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Fossil evidence for seasonal calving and migration of extinct blue antelope (*Hippotragus leucophaeus*) in southern Africa

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ABSTRACT

Aim Palaeoecological data are crucial to understanding the historical extinction of the blue antelope (*Hippotragus leucophaeus*). This study examined late Quaternary fossil evidence bearing on the blue antelope's calving and migratory habits.

Location Cape Floristic Region (CFR), South Africa.

Methods Blue antelope mortality patterns were reconstructed from dental remains from fossil assemblages spanning the last *c.* 200,000 years and located in the CFR's winter and year-round rainfall zones. Two demographic measures were examined: (1) the frequencies of juveniles relative to adults; and (2) the frequencies of neonates relative to older juveniles. Geographical trends were examined across a longitudinal gradient of decreasing winter rainfall and increasing summer rainfall.

Results There was a significant longitudinal trend in the blue antelope mortality data, with juveniles and neonates declining in frequency from west to east. This suggests that calving occurred primarily in the winter rainfall zone, probably during the winter months when seasonal rains promoted the growth of C₃ grasses. The summer drought and lack of adequate forage forced blue antelope to migrate east, in time with summer rainfall and the increased availability of C₄ grasses. The migration route probably depended in part on reduced sea levels during glacial phases of the Pleistocene.

Main conclusions Blue antelope were probably migratory. Rising sea levels at the onset of the Holocene disrupted their migration routes, limited access to west-coast calving grounds, and fragmented populations. Such disruption would have devastated the blue antelope population and contributed to its vulnerability to extinction. Blue antelope survived previous marine transgressions, however, suggesting that other factors played a role in its demise. Agricultural expansion early in the colonial era may have further disrupted migration routes and played an important role in its extinction.

Keywords

Blue antelope, Cape Floristic Region, extinct species, extinction, migration, palaeoecology, Quaternary, southern Africa, zooarchaeology.

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INTRODUCTION

The blue antelope, *Hippotragus leucophaeus* (Pallas, 1766), was endemic to southern Africa, and its disappearance *c.* AD 1800 marked the first African large mammal extinction in historical times (Klein, 1974). Although historical observations are scarce (Skead, 2011), the blue antelope is well represented in

the Quaternary fossil record (Klein, 1974), which provides a key source of insight into its ecology and the factors leading to its demise. An understanding of both is not only important in its own right, but is also relevant to contemporary large mammal conservation efforts (Kerley *et al.*, 2003, 2009; Faith, 2012a) and to understanding palaeoecological change in the region (Klein, 1983; Rector & Reed, 2010; Faith, 2011a).

Previous studies have invoked several potential mechanisms to account for the extinction of the blue antelope, including overhunting by European colonists, competition and habitat degradation associated with the spread of pastoralism, and habitat loss due to long-term environmental change (Klein, 1974, 1987; Robinson *et al.*, 1996; IUCN SSC Antelope Specialist Group, 2008; Kerley *et al.*, 2009; Faith, 2011b). A better understanding of how these processes might have contributed to the blue antelope's extinction, however, requires an improved understanding of its ecology. To this end, we examine late Quaternary fossil evidence bearing on its calving and migratory habits in southern Africa's Cape Floristic Region (CFR).

Distribution and ecology

Although the historically documented range of blue antelope was limited to 4300 km² along the southern coast (Kerley *et al.*, 2003), fossil evidence documents a broad distribution spanning the southern and western coastal plains of the CFR, and even extending beyond the CFR into the highlands

of Lesotho (Fig. 1). The prehistoric distribution encompasses significant variation in rainfall regimes (Chase & Meadows, 2007) (Fig. 1). The west coast receives the majority of its rainfall during the winter (winter rainfall zone: > 66% of annual precipitation from April to September), reflecting the annual north–south migration of westerly frontal systems. The south coast receives rainfall throughout the year (year-round rainfall zone), receiving winter rains from the west and summer rains from easterly fronts associated with the migration of the Intertropical Convergence Zone (ITCZ). To the north and east of the CFR, summer rains are dominant (summer rainfall zone: > 66% of annual precipitation from October to March). This variation in rainfall seasonality strongly influences the distribution of C₄ and C₃ grasses, which track the proportion of summer and winter rains, respectively (Vogel *et al.*, 1978; Cowling, 1983; Rebelo *et al.*, 2006).

