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Population genetics of the springbok *Antidorcas marsupialis* – a preliminary study

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Biochemical-genetic variation was studied in springbok *Antidorcas m. marsupialis* (Zimmermann, 1780) from a large ($N > 2000$) "wild" population ($n = 24$) and a small ($30 > N > 20$) isolated farm population ($n = 10$) using electrophoretic allozyme analysis. Springbok showed polymorphisms at eight out of 46 loci. The springbok from the large population had a higher proportion of polymorphic loci ($P = 15.6\%$) than those from the small population ($P = 8.9\%$). Average heterozygosity ($H = 5.1\%$ and $H = 4.1\%$, respectively) was similar for the two populations. This unexpected result is an artefact of the method for calculating H. $H:P$ ratios are lower for the large population than the small one. The distribution of genotypes differed significantly from Hardy-Weinberg equilibrium for two loci. These were found to have a preponderance of homozygotes. This could not be explained by population fragmentation. The levels of polymorphism and heterozygosity are high compared to results from other African bovids.

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Introduction

Little attention has been given to genetic studies of African *Bovidae*, much less, for example, than to members of the *Cervidae* (e.g. Hartl *et al.* 1990a). This paper is a contribution to knowledge of the population genetics of the springbok *Antidorcas marsupialis* (Zimmermann, 1780), a widespread south-western African gazelle. It is a variable species and recent taxonomic usage has been to recognise three subspecies: *A. m. angolensis* (Blaine, 1922) from south-western Angola and northern Namibia (or only from Angola), *A. m. hofmeyri* (Thomas, 1926) from southern Namibia, adjacent parts of the northern Cape Province of South Africa and southern and western Botswana, and *A. m. marsupialis* from the central and south-western parts of South Africa (Ansell 1972, Meester *et al.* 1986). However,

Robinson (1979) considered the continued recognition of subspecies unjustified and in this he was followed by Skinner and Smithers (1990).

Springbok are of particular interest from the point of view of population genetics. They undertook irregular, large-scale nomadic movements or "treks" until late in the 19th century (Cronwright-Schreiner 1925), which must be expected to have caused major genetic mixing from time to time. The species was exterminated in many parts of the Republic of South Africa but reintroductions of *A. m. marsupialis* in particular to fenced farms, have created many isolated sub-populations. The widespread belief that there has been a size deterioration of these farm animals as a result of inbreeding and selection of large animals by hunters, has led an unrecorded but probably quite large number of South African farmers to introduce big "Kalahari" animals from Botswana or Namibia in the belief that this will improve their own herds. No results of such introductions have been published.

Two colour variants of *A. m. marsupialis* – "black" and "white" springbok – have arisen on farms and have been preserved and reintroduced on a limited scale as novelties or for sale as unusual trophy animals. Kruger *et al.* (1979) found no consistent physical differences other than those of colour between normal *A. m. marsupialis* and the colour variants.

Robinson and Skinner (1976) reported a diploid number of 56 for the springbok and found the subspecies to be characterised by a monomorphic karyotype at the gross level. Robinson *et al.* (1978) carried out electrophoretic analysis of blood plasma and liver homogenates from 12 populations drawn from the three subspecies. Hardy-Weinberg genotype distributions computed for the species using the isozymes IDH and PGD resulted in a highly significant preponderance of homozygotes. Similar estimates computed within the putative subspecies showed significant deviations for both isozymes in farm populations of *A. m. marsupialis*, and for PGD in *A. m. hofmeyri*. These authors conclude that the isolation of populations on farms has been largely responsible for the increase in homozygosity. Gene frequency differences among subspecies are at best no greater than those between fenced isolates. They suggest that differences between subspecies may be being swamped by the formation of artificial isolates.

Study area

The present study is based on material from 24 springbok, 12 of each sex, collected on the farm Susanna near Kimberley, Cape Province (24°45'E, 28°40'S). The farm is 4046 ha in extent and carries 1000 – 1500 springbok. Some interchange is believed to take place between this population and the 800 – 1000 animals on two neighbouring properties (Olifantskop and Olifantsdam, area 5174 ha). The springbok represent *A. m. marsupialis* and are descendents of the original wild stock which was preserved when the farms were established in the second half of the nineteenth century. No introductions are known to have taken place. Populations are managed by hunting and cropping by helicopter. Although isolated, these springbok are probably as close to representing a large "wild" *A. m. marsupialis* population as can be found at the present day.

