Temporal variation in Plio-Pleistocene *Antidorcas* (Mammalia: Bovidae) horncores: the case from Bolt's Farm and why size matters

Sally Christine Reynolds*

Morphological differences in samples of fossil (*Antidorcas recki*) and modern (*A. marsupialis*) springbok horncores suggest that the ancestral species shows less sexual dimorphism than is observed in the horn dimensions of modern springbok. This pattern may prove useful when evaluating fossil springbok specimens in South African Plio-Pleistocene faunal assemblages. Undated *Antidorcas* craniodental specimens from Pit 3, Bolt's Farm (Cradle of Humankind, Gauteng, South Africa) have previously been referred to *A. recki* by Cooke.[1] However, comparison with numerous other springbok samples suggests that these specimens are more likely to represent male and female fossils of the extant species, *A. marsupialis*. This re-evaluation adds weight to the fossil evidence implying that the modern form of springbok is a southern African endemic species which first appeared around 1.5–1.0 million years ago in Swartkrans Member 1.[2,3] Bolt's Farm Pit 3 fossils are inferred to be of a similar age.

Introduction

The springbok (*Antidorcas marsupialis*) is a common antelope species from southern Africa, represented by three subspecies across a continuous range (Fig. 1). Sexual dimorphism is evident in body size and in horn shape in each subspecies. The largest springbok populations are of *A. m. hofmeyri* in the arid areas of Namibia whereas those of the subspecies from South Africa (*A. m. marsupialis*) are the smallest.[4,5] Mean body mass varies from 41 kg recorded for males to 37 kg for females.[6,7] Although both sexes are horned, males possess heavily ridged horns that sweep backwards from the base before diverging outwards and hooking inwards at the tips. In contrast, females possess horns that are 'distinctly smaller, wider apart at the base, lightly ridged and much thinner than in the males'.[7]

The ancestral springbok species (*A. recki*) is abundant in East and South African Plio-Pleistocene deposits (Fig. 1) from roughly three million years ago but disappears entirely from the eastern African fossil record after about 330 000 years ago.[8] The ancestral form possessed more mediolaterally compressed horncores and smaller overall body size than the descendant species. The earliest fossils of the extant springbok (*A. marsupialis*) are from Swartkrans Member 1 (in the Sterkfontein Valley, South Africa), and this species is common throughout the entire Swartkrans sequence and at numerous other sites in the Sterkfontein Valley. Ecomorphological studies on both East and South African samples suggest that the ancestral species was adapted to more closed, woodland habitats and a predominantly browse (C_3) diet.[9,10]

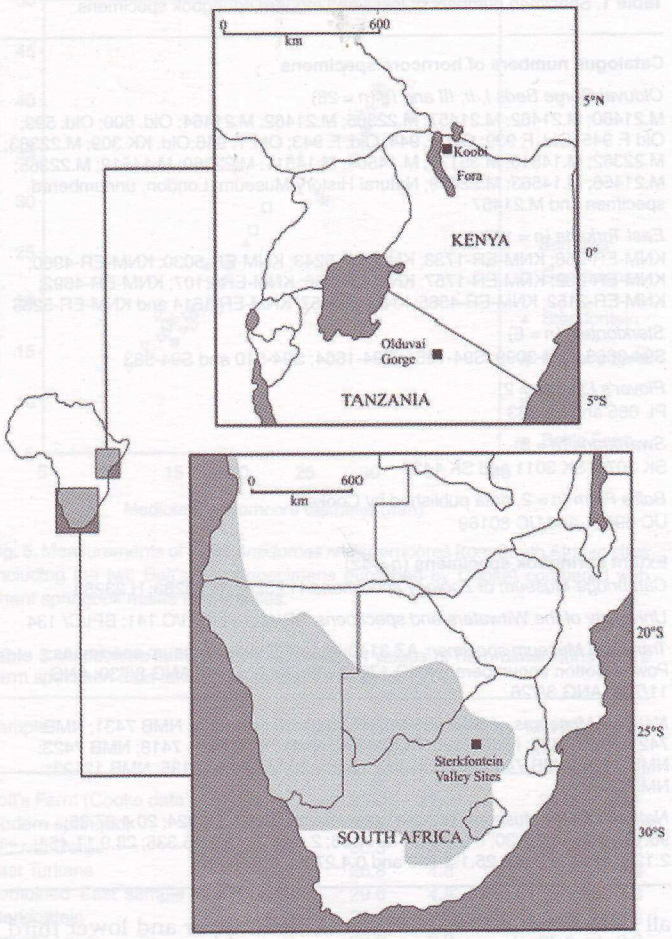

Fig. 1. Modern-day geographic range of *Antidorcas marsupialis* (shown in grey shading), with fossil sites in eastern and southern Africa, from which samples discussed in this study derive.