Because the blue antelope disappeared before zoologists could make systematic observations of living populations, its ecology must be reconstructed from fossil data (Klein, 1974, 1987), historical observations (Skead, 2011) and our knowl-

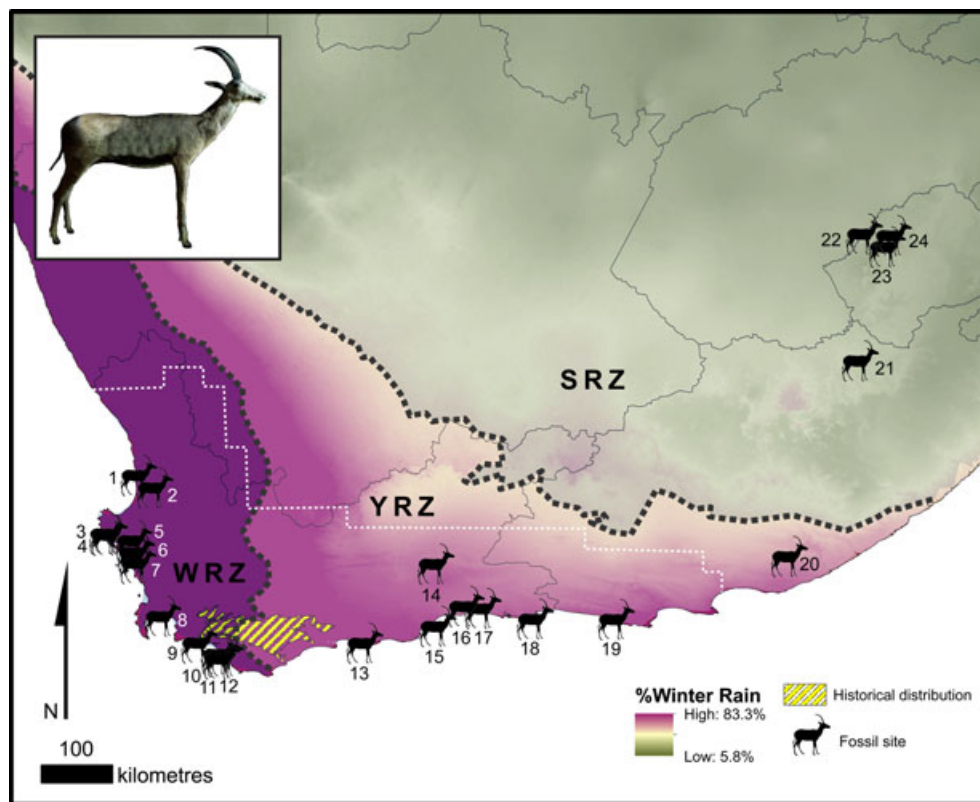


Figure 1 The historical and fossil range of blue antelope (*Hippotragus leucophaeus*) in southern Africa (after Faith, 2011b), and the distribution of winter (WRZ: > 66% of annual precipitation from April to September), year-round (YRZ), and summer rainfall zones (SRZ: > 66% of annual precipitation falls from October to May). Precipitation data are from Hijmans *et al.* (2005). The white dashed line indicates the boundaries of the Cape Floristic Region. The inset depicts the specimen on display at the Muséum National d'Histoire Naturelle (Paris, France). Key to fossil sites: (1) Elands Bay Cave; (2) Diepkloof Rockshelter; (3) Sea Harvest; (4) Hoedjiespunt; (5) Elandsfontein; (6) Bloembos; (7) Duinefontein 2; (8) Swartklip 1; (9) Hawston; (10) Die Kelders Cave 1; (11) Eyre's Cave; (12) Byneskranskop 1; (13) Blombos Cave; (14) Boomplaas Cave; (15) Pinnacle Point; (16) Oakhurst; (17) Lake Pleasant; (18) Nelson Bay Cave; (19) Klasies River Mouth Caves 1/1A/1B; (20) Uniondale; (21) Colwinton; (22) Rose Cottage Cave; (23) Ha Makotoko; and (24) Ntloana Tsoana.

edge of its extant relatives. The blue antelope was almost certainly a grazer, as suggested by dental similarities to its grazing congeners – roan (*Hippotragus equinus*) and sable (*Hippotragus niger*) – and accounts of it grazing in sheep pastures (Klein, 1974, 1987). Dental mesowear analysis of mid-Pleistocene fossils further indicates a diet of grasses (Stynder, 2009), although its relatively long premolar row suggests that blue antelope may occasionally have consumed some dicotyledonous plants (Klein, 1987). Consistent with its reconstructed diet, blue antelope probably favoured grassy habitats. This can be inferred from observations that blue antelope tend to be most numerous in fossil assemblages dominated by other grassland species (Klein, 1983; Faith, 2012b).

