Aspects of the expressive behaviour of the waterbuck *Kobus ellipsiprymnus ellipsiprymnus* in a Rhodesian Game Park

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Aspects of the expressive behaviour of waterbuck *K.e. ellipsiprymnus* are described and the results of this study support the contention that *K.e. ellipsiprymnus* and *K.e. defassa* are conspecifics. Comparisons with observations on waterbuck behaviour recorded by other authors show a number of differences as well as similarities in behaviour patterns.

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Aspekte van die ekspressiewe gedrag van waterbokke *K.e. ellipsiprymnus* word beskryf en die resultate van hierdie studie ondersteun de bewering dat *K.e. ellipsiprymnus* en *K.e. defassa* gelyksoortig is. Vergelykings met waarnemings van waterbokgedrag deur ander skrywers wys 'n aantal verskille sowel as ooreenkomstes in gedragspatrone.

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Lake McIlwaine is a man-made reservoir situated some 32 km south-east of Salisbury at 30°50′E and 17°55′S. A fenced game park measuring about 1867 ha in extent borders the southern edge of the lake and contains a variety of ungulates including waterbuck.

There are two kinds of waterbuck in Africa *Kobus ellipsiprymnus ellipsiprymnus* (Ogilby 1833) and *Kobus ellipsiprymnus defassa* (Ruppel 1835) recorded in the literature. These are regarded as conspecifics by some authors (Haltenworth 1963; Ansell 1968 & Heyden 1969) owing to their more or less continuous distribution and lack of distinguishing characteristics, other than rump markings. Smithers (1966) and Dorst and Dandelot (1970), however, regard them as separate species and indicate that their distribution is clearly separated geographically. Kiley-Worthington (1965) comments that there are at least two areas where these species interbreed in Kenya and where this occurs the offspring have a variety of rump markings.

Spinage (1969) has briefly described aspects of the social behaviour of *K.e. defassa* but to date very little has been written on the behaviour of *K.e. ellipsiprymnus*. Walther (1974), in his review on the expressive behaviour of certain horned ungulates, provides a number of tables which compare aspects of ungulate behaviour, including that of *K.e. ellipsiprymnus*. He has, however, indicated that most of his work on waterbuck is from unpublished personal observations.

The aim of this paper is, therefore, to describe in detail certain aspects of the expressive behaviour of *K.e. ellipsiprymnus* and to compare the findings of this study with those of other authors.

Materials and Methods

The game park comprised a total of 90 waterbuck, which were encountered commonly as territorial males (T♂♂), bachelor males (B♂♂) or female/immature groups (♀♀/Imm) (Tomlinson 1979). A number of individuals were identified and named by natural scars along the edges of their ears and by horn shape and size (Figs. 1 & 2). A Landrover was used to follow the different social groups of waterbuck on a daily (06h00 – 18h00) or nightly (18h00 – 06h00) basis and a combined total of 156 'waterbuck-days' (1 872 h) and 17 'waterbuck-nights' (204 h) were spent on observations over one calendar year.

Fig. 1 Bachelor male 'Left Dent'.