Modern springbok are ecologically different and are arid-adapted, showing dietary flexibility to cope with drought conditions.[11,12] Climatic shifts towards more open, savanna-dominated environments during the Pleistocene are likely to have altered ancestral springbok habitats,[13] prompting increases in body size, and concomitant changes in diet. Accompanying this suite of changes, *A. marsupialis* displays a slightly less mediolaterally compressed horncore morphology than its ancestor, with marked horncore differences between sexes. Less is known about the extent of horncore sexual dimorphism in *A. recki*. Cooke suggested that certain horncores from Pit 3, Bolt's Farm, represent dimorphic male and female *A. recki*, and imply a degree of sexual dimorphism 'very similar to that shown by the living *A. marsupialis*, or perhaps even more marked'.[1] The study reported here compares large samples of modern springbok and fossils from southern Africa and East Africa to re-evaluate Cooke's assessment of sexual dimorphism in ancestral springbok.

Materials and methods

Variation in body size has been reported in the three extant subspecies of springbok, necessitating a total of 42 crania of wild-caught specimens from across the geographic range of *A. marsupialis*, including Angola, Namibia (Kalahari) and South Africa (Table 1). The sample comprised 19 males and 23 females,

*School of Anatomical Sciences, University of the Witwatersrand Medical School, 7 York Road, Parktown 2195, South Africa, and School of Biological and Earth Sciences, Liverpool John Moores University, Byrom Street, Liverpool L3 3AF, U.K.
E-mail: sally.reynolds@wits.ac.za

Table 1. Specimen numbers of fossil and modern springbok specimens.

Catalogue numbers of horncore specimens

Olduvai Gorge Beds I, II, III and IV (*n* = 28)
M.21460; M.21462; M.21457; M.22365; M.21462; M.21464; Old. 600; Old. 599; Old F. 945; Old. F. 939; Old. F. 944; Old. F. 943; Old. F. 946;Old. KK 309; M.22363; M.22362; M.14510; M.35170; M.14509; M.14511; M.22360; M.14512; M.22365; M.21456; M.14563; M.22479; Natural History Museum, London, unnumbered specimen and M.21457

East Turkana (*n* = 15)
KNM-ER-258; KNM-ER-1738; KNM-ER-5243; KNM-ER-5030; KNM-ER-4960; KNM-ER-232; KNM-ER-1757; KNM-ER-456; KNM-ER-2107; KNM-ER-4692; KNM-ER-2152; KNM-ER-4565; KNM-ER-457; KNM-ER-1614 and KNM-ER-5265

Sterkfontein (*n* = 6)
S94-3663; S94-3099; S94-1661; S94-1664; S94-510 and S94-983

Plover's Lake (*n* = 2)
PL 665 and PL 863

Swartkrans (*n* = 3)
SK 3071; SK 3011 and SK 1428

Bolt's Farm (*n* = 2, data published by Cooke)
UC 69521 and UC 80169

Extant springbok specimens (*n* = 42)
Cambridge Museum of Zoology specimens: H.23282; H.23283; H.23288

University of the Witwatersrand specimens: BP/4/1141; BPI/C 141; BPI/C/ 134

Transvaal Museum specimen: AZ 3140; Powell-Cotton Museum specimens: Powell-Cotton unnumbered; ANG 172; ANG 178 ANG 35; ANG 8/730; ANG 11/728; ANG 3/726

National Museums of Bloemfontein (Florisbad) specimens: NMB 7431; NMB 7421; NMB 7425; NMB 7420; NMB 6096; NMB 7426; NMB 7418; NMB 7423; NMB 7434; NMB 7433; NMB 12117; NMB 12022; NMB 12135; NMB 12123; NMB 9499

Natural History Museum (London) specimens: 1926.12.7.324; 20.4.27.35; 96.11.28.8; 31.2.1.30; 64.446; 27.2.11.86; 2.4.11.1; 19.7.15.335; 28.9.11.454; 2.12.1.41; 2.12.1.42; 25.1.2.253 and 0.4.27.34

all fully adult individuals (that is, with upper and lower third molars erupted).