Both roan and sable are gregarious, with roan typically associating in small herds of 5–12 individuals and sable in herds of 10–30 (Skinner & Chimimba, 2005). Historical records confirm the same gregarious behaviour in blue antelope (Skead, 2011). The calving schedule of roan and sable varies over their geographical range, with the southernmost populations characterized by more pronounced seasonality (Wilson & Hirst, 1977; Sekulic, 1978; Skinner & Chimimba, 2005). In southern Africa, most sable antelope are born between January and March, coinciding with summer rains and peak forage availability. Roan antelope are generally considered to be aseasonal breeders, although they exhibit similar summer peaks in some parts of South Africa. Observations are unavailable for blue antelope, but the seasonality of rainfall and forage availability across its prehistoric range raises the possibility of pronounced breeding seasonality.

Female roan and sable calve away from the herd, leaving the calf concealed and returning regularly to feed it (Skinner & Chimimba, 2005). Only after 2 months does the calf join the herd. The same behaviour in blue antelope is supported by an 18th-century account noting the tendency of females to neglect their young (Skead, 2011), presumably a reference to the females leaving neonate calves in isolation.

Prehistoric migration?

It has long been noted that Pleistocene faunal assemblages from the CFR are dominated by large grazing ungulates, in contrast to the dominance of small-bodied browsers today (Klein, 1980, 1983). Marean (2010) proposed that this was made possible by the existence of a prehistoric migratory ecosystem, and we build on this hypothesis here. Ungulate migration across a range of habitats is thought to be motivated by seasonal precipitation and its influence on forage availability and quality (Fryxell & Sinclair, 1988; Williamson *et al.*, 1988; Wilmshurt *et al.*, 1999; Holdo *et al.*, 2009). The longitudinal gradient in rainfall seasonality in the CFR (Fig. 1) sets the stage for such migration. In particular, the C₃ grasses of the winter rainfall zone become moribund and unpalatable during the hot and dry summer months (Pierce & Cowling, 1984; Radloff, 2008). Ungulates that are unable to consume large quantities of low-quality forage (e.g.

equids) or that are not adapted to consume and digest dry, fibrous grasses (e.g. hartebeest, *Alcelaphus buselaphus*) would have been compelled to migrate east to the year-round rainfall zone in search of fresh grass associated with summer rains. This is likely to have included the blue antelope, as there is little about its morphology, by way of massive body mass or extreme hypsodonty, to suggest that it was capable of surviving the summer drought in the winter rainfall zone. Such migration should translate to geographical and seasonal variation in blue antelope calving grounds, as forage availability is a key determinant of breeding seasonality in most grazing antelopes (Kingdon, 1982; Skinner *et al.*, 2002; Skinner & Chimimba, 2005). It is anticipated that blue antelope preferentially calved when rainfall promoted maximum grassland productivity; that is, in the western margin of the CFR during the winter or in the eastern margin of the CFR during the summer.

The east–west dichotomy between summer and winter rains is likely to have characterized the prehistoric landscapes inhabited by blue antelope. Isotopic analysis of presumed grazers from Langebaanweg (20 km north-west of Elandsfontein, Fig. 1) indicate diets of C₃ grasses, suggesting that the dominance of winter rainfall on the west coast dates to at least the early Pliocene (Franz-Odenaal *et al.*, 2002). Parallel evidence has been obtained from mid-Pleistocene grazers at nearby Elandsfontein (Luyt *et al.*, 2000) and Hoedjiespunt (Hare & Sealy, 2013). Isotopic evidence from grazers in the modern summer rainfall zone consistently indicate the dominance of C₄ grasses and summer rains during glacial and interglacial phases since the middle Pleistocene (Lee-Thorp & Beaumont, 1995; Codron *et al.*, 2008). In the year-round rainfall zone, blue antelope and African buffalo (*Syncerus caffer*) at Nelson Bay Cave consumed mixed diets of C₄ and C₃ grasses from the Last Glacial Maximum through the Holocene (Sealy, 1996). This may reflect the persistence of both summer and winter rains under glacial and interglacial conditions, but we caution that the signal could be influenced by seasonal migration. Although the precise boundaries of the winter and summer rainfall zones have changed over time (Chase & Meadows, 2007; Bar-Matthews *et al.*, 2010; Faith, 2013), these observations suggest that seasonal variation in rainfall and forage availability are likely to have characterized blue antelope habitats throughout the Quaternary.