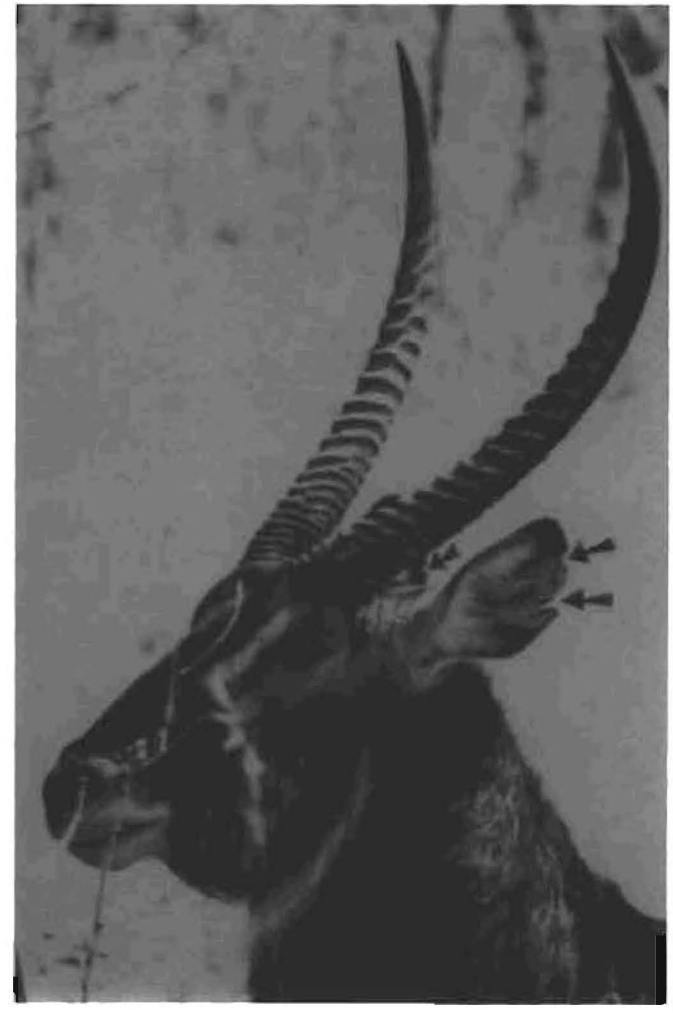

Fig. 2 Territorial male '3 Notch'.

Results

Social dynamics

Interactions between neighbouring territorial males

A total of seven adjacent territories were found situated along the entire game-park with a mean territory size of 89,5 ha.

Interactions between neighbouring territorial bulls occurred in the vicinity of territorial boundaries and the normal sequence of events (seven observations) were as follows:

Two individuals would sight each other at some distance apart (50 – 100 m) and would advance slowly while feeding, stopping occasionally to look up. On reaching a posi-

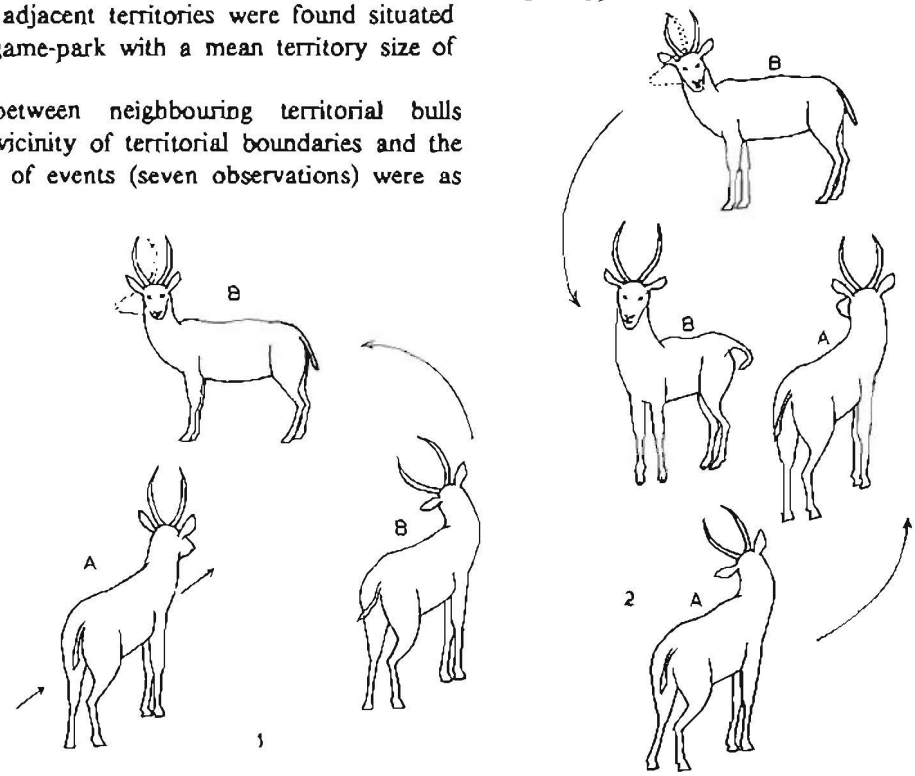

Fig. 3 *Interactions between neighbouring territorial males and/or challenging bachelor males:* (1) Broadside blocking movement with horn threat and ending in head held-high position (Proud Posture) by animal B. (2) Return movement with horn threat by animal A – ending in reverse-parallel position.

tion where they were about 5 — 10 m apart, one individual would move in a sideways movement around and to the front of its opponent where it would stand in a broadside position (Animal B. Fig. 3(1)). This movement was accompanied by the chin being tucked tightly into the throat with head and horns tilted towards its opponent, and then ending with head high and horizontal (Proud Posture) for a few seconds before turning to face its opponent.

