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Mixed herds of Common and Defassa waterbuck, *Kobus ellipsiprymnus* (Artiodactyla: Bovidae), in northern Kenya

by

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With few exceptions like Walther (1984) there is general agreement today that Common and Defassa waterbuck are conspecific (Haltenorth 1963, Heyden 1969, Ansell 1972, Grubb 1978, Corbet & Hill 1980, Tomlinson 1980, Honacki et al. 1982, Kingdon 1982). Most authors follow Ansell (1972) in distinguishing an *ellipsiprymnus* and a *defassa* group of subspecies within the species *Kobus ellipsiprymnus* (Ogilby 1833) (e. g. Spinage 1982, Smithers 1983, Yalden et al. 1984).

The first to point out that contrary to long-held taxonomic views Common and Defassa waterbuck may be conspecific, were Ellerman et al. (1953). Indeed, they listed *Kobus ellipsiprymnus* and *Kobus defassa* (Rüppell 1835) as separate species, but in a footnote (l. c.: 194) commented "G.H.E. Hopkins (in litt.) tells us that according to V. G. L. van Someren *ellipsiprymnus* and *defassa* interbreed in Kenya, and form intermediate herds. If this is so then the latter should be regarded as a race of the former?" Obviously unaware of this annotation Backhaus (1958) dealt with the problem of the taxonomic status of the two waterbuck forms. Because of hybrids with intermediate rump patterns observed by C.A.W. Guggisberg (reported to Backhaus in litt.) in Nairobi National Park, Kenya, and Ngorongoro Crater, Tanzania, he concluded that Common and Defassa waterbuck had not yet attained full species status. Finally, in his monograph on the taxonomy of the Artiodactyla Haltenorth (1963) cited Ellerman et al. (1953) and Backhaus (1958) as references in listing both Common and Defassa waterbuck as conspecific under *Kobus ellipsiprymnus*. Haltenorth's statement, however, that there is a broad belt with intermediate waterbuck populations in central East Africa between about 1° and 3°S and 35° and 38°E is not borne out to that extent by the data presented in the publications cited.