MATERIALS AND METHODS

We test the migration hypothesis through an examination of geographical variation in blue antelope mortality patterns. The immobility of blue antelope neonates, presumably for the first 2 months of life, means that their presence in a fossil site is unequivocal evidence that calving occurred nearby. Mortality data are reconstructed using blue antelope dental remains from archaeological and palaeontological sites in the CFR's winter and year-round rainfall zones (Table 1). Two demographic measures are examined. The first considers the relative abundance of juveniles, which is estimated by the

Table 1 Details of blue antelope (*Hippotragus leucophaeus*) assemblages examined here. Sites are arranged from west to east.

Site	Context	Age
Winter rainfall zone		
Sea Harvest	Hyena den assemblage	middle-late Pleistocene (biochronology)
Swartklip 1	Hyena den assemblage	186–130 ka
Die Kelders Cave 1 (MSA)	Archaeological cave site	70–60 ka
Byneskranskop 1	Archaeological cave site	12,730 ± 185 to 255 ± 50 ¹⁴ C yr BP
Year-round rainfall zone		
Blombos Cave	Archaeological cave site	100–70 ka
Pinnacle Point 30	Hyena den assemblage	151 ka
Nelson Bay Cave	Archaeological cave site	18,660 ± 110 to 455 ± 30 ¹⁴ C yr BP
Klasies River Mouth (MSA)	Archaeological cave site	115–50 ka

number of specimens with deciduous premolars (dP2–dP4) relative to those with only permanent premolars (P2–P4). Among the juveniles, we also examine the number of specimens with unworn deciduous teeth relative to those with only worn deciduous teeth, which reflects the proportion of immobile calves relative to older and more mobile juveniles that had begun grazing. Tooth eruption sequences for blue antelope are unavailable, although unworn deciduous teeth are only found in sheep and goats younger than 2 months (Zeder, 2006). This corresponds to the time when we expect that blue antelope calves remained immobile and apart from the herd. Longitudinal trends in the mortality data are examined using a chi-square test for linear trend (Lyman, 2008), conducted in Microsoft Excel on a 2 × 8 contingency table with sites arranged from west to east.

The fossil samples considered here were recovered from archaeological sites and hyena dens located on the west and south coast of the CFR (Table 1): Sea Harvest (Klein, 1983), Swartklip 1 (Klein, 1975, 1983), Die Kelders Cave 1 (Klein & Cruz-Urbe, 2000), Byneskranskop 1 (Schweitzer & Wilson, 1982), Blombos Cave (Henshilwood *et al.*, 2001; Thompson & Henshilwood, 2011), Pinnacle Point 30 (Rector & Reed, 2010), Nelson Bay Cave (Klein, 1972, 1983; Inskip, 1987), and Klasies River Mouth (Klein, 1976). These samples fall within the modern winter and year-round rainfall zones and range in age from the late middle Pleistocene at Swartklip and Pinnacle Point 30 through the Holocene at Byneskranskop and Nelson Bay Cave. We recognize that these samples encompass a broad time interval and substantial environmental variation, but also note that the longitudinal dichotomy between summer and winter rainfall appears to have been present under glacial and interglacial conditions. Although time-averaging is therefore unlikely to affect the results presented here, a chronologically controlled analysis is provided for some sites using Fisher's exact test in the software package PAST 2.17 (Hammer *et al.*, 2001).

We focus on the CFR, because this region is thought to have supported a prehistoric migratory ecosystem (Marean, 2010) and because it encompasses the blue antelope's historical range and the vast majority of its fossil occurrences (Fig. 1). The summer rainfall zone is not considered here as

it includes only a small number of blue antelope fossils (minimum of 10 individuals) scattered across four localities in and around the Lesotho highlands (Plug, 1997). This sparse sampling, despite a large number of Quaternary fossil sites in the region (Klein, 1980), not only precludes an analysis of mortality profiles, but also suggests that past migrations are unlikely to have involved the summer rainfall zone.

RESULTS

Blue antelope mortality data are presented in Table 2. A chi-square test for linear trend indicates a highly significant west-to-east decline in the abundance of juveniles (with deciduous premolars) relative to adults (with permanent premolars) ($\chi^2_{\text{trend}} = 41.275$; $P < 0.001$). A longitudinal trend is also evident within the sample of juveniles, with sites from the west including primarily neonates (with unworn deciduous teeth) and those from the east including more older juveniles (with worn deciduous teeth) ($\chi^2_{\text{trend}} = 10.732$; $P = 0.001$).

Chronological bias does not appear to be driving the overall trend, with the juvenile-dominated samples and adult-dominated samples spanning similar age ranges (Table 1). A chronologically controlled comparison is possible for the

Table 2 The number of blue antelope (*Hippotragus leucophaeus*) specimens (NISP, number of identified specimens) with deciduous (worn and unworn) or permanent premolars at Cape Floristic Region sites examined here. Sites are arranged from west to east.