The other individual 'A' responded by repeating the same performance (Fig. 3(2)), and after both had repeated this display two or three times, they would finally end in the reverse-parallel position, standing side by side. Eventually both individuals would swing around and face each other with tails flicking intermittently from side to side (Fig. 4(1)). From time to time one or the other would suddenly drop its head in a mock attack and the other would respond in an identical blocking movement but without making any physical contact. One of the bulls would then advance slowly and the other would step backwards with its head swaying from side to side; the situation would then be reversed and the other bull, in turn, would step backwards swaying its head from side to side (Fig. 4(2)). Physical contact still did not occur and both bulls would back off simultaneously. This normally heralded the end of the encounter and both bulls would move off to continue grazing.

Another feature of these encounters was the horning of

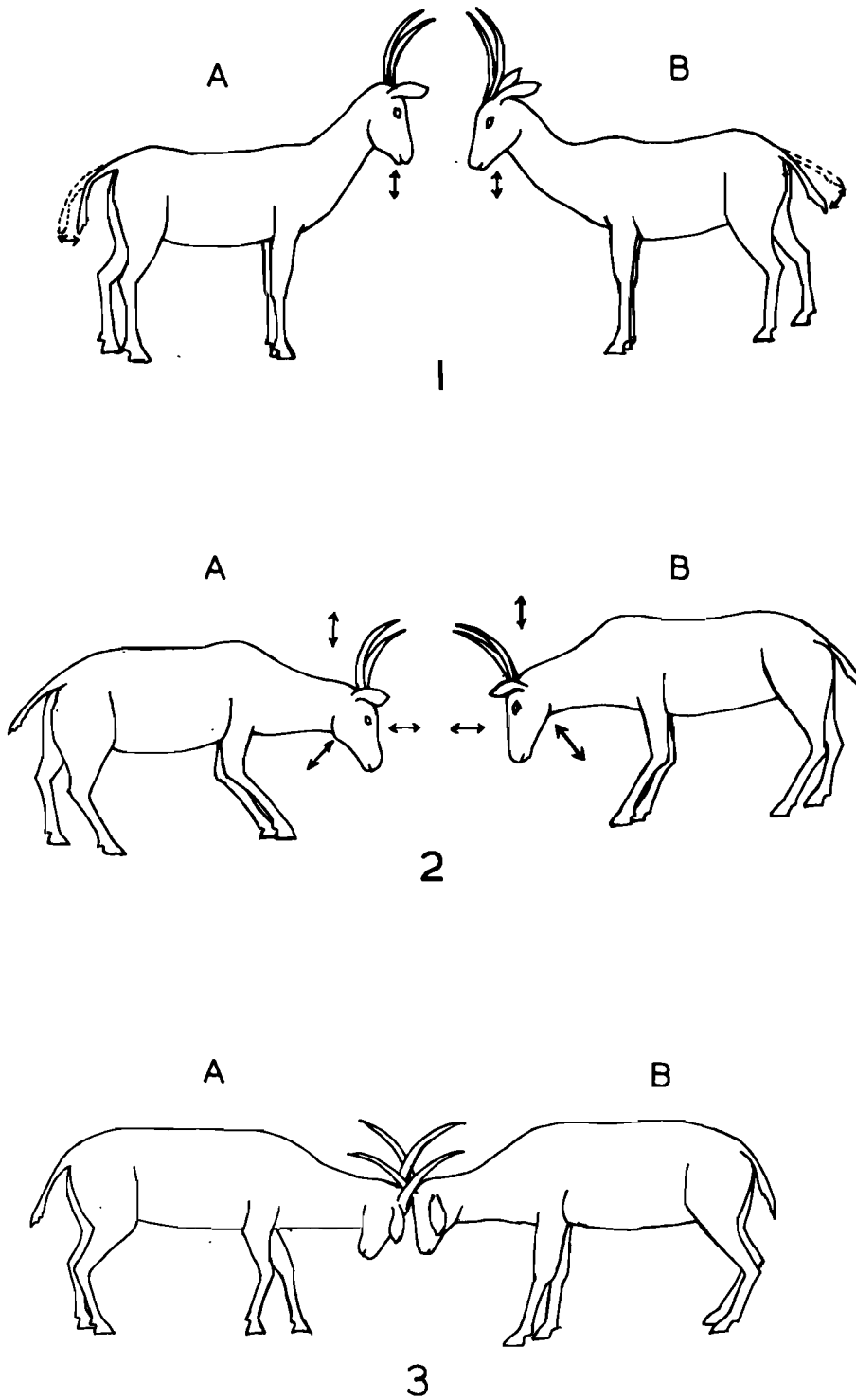

Fig. 4 *Interactions between neighbouring territorial males and/or challenging bachelor males* (cont'd): (1) Animals facing each other with intermittent tail wagging. (2) Crouch position with sudden head lowering and raising in unison. Intermittent slow head-shaking from side to side by either A or B. (3) Horns locked in aggressive pushing contest.

the grass or low bush by one or the other of the bulls, on sighting its neighbour, while still at some distance away. This involved aggressive horn thrusts into the grass and swinging of the head in a sudden upwards movement, often tossing tufts of grass into the air (Fig. 5(1)). Head-flagging (David 1973) was an additional feature of these rituals and was observed on all seven occasions (Fig. 5(2) & (3)).

Estes (1969) working on *Connochaetes taurinus* and David (1973) working on *Damaliscus dorcas* have both described a 'challenge ritual' between adjacent territorial males which contains similar components to those described for *K. ellipsiprymnus.*

Interactions between territorial males and challenging bachelor males

The following are three protocols giving an account of a situation where a bachelor male 'Left Dent' (LD) successfully established himself in part of an occupied territory belonging to 'Three Notch' (3N).