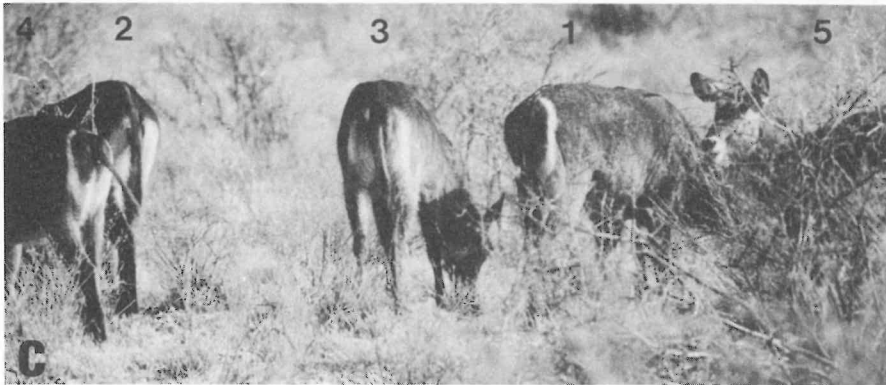
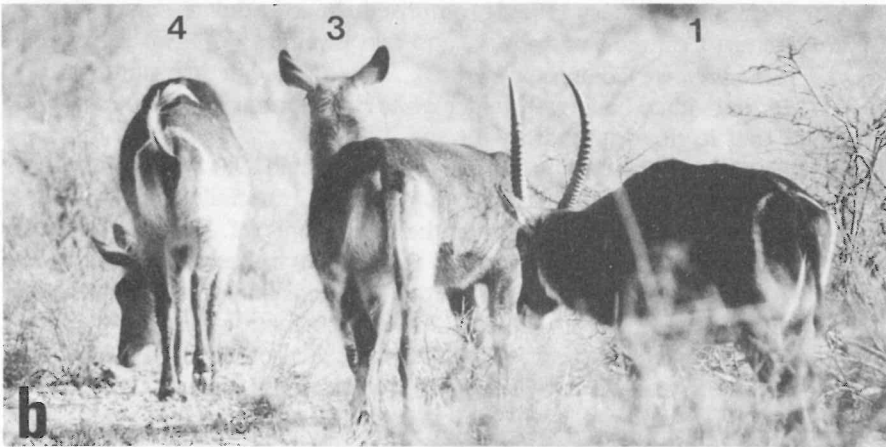
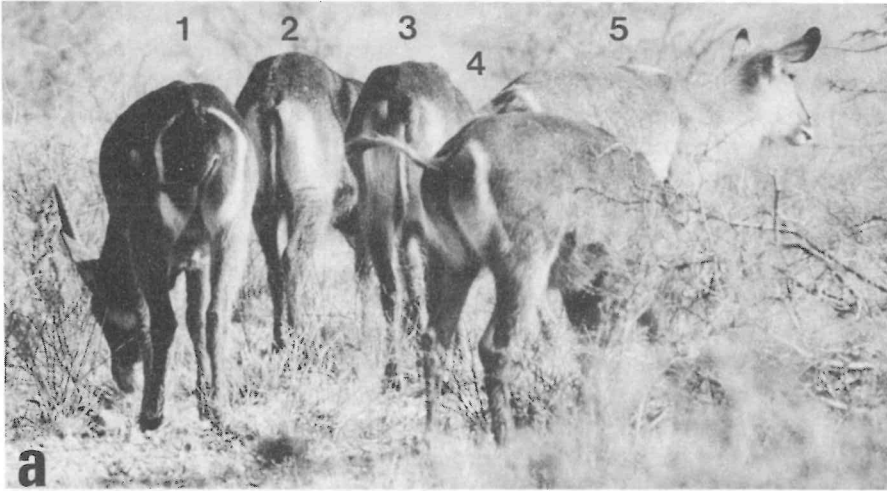
Kingdon (1982: 385) in a general remark on both forms of waterbuck notes that "In the areas of overlap in Kenya and Tanzania a variety of intermediate rump patterns can be seen which are presumably the result of hybridization." No definite localities or exact descriptions of intermediate rump patterns are given, though. The distribution map presented shows a broad belt of overlap between Common and Defassa waterbuck from south of Lake Turkana, Kenya,

southward through Kenya, passing through central and sw Tanzania and from there extending in southwestern direction through Zambia to about the Kafue River.

Detailed distributional records document several regions in East Africa where populations of Common and Defassa waterbuck may be in contact or may come into, or where both forms actually are sympatric and interbreeding may occur (Stewart & Stewart 1963, Anon. 1977). Nevertheless, full sympatry with mixed herds and hybrids have only been reported from three places in East Africa: Ngorongoro Crater, Tanzania; Nairobi National Park, Kenya; Ewaso Ngiro River, northern Kenya (Backhaus 1958, Kiley-Worthington 1965, Spinage 1982).

Hybrid waterbucks in Nairobi National Park are documented in a photograph and with several sketches of animals with different intermediate rump patches (Kiley-Worthington 1965, Pl. XII). Individuals of the population Kiley-Worthington observed in 1963 were again photographed by Spinage in 1966 (one photo published in Spinage 1982). The 6 hybrid individuals altogether whose rump pattern is visible in the photos in the two publications (1 ♂, 3 ♀ in Kiley-Worthington 1965, 2 ♂ in Spinage 1982) with some variation basically show the same type of intermediate rump patches: an incomplete '*ellipsiprymnus*' ring, lacking a portion of the upper arch above the tail head. The lower part of the ellipse varies in its relative upward extension and the thickness of the white ring. The sketches in Kiley-Worthington (1965) show 3 intermediate rump patterns: one classified as $\frac{3}{4}$ '*ellipsiprymnus*' by the author represents the type also depicted in the photos, another also classified as $\frac{3}{4}$ '*ellipsiprymnus*' with a nearly complete ellipse, thick white ring and a diffuse area of brown hair around the tail head, and a third classified as $\frac{1}{4}$ '*ellipsiprymnus*' with only the bottom portion of the ellipse on the lower thighs, with thick white lines and an indefinite junction of the white and brown hair. There is no information as to the heredity of the rump pattern. No documentation exists on mixed waterbuck herds and/or hybrid waterbucks and their rump pattern from Ngorongoro Crater, Tanzania, and Ewaso Ngiro River, northern Kenya, the other two places in East Africa from where they have been reported. The only other region in Africa where occasionally both forms of waterbuck come into contact and from where hybrids are recorded in the literature are in Zambia (Ansell 1969, 1978). No details, though, on the rump pattern of these hybrids are given. A photo of a Common waterbuck female together with two Defassa females is published in Ansell (1969).