A sample of 54 fossil springbok horncore specimens from eastern and southern Africa was examined (Table 1). Fossil individuals associated with teeth could be aged, so that subadult and juvenile specimens could be excluded from the study. Isolated horncores were included in the fossil samples, which are likely to have included a range of ages for the fossil species. The eastern African sample comprised 28 specimens from Olduvai Gorge and 15 from the Koobi Fora Formation, East Turkana locality. The South African sample derives from three sites in the Sterkfontein Valley (Fig. 1), and consists of six horncores from Sterkfontein, two from Plover's Lake and three from Swartkrans; Cooke's measurements from the two Bolt's Farm specimens are also included.

Fossil springbok are common in the Swartkrans members, but not all specimens are included here. These fossils have been

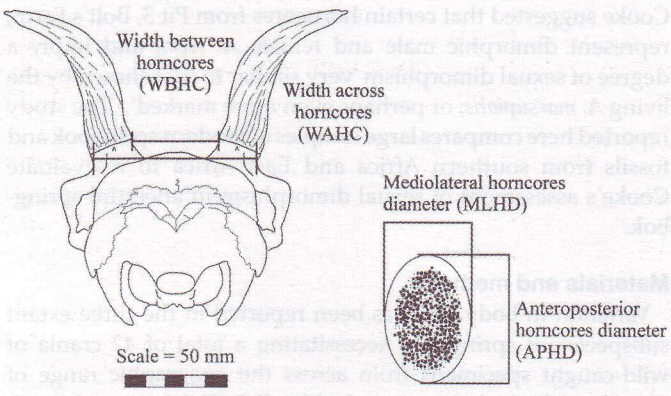

Fig. 2. Four measurements taken on springbok crania and horncore diameters.

Table 2. Extant *Antidorcas* sexual dimorphism in the four horn dimensions measured for this study. Student's *t*-tests (comparing male and female values) were calculated for each regional sample and as a combined regional sample.

Samples	*n*	WAHC (mm)	WBHC (mm)	APHD (mm)	MLHD (mm)
Angola males	5	78.3	25.4	37.3	29.8
Angola females	3	62.0	25.6	22.5	18.7
t-test *P*-value: Angola		<0.001	n.s	<0.001	<0.001
Namibia males	6	80.5	25.6	38.2	30.7
Namibia females	9	60.7	27.2	19.7	17.2
t-test *P*-value: Namibia		<0.001	n.s	<0.001	<0.001
S. Africa males	8	75.5	22.6	36.8	29.3
S. Africa females	11	58.2	28.3	17.5	15.1
t-test *P*-value: S. Africa		<0.001	<0.05	<0.001	<0.001
Combined males	19	77.8	24.3	37.4	29.9
Combined females	23	59.5	27.5	19.0	16.4
t-test *P*-value: All		<0.001	<0.05	<0.001	<0.001

assigned to *A. marsupialis/australis*, *A. bondi* and *A.recki*,[2,3] whereas Plover's Lake specimens have been assigned to the grazing springbok (*A. bondi*).[14] The purpose of using such a wide temporal, geographic and taxonomic range of animals is to define the limits of variation in modern and fossil samples to evaluate better the taxonomic assignment of the Bolt's Farm specimens.

Four measurements were recorded at the proximal border of the horncores with Mitutoyo digital callipers (Fig. 2). Width across the horncores (WAHC) and width between the horncores (WBHC) can be taken only when the frontal area of the cranium is preserved and undamaged. Anteroposterior horncore diameter (APHD) and mediolateral horncore diameter (MLHD) can be recorded on isolated horncores, provided the proximal horn base is complete (Fig. 2). The four horncore measurements were statistically compared using the parametric Student's *t*-test.