16th September 1977: 3N had been seen to chase LD on five different occasions and the latter always fled at the first sign of a charge. On this occasion 3N sighted LD at a distance of about 50 m and as usual LD started to run away. After having fled for about 10 m, he suddenly halted and turning broadside on, head held high and froze in that position. 3N immediately stopped in his tracks and also turned broadside on with head held high. LD turned to face 3N, who did the same and the former then slowly moved off. 3N immediately charged again and this time LD turned aside on and presented the tips of his horns towards 3N by tilting the head in an exaggerated fashion. 3N immediately froze with head held high. LD then moved off and 3N did the same.

This specific reaction was apparently the start of LD's challenge for a territory and, after 3N had walked away, LD followed at about 50 m distance for the rest of the day.

20th September 1977: 3N and LD approached each other with the normal lateral approaches and after a few mock lunges they locked horns (Fig. 4(3)) and a pushing match ensued. 3N had the advantage for most of the fight but LD did push 3N back a few times, although the fight ended without any specific winner. For one brief moment during a rest spell between bouts, LD backed off with ears back and carried out side to side swinging of the head.

21st September 1978: 3N was seen approaching LD which initiated the first locking movement which was not repeated by 3N. Instead, he moved off slowly back towards his own territory, horning a bush as he went. After this date 3N never attempted to enter this particular area and it was assumed that at this stage LD had been successful in claiming a territory for himself.

At the start of the third research period (rainy season) LD was always sighted alone, which was a complete change from the situation during the hot dry season when he had frequently joined the bachelor herd.

On the 4th December LD sighted 3N at about 70 m away and approached. 3N did the same and when both bulls were about 30 m apart LD suddenly stopped and proceeded to horn a bush in his immediate vicinity. He stopped and looked up at 3N, who then repeated the procedure on a bush in his vicinity. Both bulls then walked parallel to each other in the same direction while still remaining at 30 m apart and then stopped in turn in the head 'held high' position for a brief moment before turning to look at each other. Both bulls then repeated the bush-horning action and continued walking parallel to each other, never coming closer than 30 m. Eventually one bull lay down and the other followed suit by lying down with its back towards its rival.

