A Territorial Antelope:

THE UGANDA WATERBUCK

C.A.Spinage





A Territorial Antelope: The Uganda Waterbuck

A Territorial Antelope: The Uganda Waterbuck

C. A. SPINAGE UNDP, B.P. 872, Bangui, Central African Republic

1982



ACADEMIC PRESS

A Subsidiary of Harcourt Brace Jovanovich, Publishers London New York Toronto Sydney San Francisco Academic Press Inc. (London) Ltd. 24–28 Oval Road London NW1

US edition published by Academic Press Inc. 111 Fifth Avenue, New York, New York 10003

Copyright © 1982 by Academic Press Inc. (London) Ltd.

All Rights Reserved

No part of this book may be reproduced in any form, by photostat, microfilm or any other means, without written permission from the publishers.

British Library Cataloguing in Publication Data

Spinage, C. A. A territorial antelope. I. Uganda Kob 2. Territoriality (Zoology) I. Title 599.73'58'096761 QL737.U5

ISBN 0-12-657720-X LCCCN 81-66687

Contents

	Preface	•	•	•	•	•	•	•	•	vii
	List of figures .	•			•			•		xi
	List of plates .	•	•	•				•	•	xv
Ι.	Classification and	Distr	ibuti	on of	Wat	terbu	cks	•	•	I
2.	The Study Area				•				•	20
3.	Methods of Study	•		•	•				•	47
4.	Growth and Senes	cence	•		•	•			•	56
5.	Reproduction and	Repro	ducti	ve Be	havic	our	•	•	•	87
6.	Parturition and Ma	aternal	l Beh	aviou	r.			•		119
7.	Population Structu	re and	Fact	ors A	ffecti	ng Su	rvival	•	•	131
8.	Population Density	, Food	ł Sup	ply ar	nd Ha	abitat	Prefe	rence	•	159
9.	Daily Life .				•		•	•	•	198
10.	Social Organization	n							•	215
11.	Buck Behaviour	•			•	•	•	•	•	256
12.	Territorial Concep	ts and	Fun	ction	•		•		•	278
	References .	•	•	•	•	•		•	•	314
	Index		•	•		•		•		327

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

viii The Uganda Waterbuck

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

Preface ix

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

List of Figures

- Fig. 1. The distribution of waterbuck in Africa. Blocked squares Kobus ellipsiprymnus defassa, hatched squares K. e. ellipsiprymnus. Circle shows where type specimen originally occurred. Based on a map by W. F. H. Ansell, with additions.
- Fig. 2. Horn shapes in waterbuck: (a) "straight", (b) "intermediate", (c) "bowed".
- Fig. 3. The grouping of Rowland Ward's waterbuck divisions.
- Fig. 4. The overlapping of *Kobus ellipsiprymnus defassa*, large dots, and *K. e. ellipsiprymnus*, small dots, in East Africa. Based on a map by Stewart and Stewart (1963).
- Fig. 5. The phylogeny of the waterbuck, after Gentry (1978).
- Fig. 6. The phylogeny of the main groups of waterbuck.
- Fig. 7. Hypothetical dispersal of the groups of waterbuck from a common waterbuck origin.
- Fig. 8. Location map of the Rwenzori National Park in East Africa.
- Fig. 9. The clearing of bush for tsetse fly control on and around Mweya Peninsula, based on a copy of G. D. Hale-Carpenter's 1921 sketch map.
- Fig. 10. Map of the Rwenzori National Park, showing the main study areas, blocked, and the game count areas, stippled.
- Fig. 11. Map of the north-east part of the Rwenzori Park, showing the Crater Highlands.
- Fig. 12. Isohyets of the Rwenzori National Park. Lakes are shown stippled.
- Fig. 13. Graph of the mean monthly rainfall in mm, recorded at Mweya, for 1954–1963 and 1964–1966.
- Fig. 14. Map of the Mweya Peninsula showing main topographical features.
- Fig. 15. Map of the Overgrazed Study Area, showing main topographical features.
- Fig. 16. Map of the Kayanja area, showing main topographical features.
- Fig. 17. The logistic curve of growth in weight for bucks circles, and does inverted triangles. Open symbols are calculated values, blocked symbols are observed values.
- Fig. 18. Graph of logⁿ kidney weight against log metabolic weight. el—elephant, hi hippopotamus, bu—buffalo, bo—boran steer, wa—waterbuck, wi—wildebeest, to—topi, ko—kob, gr—Grant's gazelle, ty—Thompson's gazelle.
- Fig. 19. Mean monthly kidney fat index for bucks and does, with mean monthly rainfall.
- Fig. 20. Growth in horn length of waterbuck from 1 to 6 years.
- Fig. 21. Fighting attitudes of the waterbuck and sable, showing how, although the horns are inversely curved in the two species, the ridges oppose stresses in the same way.
- Fig. 22. Wear of the first incisors, showing root absorption in old age, and the undercutting of the crowns.
- Fig. 23. Predicted and observed births each month, with mean monthly rainfall.