Fig. 1 a—c. Small mixed herd of Common and Defassa waterbuck observed in 1984. In all photos identical individuals whose rump pattern is visible are labeled with the same number. (1 — ♂ Common, 2 — ♀ Defassa, 3 — ♀ Defassa (?) (potential hybrid), 4 — ♀ Common, 5 — ♀ Common).



New observations

The photographs (Figs. 1, 2) presented here were taken during short occasional observations and show two mixed herds of Common and Defassa waterbuck seen near Ewaso Ngiro River, northern Kenya, the second region in Kenya from where their sympatric occurrence is known.

The small herd shown in Fig. 1 a-c was seen in the western part of Buffalo Springs Game Reserve in August 1984 and consisted of 5 adult individuals: 1 ♂ Common, 2 ♀ Common and 2 ♀ Defassa (?) waterbuck. The 2 ♀ Common (Fig. 1 a-c) differed as clearly in their rump patterns as those from Tsavo West National Park, Kenya, figured by Spinage (1982: 11, Plate 3). One of the ♀ Defassa (?) (Fig. 1 a-c) had a roughly elliptic area of light-brown hair extending from the tail head down on the thighs with an indefinite junction with the surrounding white hair, like a faded '*ellipsiprymnus*' pattern and thus may have been a hybrid. This characteristic is much more obvious in the original colour slide than in its black-and-white reproduction figured here.

The other mixed herd (Fig. 2 a-c) was seen in the same game reserve near Buffalo Springs in February 1986. It comprised about 8 adult ♀, one a Defassa (?) and the rest Common waterbuck, and two juveniles. The two calves (Fig. 2 c) very probably were Common waterbuck. They differed in their rump patches, the younger individual having the wider white ring, contrary to Herbert's (1972) statement that it grows in width with age. There was no buck with this herd during the period of observation. Like in the herd seen in 1984 the rump patterns of the Common waterbuck differed to some extent, especially in the thickness of the white ring in its lower portion on the inner thighs (cf. Fig. 2 a). Likewise, the rump patch of the one Defassa (?) ♀ (Fig. 2 a, b) had an inner faint ellipse of light-brown hair, especially around the tail base, indicating that this individual may have been a hybrid. From these two casual observations it cannot be ruled out that one or several of these individuals were seen on both occasions. The linear distance between the two places of observation in 1984 and 1986 is about 8 km. Home range sizes published for waterbuck are smaller (Hanks et al. 1969, Spinage 1969, 1982, Herbert 1972) but movements of females over longer distances have been recorded (Herbert l.c.).

Discussion

There is no detailed study of the range of variability of the rump pattern in Common and Defassa waterbuck, only Herbert (1972: 23, 24) makes a general remark for the former: "It grows in width and brightness with age, reaching its maximum width and distinctiveness in territorial males." So, at least some of the variability in the rump pattern of adult Common waterbuck documented here (Figs. 1, 2) and by Spinage (1982: 11, Plate 3) may be due to age differences. A reliable classification of waterbuck individuals with various 'intermediate' rump patterns as hybrids between Common and Defassa waterbuck requires