Interactions between territorial males and subservient bachelor males

When territorial males encountered bachelor males the following was the normal sequence of events (n = 31): On sighting a group of bachelors the territorial male would

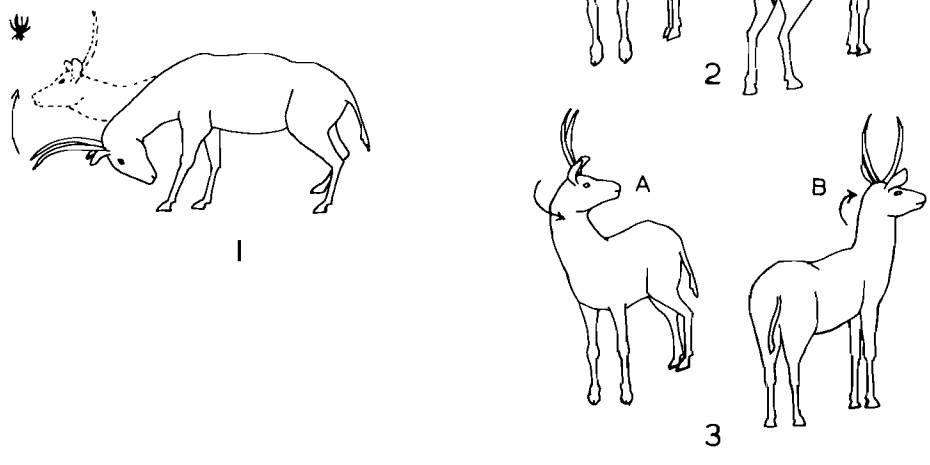

Fig. 5 *Aggressive and Dominance displays:* (1) Aggressive horn thrusts into the grass and soil. (2) & (3) A & B in reverse-parallel position with alternate, exaggerated head facing-away postures.

approach slowly to a distance of about 30 – 50 m and, facing the latter, would stand with head held high in the 'proud' posture. This attitude would initiate an immediate response by one or more of the bachelors in that they would proceed to nod their heads (Fig. 6(1)) in short up and down movements, which had the effect of 'flashing' the white collar situated on the underside of the upper neck. In addition, they would utter a bleating noise while nodding their heads, and tails would be flicked rapidly from side to side. The territorial male would remain standing in his original position.

One bachelor would then stretch its tail straight out behind it or in a position slightly above horizontal, and approach the territorial male very cautiously with head and neck stretched forward and slightly below the level of its shoulders (Fig. 6(2)). The tail would be wagged intermittently as it approached normally from the side (n = 18) or from the rear (n = 10), of the territorial male.

The territorial male would slowly lower its chin into its throat (Fig. 6(2)) and then suddenly tilt its head or sweep the head and horns in a downwards movement in the direction of the approaching animal (Fig. 6(3)). This would result in an immediate reverse and sideways movement by the bachelor who would then run off. When the head was tilted it was often (n = 21) accompanied by a curling of the tail around the side of the animal's flank.

Interactions within bachelor groups

Within the bachelor herd there was a distinct rank structure which was continually reinforced by sparring activities between members of the group. During these encounters preliminary displays consisted simply of an individual moving into a position in front of another individual and placing its forehead against that of its rival. A pushing

