© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/

Studies on the Breeding Biology of the Reedbuck *(Redunca arundinum* Boddaert, 1785) in the Krüger National Park

By Hartmut Jungius

From the Institut für Haustierkunde der Christian-Albrechts-Universität zu Kiel
Director: Prof. Dr. Dr. h. c. W. Herre

Eingang des Ms.: 14. 3. 1970

Introduction

This paper is part of a field study of the reedbuck, in which the author was engaged in the Krüger National Park (KNP), from March 1967 to April 1968. The main study area was the district of Pretoriuskop in the SW of the park and the Shawu-vleis in the N of Letaba, near to the center of the park.

These areas constitute the most magnificent reedbuck habitats of the KNP. The biotope consists of tall grass savanna and tree savanna, in which *Hyparrhenia dissoluta* and *Sporobolus robustus* (in vleis) form the most important cover of all grass species. As long as water is available, during the dry season, these areas are inhabited by reedbuck all year round. The environment of Pretoriuskop appears to be a well drained, rolling countryside with insular mountains. The vleis of the north, which are mostly inundated during the rainy season, are shallow and poorly drained grassy valleys.

In these areas reedbuck ♂♂ establish their territories, which seem to be occupied permanently if the habitat is not destroyed (by fire, drought, etc.). In their territory reedbucks live in pairs (♂+♀), ♂–♂-mother-families (♂+♀+fawn or yearling, fig. 2), or in mother-families (♀+fawn stay together, the ♂ lives separately, fig. 4). For further information see: Alverdes (1925), Remane (1960), Portmann (1953), Jungius (1970). Only during the dry season are groups of more than 3 animals to be found around water holes or in favoured grazing areas. For more details see Jungius (1970).

Acknowledgements

Grateful acknowledgement is made to the Director of the National Parks Board, Mr. R. Knobel and Nature Conservator R. J. Labuschagne who provided the necessary study facilities within the KNP.

I am indebted to Dr. U. de V. Pienaar and Mr. P. van Wyk from the Department of Nature Conservation in Skukuza, who assisted with their advice and their experience. Thanks are also expressed to Mr. Brynard, the gamewardens G. Adendorff and M. G. Mostert, as well as to the African game scout Nguela.

I am very much obliged to Dr. J. Meester and Prof. F. C. Eloff from the University of Pretoria for helpful support.

I. Mating behaviour

The whole sequence of a mating ceremony, starting with courtship (premating behaviour) and culminating in copulation has only been observed three times. Sequences of premating behaviour, which did not terminate in copulation, have been observed

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/

many more times. It was possible to observe mating behaviour all year round but the main season seems to occur between May-June, during which mating has been recorded most frequently. In mating behaviour the following phases have be distinguished, (fig. 1)

1. Premating behaviour
2. Mounting and copulation
3. Postcopulatory behaviour.

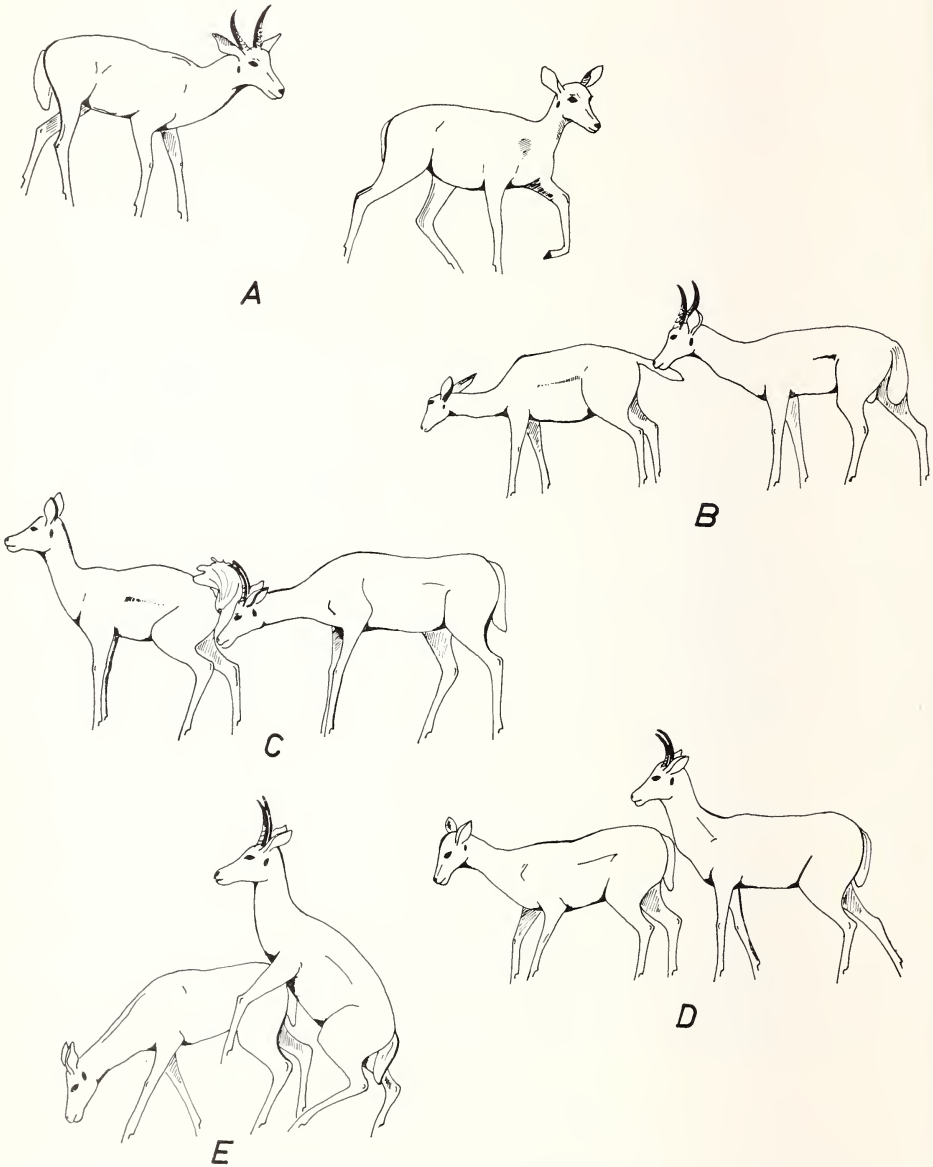

Fig. 1. Mating behaviour: A. ♂ follows ♀, B. naso-anal-contact, C. ♀ urinates, ♂ places his nose in the stream of urine, D. ♂ before mounting, E. mounting

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/

1. Premating behaviour

A ♂ approaches a feeding or standing ♀ from behind. Thereby he shows "nose forward posture"; he puts his head down, and ears back and then he starts nuzzling the base of the tail of the ♀ (fig. 1 B). Thereupon the ♀ normally adopts a submissive position ("Demutstellung") (fig. 2), she twists up her tail and urinates, jumps forward or moves only a few steps sideway (2—4 m) flicking her tail and standing still again. If the ♀ urinates, the ♂ places his nose in the stream of urine (fig. 1 C). After this he lifts his head to a horizontal position, moves it several times from side to side, retracts his lips and wrinkles his nose in the "Flehmen" posture (Schneider 1930)[1]. Flehmen was also observed after smelling urine on the ground or after smelling the resting place of a ♀. If the ♀ jumps very far away (8—10 m), after the ♂ has sniffed at her anal region, he usually does not follow. If she moves a few steps forwards or sidewards, with or without flicking of the tail, the ♂ follows her (sometimes performing a licking gesture) and starts again smelling at the anal region or licking the female's upper tail. If the ♀ moves again a few steps forward with tail flicking the ♂ follows once more and starts sniffing or licking anew. This moving away a few metres can be repeated several times, and leads to the first mounting attempts of the ♂ after he has followed the ♀ once, twice or three times. The following of the ♂ can be released as well without preceding Flehmen, either after sniffing, licking or an "invitation" of the ♀. It was once observed that the ♀ passed a ♂ for the 2nd time very closely flikking her tail; when the ♀ passed him, the ♂ followed, the ♀ stopped, the ♂ sniffed, the ♀ walked away, the ♂ followed and mounted.