Results

Variation in modern springbok horns

In all horncore dimensions, males and females fell into two discrete clusters which did not overlap (Table 2, Fig. 3). Both the smallest female and male horn metrics derived from the smallest subspecies (*A. m. marsupialis*) from South Africa (Fig. 3). In contrast with Namibian and Angolan specimens, however, which

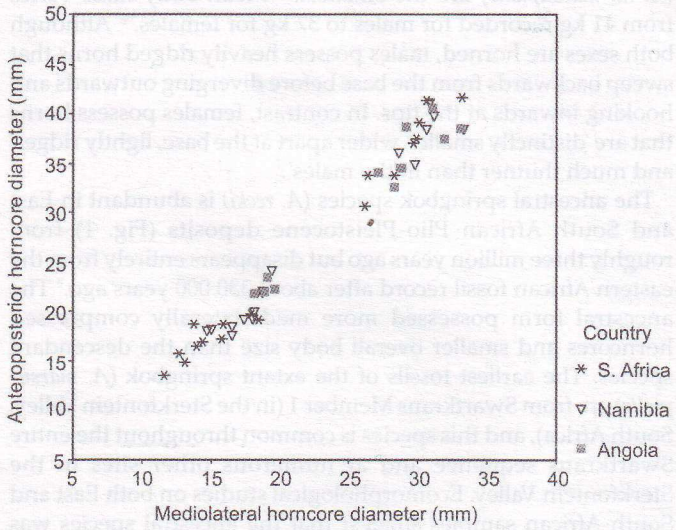

Fig. 3. Extant springbok male and female horncore dimensions according to the three separate geographic regions. Clusters of smaller females are clearly differentiated from larger males, with no overlap in anteroposterior or mediolateral horncore diameters.

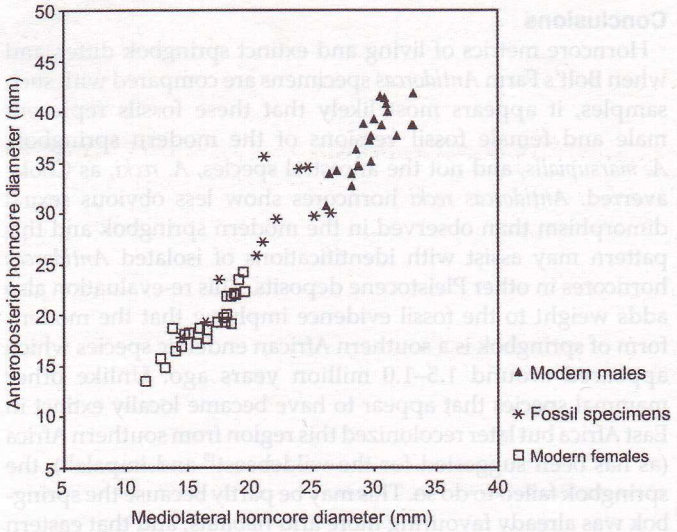

Fig. 4. Horncore dimensions of extant male and female springbok compared with a combined sample representing East African and South African *Antidorcas recki*.

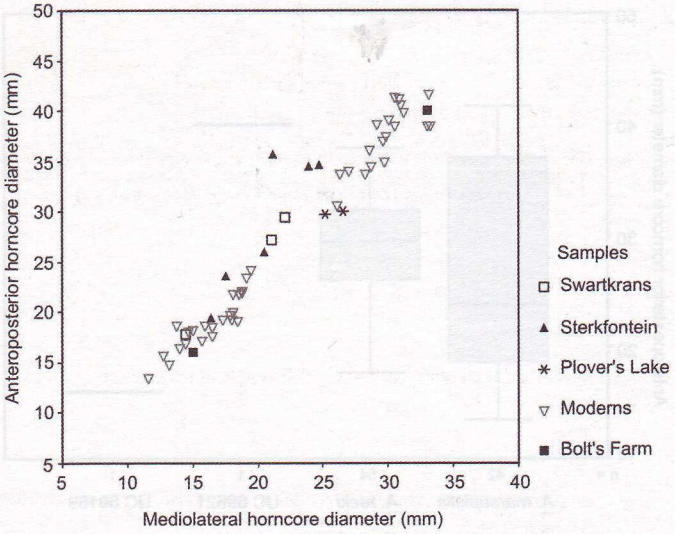

Fig. 5. Measurements of fossil *Antidorcas recki* horncores from South African sites (including the two Bolt's Farm specimens published by Cooke) compared with extant springbok males and females.

differed between males and females in only three of the four horncore measures, South African specimens showed significant differences in all four measures (Table 2).