xii The Uganda Waterbuck

- Fig. 24. Monthly conceptions in (a) waterbuck, hippopotamus, (b) warthog and buffalo, with mean monthly rainfall.
- Fig. 25. Monthly conceptions compared with the mean monthly kidney fat index.
- Fig. 26. Smoothed curves of the monthly conceptions in (a) buffalo, waterbuck, (b) hippopotamus and warthog, compared with time of sunrise and sunset at the equator. Arrows indicate the summer and winter solstices.
- Fig. 27. Monthly births compared with the mean monthly kidney fat index.
- Fig. 28. The change in rumen contents with change in fetal weight. Horizontal lines show the mean rumen fill index from 0 to 5 kg fetal weight, and from 5 kg to term. The vertical line shows the range in the rumen contents index in non-pregnant animals, and "X" shows the mean.
- Fig. 29. Survivorship curves of fawns based on lactation state of the doe.
- Fig. 30. Frequency distributions of the numbers of found skulls.
- Fig. 31. Survivorship curves for bucks and does in the Rwenzori Park.
- Fig. 32. Smoothed force of mortality curves for bucks and does in the Rwenzori Park.
- Fig. 33. Force of mortality curves for cropped does, dotted line, and natural mortality, continuous line.
- Fig. 34. "Survivorship" curve of Peninsula bucks.
- Fig. 35. "Survivorship" curve of Peninsula does.
- Fig. 36. Changes in the numbers of waterbuck inhabiting the Mweya Peninsula from 1955 to 1973. Dotted line shows the calculated increase from 1960, vertical lines show the range.
- Fig. 37. Monthly changes in the Peninsula and Ogsa waterbuck numbers from 1956 to 1967, with mean monthly rainfall. Horizontal lines show the means.
- Fig. 38. Monthly changes in the crude protein values in the stem and leaf of four principal grass species. Changes in calcium and phosphorus for 9 months are also shown; "d"—dry, "w"—wet.
- Fig. 39. The types of grass eaten by waterbuck through the year. Adapted from Field (1972).
- Fig. 40. Comparative analysis of occupation of the bachelor bucks and territorial bucks and does on the Peninsula from April 1965 to March 1967, expressed as cumulative numbers per 0.4 ha. a — does, b — bachelor bucks, c — territorial bucks.
- Fig. 41. Rectal temperature change, respiratory rate and evaporation in the waterbuck with increase in ambient temperature, after Taylor *et al.* (1969).
- Fig. 42. The thermoneutral zone of the waterbuck, after Taylor et al. (1969).
- Fig. 43. Water requirements of the waterbuck compared with three other species, after Taylor *et al.* (1969).
- Fig. 44. The daily activity pattern of the adult buck Y7 for three periods, each on three consecutive days: (1) 16–18.2.66; (2) 18–20.5.66; (3) 19–21.9.66. Blocked areas = "other activities"; dense dots = lying resting; medium density dots = ruminating; blank = feeding.
- Fig. 45. The daily acitivity patterns of: (1) adult doe Y128 for two consecutive days 7-8.2.67; (2) 6-month-old fawn for two consecutive days 7-8.2.67; (3) adult doe Y123 for two consecutive days 22-23.2.66; (4) adult buck Y22 for two consecutive days 28-29.6.66.
- Fig. 46. The daily acitivity pattern of: (1) adult doe Y114 for three consecutive days 22–24.2.66: and (2) the nocturnal activity pattern of adult buck Y7 for three separate nights: 7–8.3.66; 28–29.10.66 and 25–26.1.67.
- Fig. 47. The mean time spent in feeding per hour for bucks (24 h) and does (12 h), as a percentage of the total activity per hour.
- Fig. 48. Diurnal movement of adult doe Y114 for three consecutive days, and adult doe

