BEHAVIOURAL ASPECTS OF THE REPRODUCTIVE PHYSIOLOGY OF THE IMPALA, *AEPYCEROS MELAMPUS* (LICHT.)*

N. FAIRALL

Department of Nature Conservation,
Cape Provincial Administration.

ABSTRACT

The reproductive physiology of the impala was studied in the Kruger National Park. The data concerning the hypophysial hormones, the androgenic hormones and ovarian histology are discussed in relation to the behaviour of the animal.

It was found that the male animal shows the most profound behavioural changes which occur during the mating season. These changes are induced by an increase of interstitial cell-stimulating hormone which leads to an increase in androgenic hormone. The female shows relatively few behavioural changes during the mating season, the only change being at the time of oestrus.

On the basis of the data presented and information reported for domestic animals, it is postulated that the behaviour of the male impala plays an important role in determining the breeding season.

The impala is the most abundant of the larger mammals in the Kruger National Park where this study was undertaken. They are not shy and are commonly seen next to the roads and at watering points. During the last few years it has become apparent that impala numbers were not being controlled sufficiently and that they were endangering the available habitat. For this reason a culling programme was started and this provided a source of material that was used to study the reproductive physiology.

As the study progressed, it became clear that certain findings about the physiology were correlated with behaviour patterns which were observed in the population. Eventual analysis indicated a reciprocal interaction between behaviour and physiology that should be of use to workers in both fields.

PROCEDURE

Information on the behaviour of the impala was available from observations made on the population over a period of eight years. Schenkel (1966) made an intensive study of the behaviour of the impala in Kenya and this was used in the evaluation of my observations on behaviour.

Histological studies were done on the ovaries of five ewes per month for six years. The ovaries were fixed, embedded in wax and sectioned. Sections were taken from the anterior, median and posterior thirds of each ovary. These were placed on a single slide, stained by the Masson technique (Culling 1957) and examined to determine the number of developing and degenerating follicles as well as the size of follicles.

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Pituitaries were collected from five male impala each month during 1968 and 1969 and from five female impala per month during 1969. The pituitaries collected during 1968 were frozen and stored in a deep freeze for later assay of total gonadotrophin. To perform the assay the anterior pituitary was obtained by dissection and each month's supply was pooled and ground in a tissue grinder in 5 ml normal saline. The tissue grinder was rinsed with a further 5 ml of the saline solution: the two volumes were then combined and stored in a refrigerator during a three day injection period.

Day-old male chicks of a Leghorn-Australorp cross were obtained from a commercial breeder. Ten chicks were used for each month's assay and were injected subcutaneously with 0,3 ml of ground pituitary per day for three days. On the fourth day the chicks were killed, their testes were removed, placed in Bouin's solution blotted dry and weighed. The difference in weight between the testes of the control group and the test groups was taken as a measure of total gonadotrophin.

The pituitaries collected during 1969 were collected in ice-cold acetone, dried on blotting paper and stored in a deep freeze in a sealed vessel, containing silica gel. Each month's sample of male and female glands were separately pooled, then ground in a peppermill and tested for follicle stimulating hormone (FSH) by the method of Steelman and Pohley (1953). Five female rats of about 21 days of age were used per test. They were injected with 0,5 ml of a mixture of 150 mg of pituitary powder and 100 IU chorionic gonadotrophin in 7,5 ml normal saline, each day for three days. The rats were killed on the fourth day, the ovaries were removed, placed in Bouin's solution blotted and weighed. The average monthly weights were taken as indicating the FSH content of each sample.

One testis each from five male animals per month was collected in 1968 and stored in the deep freeze. Before analysis these organs were thawed, the epididymis and tunica vaginalis was dissected away, and each month's sample was weighed and ground in a Waring blendor. Ethanol (95%) was added at a rate of 1 ml per gram of testis and blended into the tissue, which was left in the refrigerator overnight. The following morning the mixture was centrifuged and 300 ml of the supernatant was taken, evaporated to dryness and the residue redissolved in 10 ml of 95% ethanol. These samples were kept in a refrigerator before use and during the period of administration.

Assay of the extract was performed as outlined by Gallagher and Koch (1935) using five capons per month. The height and length of the combs were measured and these measurements were combined by addition. Extract was applied to the comb at a rate of 0,1 ml per day for five days, on the eighth day the combs were remeasured and the increase in size was taken as a measure of androgenic activity.

RESULTS

Behaviour

The impala in the study area are herd-forming animals with a single breeding season each year. This season consists of a mating period from the end of April to the middle of June and a lambing period from the middle of November to the beginning of January.