Additional material (n = 10) comes from a small, isolated population of *A. m. marsupialis* introduced to a 156 ha paddock on the farm Brakkekuil in the southern Cape Province (34°18'S, 20°51'E) from an unknown source sometime between 1930 and 1956 (Mrs G. Uys, pers. comm.). In the past five years numbers have been limited by shooting to 20 – 30, and this probably reflects the pattern of management practised since the animals were introduced.

The paddock is also occupied by 50 – 80 introduced blesbok *Damaliscus dorcas phillipsi*. This population has already been examined for genetic variation by R. C. Bigalke *et al.* (in prep.), who screened almost the same set of isozymes. In order to assess genetic divergence between the springbok and the blesbok, marker samples of the latter were included in the present study.

Material and methods

Liver, kidney and heart samples were frozen immediately after death of the specimens and stored frozen at –20°C until electrophoresis. Preparation of tissue extracts, horizontal starch gel electrophoresis and enzyme specific staining procedures were performed according to routine methods (Hartl and Höger 1986, Grillitsch *et al.* 1992). The following 30 isozymes representing a total of 46 presumptive structural loci were screened (abbreviation, E.C. number and loci detected are given in parentheses): α-glycerophosphate dehydrogenase (GDC, E.C. 1.1.1.8, *Gdc*), sorbitol dehydrogenase (SDH, E.C. 1.1.1.14, *Sdh*), lactate dehydrogenase (LDH, E.C. 1.1.1.27, *Ldh-1*, *Ldh-2*), malate dehydrogenase (MDH, E.C. 1.1.1.37, *Mdh-1*, *Mdh-2*), malic enzyme (ME, E.C. 1.1.1.40, *Me-1*, *Me-2*), isocitrate dehydrogenase (IDH, E.C. 1.1.1.42, *Idh-1*, *Idh-2*), 6-phosphogluconate dehydrogenase (PGD, E.C. 1.1.1.44, *Pgd*), glucose dehydrogenase (GDH, E.C. 1.1.1.47, *Gdh*), glucose-6-phosphate dehydrogenase (GPD, E.C. 1.1.1.49, *Gpd*), xanthine dehydrogenase (XDH, E.C. 1.2.3.2, *Xdh*), glutamate dehydrogenase (GLUD, E.C. 1.4.1.3, *Glud*), catalase (CAT, E.C. 1.11.1.6, *Cat*), superoxide dismutase (SOD, E.C. 1.15.1.1, *Sod-1*, *Sod-2*), aspartate aminotransferase (AAT, E.C. 2.6.1.1, *Aat-1*, *Aat-2*), hexokinase (HK, E.C. 2.7.1.1, *Hk-1*, *Hk-2*, *Hk-3*), pyruvate kinase (PK, E.C. 2.7.1.40, *Pk*), creatine kinase (CK, E.C. 2.7.3.2, *Ck-1*, *Ck-2*), adenylate kinase (AK, E.C. 2.7.4.3, *Ak-1*, *Ak-2*), phosphoglucomutase (PGM, E.C. 2.7.5.1, *Pgm-1*, *Pgm-2*, *Pgm-3*), esterases (ES, E.C. 3.1.1.1, *Es-d*), acid phosphatase (ACP, E.C. 3.1.3.2, *Acp-1*, *Acp-2*), fructose-1,6-diphosphatase (FDP, E.C. 3.1.3.11, *Fdp*), peptidases (PEP, E.C. 3.4.11, *Pep-1*, *Pep-2*), aminoacylase-1 (ACY-1, E.C. 3.5.1.14, *Acy-1*), adenosine deaminase (ADA, E.C. 3.5.4.4, *Ada* – kidney), aldolase (ALDO, E.C. 4.1.2.13, *Aldo*), fumarate hydratase (FH, E.C. 4.2.1.2, *Fh*), aconitase (ACO, E.C. 4.2.1.3, *Aco-1*, *Aco-2*), mannose phosphate isomerase (MPI, E.C. 5.3.1.8, *Mpi*), and glucose phosphate isomerase (GPI, E.C. 5.3.1.9, *Gpi-1*, *Gpi-2*).

At the polymorphic or differential diagnostic loci, the most common allele in the springbok population at Susanna was designated arbitrarily "*100*". Variant alleles were designated according to the relative electrophoretic mobility of the corresponding allozymes. The proportion of polymorphic loci (P), expected (H_e) and observed (H_o) average heterozygosity were calculated according to Ayala (1982). Genetic distances between populations or species were calculated according to Nei (1972). Relative genetic differentiation among populations was estimated using Nei's (1975) G-statistic.