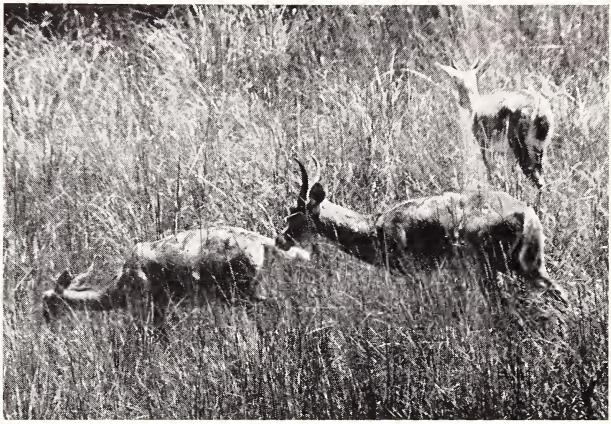

Fig. 2. ♂-mother-family (♂+♀+yearling ♂) in tall-grassveld. ♂ sniffing at the base of the tail of the ♀, ♀ adopts submissive position

Whether or not the penis was erect during one of these courtship sequences, as in the waterbuck (Spinage 1969; Kiley-Worthington 1965) or in the Uganda kob (Buechner et al. 1965) could not be observed because of the tall grass.

2. Mounting and copulation

Before the ♂ mounts he approaches the ♀ very closely (fig. 1 D). He suddenly rises on his hindlegs and throws up his frontlegs simultaneously. If mounting has been accomplished the upper part of his body leans on the female's croup, the ♂ holds his neck erect, the tail hangs freely, the forelegs clasp the flanks of the ♀ or her hindlegs (fig. 1 E).

During the first mounting attempts the ♂ does not succeed in laying himself upon

[1] This posture of "Flehmen" is widespread among ungulates, but occurs also in lions and tigers. Its function is chemoreceptory testing by means of the Organon Vomeronasale (O. Jacobsohni).

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/

the ♀. As soon as the ♂ rises on his hindlegs, the ♀ steps forwards, flicking her tail and stops, which causes the ♂ to drop on to his forelegs again. He does not follow the ♀ on his hindlegs as do impala (Schenkel 1966) and gerenuk (Backhaus 1958). After some fruitless efforts the ♂ usually succeeds in laying himself on the female's rump, but usually the ♀ moves a few steps forwards again (2—3 m) and the ♂ glides down, touching with his neck the rump of the ♀ and dropping back on to his forelegs.

The ♂ follows the ♀, licking or sniffing her tail. The ♀ moves away in wide circular paths (once in a closed circle, diameter 6—8 m). Mounting occured at intervals of 8—15 sec. With increasing frequency (3—53 times) it became more intensive, because the ♀ stayed still longer (3—6 sec.) so that the ♂ was able to lean high on the ♀. Chasing the ♀ with "Laufschlag" (Walther 1958)[2], as is typical for many antelopes (see below), has not been observed.

Only once has similar behaviour been noticed. A ♂ repeatedly tried to mount a ♀ but in vain, because she always moved away. The ♂ stood on one foreleg, the other foreleg was lifted and stroked the outside of the hindleg of the ♀ in a curved position. This was probably intended to lead to mounting but this was not accomplished because the ♀ stepped forward. It is still debatable whether it is possible to assume that the Laufschlag originates from this intentional mounting movement which occurs in many ungulates (Walther 1958). Walther (1958) explains Laufschlag as a ritualised aggressive motion, which derived from "Drohscharren" (pawing threateningly), or from "Feindabwehr" (aggressive behaviour); Backhaus (1958) explains Laufschlag as a displacement activity deriving from the process of taking food by pawing.

Despite frequent mounting by the ♂ it is possible that the ♀ does not permit copulation.

Observation No. 1: A ♂ is in the territory of his neighbor; he chases him away and tries to copulate with his ♀. The ♀ allowes mounting but not copulation. She defended herself as follows: stepping forward, short turns of 90° or 180°, kicking. The ♂ mounted 53 times without success and after an interval of 12 minutes another 25 times, but also in vain.

If copulation takes place, it happens during the last mounting. The ♂ maintains the same position, but clasps the flanks of the ♀ very tightly with his forelegs and gives a vigorous ejaculatory thrust, after which he dismounts. This last mounting is very quick and lasts about 2 seconds.

3. Postcopulatory behaviour

Immediately after dismounting ♂ and ♀ stand immobile for a few seconds. Then the ♂ walks to the ♀, licks her neck or possibly rubs it with his head for 4—6 sec. Because of the tall grass it could not be observed if this action is followed by a Laufschlag as has been observed in the case of Uganda kob (Buechner et al. 1969). After this the ♂ starts feeding or shows grooming behaviour. The ♀ mostly licks her flanks or her back and starts feeding as well.

4. Comparison of the mating behaviour of the reedbuck with that of other antelopes

To secure successful copulation it is necessary that the behaviour pattern of ♂ and ♀ are co-ordinated. Normally approaching within a definite distance of an animal results either in flight or aggression. But to assure copulation these reactions have to be suppressed. Therefore so-called "Beschwichtigungsgebärden", (appeasing ceremony; Tinbergen 1953) are performed, which remove the barrier between ♂ and ♀ (Eibl-Eibesfeldt 1966). In each species mating takes place according to a certain pattern.

[2] The ♂ touches the underparts of the ♀ with his stiff foreleg in the flanks region from the side, or between the hindlegs from behind, or laterally strikes the outside of the hindlegs.

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/

Very often small, but significant, divergencies from this pattern are the reason why no interbreeding occurs between closely related species. Therefore these behaviour patterns make it possible to distinguish between closely related species within systematic groups. Thus it is striking to notice that no chasing occurs during the premating phase in the reedbuck nor in other species of the genus Reduncini: Uganda kob, (Buechner et al. 1965) and waterbuck (Kiley-Worthington 1965; Spinage 1969), although it has been recorded in many gazelles (Brooks 1961; Walther 1958, 1968), impala (Schenkel 1966) and also in the roe deer (Kurt 1968).

If a ♀ of the Uganda kob stops within the territory of a ♂ he approaches with a stiff-leged gait of short, accentuated steps ("prancing") and starts nuzzling the inguinal region of the ♀. After this the ♀ urinates and often the ♂ places his nose in the stream of urine (like the reedbuck) and shows Flehmen (like the reedbuck). A similar behaviour pattern is to be found in the waterbuck (cit. above). Prancing does not occur, but the ♀ stands still and urinates or jumps a few steps forward when the ♂ starts Laufschlag, rubbing, smelling or licking of the anal region. Flehmen of the ♂ is similar to that in the case of the reedbuck. With the impala for instance (Schenkel 1966), Flehmen does not play a fixed part in premating behaviour and gazelles usually take the scent from the ground (cit. above).

After Flehmen, chasing ("Treiben") of the ♀ starts in gazelles, caused by the Laufschlag of the ♂, evoking avoidance behaviour in the ♀. In the reedbuck this has not been observed, but it is known in the waterbuck (cit. above), Uganda kob (cit. a.), puku, lechwe (Robinette et al. 1964; de Vos et al. 1966) and other antelopes, for example sable, (own observation in zoos) roan (Backhaus 1958), duiker and steenbuck (own observations, KNP). This behaviour does not occur in the Bovini and in the genus *Tragelaphus* (Backhaus 1958; Walther 1964). Before mounting takes place the ♀ of the reedbuck does move forward as well, but this happens slowly and only a few steps are taken. Tight circling of ♂ and ♀, "Paarungskreisen" (Walther 1958) does not occur, as Walther describes it in gazelles (1958, 1968), Backhaus (1958) in oryx *(O. algazel),* nilgau, nyala and sable, Buechner et al. (1965) in Uganda kob, Kiley-Worthington (1965) in waterbuck.

