <i>N</i> + Log Rain + Log Lion	4	59.2677	65.9344	4.4677	0.0445
Carcass ~ Log <i>N</i> + Log Rain	3	63.44387	66.8724	5.4058	0.0278
Carcass ~ Log <i>N</i> + Log Rain b + Log Dry + Log Lion	5	56.91274	68.9127	7.4461	0.0100
Carcass ~ Log <i>N</i> + Log Dry + Log Dry b + Log Lion	5	57.12773	69.1277	7.6611	0.0090
Carcass ~ Log <i>N</i> * Log Rain + Log Lion	5	57.36136	69.3614	7.8947	0.0080
<i>Wildebeest models</i>					
Carcass ~ Log <i>N</i> + Log Dry + Sex	4	133.1735	135.5264	0.0000	0.1912
Carcass ~ Log <i>N</i> + Sex	3	134.3896	135.7229	0.1965	0.1733
Carcass ~ Log <i>N</i> * Log Dry + Sex	5	132.4284	136.1784	0.6520	0.1380
Carcass ~ Log <i>N</i> + Log Dry b + Log Lion + Sex	5	133.0768	136.8268	1.3004	0.0998
Carcass ~ Log <i>N</i> + Log Rain + Sex	4	134.5175	136.8704	1.3440	0.0976
Carcass ~ Log <i>N</i> + Log Dry b + Sex	4	135.0352	137.3881	1.8617	0.0754
Carcass ~ Log <i>N</i> + Log Lion + Sex	4	135.0370	137.3899	1.8635	0.0753
Carcass ~ Log <i>N</i> + Log Rain b + Sex	4	135.4725	137.8254	2.2990	0.0606
Carcass ~ Log <i>N</i> * Log Rain b + Sex	5	134.4056	138.1556	2.6292	0.0514
Carcass ~ Log <i>N</i> + Log Dry + Log Dry b + Sex	5	135.0349	138.7849	3.2585	0.0375
<i>Zebra models (without sex)</i>					
Carcass ~ Log <i>N</i>	2	61.80893	63.3089	0.0000	0.4094
Carcass ~ Log <i>N</i> + Log Dry	3	60.79537	64.2239	0.9150	0.2591
Carcass ~ Log <i>N</i> + Log Rain	3	63.39063	66.8192	3.5103	0.0708
Carcass ~ Log <i>N</i> + Log Dry b	3	63.63124	67.0598	3.7509	0.0628
Carcass ~ Log <i>N</i> + Log Rain b	3	63.7037	67.1323	3.8233	0.0605
Carcass ~ Log <i>N</i> + Log Lion	3	63.77105	67.1996	3.8907	0.0585
Carcass ~ Log <i>N</i> + Log Dry + Log Lion	4	62.53391	69.2006	5.8916	0.0215
Carcass ~ Log <i>N</i> + Log Dry + Log Dry b	4	62.75402	69.4207	6.1118	0.0193
Carcass ~ Log <i>N</i> + Log Rain + Log Dry	4	62.76325	69.4299	6.1210	0.0192
Carcass ~ Log <i>N</i> + Log Rain b + Log Dry	4	62.79419	69.4609	6.1519	0.0189

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