Locality	Deciduous		Permanent
	NISP worn	NISP unworn	NISP
Sea Harvest	5	7	1
Swartklip 1	17	20	9
Die Kelders Cave 1	16	11	5
Byneskranskop 1	3	2	7
Blombos Cave	5	20	0
Pinnacle Point	0	0	3
Nelson Bay Cave	30	15	53
Klasies River Mouth	36	7	58

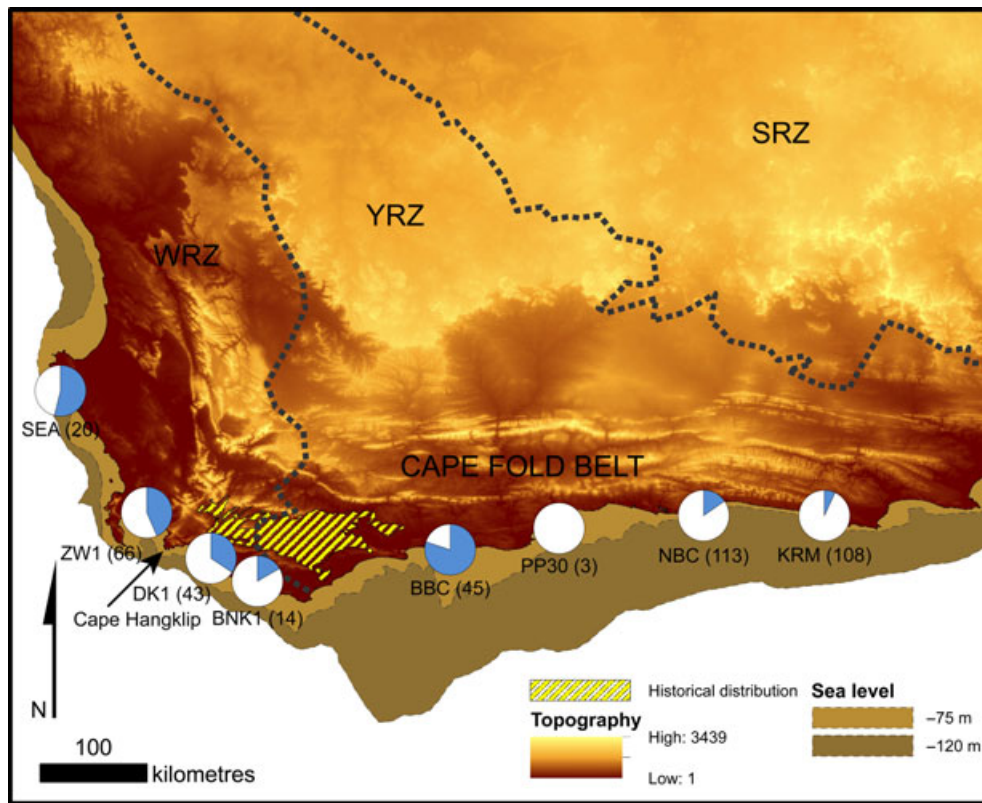


Figure 2 Topographical map illustrating the location of blue antelope (*Hippotragus leucophaeus*) assemblages examined here. SEA, Sea Harvest; ZW1, Swartklip 1; BNK1, Byneskranskop 1; DK1, Die Kelders Cave 1; BBC, Blombos Cave; PP30, Pinnacle Point 30; NBC, Nelson Bay Cave; KRM, Klasies River Mouth. Pie charts illustrate the abundance of fossil specimens belonging to neonate calves (in blue) relative to older juveniles and adults (in white) (sample sizes in parentheses). Approximate coastline at sea levels of 75 and 120 metres below present are also shown. Dashed lines correspond to the boundaries of the winter (WRZ), year-round (YRZ), and summer rainfall zones (SRZ).

archaeological samples from Die Kelders Cave 1 and Klasies River Mouth, with the former dating to 60–70 ka (Feathers & Bush, 2000) and the latter to 50–115 ka (Feathers, 2002). Die Kelders Cave 1 is found along the western margin of the south coast in the winter rainfall zone, while Klasies River Mouth is located along the eastern margin of the year-round rainfall zone, where summer rains are more common (Figs 1 & 2). Consistent with the overall pattern, Die Kelders Cave 1 includes a greater number of neonates (Fisher’s exact test: $P = 0.028$) and fewer adults (Fisher’s exact test: $P < 0.001$) than Klasies River Mouth.