Mounting with head erect, such as does not seem to occur in all *Tragelaphus* sp. (cit. a.), is to be found in the reedbuck, as well as in the waterbuck, Uganda kob, Hippotragini, duikers, and (all?) Neotragini (cit. a.). The position during copulation of the reedbuck is similar to that of the kob and the waterbuck. On the other hand, many gazelles (cit. a.) and impala (cit. a.) hold the neck and the body in a raised position. The ♂ does not lean on the female's croup, nor does he hold her loins with his forelegs; he rushes forward on his hindlegs bipedally to perform penetration, which does not last longer that one second in impala (Schenkel 1966).

The postcopulatory behaviour of the reedbuck is very different from that of other Reduncini. Nothing similar to the Uganda kob has been observed (cit. a.), such as whistling, licking of the erect phallus, licking of the vulva, nuzzling of the inguinal region, licking of the udder or Laufschlag. In the waterbuck as well an intensive pattern of post copulatory display is obvious, although there is a quiet period of 1—4 minutes, during which both partners stand immobile. After this the ♂ may repeat mounting without erection, Laufschlag, rubbing his face against various parts of the female's body, smelling of the vulva, Flehmen.

All aggressive behaviour patterns as they have been observed for instance in impala (cit. a.) are absent in the mating behaviour of the reedbuck, as well as "pronking" with erected tail, as has been stated in the case of the Bohor reedbuck (Redunca redunca wardii) by Versey-Fitzgerald (1958). After copulation, the reedbuck is very inactive like the gazelles (cit. a.) or the hartebeests (Backhaus 1958).

If compared with other Reduncini, mating behaviour in the reedbuck (so far as

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/

known), seems to be relatively uncomplicated. It is not composed of as many different sequences as is the case with other species. Although there are similarities to be found in mating behaviour in which the Reduncini differ from all other species, for example in courtship during the phase of premating, in mounting and in the position during copulation, there exist distinct differences in mating behaviour between the reedbuck and most of the Kobus sp.: Laufschlag, prancing, whistling, smelling of the inguinal region and tight circling ("Paarungskreisen") do not occur. Until detailed informations exist from *Redunca redunca* and *Redunca fulvorufula,* it seems justified to state that there are profound variations in mating behaviour between the genus *Kobus* and *Redunca,* even though there are certain similarities.

II. Reproduction

All information available on this problem is very contradictory.

1. Kirby (1896): Lambs are born between December and March and in the plains earlier than in the mountains.
2. Wilhelm (1933): Between December and May.
3. Stevenson-Hamilton (1947): In East-Africa between August and September.
4. Zuckermann (1953): In the London Zoo all 7 lambs were born between October and May, (northern hemisphere!).
5. Asdell (1946): Between August and May, no definite season.
6. Brand (1963): Zoo of Pretoria, all year with a peak between February and May.
7. Fairall (1968): KNP, not much information; young fawns have been observed throughout the year.

According to my own observations (3.67—4.68) the peak of reedbuck births seems to be between December and April, when pasture, water and cover are abundant. Particularly in the N some lambs have been born in wintertime and in spring (May-November), as well as during an unfavourable season. If these observations are compared with those of the authors mentioned above, one may conclude:

1. The reedbuck is not a strictly seasonal breeder. Lambs are born throughout the year. (Brand, Asdell, Fairall, own obs.).
2. Most of the lambs are born between December and May (Kirby, Wilhelm, Asdell, Brand, own obs.).

Hence we may infer that the reedbuck belongs to those African antelope species that have a lambing peak. But relatively few are strictly seasonal breeders and the presence of young fawns throughout the year indicates that the reedbuck is no exception, just as waterbuck (peaks in summer and spring), bushbuck, sable, duiker, steenbuck (?), (Fairall 1968).

It is difficult to determine the gestation period of the reedbuck, because seasonal rut does not occur (mating has been observed in June, July, December), and lambing thus takes place all year round. Brehm (1930) records 7³/₄ months (Zoo Frankfurt), Wilhelm (1933) states 7³/₄ months for SW-Africa (soucre unknown), Kenneth (1943) refers to Wilhelm and gives 233 days. Asdell (1946) and Brand (1963) refer to Kenneth.

As mentioned above, lambs are born all year round. This can be caused by a miscariage after which the ♀ comes into heat again outside the normal rutting season, (so-called "Folge-" or "Ersatzbrunft", Prell 1937), during which she is mated again. Cases like this are well known from our European game species (Prell 1937). With regards to the reedbuck I could observe that this "Ersatzbrunft" also occurs if ♀♀ lose their lambs to predators during the first weeks after parturition (see above).

Observation No. 2: A ♀ had dropped her lamb between 17. and 20. 12. At the age of about 2 weeks on 3. 1. the lamb was killed. Some days later this ♀ was observed with a ♂.

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/

8. 1. mating took place. If fertilization was achieved, the new fawn would be born in September (gestation period as mentioned above).

An other possibility to explain births throughout the year, could be due to delayed implantation, as is known in the case of the roe deer (Prell 1938) and some Mustelidae. In the roe deer a variation of the gestation period has been found in those ♀♀ which reproduced only once. In these young ♀♀ the control and regulation of the endocrine system, which partially determines reproductive behaviour, has not been fixed as in old ♀♀. Therefore an extension or an abridgement of the gestation period may occur. In the roe deer this is well testifield (Prell 1938). Theoretically similar cases could appear in other species as well and thus be a further explanation for the appearance of young ones throughout the year.

According to Dittrich (pers. com. 1970), so far no signs of delayed implantation have been found in antelopes (Zoo of Hannover), and he explains the birth of fawns throughout the year by the fact that young ♀♀ reach maturity at different times and also because some fawns are lost in the first weeks after parturition (see above) and thus the ♀ comes into rut outside the normal season. But until further investigations have been undertaken, I would not totaly deny the possibility of delayed implantation in antelopes, which would be an other step towards understanding all year round reproduction.

III. The mother-child bond

During the time of my studies I succeeded in observing the bond between ♀♀ and older lambs (from 3—5 month of age) throughout the whole year. It was very difficult to observe younger animals, on one hand because of their low activity, on the other hand due to the tall grass which provides a good cover, but primarily because of the great vigilance and the secluded life of the mother. Some observations on lambs aged between 2 and 3 months have been made in April and May. Once it was possible to make a continuous observation for 8 days in December of a lamb (L 1) about 10 days old.

A. The period before parturition

1. The separation of the ♀

Observations have particularly been carried out on the ♀ of L 1. Heavily pregnant ♀♀ leave the family unit (♂, ♀, yearling) 3—4 weeks before giving birth. They avoid meeting the ♂ and withdraw mostly into the outskirts of the territory. The ♀ does not show any relationship to the ♂ and thus she usually lives alone during this time. Only her lamb born in the previous year stays with her. Before I found L 1 (27. 12.) the ♀ had been observed for the last time with the ♂ on 2. 12. and thereafter only with the yearling. ♂ and ♀ did not meet even though they were once found grazing only 60 m away from each other. On December 12th, restless wandering around of the ♀ was observed for the first time, obviously as an attempt to discourage the further company of the yearling, as the time had approached for her fawn to be born and thus it became necessary for her to retire into isolation and find a suitable place for giving birth. During 30 minutes 800 m were covered. The borders of the territory were crossed.

Similar behaviour has also been observed in an other ♀ which was heavily pregnant and still accompanied by her lamb of the previous year.

Observation No. 3: 15. 4. 68 Pretoriuskop
8.15 ♀ and yearling ♂ (1 year and a half) get up, graze.
26 ♀ runs 5 m, lies down.