Different types of herds may be identified at different seasons. These are female herds, male herds and breeding herds. The female herd normally consists of ewes of all ages, immature males

and one or two mature males either in the herd or just on the perimeter. After the lambing season large numbers of lambs are also seen in the female herds. These are the normal large mixed herds of impala that are always seen, other than during the mating season. Male herds consist solely of rams of all ages and vary in size from two or three individuals to twenty or more. These herds increase in size during the mating season and later decrease again as individuals rejoin the mixed herd. The breeding herd is very like the normal mixed or female herd but one now finds that they are smaller and consist of only one or at the most two mature males and females of different ages.

The behaviour of these three groups vary and in fact this is the reason for the difference between the mixed herd and the breeding herd. During the greater part of the year rams mix with the female segment of the population, mature rams being found on the edges of the herd where they show symbolic herding behaviour but do not interfere with the younger rams in the female herd.

The male herds have a loose structure and some individuals graze alone more than 50 meters away from the rest. There is no clearly defined dominance by any of the individuals and all age groups seem to have the same status.

Just before the onset of the breeding season in April, there is a marked change in individual male behaviour and this brings about changes in the herd structures. This change is characterised by the males becoming more aggressive, all young and subordinate rams are chased out of the female herds, the males patrol the borders of the herd and actively herd the females. Females attempting to leave the herd are chased and returned to the herd. This is usually followed by strutting and "roaring" displays by the male which are a characteristic and noisy feature of this time of the year. As the mating season reaches its peak this male behaviour increases in intensity after which it tails off towards the end of July. The male herds increase in size at this time, absorbing most of the young males from the other groups. There is also much display and both active and symbolic fighting are in evidence. There is, however, no evidence of dominance or herd-forming behaviour by any individual male.

The female shows no great change in behaviour at this time. When they come in oestrus, however, there is a change. The ewe shows an active interest in the ram but tries to evade him when he reciprocates. She sometimes tries to escape from the herd and join other herds or single male impala in the vicinity. Eventually however, she stands, and mating takes place.

Physiology

The histological data from the study of the ovaries are summarised in Table I. It can be seen that the numbers of developing follicles are high during most of the year, the most notable change being a decrease during September, October and November. The same tendency is seen in the size of the follicles throughout the year. In some years, however, it is evident that the largest follicles occur during the mating season. This tendency however, does not emerge clearly enough, as it was in fact found that the only follicles larger than 5 mm were found during April and May, which is in the breeding season.

The data from the total gonadotrophin test are presented graphically in Fig. 1. (The material collected during July, August and September was lost because of a power failure). These data show a very distinct peak at the time of the mating period. In Table 2 the results of the two FSH assays are presented.

TABLE 1

AVERAGE NUMBERS OF DEVELOPING FOLLICLES AND SIZE OF THE LARGEST FOLLICLE THROUGHOUT THE YEAR – FOR THE PERIODS 1962–1965 AND 1968

Year	JAN.		FEB.		MAR.		APRIL		MAY		JUNE		JULY		AUG.		SEPT.		OCT.		NOV.		DEC.	
	Dev. No.	Size mm	Dev. No.	Size mm	Dev. No.	Size mm	Dev. No.	Size mm	Dev. No.	Size mm	Dev. No.	Size mm	Dev. No.	Size mm	Dev. No.	Size mm	Dev. No.	Size mm	Dev. No.	Size mm	Dev. No.	Size mm	Dev. No.	Size mm
1962 ..	—	—	—	—	19	3,24	21	3,00	10	3,12	10	3,06	12	2,70	7	2,70	4	1,98	8	1,50	2	1,44	7	2,64
1963 ..	8	3,60	10	3,80	9	3,60	11	4,45	11	3,79	13	3,42	12	3,42	15	2,28	6	2,22	9	2,28	6	1,80	7	3,42
1964 ..	5	3,12	14	3,12	8	4,80	6	3,00	8	3,96	9	3,36	8	2,46	4	2,46	12	2,22	10	2,34	7	2,28	9	1,80
1965 ..	7	2,70	6	1,98	—	—	—	—	17	3,12	6	3,42	6	3,06	5	2,04	2	1,08	1	1,14	1	1,14	4	1,64
1968 ..	20	2,22	23	3,12	14	3,60	16	4,45	15	3,45	9	3,10	16	3,24	9	3,12	3	2,46	4	1,83	5	1,98	12	2,50

TABLE 2

AVERAGE WEIGHTS (mg) OF RAT OVARIES USED IN THE FSH ASSAYS OF MALE AND FEMALE IMPALA

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Male ..	24,88	23,23	24,79	24,25	24,25	24,48	24,55	—	23,54	23,97	18,59	25,08
Female ..	—	27,7	27,7	26,3	26,3	18,4	18,0	—	21,6	14,8	17,1	—