DISCUSSION

Blue antelope mortality profiles show a pronounced west-to-east decline in the frequencies of neonate calves and juveniles. This trend is not readily explained by differential chronological sampling, although it is possible that different taphonomic agents (human versus hyena) preferentially accumulated blue antelope of different ages. This is unlikely to explain the patterns observed here, however, as hyena and anthropogenic accumulations are represented in both the winter and year-round rainfall zones (Table 1). The possibil-

ity that faunal remains were accumulated on a seasonal basis (e.g. seasonal occupation of archaeological sites) could contribute to variance in the mortality data, including the large number of neonates at Blombos Cave. The site seasonality data needed to explore this possibility in further detail are unavailable.

In the absence of systematic taphonomic and chronological bias, the mortality data provide evidence that blue antelope calved and migrated on a seasonal basis. The longitudinal trend in the frequency of blue antelope neonates indicates that calves were born primarily in the west (winter rainfall zone). Given the pronounced seasonality of rainfall (Fig. 1), calving in the west is expected to have occurred only during the winter, when seasonal rains promoted the growth of C_3 grasses. The summer drought and moribund C_3 grasses would have required blue antelope to migrate east to the year-round rainfall zone in search of summer rainfall and fresh C_4 grasses, only returning west to complete the migratory cycle in the winter. The rarity of neonates and greater abundance of older juveniles in the east are consistent with west-to-east migration after calves joined the herd. Likewise, the dominance of adults relative to juveniles in the east may reflect attrition of juveniles during the course of

migration, as mortality in ungulates is highest in the youngest individuals (Klein, 1982). The presence of neonates at most sites indicates that some calving occurred throughout its range and perhaps at other times of the year, but the peak was concentrated to the west and in the winter.

It remains to be determined why calving preferentially occurred in the west during the winter as opposed to the east during the summer. However, there is evidence that some C_3 grasses are generally more nutritious and more readily digested than their C_4 counterparts (Caswell *et al.*, 1973; Ehleringer & Monson, 1993; Sponheimer *et al.*, 2003; Barbehenn *et al.*, 2004). Preferential calving in the western C_3 grasslands may have provided blue antelope females with a crucial nutritional advantage at a time when they had to invest a substantial amount of energy into producing milk.

Migration corridors and sea-level change

Quaternary sea-level changes are likely to have played a central role in the opening and closing of blue antelope migration corridors. Today, the western and southern coastal plains are isolated from each other and from the South African interior by the Cape Fold Belt, which is divisible into southern and western branches that intersect at the Cape Syntaxis (Fig. 2). The southern branch consists of a series of folded mountains that rise up to 2000 m in elevation and run parallel to the coast for more than 600 km. Cape Hangklip represents the coastal spur of the Cape Syntaxis, from which the western branch extends *c.* 250 km to the north and defines the eastern boundary of the western coastal plain. The intersection of the Cape Syntaxis with the shoreline at Cape Hangklip creates a biogeographical barrier in a series of rocky cliffs that restrict the movement of large terrestrial mammals between the south and west coast (Compton, 2011). With the exception of the Cape mountain zebra (*Equus zebra zebra*), which tolerates rugged terrain, most large grazers are unable to find adequate habitat or forage across the Cape Syntaxis barrier (Boshoff & Kerley, 2001). Migration to the eastern margin of the southern coastal plain (e.g. Klasies River Mouth) is inhibited by dense Afromontane forest along the narrow coastal plain (4 km wide) (Cowling & Hejnis, 2001; Mucina *et al.*, 2006) and deeply incised river gorges just beyond Nelson Bay Cave (Compton, 2011).

Reduced sea levels during glacial phases of the Pleistocene exposed the shallow continental shelf off the southern coast (the Agulhas Bank), creating a broad coastal plain and increasing the land area by more than 60,000 km² (van Andel, 1989; Fisher *et al.*, 2010) (Fig. 2). Drawing upon bathymetric data, Compton (2011) showed that marine regressions would have allowed large mammals to move across the coastal plains unimpeded by biogeographical barriers. Past migrations of blue antelope across the Cape Syntaxis or between the western and eastern limits of the southern coastal plains were probably dependent on lower sea levels.