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/

27 ♂ follows, still grazing.
28 ♂ is 3 m away from the ♀; ♀ gets up, shakes her head, adopts submissive position, runs 8 m, doubles, stops, licks her flanks; ♂ follows slowly.
31 ♀ runs away, ♂ follows at a distance of 13 m. After 50—60 m the ♀ slows down, walks 8 m and lies down.
33 ♂ has followed; ♀ gets up walks 8 m.
36 ♀ lays down.
37 ♂ lays down at a distance of 10 m.
47 ♂ gets up, passes the ♀ and lies down 4 m away from her.
10.10 ♀ gets up as does ♂; both clean their fur; ♀ walks 10 m and lies down.
14 ♂ follows and lies down 2 m away from her.
12.15 ♂ rises grooming himself; ♀ gets up, grooming herself and defecating.
17 ♂ walks up to ♀.
20 ♀ runs away flicking her tail; ♂ follows. After 30 m the ♀ starts walking, walks 10 m and lies down; ♂ is grazing.
50 ♀ gets up and starts grazing.
14.10 ♀ lies down; ♂ is grazing nearby, lies down 4 m away from the ♀.
47 ♀ rises, grooming herself, and starts to graze.
49 ♀ lays down at a distance of 15 m from the ♂.
16.51 ♀ gets up, grooming herself and grazing.
52 ♂ rises and grazes.
17.30 the observation was stopped; both animals were still grazing.

The most remarkable point of this observation was that the ♀ attempted again and again to widen the distance between her and the yearling ♂, and once she even adopted a submissive position when the yearling approached too close.

It is not known with certainty when the relation between ♀ and yearling actually breakes up. In the ♀ of L1 the separation from the yearling must have taken place about 5 days before the new lamb was born. Both, ♀ and yearling were seen together on December 15th, and the lamb was born shortly before December 20th, or a few days later.

This separation of the ♀ before giving birth is very common in ungulates which live in small groups (bushbuck, duiker, Neotragini, small Cervidae). It also occurs in some gregarious species like impala, where the heavily pregnant ♀♀ leave the herd and give birth in the isolation of dense undergrowth or in the cover of a bush thicket. The newly born fawn follows its mother only after a few days (Schenkel 1966). In the Grant's gazelle (Walther 1965) similar behaviour seems to occur (observation in the Ngorongoro crater). In other species, like the wildebeest, the young ones are born in or near the herd, without isolation of the ♀ (Talbot & Talbot 1963). Very exact studies of the female's behaviour before giving birth exist on our indigenous deer species as the roe deer (Kurt 1968; Bubenik 1965) and the red deer (Bubenik 1965). In the roe deer, which lives in small groups like the reedbuck separation of the ♀ from the yearling before giving birth has also been observed. It is clearly shown by display and threatening behaviour in the ♀, by which she tries to establish a larger distance (so-called individual distance) between herself and the yearling and to shake him off. The separation occurs some days before the fawn is born.

2. *The choice of the place for parturition*

The mother of L1 gave birth high on the slope, directly at the foot of a mountain in the open tall-grass-veld. This place belonged to the outskirts of the territory and was remote from the core-areas of other reedbuck territories, as well as from those of other species. Because of bordering at the mountain, the area was very peaceful. Only a bushbuck-family and a pair of klippspringers lived around this mountain. However the bottom of the valley was often traversed by kudu, giraffe, sable, reedbuck, and wildebeest and was thus not as undisturbed.

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/

B. The first weeks after parturition

1. Hiding of the young („Abliegen")

In the young of ungulates, WALTHER (1958) distinguishes two different types according to varying behaviour pattern. Those are: "Nachfolgertyp" and "Abliegetyp".

In the "Nachfolgetyp", as for instance in the wildebeest, the calf follows its mother 5—10 minutes after parturition and always stays with her.

In the "Abliegetyp", as is kudu, waterbuck, gazelles (ESTES 1967, WALTHER 1958, 1968) and the reedbuck, the young one does not follow its mother after birth. During most of the day the lamb remains constantly hidden in dense cover. The mother mostly remains in the vicinity or stays a few 100 m away. If not disturbed she regularly visits the lamb in the course of the day (once in the case of the reedbuck), to nurse and to clean it, whereupon the lamb hides itself again from its mother.

This hiding is a deliberate action on the part of the lamb, undertaken without guidance or influence from its mother. This applies to the reedbuck as well as to kudu, gazelles, roe deer (KURT 1968), Grant's gazelle (WALTHER 1965; ESTES 1967), lechwe and puku (DE VOS et al. 1966). The ♀ was not observed to nudge the fawn into a lying position as RUE (1962) recorded in the case of the white-tailed deer, and ALTMANN (1965) for the wapiti.

The ♀ does not follow the lamb when it seeks a suitable place but observes it before moving away and evidently memorizes the place where it lies down. Comming back to visit her lamb, she usually approaches it from an other direction, and seems to orientate herself optically and olfactorily. Particularly during the night time orientation seems to be mainly olfactorily.

It is assumed with great certainty that this concealment period of the lamb is well demonstrated during the first 1½—2 months, but possibly even longer (3 months). It is hard to give exact information on this because it was very difficult to determine the age of lambs exhibiting this behaviour and it was only possible by comperative field-observations; moreover, only few lambs have been seen due to this habit of concealing themselves.

As to the mother-child relationship during the first weeks after birth, only one observation of 8 successive days has been made (♀ of L 1) from 27. 12.—3. 1. Although these observations were only of short duration, it is possible to distinguish a distinct activity pattern, due to its repeated periodicity (fig. 3).

♀ and lamb rest before sunrise. The ♀ lies 20—30 m away, (minimum 5 m, maximum 80 m). Between 9 and 10 o'clock the ♀ gets up, grooms herself, looks around carefully and starts grazing. If she has rested near the lamb she starts grazing in a wide circle, working away from the lamb but later returning. If the distance between her and the lamb was greater (80 m), she starts grazing in the direction of the hiding place of the lamb and lies down 5—8 m away from it. The lamb does not show any reaction while its mother approaches and stays lying down. While grazing, the ♀ does not cover large areas but stays at a distance of 20—30 m from the lamb's hiding place; she grazes about an hour.

Between 11 a. m. and 2 p. m. the only diurnal visit of the lamb by the ♀ was confirmed during a second grazing period. But this happens only when the ♀ has not been alarmed or badly disturbed. If alarmed, the ♀ would become very vigilant and nervous; this often results in the lambs not being visited during the day time (30. 12.), fig. 3.

The resting and hiding lamb was either approached in a straight line, in a circle or in a zigzag by the ♀ while she was grazing. Sometimes the ♀ walked the last 5—10 m without grazing, but stopping repeatedly to observe the lamb; for instance

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/

she would lower her head as if about to start feeding and then suddenly look up, remaining motionless, or stop suddenly and adopt a watchful posture (every 1/2–2 m), looking around carefully. When she was 1–2 m from her lamb she stopped again and cautiously examined the environment. At this moment the lamb might get up and bound to its mother. If the lamb remained lying down, the ♀ approached with lowered head and started to lick its body until it rose.

Calling of the lamb by its mother or vice-versa has not been heard as was recorded in the case of the Uganda kob (LEUTHOLD 1967) and the waterbuck (SPINAGE 1969). The activity bond of the lamb which now starts when visited by its mother, is composed of the following: it is cleaned with thoroughness and nursed and jumps and walks around. This activity lasts not longer than 10–30 minutes. During all this the ♀ remains in the same position in a watchful posture.

After this period of activity, the lamb turned away from the mother and looked for a suitable hiding place, usually 3–10 m away from the ♀, and lied down. The ♀ remained at the same place and stared at the spot where it disappeared; then she started ruminating or grazing an bedded down as well or else walked slowly some meters away, grazing and watching. After this she lied down and rested until it got dark. The distance between her and the lamb was about 5–25 m as in the morning.

Other observations of lambs that were a little bit older (1–2 months) showed the same activity of the young one, starting only with the arrival of the ♀. Therefore it is supposed to be the fundamental behaviour pattern during the hiding period, with this one difference: in autumn, lambs were active in the morning and after sunset; (fig. 3, 21. 6.). Lambs in December were active in the early afternoon.