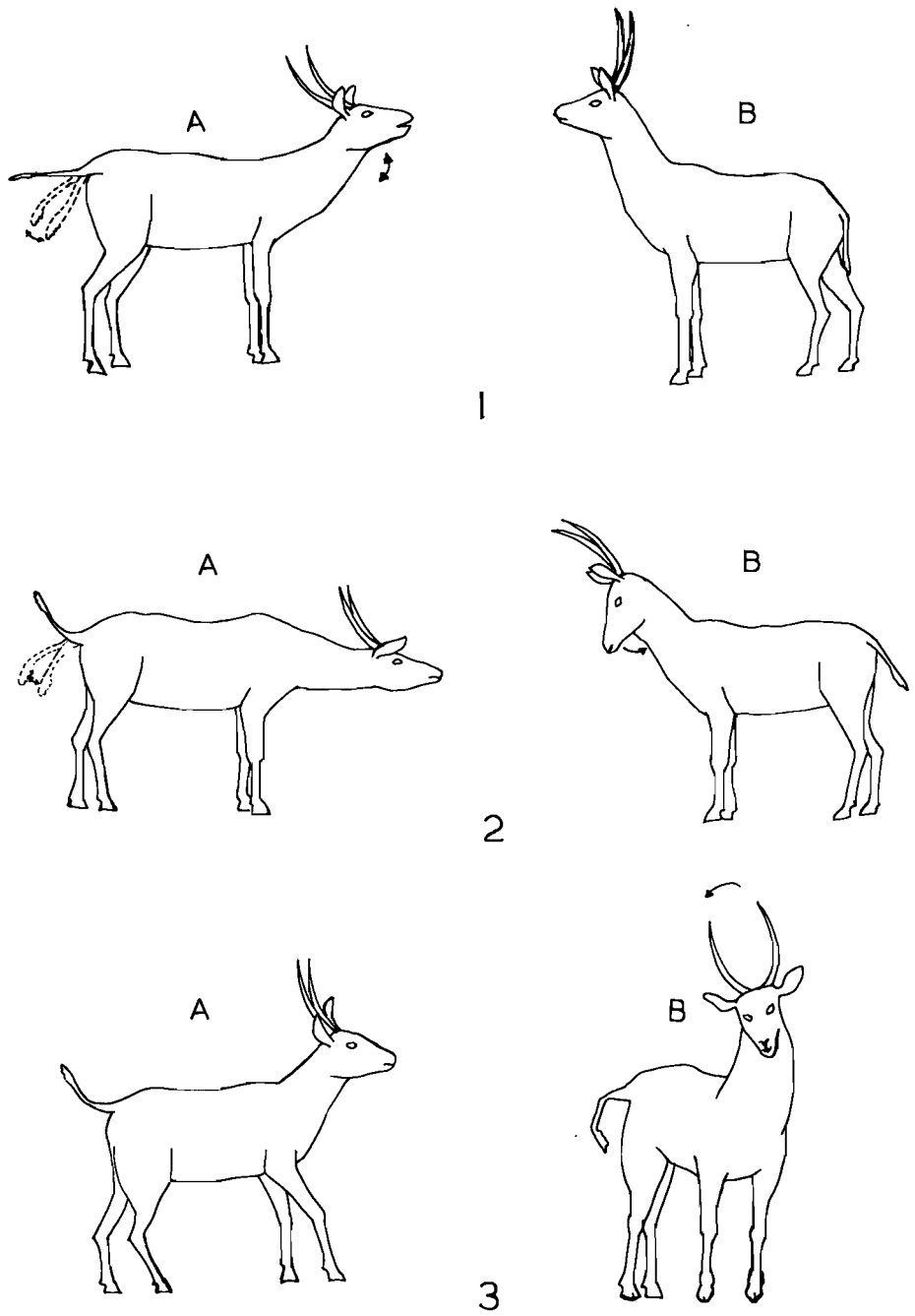

Fig. 6 *Interactions between territorial males* (B) *and subservient bachelor males* (A): (1) A = Head nodding accompanied by tail wag and submissive bleat; B = Proud Posture facing A. (2) A = Cautious approach with tail up, head low and neck outstretched; B = Chin tucked tightly into throat with horns pointing forward. (3) A = Rapid retreat with tail up; B = Horn threat.

match then ensued which varied in duration from a very brief encounter to seven minutes, with the loser eventually breaking away and trotting off for a few yards.

To depict the rank structure within a bachelor herd, an interaction matrix (Table 1) is drawn up showing the number of times each individual 'wins' or 'loses' a pushing contest. The 'loser' in these encounters was the one that broke away first.

From Table 1 it can be seen that rank is based largely on age, with animals of similar ages holding equal rank.

Table 1 Interaction matrix showing numbers of wins in encounters between different individuals of a bachelor group

Losses:						
	6y	4y	3y	3y	2y	2y
6y	—	14	2	3	—	—
4y	0	—	18	13	3	5
3y	0	0	—	23	19	12
3y	0	0	17	—	9	11
Wins:						
2y	0	0	1	2	—	28
2y	0	0	0	0	3	—

N.B. y = years of age

Interaction between females

Females appeared to be indifferent to the presence of other females and when two groups joined up, there were no outward signs of recognition and no form of greeting took place. In addition, no leadership by any particular individual within a herd was apparent and when moving off any individual taking the lead was followed.