Results

The following 8 loci were polymorphic in the springbok populations: *Gdc*, *Me-1*, *Idh-2*, *Pgm-2*, *Pgm-3*, *Acp-2*, *Es-d*, and *Mpi*. Allele frequencies, single locus heterozygosities, and indices of genetic variation are given in Table 1 together with the corresponding data of the blesbok (taken from R. C. Bigalke *et al.*, in prep.). In springbok from Susanna, observed genotypes at *Idh-2* and *Me-1* deviated significantly from Hardy-Weinberg expectations (Table 2); in Brakkekuil n is too small

Table 1. Genetic variation in the springbok from two populations (this study) and in blesbok (data from R. C. Bigalke *et al.*, in prep.). P – proportion of polymorphic loci, h_e (h_o) – expected (observed) heterozygosity, H_e (H_o) – expected (observed) average heterozygosity.

Locus	Allele	Springbok		Blesbok
		Susanna (n = 24)	Brakkekuil (n = 10)	Brakkekuil (n = 27)
Gdc	*100*	0.762 h_o 0.476	0.250 h_o 0.500	0.0
	67	0.238 h_e 0.363	0.750 h_e 0.375	1.0
Me-1	*100*	0.438 h_o 0.333	0.350 h_o 0.600	0.0
	109	0.292 h_e 0.650	0.050 h_e 0.515	0.0
	94	0.0	0.0	1.0
	78	0.270	0.600	0.0
Idh-2	*100*	0.708 h_o 0.250	0.500 h_o 0.400	0.0
	123	0.292 h_e 0.414	0.500 h_e 0.500	0.0
	77	0.0	0.0	1.0
Pgm-2	*100*	0.896 h_o 0.208	1.0	1.0
	85	0.104 h_e 0.186	0.0	0.0
Pgm-3	*100*	0.875 h_o 0.167	0.650 h_o 0.500	0.0
	95	0.0 h_e 0.219	0.0 h_e 0.455	1.0
	90	0.125	0.350	0.0
Acp-2	*100*	0.562 h_o 0.542	unscorable	
	87	0.438 h_e 0.492		
Es-d	*100*	0.958 h_o 0.082	1.0	0.0
	150	0.0 h_e 0.042	0.0	1.0
	50	0.042	0.0	0.0
Acy-1	*100*	1.0	1.0	0.0
	91	0.0	0.0	0.426 h_o 0.556
	80	0.0	0.0	0.574 h_e 0.489
Mpi	*100*	0.750 h_o 0.292	1.0	0.0
	113	0.146 h_e 0.405	0.0	0.0
	83	0.104	0.0	0.0
	62	0.0	0.0	1.0
45 Loci (*Acp-2* excluded)	P	0.156	0.089	0.022
	H_o	0.040	0.044	0.012
	H_e	0.051	0.041	0.011
46 Loci (*Acp-2* included)	P	0.174	×	×
	H_o	0.051	×	×
	H_e	0.060	×	×

Table 2. Test for Hardy-Weinberg equilibrium within the Susanna population for *Me-1* and *Idh-2*. O – observed, E – expected, * – $p < 0.05$, ** – $p < 0.01$.

Me-1	Genotype						χ^2
	100/100	*109/109*	*78/78*	*100/109*	*100/78*	*109/78*	12.14**
O	7	5	4	3	4	1	
E	4.6	2.0	1.8	6.1	5.7	3.8	

Idh-2	Genotype			χ^2
	100/100	*100/123*	*123/123*	3.86*
O	14	6	4	
E	12.0	9.9	2.0	

for a meaningful test. In both species P, H_e, and H_o are calculated over 45 loci, but their composition is slightly different. Since the respective isozymes were not consistently scorable, three esterase loci and *Np* evaluated only in the blesbok are replaced by *Xdh*, *Hk-3*, *Pgm-3*, and *Pep-2* evaluated only in the springbok. *Acp-2* was scorable only in springbok from Susanna and is therefore excluded from calculations for all comparisons within the present study. In contrast to population genetic data, genetic distance between springbok and blesbok ($D = 0.475$) is based on 45 homologous loci. The following 11 loci were monomorphic in both species, but fixed for different alleles: *Gpd*, *Gdh*, *Glud*, *Aat-2*, *Acp-1*, *Ck-2*, *Hk-1*, *Ada*, *Sod-1*, *Sod-2*, and *Fh*. D between springbok from Susanna and Brakkekuil is 0.012, and 11.5 per cent of the total gene diversity is due to diversity among populations ($G_{ST} = 0.115$, $D_{ST} = 0.006$, $H_T = 0.052$, $H_S = 0.046$).