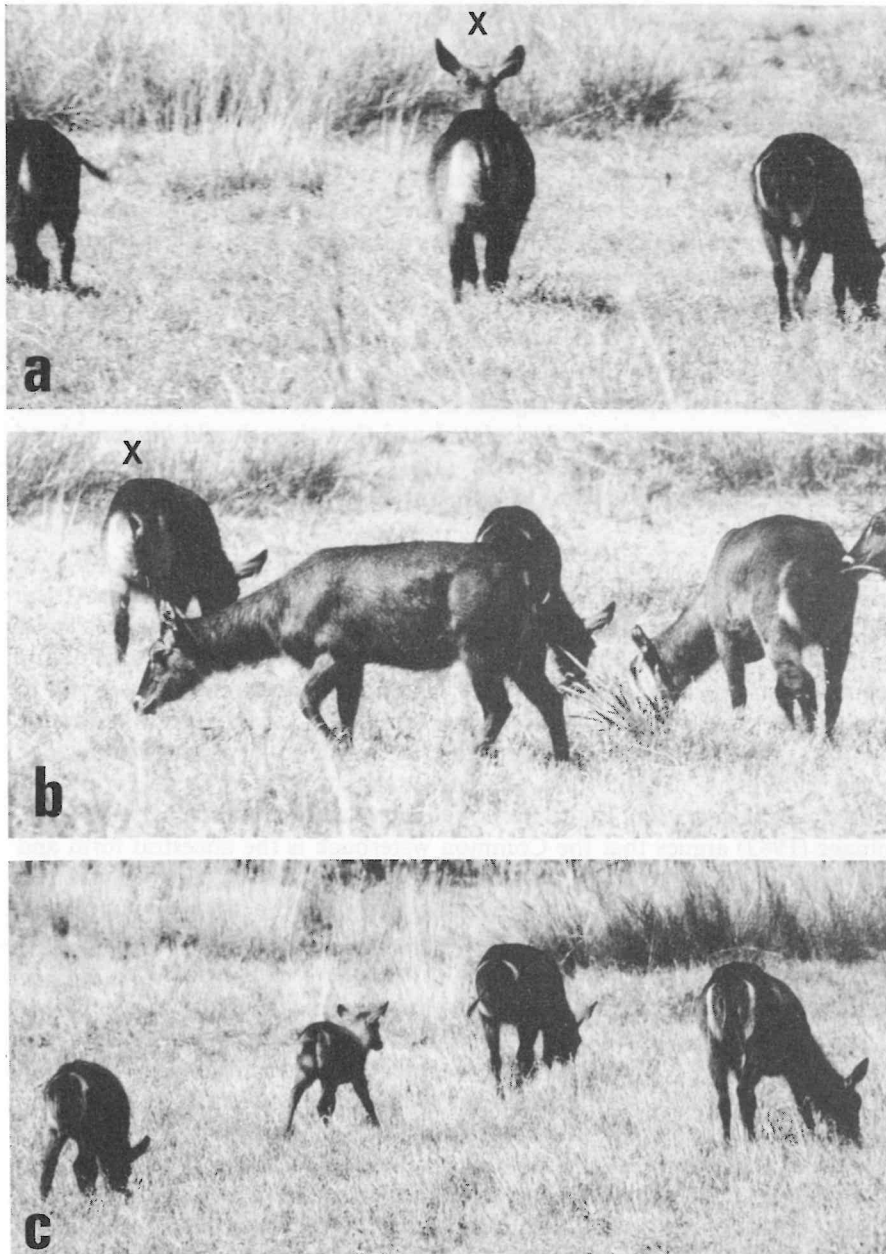


Fig. 2 a—c. Some individuals of the mixed waterbuck herd seen in 1986. The Defassa (?), potential hybrid waterbuck is marked with an 'X'. All other adult animals in the herd were ♀ Common, the sex of the two calves in c could not be ascertained.

that the range of variability in this characteristic is well documented at all ages in both forms — unless an individual is positively known as the offspring of a mating between the two.

The potential hybrid waterbucks reported here are very similar in their rump pattern to the sketch of a hybrid depicted in Kiley-Worthington (1965, Pl. XII, Sketch I A, mid right), classified by her as $\frac{3}{4}$ '*ellipsiprymnus*'. Of course, this statement can only be a phenotypic classification according to the individual's rump patch and is no specification of its genotype.