The importance of marine regressions to the blue antelope migration is consistent with its fossil history. Large samples of neonate blue antelope are found at both Swartklip 1 and Sea Harvest, west of the Cape Syntaxis (Fig. 2). At Swartklip 1, an amino acid racemization date (186–130 ka) on ostrich eggshell (Klein *et al.*, 2007), and an optically stimulated luminescence date (131 ± 6.4 ka) for a palaeosol overlying the fossil deposit (Roberts *et al.*, 2009), suggest an age corresponding to glacial Marine Isotope Stage 6. Radiometric dates for Sea Harvest are lacking, although the exceptionally diverse grazing community suggests that it also represents a glacial phase during the middle–late Pleistocene (Klein, 1983). Swartklip 1 – and probably also Sea Harvest – sample faunal communities from a time when sea level was substantially reduced (Fisher *et al.*, 2010) and migration between the west coast and south coast was possible (Compton, 2011). Further east, blue antelope are found throughout the Middle Stone Age sequence at Klasies River Mouth (Klein, 1976), which dates to 115–50 ka (Table 1). Sea levels were anywhere between 17 and 85 m lower than at present (Fisher *et al.*, 2010), potentially opening the eastward migration corridor beyond Nelson Bay Cave (Compton, 2011).

Rising sea levels at the onset of the Holocene would have disrupted the blue antelope migration route, limited access to the west coast calving grounds, and fragmented populations. Migration across the Cape Syntaxis barrier was restricted, and populations isolated on the west coast would have struggled to find adequate forage during the summer drought. Although blue antelope fossils are consistently found in west-coast Pleistocene sites (Klein & Cruz-Uribe, 1987; Cruz-Uribe *et al.*, 2003; Halkett *et al.*, 2003), they are largely absent from the Holocene record, with the exception of a single specimen from a stratum dated to 3510 ± 45 ¹⁴C yr BP at Elands Bay Cave (Klein & Cruz-Uribe, 1987). This record indicates that a population survived on the west coast well into the Holocene, or that limited interchange across the Cape Syntaxis barrier was possible. Blue antelope persisted on the southern coastal plain throughout the Holocene, with fossil occurrences ranging from Die Kelders Cave 1 (Klein & Cruz-Uribe, 2000) in the west to Nelson Bay Cave (Klein, 1983) in the east. The absence of blue antelope from the Holocene units at Klasies River Mouth (Klein, 1976) suggests that the migration corridor beyond Nelson Bay Cave was closed. The summer rainfall zone documents a relatively short-lived presence of blue antelope dating from the end of the Pleistocene to the middle Holocene (Plug, 1997) (Fig. 1). This population is likely to have expanded into the region while sea levels were lower during the terminal Pleistocene, only to become isolated from the CFR population on the southern coastal plain at the onset of the Holocene.

The persistence of blue antelope on the southern coastal plain into historical times is likely to reflect the ability of this population to access both winter-rainfall calving grounds (winter rainfall zone) and summer grazing pastures (year-round rainfall zone). It is striking that the historical range of the blue antelope straddles the boundary between the winter

and year-round rainfall zones (Fig. 2), suggesting that even small-scale migrations may have occurred until recently. Access to summer rainfall would not have been possible for the population isolated on the west coast, whereas the population in the interior would have been unable to access winter-rainfall calving grounds or substantial winter rains.

Extinction

We propose that the rise in sea levels at the onset of the Holocene played a crucial role in the demise of the blue antelope. Populations were fragmented and the migration route disrupted, leaving only the isolated population on the south coast with access to winter calving grounds and summer rains. The consequences of these changes would have been devastating (Newmark, 2008). For example, when a wildebeest (*Connochaetes taurinus*) subpopulation in Kruger National Park had its migration route disrupted by the erection of a fence, the subpopulation crashed by 87% (Whyte & Joubert, 1988). Similarly, following the disruption of migration routes associated with the fencing of Etosha National Park in Namibia there was an 85% decline in wildebeest populations (Berry, 1997). Such a reduction in blue antelope population size, together with geographical isolation, would have contributed to a substantial decline in genetic diversity and increased the risk of extinction (Franklin, 1980; Lacy, 1997). These factors probably contributed to the prehistoric extinction of sub-populations along the west coast and in the interior.

Although rising sea levels and geographical isolation probably set the stage for the blue antelope's demise, previous interglacial high-stands witnessed higher sea levels than the Holocene (Fisher *et al.*, 2010). This suggests that sea level change alone is an insufficient extinction mechanism. Other contributing factors could include hunting and landscape transformation by European colonists, the introduction of livestock *c.* 2000 years ago, or long-term vegetation change.