Discussion

Most of the isozymes polymorphic in the springbok are variable also in several other species of the *Artiodactyla*. Various possible explanations for the non-random distribution of genetic polymorphism among protein coding loci, such as different mutation rates and different kinds of selection are under discussion (c.f. O'Brien *et al.* 1980). Regarding the latter, genotypes at some isozyme loci (*Me-1*, *Idh-2*, *Acp-2*, and *Mpi*) are associated, for example, with fitness and morphological traits in the red deer (Pemberton *et al.* 1988, 1991, Hartl *et al.* 1991a, b, in press), with body condition in wild boars (*Pgm-2*, Hartl 1990), and with the "Porcine Stress Syndrome" (*Pgd*, *Gpi*) in pigs (Gahne and Juneja 1985). Thus, because of functional or chromosomal linkage, especially at polymorphic loci with a low number of ubiquitously occurring alleles (c.f. Hartl *et al.* 1990a, b), the distribution of genotypes and allele frequencies is likely to be influenced by selection also in other species.

In our springbok material, we observed a significant preponderance of homozygotes at two loci (*Me-1*, *Idh-2*), which is in agreement with previous results of Robinson *et al.* (1978) for the loci *Pgd* and *Idh-2*. Since in our case the deviations from Hardy-Weinberg equilibrium were detected within one population and not in a pooled sample of animals from various provenances, they are apparently not only due to the formation of geographical isolates, but may as well be brought about by the mating system of the species (c.f. Leuthold 1977, Apollonio and Hartl 1993). Also some disruptive selection could be involved, but the collection of appropriate data is necessary for testing this hypothesis.

In contrast to Robinson *et al.* (1978) there was no variation at the *Pgd* locus in our samples consisting of pure *A. m. marsupialis*. Due to the high incidence of this polymorphism in both the other subspecies, the presence of a second *Pgd* allele may be indicative of the introgression of *A. m. hofmeyri* genes into *A. m. marsupialis* populations (see Introduction). This would explain the occurrence of the variant *Pgd* allele in only two out of five *A. m. marsupialis* stocks in the study of Robinson *et al.* (1978), where, in one case, the genotypes deviated considerably from Hardy-Weinberg expectations.

If the Susanna population is considered representative of the gene pool of *Antidorcas marsupialis*, the P and H values obtained in this species are amongst the highest ones observed in antelope so far (Table 3), but in the present state of knowledge this result is not very meaningful. The collection of data on biochemical-genetic variation in antelope by electrophoretic multilocus investigations has only recently been started and a reference system of genetic diversity within and among populations, subspecies, and species, comparable to that already available in the *Cervidae* (see Hartl *et al.* 1990a, Dratch and Pemberton 1992, for reviews), is completely lacking. The Brakkekuil population appears to have lost a great deal of biochemical-genetic variation due to its population size and history, which is, however, much more evident in terms of P than in terms of H. This result can readily be explained as follows: As can be seen in Table 1, the calculation over all loci examined yields almost the same H-value when there are several moderately or only a few highly polymorphic loci. Since variant alleles occurring at high

Table 3. Genetic variation in various antelopes [only studies based on a reasonable number of loci (> 35) were considered]. P – proportion of polymorphic loci, H_e – expected average heterozygosity, nL – number of loci, nI – number of individuals examined. 1 – present study, 2 – Georgiadis *et al.* (1990), 3 – R. C. Bigalke *et al.* (in prep. – note that this is a small, inbred population).