Y128 with her 6-month-old fawn for two consecutive days. 1st day — broken line; 2nd day — dotted line; 3rd day — continuous line.

- Fig. 49. Frequency distribution of mean doe group size.
- Fig. 50. Map of observed emigrations from the Peninsula.
- Fig. 51. Home ranges of Peninsula does. Inset shows the extent of some ranges into the Ogsa (hatched area), and the two discrete home ranges of doe Y106 (blocked areas); 13.4.65 to 7.3.67. Ages of the does are given.
- Fig. 52. The ranges of some does in the Ogsa, 7.8.65 to 11.3.67. Ages of the does are given.
- Fig. 53. The Ogsa bachelor groups. Open circles up to 12.7.66, blocked circles from 5.12.66. Figures show mean group size.
- Fig. 54. Age structure of the Ogsa buck population, July 1965.
- Fig. 55. Some sparring contacts amongst the Peninsula bachelor group.
- Fig. 56. Bachelor groups Peninsula ranges: a 10.64-11.64; b 4.65-5.65; c 6.65-7.65; d 8.65-9.65; e 11.65-12.65; f 1.66-2.66; g 3.66-4.66; h 9.66-10.66; i 2.67-3.67; j 11.68.
- Fig. 57. Peninsula buck territories from November 1964 to November 1968. Numbers indicate buck. a = 10.64-11.64; b = 4.65-5.65; c = 6.65-7.65; d = 8.65-9.65; e = 11.65-12.65; f = 1.66-2.66; g = 3.66-4.66; h = 9.66-10.66; i = 2.67-3.67; j = 11.68. The plotted observations on which the boundaries are based can be found in Spinage (1969C).
- Fig. 58. Age structure of the Peninsula bucks 1964–1966. t = territorial, b = bachelor, e = emigrated, d = died.
- Fig. 59. Mean territory size in ha according to age of the territory holder for Peninsula bucks.
- Fig. 60. The percentage of the total territorial area available expressed as buck occupation according to age, compared with the number of doe visits, for the Peninsula.
- Fig. 61. Real and hypothetical age structure of the Peninsula bucks for November 1968. Continuous lines — observed presence, dotted lines — hypothetical presence.
- Fig. 62. Territories in the Ogsa, July 1965–March 1967. Blocked circles indicate observations of Y35.
- Fig. 63. Mean territory size in ha according to age of the territory holder for Ogsa bucks, July 1965.
- Fig. 64. Territories at Kayanja, November 1966–February 1967. Dot-dash lines indicate routes taken to water, dashed lines indicate park tracks.
- Fig. 65. Buck movements on the Peninsula. a-c-diurnal movements of Y7; dnocturnal movements of Y7; e-diurnal movements of Y22; f-diurnal movements of the bachelor group. 1st day-dashed line; 2nd day-dotted line; 3rd daycontinuous line. Long dashed line indicates the maximum plotted boundaries of the territorial bucks.