During night time an other meeting must have taken place between mother and L1 regularly, because in the next morning the lamb was always found in a new place

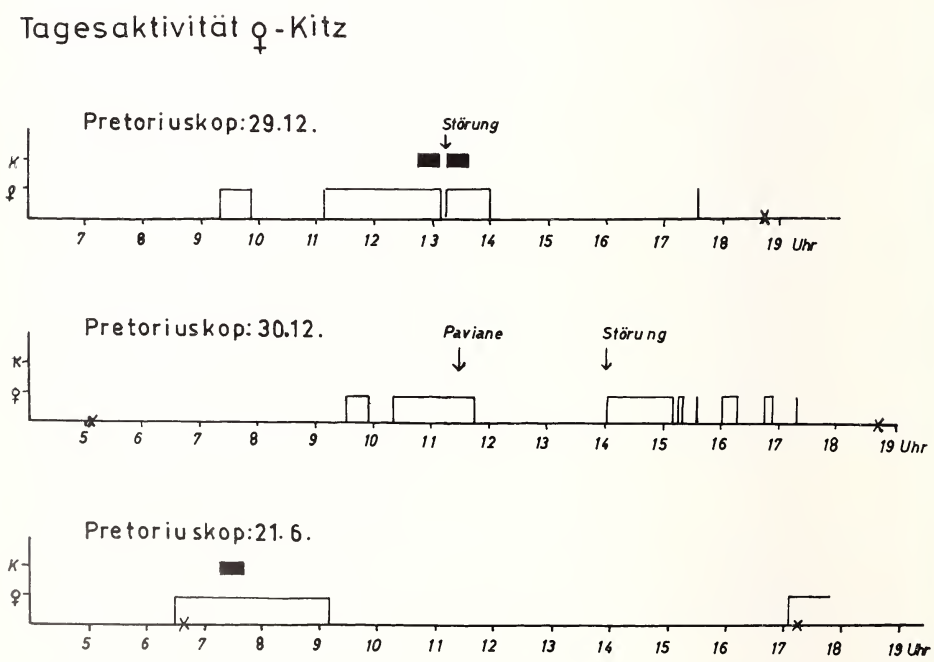

Fig. 3. Daily-activity of ♀ and very young lamb (K) (black: activity of fawn, Störung: disturbance, Paviane: baboons x sunrise, sunset)

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/

15—60 m away from the previous one. Within 5 days 150 m were covered. The same hiding place was never used twice.

Until they are 2 month old all lambs seem to leave their hiding place only after the ♀ has arrived ("festes Abliegen"). Later it happens frequently that they graze with their mother (fig. 4), but after grazing or when alarmed (avoidance of predators, see below), they still hide themselves deliberately, and the ♀ takes up her resting place nearby (40—150 m). About 4 months after the birth of the lamb, the ♀ and the lamb (mother-family, see above) join the ♂ (Jungius 1970) and form the so-called ♂-mother-family (see above). Even now the lamb still partly keeps to his hiding habits and leaves the ♂ and ♀ when bedding down. I have repeatedly observed that young ones start resting earlier than the adults and also appear later (20—30 minutes) in the evening, when ♂ und ♀ are already feeding.

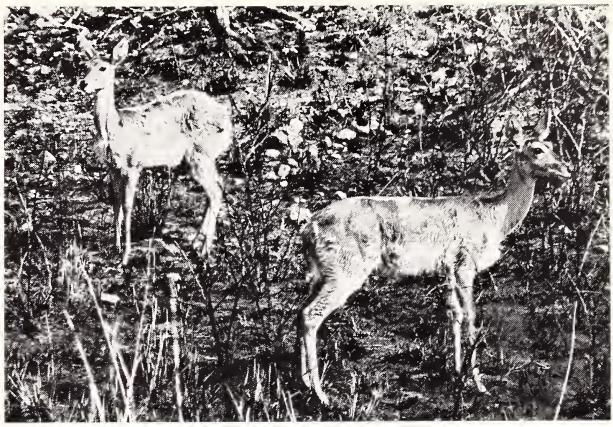

Fig. 4. Mother-family on burnt veld, lamb about 4 months old

As they grow up (3—4 months) behaviour regarding "Abliegen" changes. The lamb not only hides but also gets up independently. More than once it has been observed that the ♀ returned to her resting lamb and started grazing 10—30 m away, constantly observed by the young one. As mentioned above, the lamb got up after at least 30 minutes and ran up to the ♀. Sometimes a greeting ceremony took place (Jungius 1970) but often the lamb started grazing near the ♀ without taking any particular notice of her presence.

3. Grooming behaviour

The first action af the ♀ after having approached the resting lamb is licking. This starts at the anus (fig. 5 B) during which the lamb stands immobile with its tail twisted up; then the ♀ continues licking it, progressing from the back to the flanks and then to the head (fig. 5 C), after this she sometimes starts at the anus again. The whole ceremony can last about 8 minutes, at intervals of 1—2½ minutes and at any time during this period of activity.

The first licking period just after ♀ and lamb have met is the longest and is carried out most carefully. Licking stops only when the lamb starts to suckle or to walk around. It may happen that the ♀ follows still continuing to lick its anus, which makes it stop and twist up its tail again. During nursing, licking of the anus or of the body may occur as well, but this is only of short duration.

The significance of this anal-licking by the ♀ has already been stated by Hediger (1949). According to him, this stimulus is necessary during the first weeks of life to effect urination and defecation in the lamb. The first autonomous performance of grooming behaviour has been observed in lambs about 2 weeks old. It consisted in licking of flanks and back.

It seems that lambs older than 4 months are only cleaned after the ♀ has been animated. For that purpose the young one walks to the ♀ and touches her nose or the sides of her muzzle with its nose. Then it presents that part of the body which it wants

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/

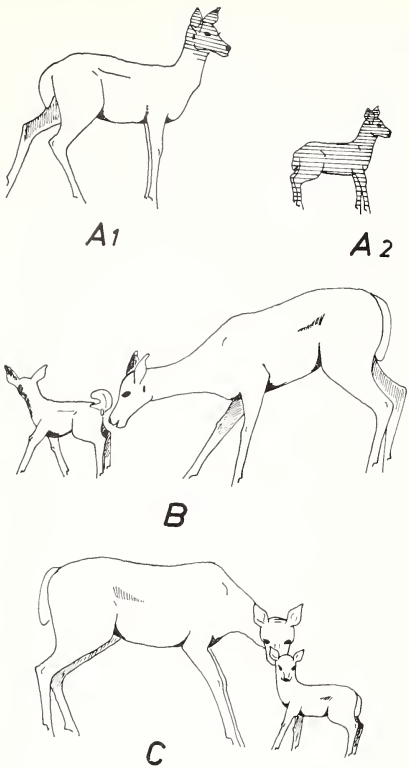

Fig. 5. Grooming behaviour: A1, A2. hatched parts are groomed by the ♀, B. licking of the anus, C. licking of the body

to be cleaned, either the head or the ears (fig. 5 A 1). Thereupon the ♀ starts licking the head very carefully and sometimes the neck as well. The ears are licked inside or outside or cleaned by the mother's rapidly nibbling incisors; sometimes they are taken into the mother's mouth and then pulled through between incisors and upper jaw by the mother throwing back her head (up to 5 times). If the ♀ stops before the lamb is satisfied, the latter lifts its head with its nose pointing upwards and the ♀ continues. This behaviour pattern seems to be wide spread in ungulates, because it has also been observed by Kurt (1968) in the roe deer. After 6—8 months the young animal usually masters the technique of scratching its muzzle, cheeks and ears with the hoof of a hindleg and thus all further assistance by the ♀ is unnecessary.

4. *Nursing*

When the lamb (L 1) was just a few weeks old, (8—14 days), only a single diurnal nursing took place (observation from sunrise to sunset).