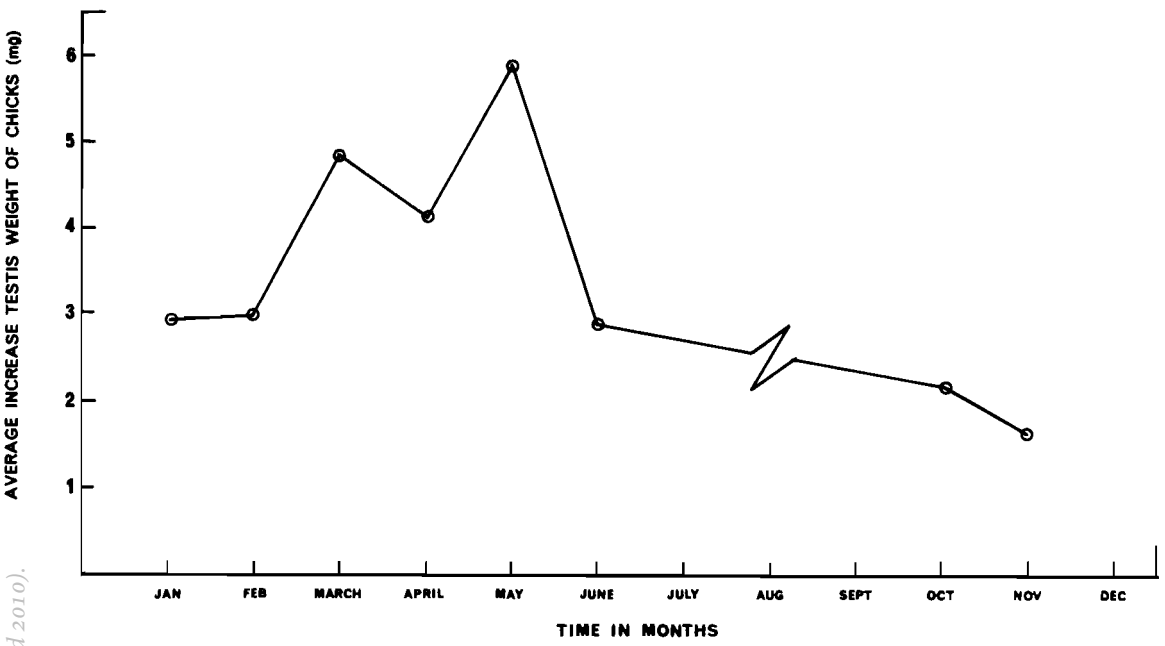

FIGURE 1
Monthly variation in total gonadotrophin.

It is clear, from these results, that there is a large difference between the male and female segment of the population. The males show a more or less constant concentration that declines during November. This is not, however, statistically significant. In the female, activity is high during February, March, April and May and low during the period from June to November. Analysis of variance shows this difference to be statistically significant. September is statistically different from the low period and falls in the active period. The reason for this is unknown but was also seen in some of the other data.

The androgenic activity of the male testis is shown graphically in Fig. 2. Statistically the data can be divided into three periods namely 1. May, June, July and January; 2. August, September, October, and November and 3. December, February, March and April. In the first period the androgenic reaction is high and there is no difference between each month, the second period is of low androgenic activity and there is no difference between months, whereas the third period comprises the transition from low to high and high to low, and these months all differ from all other months.