The distributional pattern of the two waterbuck forms (Fig. 3) and the existence of a narrow hybrid zone constitutes a case of "allopatric hybridization" (Mayr 1942, 1963), better termed "secondary intergradation" (Bigelow 1965, Mayr 1969), defined as "If two taxa that were previously recognized as two allopatric species completely intergrade in a zone of secondary contact, it proves that they are not reproductively isolated and that they should be considered subspecies of a single polytypic species" (Mayr 1969: 195). As such it is discussed in detail by Spinage (1982) and to some extent by Grubb (1978, 1985) and by Sinclair (1983).

According to these authors the main causes for the present situation were tectonic activities in the Rift Valley and long-term climatic changes in East Africa. The waterbuck is adapted to mesic savannah and dependent on permanent water, so suitable habitat was disrupted repeatedly during drier periods, isolating populations. This occasionally resulted in allopatric divergence subsequent to which these populations may have come into secondary contact when mesic conditions made range extensions possible. The existence of a small hybrid zone in the waterbuck suggests that allopatric separation of the two forms was relatively short and recent as there is no full reproductive isolation between them. Spinage (1982) argues that the Common waterbuck is the ancestral form and originally was distributed in the coastal regions of East Africa. From there around 10 000 BP during the last East African pluvial a founder population crossed the Rift Valley and, expanding west of it into several directions, gave rise to the Defassa waterbuck.

The Defassa waterbuck is thought to be the ecologically more specialized of the two forms in its requirement of a high protein diet and its dependence on permanent water, whereas there is some indication that the Common waterbuck may have a less specialized diet (Spinage 1982). There is no substantial evidence for this author's statement that hybrids between the two are less viable than their parental forms. A reduced viability of the hybrids and differing ecological requirements of the parental forms would be factors stabilizing the narrow hybrid zone (Bigelow 1965, Moore 1977). Indeed, the hybrid population in Nairobi National Park seems to have been stable for a considerable time, numbering between 40 and 50 individuals and remaining localized (Spinage 1982). More than two decades have passed since the compilation of the distribution map published by Stewart & Stewart (1963) documenting the

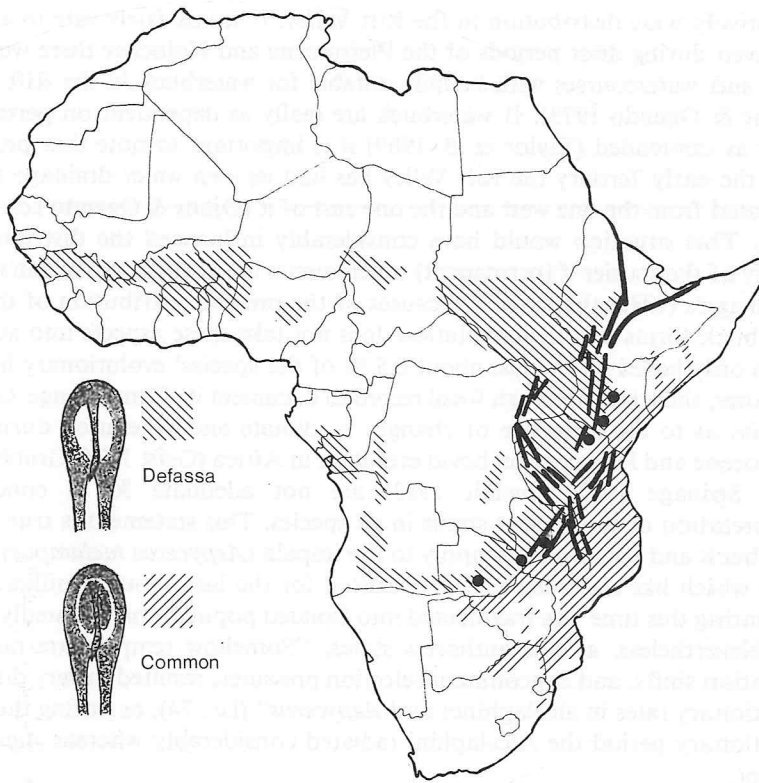


Fig. 3. Approximate present distribution of waterbuck with major faults of Rift Valley system. Places from where potential hybrids are known are marked with a black circle. (Compiled from various sources).

sympatry of the two waterbuck forms on the Ewaso Ngiro River, northern Kenya, and the observation of the two mixed herds and the potential hybrids from that region reported here, also indicating a fairly stable situation there. No recent information is available from the other places where both forms are known to be sympatric and from where hybrids were recorded.