One observation proved that it may go a whole day without being nursed.

Observation No. 4; 30. 12. 1967 Pretoriuskop (fig. 3).

Time of observation: 4.30 a. m. — 6.30 p. m. (14 hours). The ♀ tried twice to visit the lamb. Once it was disturbed by baboons, an other time it was alarmed by something unindentified. As a result she always grazed around the hidingplace of the lamb but did not approach and establish contact.

If no disturbance occured, a single nursing period took place around noon. After the lamb had been licked by its mother and after it had run around for a while, it went to the ♀, put its head under her belly and found the udder at once, without being pushed or nosed into the sucking position. The young reedbuck suckles calmly and continuously in a standing position, not kneeling down. The duration of suckling varied from $2^1/_2$—$4^1/_2$ minutes.

Comparison with other species: Observations on the nursing behaviour except the waterbuck (Spinage 1969) do not exist for species closely related to the reedbuck. A comparison with fawns of the roe deer (Bubenik 1965), red deer, the waterbuck (Spinage, 1969) and other antelopes show that this is an extraordinarily long period of nursing.

In the fawn of the *roe deer* 9—11 nursing periods occur within 24 hours, and 4—6 periods during day-time. The suckling periods are very short and last about 30 seconds; thus the whole period of food intake is 2—3 minutes per day. In the *red deer* there is a different behaviour pattern, corresponding to some degree with that of the reedbuck. Between two to four weeks after birth, 6 periods of sucking, lasting altogether about 600 seconds, have been observed in 24 hours. The ♀ did not allow nursing of the calf

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/

at any time but only during certain periods of the day and during the night. The calfs nursed for periods of 1—3 minutes. In daytime the nursing period was longer than during the night.

WALTHER (1968) noted 3—5 periods of sucking in the *Grant's gazelle* during 24 hours of field observation. During day time the young ones nursed at intervals in the morning, during noon and in the evening. The duration of each period varied from 30 sec. to 5 min. Very long suckling is recorded in the *waterbuck*, (SPINAGE 1969). A 6 months old calf was timed suckling for 9 minutes.

This single diurnal nursing period and the long duration of suckling in the reedbuck lamb, which occurs either in the morning (June) or at noon (December), certainly has to be related to its low activity rate, due to its concealed behaviour ("Abliegen"). This behaviour pattern constitutes essential means of protection for the young animal. Walking around of the ♀ is reduced to a minimum and the infant exposes itself only during a relatively short period and spends the rest of the day in cover.

Suckling has still been observed in lambs 3—4 months old that already grazed with their mother. Frequently the young animal only commenced to nurse when its mother was busy looking around or while she was in a watchful posture. The ♀ either interupted its nursing by turning away or stepping forward. If she continued watching, the lamb very often succeeded in suckling for about one minute.

5. *The behaviour of following in the lamb*

During the first weeks after birth the lamb hardly ever follows its mother. If it does follow her, this is just for a very small distance and only takes place when danger forces the ♀ to move into an other area. A complete change of this behaviour is accomplished as the lamb gets older and as behaviour of hiding ("Abliegen") disappears (see right). During the first weeks of its life the lamb left its mother to hide itself in dense cover, but as it gets older it starts to follow her. The young reedbuck does not follow continuously, at a certain distance, but at intervals. The young animal waits until its mother has advanced for about 15—30 m and then follows at a canter and stops 1—2 m in front of her or beside her. If the ♀ has passed by again and sets up a distance of more than 15 m between herself and her lamb, the latter follows once more. The lamb follows without invitation of the mother. As the reedbuck gets older (about 8 months) this behaviour is gradually lost and it happens more and more often that the young reedbuck walks at the same pace as its ♀, either following at her side or diagonally behind. At this age it also happens that young reedbuck join other ♀♀ or families (fig. 6). They graze, drink, rest and move around with them. Conflicts have never been caused by this behaviour and it can be assumed that young

Fig. 6. Mother-family joined by an other lamb

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/

reedbuck are also tolerated by other ♂♂ and ♀♀ and are not chased away. This process of following other adults occurs particularly when reedbucks associate in large groups and when many ♀♀ rest with their young ones in a confined area in visual range (Jungius 1970), In the Shawu-vleis it was very common for lambs of about 6 months to join other ♀♀ or families on burned areas during winter-time.

Observation No. 5: A ♀ gets up and moves towards a water hole. After she has walked for 20 m a lamb rises and follows; both pass an other ♀ at a distance of 10 m. The fawn of this second ♀ rises and joins them (fig. 6) while the ♀ remains lying down. All 3 approach the water and drink; then they return the same way, the 2nd lamb following behind. When passing the ♀, this lamb leaves the others and lays down beside her. The ♀ shows no reaction.

A group composition like this can exist for a whole day.

6. *Avoidance of predators*

In the "Nachfolger" (see above), which also could be called "nidifogous" (as in birds), the nervous system and the organs for movement are usually well developed and the young ones are able to follow their mother shortly after parturition, as for instance in the wildebeest (Talbot & Talbot 1963), (nidifogous young in mammals, Portmann 1953). On the other hand these physical abilities develop only very slowly in the "Ablieger" (see above) or "nidicolous" young.

The reedbuck that grows up in the cover of tall grass does not possess the skill and speed to escape its enemies during the first weeks of its life. Favoured by its habits and due to its concealment discipline its best means of survival appears to be avoiding detection by remaining immobile during the day and motionless when danger is near or pressing itself as close to the ground as possible so that less of it is visible. This hiding instinct is so much a part of the young animal's behaviour pattern that it does not run far if an enemy approaches within the distance (5 m for a human), which releases the flight reaction (Hediger 1934). In a clumsy canter it heads for the next cover and hides again. Older lambs (about 3 months) also run only as far as the next cover into which they disappear, although they are able to escape at considerable speed. This typical flight pattern of the young becomes evident when lamb and ♀ are alarmed together. The ♀ will escape with great leaps, while the young one lies down where it is and skulks or else runs only as far as the nearest cover where it hides.

Similar behaviour is also known in other "Ablieger", for instance puku and lechwe (de Vos et al. 1966). In the waterbuck I was able to observe this myself:

Observation No. 6: A waterbuck calf was together with 2 ♀♀. When approached, the ♀♀ ran away as did the calf, but only for 8 m and in a different direction, disappearing into thick cover. Here it lay down with its head upon the ground and its legs placed under the belly ready to jump up. When approached to within about 3 m it bounded up and ran slowly for about 30 m heading for a bush thicket at a clumsy canter, where it hid again.

If a reedbuck lamb runs away for a short distance with its parents it can happen that it runs in front "flagging" its tail (tail twisted up), behaviour which has never been observed in adults. This seems to be not the execution of a flight releasing signal, but an expression of excitement, as it is also performed in play (Jungius 1970). If panicked by its enemies or if scared by something else, the lamb may utter a bleating sound of distress or of fear which calls in the ♀ immediately if she is in the vicinity, releasing her protective instinct. In L1 this behaviour has been observed three times. The example below may elucidate this defence reaction:

Observation No. 7: 30. 12. 1967 Pretoriuskop. The ♀ walks to the water hole and is about 200 m away from the hiding place of her offspring. When she hears the noice of baboons in the distance, she stops, faces into that direction and runs straight back. Near the lamb she starts walking and approaches with caution until she is 10 m away from its hiding place; here she

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/

stops and looks around. When she notices that the baboons have passed by she starts grazing and 6 minutes later lies down.

On January 1st an encounter took place between this lamb and baboons in the course of which the young reedbuck was killed.

Observation No. 8: Pretoriuskop

10.00 ♀ rests 150 m away from the lamb.