Courtship behaviour

Courtship behaviour has been described by Kiley-Worthington (1969) and Spinage (1968) for *K.e. defassa* and is exactly the same for *K.e. ellipsiprymnus*. No further comment is necessary.

Summary of tendency indicators

Many ungulate species have been endowed with variable body and facial markings which have evolved apparently to ensure that species do not interbreed and to act as communication agents. Waterbuck have a characteristic white ring around the rump and a prominent white 'bib' under the throat. As a communication agent the white ring apparently serves to enhance tail movements and positions while the throat 'bib' can be exposed or hidden at will by the position of the head.

In this study, different tail positions have been shown to exhibit specific outward manifestations of an individual's momentary psycho-somatic state (Walther 1974) and Table 2 summarizes the tendency indicators for different tail positions (Fig. 7).

Tail positions therefore appear to represent a continuum from aggression to fear. In support of these conclusions De Vos and Dowsett (1966) observed that sparring waterbuck flicked their tails continuously when circling each other, except during the actual clash of horns when tails were depressed slightly. In addition during sparring bouts when one male pushed another backwards, the loser flicked its tail repeatedly as it was forced backwards. The vertically upright tail was also observed by these authors to occur under alarm situations.

A combination of head and horn positions together with closure and exposure of the white 'bib' are used to communicate to specific individuals (conspecifics) with the aim of releasing particular responses by the latter (Table 3, Fig. 7).

Discussion and Conclusions

Observations on the social displays of waterbuck at Lake McIlwaine have been compared with those of Spinage (1968–69) and Walther (1974) and these are summarized in Table 4.

Walther (1974) observed *K.e. ellipsiprymnus* in the standing position with nose pointing directly upwards (a) and has indicated that the display is especially pronounced and frequent. This display was never observed at Lake

Table 2 Summary of tail positions as tendency indicators

Fig.	Tail position	Situation
7A	Curved around flanks	Carried out by one animal threatening another. *Tendency:* Aggressive.
7B	Side to side flick	(a) Carried out by low ranking animals when confronted by higher ranking animals. (b) By females when approached by males. (c) By territorial males when confronted by adjacent territorial occupants along common boundaries. *Tendency:* Conflict between a desire to remain or flee.
7C	Horizontal	Carried out by bachelor males when confronted by dominant/territorial males. *Tendency:* Slight fear/submission.
7D	Vertically upright	Carried out by (a) Bachelor males when confronted by territorial males at close quarters. (b) All animals when approached by humans. *Tendency:* Extreme fear/submission.