Species	nI	nL	P (%)	H_e (%)	Source
Antidorcas marsupialis	24	46	17.4	6.0	1
Alcelaphus bucelaphus	17	40	8.7	1.9	2
Connochaetes taurinus	61	40	4.3	1.2	2
Damaliscus dorcas phillipsi	27	45	2.2	1.1	3
Damaliscus lunatus	19	40	10.9	1.0	2
Gazella thomsoni	33	40	19.6	5.5	2

frequencies are likely to be preserved even when a population bottleneck is rather severe (c.f. Nei *et al.* 1975) the consideration of H alone has led several authors to the conlusion, that the effects of genetic bottlenecking are less severe than commonly thought (e.g. Gyllensten *et al.* 1983, Gębczyński and Tomaszewska-Guszkiewicz 1987). However, in spite of the same or a similar magnitude of average heterozygosity, the biological meaning of H can be very different. If this index as calculated from electrophoretic data is considered representative for genetic variation in a certain part of the genome (c.f. Mitton and Pierce 1980, Mitton and Grant 1984), the contribution of many polymorphic loci indicates the presence of a rich gene pool, enabling a population to produce many different phenotypes through recombination. When the contribution of polymorphic loci is small, individuals are heterozygous at more or less the same loci, which dramatically reduces the possibilities for recombination and, thus, the adaptability of a population. According to these considerations, a comparison of genetic variation among populations or species is therefore not very informative when based only on H (as usually given without its variance among loci). The proportion of polymorphic loci (P) or the ratio $H : P$ (which is significantly larger in genetically depleted populations – Hartl and Pucek, in press) are important additional parameters. In our case P is reduced to one half in the Brakkekuil population and, in addition, the $H : P$ ratio (0.461 vs 0.327) is considerably larger than in Susanna animals. According to Hartl and Pucek (in press) sample size is not responsible for this result. Also in the blesbok data (Table 1), which are based on a sample size comparable to that in Susanna, the $H : P$ ratio of 0.500 is almost equal to that in Brakkekuil springbok and can be explained by similar population history and size (R. C. Bigalke *et al.*, in prep.).

Genetic distance and G_{ST} between the Susanna and the Brakkekuil springbok population reflect considerable allele frequency differences, which are probably due to the isolation of demes and/or a derivation from different source gene pools. However, in accordance with morphological observations, the D-value is not of a magnitude which would indicate the presence of different subspecies (c.f. Gyllensten *et al.* 1983, Dratch and Gyllensten 1985, for typical D-values among subspecies of artiodactyls).

The genetic distance observed between *Antidorcas marsupialis* and *Damaliscus dorcas phillipsi* reflects the taxonomic status of both species as members of separate tribes within the *Bovidae* (c.f. Georgiadis *et al.* 1990).

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References

Ansell W. F. H. 1972. Part 2.15 Family *Artiodactyla*. [In: The mammals of Africa: an identification manual. J. Meester and H. W. Setzer, eds]. Smithsonian Institution Press, Washington D. C.: 1 – 84.

Apollonio M. and Hartl G. B. 1993. Are biochemical-genetic variation and mating systens related in large mammals? [In: Ecological genetics in mammals. G. B. Hartl and J. Markowski, eds]. Acta theriol. 38, Suppl. 2: 175 – 185.

Ayala F. J. 1982. Population and evolutionary genetics: A primer. Benjamin Cummings, Menlo Park, CA: 1 – 268.

Cronwright-Schreiner S. C. 1925. The migratory springbucks of South Africa. Fisher Unvin, London.

Dratch P. and Gyllensten U. 1985. Genetic differentiation of red deer and North American elk (Wapiti). Biology of deer production, R. Soc. NZ. Bull. 22: 37 – 40.

Dratch P. and Pemberton J. M. 1992. Application of biochemical genetics to deer management: What the gels tell? [In: The biology of deer. R. D. Brown, ed]. Springer, New York: 367 – 383.

Gahne B. and Juneja R. K. 1985. Prediction of the Hal-genotypes of pig by deducing Hal, Phi, PO-2, Pgd haplotypes of parents and offspring: results from a large-scale practice in Swedish breeds. Anim. Blood Grps. Biochem. Genet. 16: 265 – 283.

Gębczyński M. and Tomaszewska-Guszkiewicz K. 1987. Genetic variability in the European bison. Biochem. Syst. Ecol. 15: 285 – 288.

Georgiadis N. J., Kat P. W., Oketch H. and Patton J. 1990. Allozyme divergence within the *Bovidae*. Evolution 44: 2135 – 2149.

Grillitsch M., Hartl G. B., Suchentrunk F. and Willing R. 1992. Allozyme evolution and the molecular clock in the *Lagomorpha*. Acta theriol. 37: 1 – 13.