Sexual dimorphism in fossil springbok (*A. recki*)

Extant springbok showed distinctly non-overlapping clusters of male and female measurements, whereas the combined East African and South African horncore sample of *A. recki* fell within the corresponding range of extant males and females (Fig. 4). The sample sizes of fossils from East Africa (n = 43) and South Africa (n = 11) are sufficiently large to permit comparison of the means of *A. recki* specimens between these regions (Table 3). Combined East African samples (from Olduvai Gorge and East Turkana) and South African samples (from Sterkfontein, Swartkrans and Plover's Lake) showed no significant differences in either anteroposterior or mediolateral horncore dimensions (APHD and MLHD both $P > 0.05$; Table 3). Standard deviations and means were compared between fossil and modern samples. For modern springbok, the means were less than those reported for almost all fossil samples, but the standard deviations were greater, indicating more variability (Table 3).

Small sample size undoubtedly affects such comparisons, but for one site, Olduvai, a large sample of 28 horncores revealed the same pattern of high means and low standard deviations as observed in the modern springbok specimens. In contrast, fossil *A. recki* from Sterkfontein, Olduvai and East Turkana have higher means, but also smaller standard deviations, implying less variability in these measures (Table 3). Some of the smaller individuals which clustered more closely with extant female springbok may represent juvenile male *A. recki*. The Bolt's Farm data reported by Cooke[1] fall closer to the modern springbok in terms of both means and also standard deviations (Fig. 5; Table 3).

Bolt's Farm *Antidorcas recki*: a case of mistaken identity?

The twenty-three Bolt's Farm localities have yielded a series of dates based on faunal correlations, ranging from 4.5 million years old to the Pleistocene.[1] Pit 3 yielded two crude stone tools, suggesting an early Pleistocene age for these fauna. Cooke described two Bolt's Farm fossil crania (held in the University of California collections) as a male *A. recki*, because the specimen (UC 69521) 'resembles in general the corresponding core of the living male springbok'.[1] A second cranium (UC 80169) has more gracile horns and is therefore identified as a female of the same species. Cooke suggests that the differences between the two crania represent morphological size variation in sexual dimorphism such as is seen in living springbok, suggesting that such differences were also present in *A. recki*. However, box-and-whisker plots show that the Bolt's Farm fossils both clearly fall outside the range of *A. recki* size variation. Instead, the two specimens fall within the range of extant *A. marsupialis*, with UC 80169 placed close to the cluster of adult females and the UC 69521 located close to adult males (Figs 6 and 7).

Table 3. *Antidorcas* sample sizes and median values of horn dimensions. Bolt's Farm specimen data taken from published reports.

Sample:	n	APHD (mm)	s.d.	MLHD (mm)	s.d.
Bolt's Farm (Cooke data[1])	2	28.0	17.00	24.0	12.7
Modern springbok	42	22.8	9.7	18.2	7.1
Olduvai Gorge	28	30.3	4.5	22.7	3.5
East Turkana	15	26.8	4.8	21.4	2.8
Combined 'East' sample	43	29.6	4.8	22.1	3.3
Sterkfontein	6	30.1	6.9	20.9	3.3
Plover's Lake	2	29.9	0.2	25.8	0.9
Swartkrans	3	27.1	6.1	21.1	4.1
Combined 'South' sample*	11	29.4	5.9	21.2	3.8
'East' vs 'South' combined sample Student's t-test P-value		APHD and MLHD both $P > 0.05$ Not significant			

*'South' sample excludes Bolt's Farm data.

Discussion

The sexes of extant adult springbok are significantly dimorphic in horncore dimensions, whereas extinct springbok do not form two groups which could be indicative of male and female individuals. This pattern is evident across the geographic range of the fossil species represented by 54 fossil horncores. Furthermore, for at least one site, Olduvai, sample size is sufficiently large (n = 28) to have encompassed both males and females. If sexual dimorphism was equal to, or greater than, that in the extant species, then *A. recki* would be expected to be illustrated by female specimens smaller than extant springbok females. Instead, the horncores of modern springbok females are smaller than those of even the smallest *A. recki* fossils (Fig. 5).