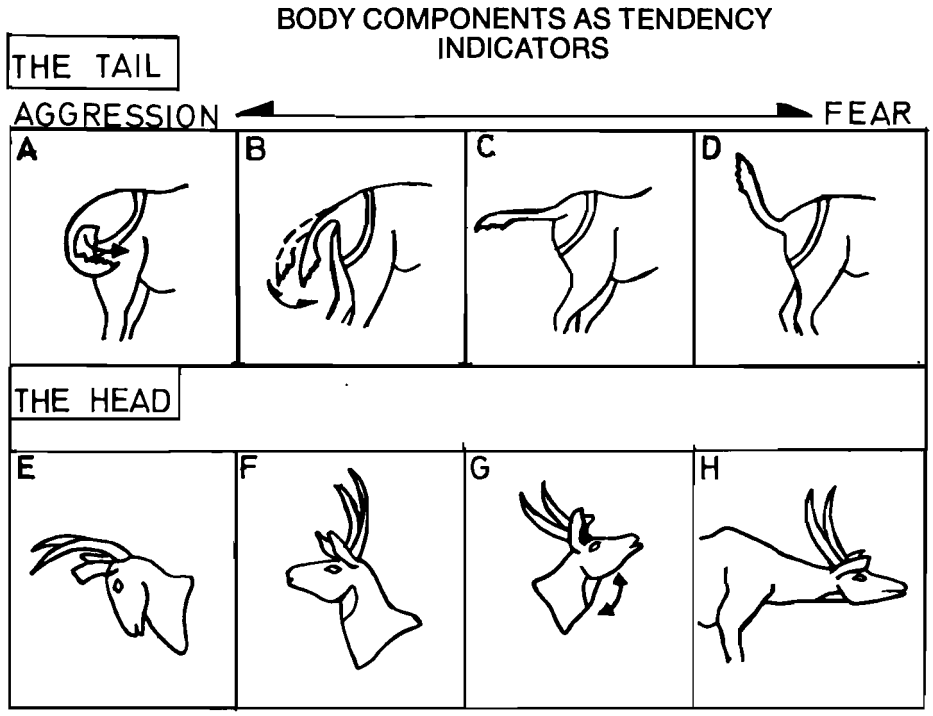

Fig. 7 *Summary of body components as tendency indicators.* A = Tail curved around flanks; B = Tail wag; C = Tail horizontal; D = Tail vertical; E = Horn presentation; F = Proud posture; G = Head nod; H = Head low. N.B. See text for explanation.

Table 3 Summary of head positions as tendency indicators

Fig.	Head position/Movement	Situation
7E	Chin against throat. Horn presentation.	Carried out by (a) Dominant bulls threatening lower ranking animals. (b) Opponent bulls just prior to a head to head sparring bout. *Tendency:* Aggressive dominance.
7F	Head horizontal and held high.	Carried out by (a) Territorial males in broadside display. (b) Towards adjacent occupants and lower ranking animals. *Tendency:* Dominance or 'I am the greatest' after Walther (1974).
7G	Head nodding (up and down) i.e. flashing of white bib	Carried out by (a) Bachelor males when confronted by territorial males. (b) Females when approached by males. *Tendency:* Open submission/fear.
7H	Head and neck extended and held in low position	Carried out by (b) Bachelor males when approaching and in close proximity to territorial males. (b) Females when approached by males. *Tendency:* Submission/fear.

McIlwaine and Spinage (1969) makes no mention of its occurrence. Head-shaking from side to side (c) was not recorded by Spinage (1969) but has been recorded in this study during encounters between neighbouring territorial males. Head nodding (j) was observed frequently during encounters between territorial males and bachelors. Spinage (1969) recorded this display in Uganda but surprisingly Walther (1974) makes no mention of this activity at all. In direct contrast to the findings of other authors working on different ungulates Estes (1969) and David (1973) Walther (1966) and Schenkel (1966), head nodding in *K. ellipsiprymnus* is an appeasement tendency indicative of fear.

A downward sweep of the horns (e) was carried out frequently by territorial males when confronting bachelor males. Spinage (1969) observed this display but Walther (1974) did not. Low presentation of the horns (h) was observed in this study and by Walther (1974) but not by Spinage (1969).

In Table 4, head and neck stretch forward (i) was a common submissive display carried out by bachelor males and females when confronted by territorial males, as confirmed by Spinage (1969) but not by Walther (1974). Head flagging (k) was observed in confrontation between neighbouring territorial males at Lake McIlwaine although neither Walther (1974) nor Spinage (1969) make any mention of this display.

Table 4 Waterbuck displays — Comparisons with observations made by other authors

	Threat/Dominance displays					Appeasement/Submissive displays					
	a	b	c	d	e	f	g	h	i	j	k
Tomlinson (1978)	—	x	x	x	x	x	x	x	x	x	x
Walther (1974)	x	x	x	x	—	x	x	x	—	—	—
Spinage (1969)	—	x	—	x	x	x	x	—	x	x	—

a = Nose vertically upwards
b = Symbolic snapping (00)
c = Head shaking (side to side)
d = Head held high (proud posture)
e = Downward sweep of head and horns
f = Medical presentation of horns
g = High presentation of horns
h = Low presentation of horns
i = Head and neck stretch forward
j = Head nodding
k = Head flagging

As far as courtship displays are concerned, those described by Kiley-Worthington (1965) and Spinage (1968) were observed in this study. However, a kick with the foreleg, combined with the head and neck stretched forward (Walther 1974), was never observed in this study or by Spinage (1968).

In conclusion, there appears to be a considerable amount of variation in the waterbuck displays observed in this study and in those recorded by Walther (1974). Spinage's (1968; 1969), observations, however, are in close agreement with those made in Rhodesia and it can be concluded, therefore, that on the basis of behavioural evidence *K.e. ellipsiprymnus* and *K.e. defassa* appear to be conspecifics.

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