12.40 Baboons approach the hiding place of the lamb; the ♀ gets up, the lamb bleats twice and the ♀ runs to where it is and rushes into the middle of the baboons. Some baboons withdraw from the reedbuck. When the ♀ begins chasing by galloping towards them, some escape into trees, while those which were further away withdraw and leave the ♀ alone. She continues to pursue all baboons within a radius of about 30 m and chases them up into trees. This lasts until 12.50. From now on she concentrates only on those sitting in 3 trees (4, 6, 5 animals) in the immediate vicinity (15—30 m) of the hiding place. The ♀ patrols from one tree to an other and attempts to prevent the baboons from leaving them. But as soon as she turns away from a tree, some of the baboons try to climb down. If they succeed before the ♀ noticed their intention, they run away very quickly. Therupon the ♀ returns and looks up into the tree and the remaining baboons climb up again.

13.30 The last of the baboons manages to escape.

14.00 All baboons return from the same direction, the ♀ starts chasing them again.

14.25 All of them have left; the ♀ restlessly moves too and fro.

14.28 ♀ lies down.

During this whole action the ♀ was not attacked once. But despite this, one of the baboons must have managed to catch and kill the lamb. I found it only the next morning, 25 m away from its hiding place of the day before; the head was smashed and everywhere typical feeding marks of baboons could be found.

A similar defensive action by a reedbuck ♀ has been described by Millar (1899): A dog flushed a reedbuck lamb and chased it. When the dog was about to catch it, the lamb bleated. The ♀, which was resting 180 m away, got up, looked around and ran out to help her offspring. She passed the dog, jumped over it and kicked at it with her hindlegs. As a result the dog stopped the chase and ♀ and the lamb escaped.

Here as well as in the observation made above, the ♀ arrived when called by the lamb. A similar behaviour of boldness and aggression is also recorded for a waterbuck ♀ by Spinage (1969). So far it is not known from other species more closely related to the reedbuck such as lechwe and puku (de Vos et al. 1966). A thorough investigation on the defence reaction of the ♀ caused by the call of her fawn has been carried out by Kurt (1968), in a study on the roe deer. Kurt worked with sound-recordings which he played back to different ♀♀. He found out that the reaction of the ♀ to the call of the fawn is an innate releasing mechanism (irm), which becomes only effective after parturition. The relation between the call of distress or fright and the mother's own fawn is only learnt later.

In connection with the concealment activity of the young and the avoidance of predators, it has been mentioned again and again that it is difficult for carnivores to detect hiding lambs, because they have no scent of their own. But Bubenik (1965) proved that dogs are able to discover fawns of the roe deer during the first weeks after birth. Moreover, one must realise that during nursing saliva and milk are mixed and rubbed into the fur, where they produce a scent. Furthermore the fawn is licked thoroughly by its mother and thus comes into close contact with the odour of her body. It thus seems questionable to assert that a fawn has no scent of its own. It is more likely to be the case that a fawn's scent is reduced due to a certain behaviour pattern:

a. during the first weeks of its life the fawn requires the active stimulus of licking by its mother before it can urinate or defecate. In doing so, all faeces that would leave a very strong scent are devoured by its mother (cit. above).

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/

b. In order to hide, the fawn leaves its mother and her scent track, thus preventing a great deal of her scent from being carried into its hiding place.
c. The same hiding place is never used twice.

7. *Disruption of the bond between mother and lamb*

The mother starts to reject the yearling a few days before she gives birth to a new fawn (see above). After being separated from the ♀, the yearling does not leave the territory at once. During the first days or weeks it may stay alone but then sometimes associates with the ♂ for a while. Yearlings ♂♂ stay with the ♂-♀-family (fig. 2) until an age of 2—2½ years (Jungius 1970). Then they leave the family unit due to the increasing aggression of the adult ♂. Heavy fighting has never been observed, but there is a permanent belligerence between them both. If vigorous pushing started, the yearling ♂ usually adopted a submissive gesture very soon and jumped away. Pursuit or chasing has not been observed. If a yearling ♂ has been driven out of the parental territory, he starts to establish his own territory at an age of about 3 years, sometimes already with a ♀. Occasionaly he also takes over the territory of an other ♂ that has been killed. Bachelor herds are not established (unlike waterbuck, impala etc.).

The yearling ♀ leaves the parental territory much earlier than the yearling ♂. As early as the age of 1½—2½ years she lives together with a territorial ♂. It has not been observed if the yearling ♀ leaves the territory of her parents of her own will or if she is driven away by her new mate.

If a ♀ does not succeed in raising her newborn-fawn (for example ♀ of L1), she is joined again by her lamb of the previous year. This is true for yearling ♂♂; yearling ♀♀ still leave the parental territory.

Summary

I. Mating behaviour in the reedbuck consists of 3 different sequences: 1. Premating behaviour, 2. Mounting and copulation, 3. Postcopulatory behaviour.
   1. The ♂ approaches a ♀ with lowered head and sniffs at her anal region. Thereupon the ♀ mostly adopts a submissive position and jumps away. If she urinats, the ♀ performs the "Flehmen"-posture. If the ♀ moves repeatedly a few steps forward, the ♂ follows and finaly mounts her.
   2. Mounting can be repeated frequently and usually terminates in copulation.
   During the phases 1 und 2 chasing and "Laufschlag" did not occur.
   3. After copulation both are very quiet.
   Comparsison with other antelopes: Mating behaviour in the reedbuck seems to be relatively uncomplicated in comparison to other Reduncini. There are similarities with the Reduncini in phase 1 and in mounting (phase 2). In this the Reduncini differ from other species. A highly ritualized postcopulatory behaviour does not occur in the reedbuck.

II. The reedbuck does not have a strict breeding season. Most of the lambs are born between December and May. The explanation for this might include the following:
   1. The appearance of so-called "Ersatzbrunft" (coming into heat out of the normal rutting season, after a young lamb has been lost).
   2. Young ♀♀ reach maturity at different times.
   3. Extension or abridgement of the gestation period.

III. Heavily pregnant ♀♀ leave the family unit and give birth in isolation. The lambs belong to the so-called "Ablieger" (concealment activity). Only a single diurnal visit to the fawn by the mother (10—30 minutes) took place for nursing and cleaning. Strict concealment behaviour or hiding seems to last for 2 months; later the lamb frequently grazes with its mother but still keeps to its hiding activity. While growing older the lamb starts to follow its mother. In young fawns as well as in older ones (about 3 months) "abliegen" is an important factor in avoiding predators. When in danger the lamb utters a call of distress which can release a protective action in the ♀.
   The ♀-child bond is desrupted a few days before the ♀ gives birth to a new fawn, but can continue longer if the new one dies early.

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/

Zusammenfassung

I. Das Paarungsverhalten des Riedbocks kann in 3 Phasen gegliedert werden: 1. Finden der Geschlechter, 2. Aufreiten und Kopulation, 3. Verhalten nach der Kopulation.
1. Der ♂ nähert sich einem ♀ mit vorgestrecktem Hals und schnuppert an ihrer Analregion. Darauf reagiert das ♀ mit Demutstellung und springt weg. Uriniert das ♀, flehmt der ♂. Weicht das ♀ dem ♂ wiederholt nur einige Schritte aus, folgt dieser und reitet auf.
2. Aufreiten erfolgt mit erhobenem Kopf und kann mehrmals wiederholt werden. Heftiges Jagen und Treiben, sowie Laufschlag, wurden nicht beobachtet.
3. Nach der Kopulation verhält sich der Riedbock ausgesprochen ruhig.

Vergleich mit anderen Antilopen: Das Paarungsverhalten des Riedbocks ist weniger reich gegliedert als das anderer Reduncini. Gemeinsamkeiten bestehen mit den Reduncini in der Phase 1 und 2. Dadurch grenzen sich diese deutlich von anderen Gruppen ab. Ein hochritualisiertes post-kopulatives Verhalten fehlt den Riedböcken.

II. Riedböcke haben keine feste Setzzeit. Die meisten Kitze werden zwischen Dezember und Mai geboren. Eine Erklärung für diese Erscheinung können folgende Beobachtungen sein: Das Auftreten von Folgebrunften (nach dem frühen Verlust eines Kitzes), unterschiedliches Erlangen der Geschlechtsreife bei jungen ♀♀ und eventuell Verkürzung oder Verlängerung der Tragezeit.