Gyllensten U., Ryman N., Reuterwall C. and Dratch P. 1983. Genetic differentiation in four European subspecies of red deer (*Cervus elaphus* L.). Heredity 51: 561 – 580.

Hartl G. B. 1990. The influence of game management on allelic variation in large mammals of Central Europe. [In: Genetics and wildlife conservation. E. Randi and M. Spagnesi, eds]. Suppl. Ric. Biol. Selvaggina 18: 95 – 108.

Hartl G. B. and Höger H. 1986. Biochemical variation in purebred and crossbred strains of domestic rabbits (*Oryctolagus cuniculus* L.). Genetical Research, Camb. 48: 27 – 34.

Hartl G. B., Köller J., Klein F. and Lang G. 1991a. Allozymes as genetic markers for the development of morphological characters in red deer (*Cervus elaphus*): further evidence. Transactions XXth Congr. IUGB, Gödöllö: 810 – 815.

Hartl G. B., Lang G., Klein F. and Willing R. 1991b. Relationships between allozymes, heterozygosity and morphological characters in red deer (*Cervus elaphus*), and the influence of selective hunting on allele frequency distributions. Heredity 66: 343 – 350.

Hartl G. B., Lang G., Klein F., Willing R and Apollonio M. (in press). Allozymes and the genetics of antler development in red deer (*Cervus elaphus*): Can. J. Zool.

Hartl G. B. and Pucek Z. (in press). Genetic depletion in the European bison (*Bison bonasus*) and the significance of electrophoretic heterozygosity for conservation. Conservation Biology.

Hartl G. B., Willing R., Lang G., Klein F. and Köller J. 1990a. Genetic variability and differentiation in red deer (*Cervus elaphus* L.) of Central Europe. Genetics, Selection, Evolution 22: 289 – 306.

Hartl G. B., Willing R. and Suchentrunk F. 1990b. On the biochemical systematics of selected mammalian taxa: empirical comparison of qualitative and quantitative approaches in the evaluation of protein electrophoretic data. Z. zool. Syst. Evolut.-forsch. 28: 191 – 216.

Kruger J. C., Skinner J. D. and Robinson T. J. 1979. On the taxonomic status of the black and white springbok, *Antidorcas marsupialis*. S. Afr. J. Sci. 75: 411 – 412.

Leuthold W. 1977. African ungulates. Springer Verlag, Berlin and New York: 1 – 307.

Meester J. A. J., Rautenbach I. L., Dippenaar N. J. and Baker C. M. 1986. Classification of Southern African mammals. Transvaal Mus. Monogr. 5: 1 – 359.

Mitton J. B. and Pierce B. A. 1980. The distribution of individual heterozygosity in natural populations. Genetics 95: 1043 – 1054.

Mitton J. B. and Grant M. C. 1984. Associations among protein heterozygosity, growth rate, and developmental homeostasis. Ann. Rev. Ecol. Syst. 15: 479 – 499.

Nei M. 1972. Genetic distance between populations. Am. Nat. 106: 283 – 292.

Nei M. 1975. Molecular population genetics and evolution. North Holland, Amsterdam: 1 – 288.
Nei M., Maruyama T. and Chakraborty R. 1975. The bottleneck effect and genetic variability in populations. Evolution 29: 1 – 10.
O'Brien S. J., Gail M. H. and Levin D. L. 1980. Correlative genetic variation in natural populations of cats, mice and men. Nature 288: 580 – 583.
Pemberton J. M., Albon S. D., Guinness F. E., Clutton-Brock T. H. and Berry R. J. 1988. Genetic variation and juvenile survival in red deer. Evolution 42: 921 – 934.
Pemberton J. M., Albon S. D., Guinness F. E. and Clutton-Brock T. H. 1991. Countervailing selection in different fitness components in female red deer. Evolution 45: 93 – 103.
Robinson T. J. 1979. Influences of nutritional parameters on the size differences of the three springbok subspecies. S. Afr. J. Zool. 14: 13 – 15.
Robinson T. J., Op't Hof J. and Geerthsen J. M. P. 1978. Polymorphic genetic markers in the springbok *Antidorcas marsupialis*. S. Afr. J. Sci. 74: 184 – 186.
Robinson T. J. and Skinner J. D. 1976. A karyological survey of springbok subspecies. S. Afr. J. Sci. 72: 147 – 148.
Skinner J. D. and Smithers R. H. N. 1990. The mammals of the southern African subregion. University of Pretoria, Pretoria: 1 – 177.

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