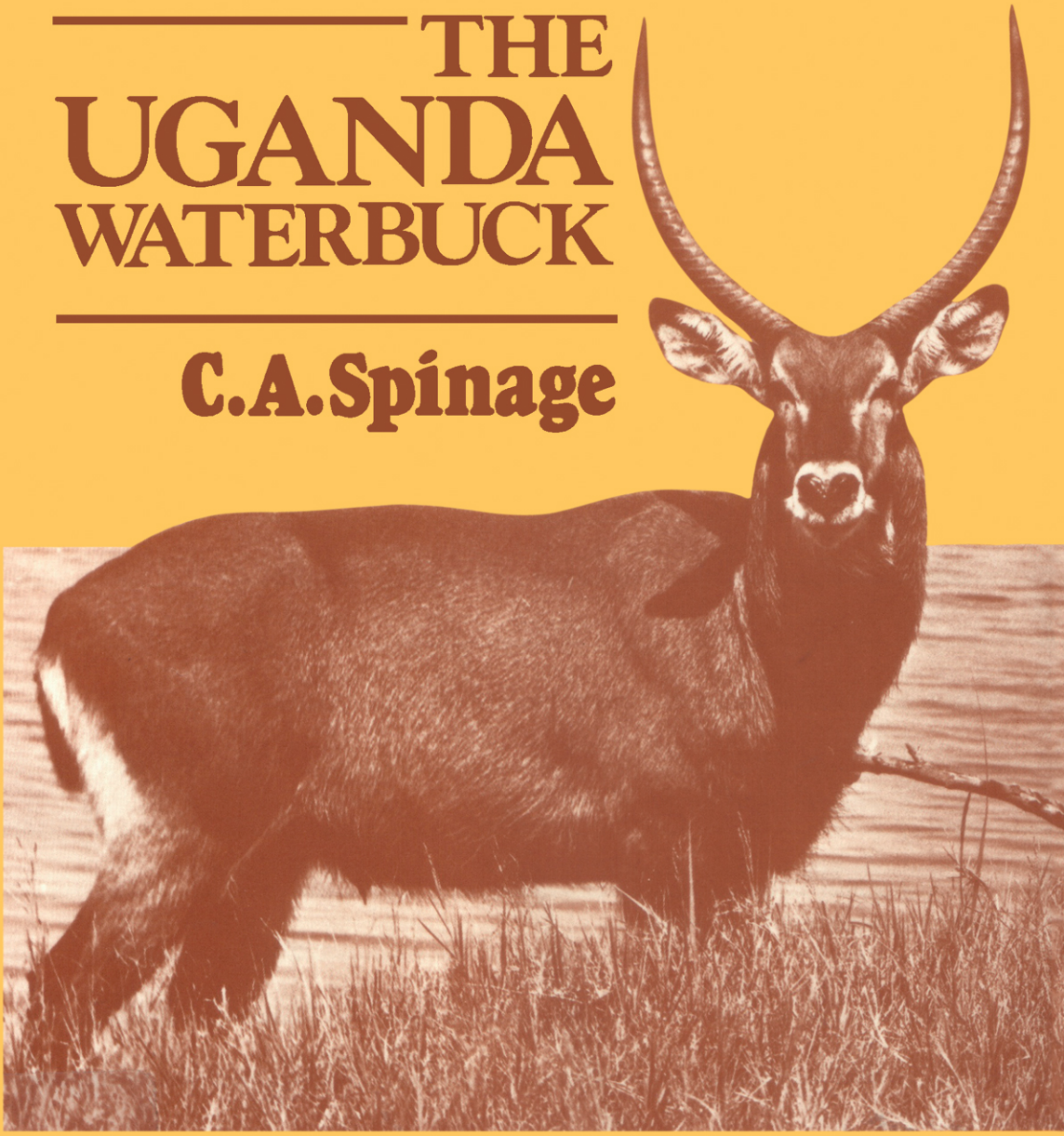
A Territorial Antelope:

THE UGANDA WATERBUCK

C.A.Spinage



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Preface

Territoriality, the name given to the social organization in which animals defend an area against competitors of their own kind, has been well known in birds since Eliot Howard defined it in 1920 in his book "Territory in Bird Life"; but in 1955 Bourlière was to write of mammals: "In general, and in so far as the paucity of observations permits judgement, it would seem that territorial behaviour is far from being as important in mammals as in birds." He was able to list only a half dozen inferences that suggested territoriality in mammals, and all of these related to smaller mammals. At the same time Bourlière quoted Hoier's observation of a buck defassa waterbuck which allegedly occupied the same area in the Congo Albert National Park from 1931 to 1939 (Hoier, 1950); and it was in 1955 that Verheyen postulated, from his observations in the same area, that the waterbuck was territorial in its behaviour (Verheyen, 1955).

It is difficult to understand today why the study of mammals, so much more closely related to the study of man than studies of birds, insects or fishes, was so neglected. Yet it was not until 1967 that a wide interest was really awakened in mammal behaviour by the popular writing of Robert Ardrey, whose book, "The Territorial Imperative", seems to have been prompted in no small measure by the observations of Buechner. In 1957 Buechner, an American Fulbright scholar working in northern Uganda, discovered, or rather his wife did, that the Uganda kob, a medium-sized antelope closely related to the waterbuck, exhibited a type of intensive territoriality, in the Semliki Valley of western Uganda, which had similarities with the "lek" behaviour of grouse on their breeding grounds in Scotland (Buechner, 1961).