Kerley *et al.* (2009) argue that the historical range of blue antelope was too small to support a viable population, in which case European colonists were incidental contributors to the extinction of a species that was already doomed. The crucial question raised by this result is why the blue antelope range had declined to this point, especially in light of the broader distribution observed in south-coast fossil deposits from the last 2000 years (e.g. at Die Kelders Cave and Nelson Bay Cave). Kerley *et al.* (2009) suggest that long-term processes (e.g. vegetation change) may be responsible, and this is supported by the steady decline in blue antelope abundances through the Holocene at Nelson Bay Cave (Klein, 1983; Faith, 2011b). Alternatively, Klein (1974, 1987) proposes that habitat deterioration associated with the arrival of domestic sheep *c.* 2000 years ago may have contributed to this decline. However, pastoralists frequently set fire to the landscape to provide grassy habitats for their stock (Skead, 2011), which may have favoured blue antelope (Kerley *et al.*, 2009). In addition, there is no quantitative support for a decline in blue antelope fossil occurrences 2000 years ago (Faith, 2011b).

Although we agree with Kerley *et al.* (2009) that long-term processes are largely responsible for the demise of the blue antelope, it may be premature to discount the impacts of European colonists. The evaluation by Kerley *et al.* rests on the assumption that the range of blue antelope during the colonial era was adequately documented. The fact that the type specimen of roan antelope has been traced to the south coast near Nelson Bay Cave (Grubb, 1999), despite only equivocal observations of this species in the region (Skead, 2011; Faith, 2012a), highlights the inadequacies of the historical record. The blue antelope's migratory behaviours would have made it particularly vulnerable to agricultural expansion early in the historical era. Any landscape transformation that disrupted the south coast migration route could have caused the blue antelope's range to contract rapidly and before it could be sufficiently documented. A massive population crash would have followed (Newmark, 2008). Perhaps relevant to the case here, agricultural expansion is widely considered to have played a central role in the near-extinction of the bontebok (*Damaliscus dorcas dorcas*), which had a historical range overlapping that of blue antelope (Skead, 2011), at the time the blue antelope disappeared (van Rensburg, 1975; Skinner & Chimimba, 2005).

Palaeoecological and conservation implications

The evidence that blue antelope migrated and calved on a seasonal basis is consistent with the proposal of an extinct migratory grazing ecosystem in the CFR (Marean, 2010). Pleistocene faunal communities from the CFR include a number of extinct grassland specialists, including the Cape zebra (*Equus capensis*), long-horn buffalo (*Syncerus antiquus*), giant wildebeest (*Megalotragus priscus*), southern springbok (*Antidorcas australis*), and an unnamed caprine antelope (Klein, 1980, 1983; Brink, 1999; Rector & Reed, 2010; Faith, 2011b, 2012b). Black wildebeest (*Connochaetes gnou*), a seasonal breeder (Skinner & Chimimba, 2005) that is unknown from the CFR in historical times (Skead, 2011), also occurred in many of the same sites as blue antelope (Klein, 1983). Although empirical evidence for migration in these taxa is not yet available, these species were probably subject to the same seasonal pressures that drove the blue antelope migration. As was the case for blue antelope, rising sea levels at the onset of the Holocene would have been devastating for any migratory species, and may have played a central role in explaining their disappearance from the CFR.

The bontebok and Cape mountain zebra, two large grazers that may have also participated in past migrations, are the focus of ongoing conservation efforts in the CFR (Novellie *et al.*, 2002; Kerley *et al.*, 2003; Watson & Chadwick, 2007; Smith *et al.*, 2011; Faith, 2012a). The bontebok nearly followed the blue antelope to extinction in the early 1800s, and the Cape mountain zebra only narrowly avoided extinction 100 years later (Skinner & Chimimba, 2005). The case of the blue antelope raises the possibility that the precipitous decline of these grazers in historical times stemmed in part from the disruption of past migration routes.

CONCLUSIONS

Blue antelope fossil assemblages from the west and south coast of the Cape Floristic Region are characterized by geographical variation in the frequencies of neonate calves and juveniles relative to other age classes. This variation indicates that blue antelope preferentially calved in the western margins of its pre-historic range during the winter rainy season and subsequently migrated across the southern coast for the summer rains. We propose that rising sea levels at the onset of the Holocene played a central role in the extinction of the blue antelope by disrupting migration corridors, fragmenting populations and limiting access to west-coast calving grounds. As a result, only the blue antelope population on the south coast survived into historical times. It remains to be determined why the historically documented range is substantially smaller than that documented in the recent (last 2000 years) fossil record. Long-term vegetation change or the arrival of pastoralists could be responsible, although it is possible that agricultural development early in the historical era disrupted the Holocene migration route and contributed to a sudden range contraction before the blue antelope's range could be accurately assessed. If so, then human impacts in the historical era could also have contributed to the demise of the blue antelope.

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