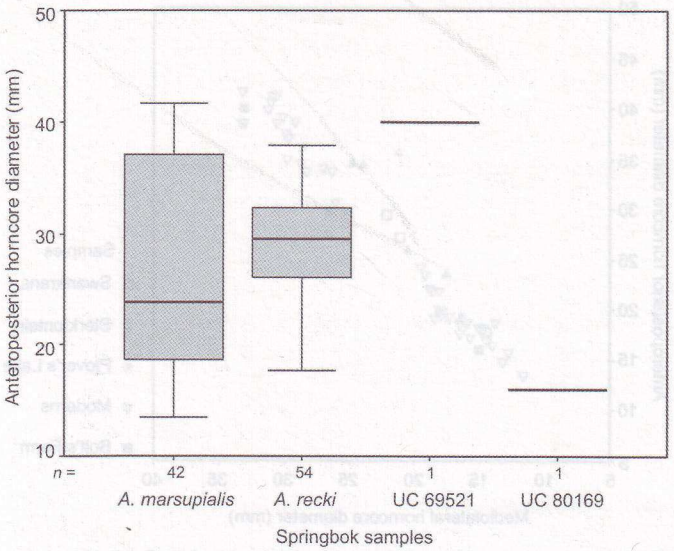

Fig. 6. Anteroposterior horncore diameter (APHD) for modern and fossil *Antidorcas*. Bold lines indicate medians, shaded areas contain 50% of dataset values, whereas whiskers indicate ranges.

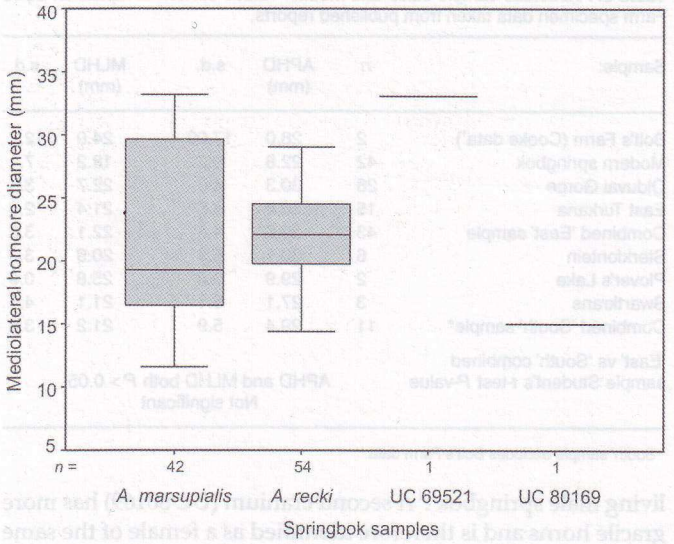

Fig. 7. Mediolateral horncore diameters (MLHD) for modern and fossil *Antidorcas*. Bold lines indicate medians, shaded areas contain 50% of dataset values, whereas whiskers indicate ranges.

This study suggests that morphological variation in fossil samples is low, possibly indicating that the East and South African fossils span similar temporal periods. It also strongly implies similarities in the degree of sexual dimorphism, and dietary and habitat preferences across the geographic range of ancestral springbok.

The two Bolt's Farm specimens do, however, exhibit large size variation, which Cooke attributes to sexual dimorphism in *A. recki*, but there are alternative explanations for this evidence. It may be that the smaller specimen represents a juvenile male *A. recki* rather than a female, or possibly that these animals do not represent *A. recki* at all. Instead, the two specimens cluster well with extant *A. marsupialis* (Figs 5–7) and so they may actually represent early fossil examples of the modern form. Although the dating for Bolt's Farm is uncertain, it may be contemporaneous with Swartkrans Member 1, a site where *Antidorcas marsupialis* is identified.[2,3]

Conclusions

Horncore metrics of living and extinct springbok differ, and when Bolt's Farm *Antidorcas* specimens are compared with such samples, it appears most likely that these fossils represent male and female fossil versions of the modern springbok, *A. marsupialis*, and not the ancestral species, *A. recki*, as Cooke averred. *Antidorcas recki* horncores show less obvious sexual dimorphism than observed in the modern springbok and this pattern may assist with identifications of isolated *Antidorcas* horncores in other Pleistocene deposits. This re-evaluation also adds weight to the fossil evidence implying that the modern form of springbok is a southern African endemic species which appeared around 1.5–1.0 million years ago. Unlike other mammal species that appear to have became locally extinct in East Africa but later recolonized this region from southern Africa (as has been suggested for the wildebeest[15] and impala[16]), the springbok failed to do so. This may be partly because the springbok was already favouring more arid habitats, and that eastern Africa offered less suitable, arid habitats over time. Alternatively, competition from highly successful sympatric gazelle species may have prevented springbok from recolonizing that region.

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