But it was not these considerations which led me, in October 1964, to study the social organization of the waterbuck. This was prompted more by the growing interest in the natural regulation of animal populations stimulated by such works as Lack's "The Natural Regulation of Animal Numbers", and Andrewartha and Birch's "The Distribution and

Abundance of Animals", both of which appeared in 1954. Wynne-Edward's "Animal Dispersion in Relation to Social Behaviour", by the criticism which it attracted when it made its début in 1962, greatly stimulated my interest in the subject.

The concept of territoriality was an important factor in the welter of speculation as to how natural population regulation might be achieved, and the apparent territorial organization of the waterbuck had been noted by the Director of the newly created Nuffield Institute of Tropical Animal Ecology, Dr R. M. Laws. This Institute was situated in the then Queen Elizabeth National Park of western Uganda, now the Rwenzori National Park and had been set up in response to the park authorities' concern at the great numbers of hippopotamuses inhabiting the area, which appeared to pose a threat of overgrazing and habitat deterioration to the detriment of the recently created park. I was invited to study the biology and social organization of the waterbuck, which was quite numerous there, as a part of an integrated overall study of the ecology of the park, which would relate to the presence of the hippopotamus.

My main objective was to try to establish whether territorial behaviour really existed in the waterbuck, and if so, what part this social system played in regulating the numbers of waterbuck, if any. However, at this period not only was virtually nothing known in detail of the social behaviour of almost all African ungulates, but also little was known of their biology. How long did they live for? How fast did they grow? When did they breed, and how often? These were just some of the questions to be answered, and this was why my study encompassed not only the behaviour of the waterbuck, but as much of its biology as I could learn in the three years which were available to me.

The result should not be considered as a book just about waterbuck. The interest of the waterbuck lies in its simple, basic type of territorial organization which the study revealed; but the book also presents the life history of an African antelope, detailing its anatomical, physiological and behavioural organization from birth to death, in which I hope that I have provided some insights into the biology of African antelopes as a whole. While, finally, I have allowed myself to speculate on the function and cause of territoriality.

The field work was carried out during 1964 to 1967, and this long gestation to the present has allowed me to put my findings into perspective in relation to studies both on the waterbuck, and to several other species on which studies have since been conducted, as well as to follow the vicissitudes of a waterbuck population for a period of some 44 years.

The original field work was financed by the Science Research Council of Great Britain, to whom I am eternally grateful. My thanks are also due

to the Director and governing body of the former Nuffield Unit of Tropical Animal Ecology for providing me with facilities at the Mweya research station; and I am especially grateful to the former director, Dr R. M. Laws FRS, for his interest and encouragement. My thanks are also due to the former director of the Uganda National Parks, the late Francis Katete, who gave permission for the study to be carried out; also to Professor Sir Alan Parkes and Dr I. W. Rowlands for providing accommodation and facilities for the writing-up of the original field work at the Wellcome Institute of Comparative Physiology at the Zoological Society of London. This writing-up formed the subject of the degree of Doctor of Philosophy of the University of London.

My thanks are also due to Dr Roger Short FRS, who initiated me into the art of darting and the study of reproductive physiology; to Dr S. K. Eltringham, a former director of the Nuffield Unit of Tropical Animal Ecology for kindly providing me with some of his data; also to Dr G. Petrides for supplying me with his data, and to W. F. H. Ansell for generously allowing me to use his map of waterbuck distribution. Finally, but not least, my thanks are due to all those other many workers and colleagues, too numerous to mention, who assisted in countless ways.

July 1981 C. A. Spinage

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1. Classification, Distribution and Origins of Waterbuck

Introduction

The antelope tribe Reduncini (Simpson, 1945) contains only two living genera: *Redunca* — the reedbucks, and *Kobus* — the kobs. The waterbuck is the largest of the kobs, and among the largest of the African antelopes. Of impressive appearance, the buck sports long, slightly curving horns, adorned with elegant chippendale ridges on the anterior faces. The body is solid, well proportioned and powerful, with a coarse but sleek coat. The hair of the coat gives the impression that it is thick, until examined closely, when it is found to be relatively sparse; but that on the neck is long, shaggy and wiry (Plates 1 and 2). The French call the waterbuck the *Cobe oncteux,* or "greasy kob", referring to the oily secretion that its skin exudes. When it is prolific this secretion imparts a dark, almost black look to the coat. The English name indicates its habit of always being found near to water; but despite its strong dependence on water it is one of the most widely distributed of the African antelopes, ranging from as far north as 14° to 29° in the south.

This wide range bears testimony to its success, wherever suitable permanent water exists; its habitat including such arid country as that surrounding the Webi and Schebeli rivers in Somalia, and the Awash in Ethiopia. Typically, however, it is a savanna and woodland species, localized near to permanent water and breeding well where not hunted by man. It seldom forms herds of larger than a hundred or so individuals, and commonly much less than this.

Ansell (1971) describes its former range in South Africa as: the north-eastern part of Natal, the eastern and northern Transvaal, the northern Cape Province along the upper Molopo River, and also along the upper Limpopo River. Today this range has been reduced in Natal to the