The earliest fossil record of *Kobus ellipsiprymnus* is from the early Pleistocene of East Africa from faunal zones A and B of the eastern Lake Turkana basin (age about 2.3–1.7 million years) and of about the same age from the Omo Sequence, southern Ethiopia, and Olduvai Gorge, Tanzania (Gentry 1976, 1978, Harris 1976). In the respective faunal zones from Lake Turkana Reduncini (*Kobus*, *Redunca*) are the most numerous bovinds, indicating mesic conditions during that period. So, already in the beginning of its existence waterbuck had

a relatively wide distribution in the Rift Valley. It seems fairly safe to assume that even during drier periods of the Pleistocene and Holocene there were still lakes and watercourses with habitat suitable for waterbuck in the Rift Valley (Ojany & Ogendo 1973). If waterbuck are really as dependent on permanent water as contended (Taylor et al. 1969) it is important to note that probably since the early Tertiary the Rift Valley has had its own water drainage system separated from the one west and the one east of it (Ojany & Ogendo l.c., Denys 1985). This situation would have considerably influenced the distributional history of the species if (permanent) watercourses are its main expansion routes.

Spinage's (1982) theory of the causes of the present distribution of the two waterbuck forms and their evolution does not take these aspects into account and is only based on the last about 0.5 % of the species' evolutionary history. Moreover, there is not enough fossil record to document its former range. General theories as to the influence of changes in climate and vegetation during the Pleistocene and Holocene on bovid evolution in Africa (Geist 1974, Grubb 1978, 1985, Spinage 1982, Sinclair 1983) are not adequate for a conclusive interpretation of the present status in all species. This statement is true of the waterbuck and seems also to apply to the impala (*Aepyceros melampus*) (Vrba 1984) which like the waterbuck has existed for the last about 2 million years and during this time was fragmented into isolated populations repeatedly (Vrba l.c.). Nevertheless, as this authoress states, "Somehow temperature/rainfall/vegetation shifts, and concomitant selection pressures, resulted in very different evolutionary rates in alcelaphines and *Aepyceros*" (l.c.: 74), as during the same evolutionary period the Alcelaphini radiated considerably whereas *Aepyceros* did not.

As regards the taxonomic status of the two waterbuck forms Grubb's (1978: 155) formulation "The formal taxonomy of these mammals implies a level of biological knowledge that has simply not been attained" is an apt description of the present state of knowledge. The situation in the waterbuck provides an opportunity to study evolutionary mechanisms in a large mammal, especially relevant factors like random vs. selective mating between the two forms where they are sympatric, their different ecological adaptations, and survival rate, reproductive success and ecological niche of their hybrids as compared with the parental forms. The very localized occurrence of hybrids and the stability of the small mixed populations suggest that this study could also clarify the taxonomic problems.

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Summary

Observations of two mixed herds of Common and Defassa waterbuck with potential hybrids of the two forms in Buffalo Springs Game Reserve, northern Kenya, are reported. Current theories published in the literature as to the distributional history and taxonomic status of the two forms are discussed.

Zusammenfassung

Die Beobachtung von 2 gemischten Herden mit Ellipsen- und Defassa-Wasserböcken und möglichen Hybriden zwischen beiden Formen in Buffalo Springs Game Reserve, N-Kenia, ist Anlaß für eine Diskussion der in der Literatur publizierten Vorstellungen zu ihrer Verbreitungsgeschichte und zu ihrem taxonomischen Status.

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