III. Hochtragende ♀♀ verlassen den Familienverband und setzen in abgelegenen Gebieten. Die Kitze gehören zum Abliegetyp. Einmal im Laufe des Tages sucht das ♀ ihr Kitz für 10—30 Minuten auf, um es zu nähren und zu putzen. Festes Abliegen scheint 2 Monate zu gelten, danach äsen ♀ und Kitz häufig zusammen, das Kitz behält aber noch sein Abliegeverhalten bei. Erst mit zunehmendem Alter folgen die Kitze ihren Müttern nach. Bei jüngeren Kitzen und auch bei älteren (um 3 Monate) spielt das Abliegen einen wesentlichen Faktor beim Vermeiden von Feinden. Bei starker Bedrängnis geben die Kitze einen Notruf von sich, der eine Verteidigungsreaktion des ♀ auslösen kann.

Die ♀-Kitz-Verbindung löst sich kurz vor dem Setzen eines neuen Kitzes, kann aber länger anhalten, wenn dieses Kitz früh umkommt.

Literatur

Altmann, M. (1956): Patterns of herd behaviour in free-ranging elk of Wyoming, *Cervus canadensis nelsoni*, Zoologica **41**, 65—71.

Alverdes, F. (1925): Tiersoziologie, Forschungen zur Völkerpsychologie und Soziologie, Bd. 1, Leipzig.

Asdell, S. A. (1946): Patterns of mammalian reproduction, London.

Backhaus, D. (1958): Beitrag zur Ethologie der Paarung einiger Antilopen. Zuchthyg. **2**, 281—293.

Brand, D. J. (1963): Records of mammals bred in the National Zoological Gardens of South Africa during the period 1908—1960. Proc. Zool. Soc. London, Vol. 140, part 4, 617—659.

Brehm, A. (1930): Die Säugetiere, Bd. 4.

Brooks, A. C. (1961): A study of the Thomson's gazelle *(Gazella thomsonii* Gunther) in Tanganyica. Her Magesty's Stationery Office, London, 147.

Bubenik, A. B. (1965): Beitrag zur Geburtskunde und zu den Mutter-Kind-Beziehungen des Reh- *(Capreolus capreolus* L.) und des Rotwildes *(Cervus elaphus)*. Z. Säugetierkunde **30**, 65—128.

Buechner, H. K., and Schloeth, R. (1965): Ceremonial mating behaviour in Uganda kob *(Adenota Kob thomasi* Neumann). Z. f. Tierpsychol. **22**, 209—225.

de Vos, A., and Dowsett, R. J. (1966): The behaviour and population structure in 3 species of the genus *Kobus*. Mammalia **30**, 30—55.

Eibl-Eibesfeldt, I. (1966): Ethologie, die Biologie des Verhaltens. Handbuch der Biologie II, 341—559.

Estes, R. D. (1967): The comparative behaviour of Grant's and Thomson's gazelles. Journal of Mammalogy, 48, No. 2, 189—209.

Fairall, N. (1968): The reproductive seasons of some mammals in the Krüger National Park. Zoologica Africana Vol. 3 No. 2, 189—210.

Hediger, H. (1934): Zur Biologie und Psychologie der Flucht bei Tieren. Biol. Zbl. Vol. 54, No. 1 und 2.

— (1944): Die Bedeutung von Miktion und Defäkation bei Wildtieren. Schweiz. Zz. Psychol. Vol. **3**, 170—172.

Jungius, H. (1970): The biology of the reedbuck *(Redunca arundinum* Boddaert, 1785) Mammalia depicta, in press.

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/

Kenneth, I. H. (1943): Gestation periods, Edinburgh.
Kiley-Worthington, M. (1965): The Waterbuck *(Kobus defassa* Rüppel, 1835 and *K. ellepsiprymnus,* Ogilby, 1833) in East Africa. Mammalia 29, 177—204.
Kirby, F. V. (1896): In haunts of wild game. Edinburgh & London.
Kurt, F. (1968): Das Sozialverhalten des Rehes *(Capreolus capreolus* L.) Mammalia depicta. Paul Parey, Hamburg, Berlin.
Leuthold, W. (1967): Beobachtungen zum Jugendverhalten von Kob-Antilopen. Z. Säugetierkunde **32**, 59—63.
Millar, A. D. (1899): An antelope protecting its young. The Zoologist **3**, 46.
Portmann, A. (1953): Das Tier als soziales Wesen. Zürich.
Prell, H. (1937): Über Tragzeitprobleme bei einheimischen Jagdtieren. Tharandter Forstl. Jb. Bd. 88, H. 11, 921—944.
— (1938): Die Tragzeit des Rehes. Z. Züchtungskunde **13**, 9, 325—345.
Remane, A. (1960): Das soziale Leben der Tiere. Rowohlts deutsche Enzyklopädie 97.
Robinette, W. L., and Child, G. F. T. (1964): Notes on the biology of the Lechwe *(Kobus leche).* Puku, Vol. 2 Lusaka, 84—117.
Rue, L. L. (1962): The world of the white-tailed deer. J. B. Lippincott Comp. Philadelphia, New York.
Schenkel, R. (1966): On soziology and behaviour in Impala *(Aepyceros melampus suara* Matschie). Z. Säugetierkunde **31**, 177—205.
Schneider, K. M. (1930—1934): Das Flehmen 1. Teil Zool. G. N. F. 3, 183—198; 2. Teil Zool. G. N. F. 4, 349—364; 3. Teil Zool. G. N. F. 5, 200—226; 4. Teil Zool. G. N. F. 6, 287—297; 5. Teil Zool. G. N. F. 7, 183—201.
Spinage, C. A. (1969): Naturalistic observations on the reproductive and maternal behaviour of the Uganda defassa waterbuck, *Kobus defassa ugandae* Neumann. Z. Tierpsychol. **26**, 1, 39—47.
Stevenson-Hamilton, J. (1947): Wildlife in South Africa. London.
Talbot, L. M. and Talbot, M. H. (1963): The Wildebeest in Western Masailand East Africa. Wildlife Monographs No. 12.
Tinbergen, N. (1959): Einige Gedanken über „Beschwichtigungsgebärden". Z. Tierpsychol. **16**, 631—665.
— (1967): Tiere untereinander, Formen sozialen Zusammenlebens. Berlin und Hamburg.
Versey-Fitzgerald, D. F. (1959): The dance of the Bohor Reedbuck. "Wildlife", Nairobi Vol. 1 No. 3, 7—8.
Walther, F. (1958): Zum Kampf- und Paarungsverhalten einiger Antilopen. Z. Tierpsychol. **15**, 340—380.
— (1964): Verhaltensstudie an der Gattung *Tragelaphus* in Gefangenschaft. Z. Tierpsychol. **21**, 393—467.
— (1965): Verhaltensstudie an der Grantgazelle im Ngorongoro-Krater. Z. Tierpsychol. **22**, 167—208.
— (1968): Verhalten der Gazellen. Neue Brehmbücherei 373.
Wilhelm, J. H. (1933): Das Wild des Okawangogebietes und des Caprivizipfels. J. S. W. Af. sci. Soc. **6**, 51—74.
Zuckerman, S. (1953): The breeding seasons of mammals in captivity. Proc. Zool. Soc. London **122**, 827—950.

Author's address: Dr. Hartmut Jungius, Institut für Haustierkunde, 23 Kiel, Neue Universität

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: Mammalian Biology (früher Zeitschrift für Säugetierkunde)

Jahr/Year: 1969

Band/Volume: 35

Autor(en)/Author(s): Jungius Hartmut

Artikel/Article: Studies on the Breeding Biology of the Reedbuck (Redunca arundinum Boddaert, 1785) in the Krüger National Park 129-146