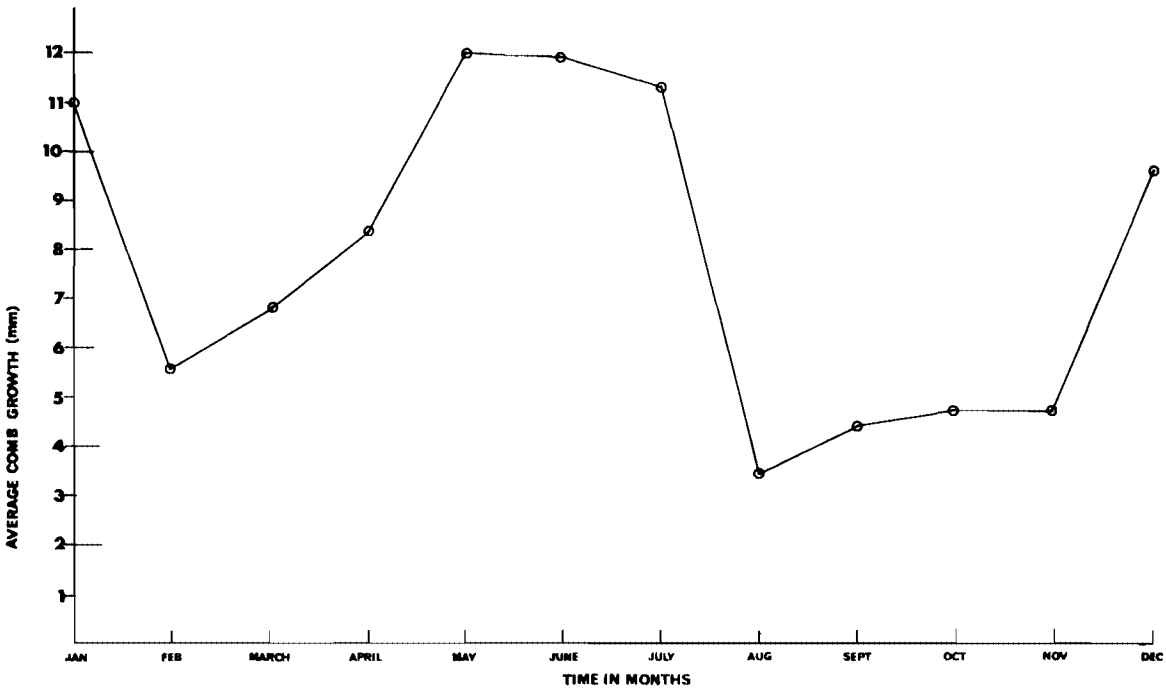

FIGURE 2
Monthly variation in androgen content of impala testes.

DISCUSSION

The main changes in the behaviour of the impala are seen in the male and these occur just prior to and during the mating season. In the present study the most marked changes in the physiology of the animals were also seen in the male and these changes occur during the mating period as well. This is seen both in the total gonadotrophin and the androgen levels. It is not, however, evident in the FSH component of the gonadotrophins.

Male behaviour is greatly influenced by the presence of male hormones (Fraser 1968) and the castrated male does not exhibit many of the behavioural characteristics of the intact male. Male hormones are produced by the testes under the influence of the interstitial cell stimulating hormone (ICSH) of the pituitary (Gorbman & Bern 1962). From the data presented it would seem as if the sequence of behaviour in the male impala is caused by an increase of total gonadotrophin of which the ICSH component is possibly the most important. This causes an increase in the output of testicular androgen and eventually the manifestation of mating season behaviour, which culminates in the mating ritual when the female comes into oestrus. The high androgen levels

during December and January are interesting since male reproductive behaviour as evidenced by roaring displays is sometimes seen at this time. The occurrence is, however, sporadic and does not affect the whole population.

In the female impala it was found that the FSH content of the pituitary was high from February to May after which it declined reaching a low point in October. This finding corresponds with the picture seen in the ovary, as the development of follicles occurs under the influence of FSH and the largest number of developing follicles are seen just before and during the mating season, after which they decline. There is, however, no clear-cut change in these functions during the mating season proper, the only difference being an increase in size of individual follicles which occurs only during the oestrus cycle.

The behaviour of the female impala changes markedly only during oestrus and this change is under the influence of estrogenic hormones. These are produced mainly in the developing follicle and especially during the final phase of development (Gorbman & Bern 1962). Ovarian follicles normally develop in two phases, the first phase occurring to about the fifth day of the cycle and final growth occurring during proestrus and oestrus (Cupps, Laben & Mead 1959). Maximum amounts of oestrogen are therefore liberated only during a very brief period.

The behaviour of the female impala is consistent with the findings obtained from the physiological data. There is no change in behaviour during the period of ovarian activity under the influence of high levels of FSH. As soon as the follicles develop to the final phase and liberate large amounts of oestrogens, the female's behaviour changes and, through the interaction of the two sexes, both stimulated by the gonadotrophic hormones, final mating behaviour occurs.

The behavioural pattern displayed by impala may be involved in the determination of the mating season. In this study it has been demonstrated that there is a definite physiological and behavioural change in the male impala before and during the mating season whereas this is not the case with the female. The only change in the latter being oestrus itself which, in individuals, is randomly spread throughout the mating period of the group. In sheep, goats and cattle it has been shown that the males can influence the onset of oestrus by causing the breeding season to occur earlier and with greater regularity (Watson & Radford 1960; Skinner & Bonsma 1964; Lamond 1964; Fraser & Laing 1968; Skinner & Hofmeyer 1969; Hunter 1969). Bullough (1951) mentions that after all other factors have reached their optimum, certain psychological factors still have to be satisfied before the mating season will occur. Robinson (1967) also mentions that social factors are important for the occurrence of oestrus.

There is a great deal of experimental evidence which shows that the central nervous system has an extremely important function in controlling the release of hypophysial hormones. In the hypothalamus there are certain areas which integrate stimuli from numerous nerve tracts; the hypothalamus reacts by releasing its hormones and these condition the same or other areas to react to psychological stimuli which cause the manifestation of mating behaviour (Harris 1959; Sawyer 1959; Grey & Phoenix 1963).

In the case of the impala it would appear as if the photoperiod conditions both the male and female animal and triggers the release of high levels of gonadotrophins. In the male this in turn causes an increase in androgenic hormones and a change in male behaviour. The demonstrative behaviour of the male, as evidenced by his chasing, fighting and vocalization, acts as a psychological trigger to bring the female into oestrus.

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