List of Plates

- Plate 1. A 10-year-old *defassa* waterbuck, known as Y1, Mweya Peninsula.
- Plate 2. Doe defassa on the Mweya Peninsula, overlooking the Kazinga Channel.
- Plate 3. Doe common waterbuck, showing the difference in rump patterns; Tsavo East National Park, Kenya.
- Plate 4. Hybrid common \times *defassa* waterbuck in the Nairobi National Park, Kenya.
- Plate 5. The glacier-capped Rwenzori Mountains from Kayanja, with waterbuck bachelor herd and does in the foreground.
- Plate 6. The northern tip of the Mweya Peninsula, December 1959.
- Plate 7. The same view, November 1968. Some change in the grass cover is evident, but there is little perceptible change in the bush.
- Plate 8. The east side of the Mweya Peninsula, December 1959, with a lone buck on the skyline.
- Plate 9. A further view of the east side of the Mweya Peninsula in December 1959, showing the exposed grassy shorelines which were later covered by a rise in the water level.
- Plate 10. A view looking west over the Peninsula from the high ground to the lower plateau, with Katwe in the distance, showing the scattered Capparis clumps and the open patches of grassland.
- Plate 11. Hippopotamus on land; note the closely-cropped grass cover.
- Plate 12. A drugged waterbuck.
- Plate 13. A 9-month-old buck with the horns just appearing.
- Plate 14. 10- and 11-month-old bucks.
- Plate 15. A 2-year-old buck.
- Plate 16. A 5-year-old buck, still in the bachelor group. Compare the body conformation with the adult in Plate 1.
- Plate 17. A horned doe.
- Plate 18. A doe with completely male-like horns, one of which had been broken off. Picture by F. E. Guinness.
- Plate 19. Hypertrophy of the female fetal gonad; Graafian follicles in the ovary of a 194day-old foetus.
- Plate 20. A waterbuck egg in the 8-cell stage.
- Plate 21. The buck follows the post-partum dam closely in anticipation of her first postpartum oestrus.
- Plate 22. Buck urine-sampling.
- Plate 23. The buck grimaces in a characteristic manner.
- Plate 24. Urine sampling.
- Plates 25 and 26. Doe champing in response to a buck.

xvi The Uganda Waterbuck

- Plate 27. Buck cajoling a doe by rubbing his chin on her rump.
- Plate 28. Rubbing the doe's udder region.
- Plate 29. Mounting an oestrus doe, the doe stands with tail held aside.
- Plates 30 and 31. Buck attempting to mount from the side.
- Plate 32. Successful copulation. Note the carriage of the doe's head, and the contraction of the buck's hindquarter musculature.
- Plate 33. Typical sucking attitude.
- Plate 34. The "follow-me" signal of the doe to her young fawn, the tail held stiffly in the air. See also Plates 31 and 32.
- Plate 35. Two fawns may sometimes follow one dam together.
- Plate 36. A young doe and a 9-month buck using a termite mound as a vantage point.
- Plate 37. A buck dying of a horn wound in the abdomen.
- Plate 38. Damalinia hilli, a biting louse common on waterbuck.
- Plate 39. Raillietia hopkinsi, the ear mite of the waterbuck.
- Plate 40. A buck attacked by a lion, whose back healed into this deformed shape.
- Plate 41. Doe browsing on Capparis.
- Plate 42. Does keeping an eye on a lion; Akagera Park, Rwanda.
- Plates 43 and 44. Young bucks sparring.
- Plates 45 and 46. The approach of a territorial buck (Y_7) by a bachelor buck; note how the adult's horns are inclined towards the bachelor.
- Plates 47 and 48. Another approach to Y7 by a bachelor buck. Note the typical broadside display of the adult and the erect penis.
- Plates 49 and 50. A fight between two territory owners.
- Plate 51. A bachelor watching the fight, preparatory to attacking one of the contestants.
- Plate 52. Uganda kob fighting in the territorial arena. Note the proximity of the other territory holders. Kikorongo, Rwenzori Park.

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 northeastern 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