

Notes on the reproduction in Hartmann zebra *Equus zebra hartmannae* in South West Africa

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ABSTRACT

In the Hartmann zebra one finds an exclusive one-male dominance over a given number of females. The subgroup population has the reproductive advantages that it ensures selective breeding and gene flow. The oestrus cycle in young females under certain given conditions is important in the formation of new breeding units. Males without a breeding unit are psychologically castrated. Stallion groups form a gene reservoir from which old males are replaced. In the females the sexual organs have reached their full development at two years of age and the female normally drops her first foal at three years of age. A distinct breeding peak from November to April was found to exist. The gestation period is 362 days.

I INTRODUCTION

In contrast with the domestic horse, very little is known about the reproductive cycle of the various zebra species in their natural state. Recently however, a comprehensive study by King (1965) was carried out. In this work he records field-work done on Grant's zebra (*Equus burchelli böhmi*) and Grevy's zebra (*Equus grevyi*). During a study on the ecology and behaviour of the Hartmann zebra (*Equus zebra hartmannae*) the author was fortunate enough to obtain some information on their reproductive behaviour and cycles. The results are given in the present paper as a small contribution to a better understanding of the reproduction of the wild species of Equidae.

II CHARACTERISTICS OF THE REPRODUCTIVE BEHAVIOUR

Although this has been dealt with by Joubert (1972), certain salient points need to be stressed. The social organization of the Hartmann zebra is an exclusive one-male dominance over a given number of females. The males possesses strong herding tendencies to ensure females against rivalry from fellow males. This herding behaviour has evolved as an innate behaviour pattern in the Hartmann zebra males. The social organization therefore results in a population made up of many sub-groups, comprizing breeding groups and bachelor groups. Reproductively speaking this has two important advantages. It ensures selective breeding and secondly gene flow. Theoretical studies in quantitative genetics show that the structure of a population is very important in governing not only the genetic variability of the population but also the speed with which new adaptive genes may spread. Wright (1950) has shown that the optimal type of population structure is one where the population is divided into semi-isolated breeding units where a certain amount of inbreeding takes place, with the units joined genetic-

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ally by a limited amount of migration between populations.

The selection for the best breeding males takes the form of a harem, where a single male takes possession of a group of females against strong inter-male competition. As one finds with territoriality this latter phenomenon, apart from selection of males, also functions with territoriality as a means of distributing the population to ensure that all available females breed. In general the sex relationship plays an unimportant role in the social organization of the Hartmann zebra except for a limited period, in the establishment of new units or the enlargement of existing small ones. As may be assumed this happens during the oestrus cycle. The influence of oestrus on the formation of new breeding units is only important under the following conditions:

- (i) when the female which comes into oestrus is a young female. Older females which have already become an inseparable part of the breeding unit through their long association with it, do not facilitate abduction by young inexperienced males. For the young females, who are undergoing their first oestrus, this period is marked by a high degree of aggression from the females in the breeding unit.
- (ii) when the number of females in the breeding unit has reached or is close to saturation point. If the breeding unit is still small, the dominant male's own herding instincts will still be so strong that a young inexperienced male would not stand a chance.
- (iii) when there is a bachelor unit in the vicinity with sexually mature males which have had the stimulating experience of competition with fellow males and have reached a high position in the hierarchy of the bachelor unit. The oestrus period of a young female serves as a trigger mechanism to ensure keen competition amongst the young males. The oestrus female also triggers the latent herding behaviour of the young male. The male which finally succeeds in herding (abducting) her mates with her forms the nucleus of a new breeding unit. Field observation has shown that experienced males, that have lost their breeding units owing to some reason or other, or only have a small breeding unit (one or two females), do not need the triggering action of an oestrus female when forming a new breeding unit.

Constant rivalry exists between dominant males and this may be considered as the continuation of natural selection of the males. In the Hartmann zebra this intermale rivalry has taken the form of phylogenetic ritualization. Ethologists agree that ritualized behaviour's primary function is that of communication. In this context it fulfills two basic functions in the reproductive organization of the animal. The first is that it suppresses actual lethal contests which endangers the survival of the individual which is also the carrier of important genes. Secondly ritualized aggressive behaviour and mating behaviour is only shown by a dominant male with a breeding unit. The chance that a Hartmann zebra without a "harem" thus possibly an inferior animal, will re-

produce is remote. Proof was also found in sexually⁰¹ mature bachelor males of a behaviour which is indi-⁹ cative of a condition that has been called by most⁸ ethologists "psychological castration". Observations⁸ in the field showed that on occasions when oestrus⁷ females were abducted by bachelor males, mating⁷ only took place after this herding activity was carried⁶ out. The influence of psychological castration is only⁶ overcome by bachelor males when they actively en-⁵ gage in herding behaviour, after being triggered by⁴ an oestrus female.

Stallion groups (bachelor units) are mainly formed³ by immature males, most of which become sexually³ mature during their association with the stallion² group, and old males past their prime which have² been ousted by younger stallions. In the stallion¹ group, selective pressure comes to bear and only the¹ more worthy young males acquire their own breed-¹ ing units. Stallion groups function thus both as a¹ natural selector for the best males as well as male¹ reservoirs for replacing dominant males that become¹ senile, or are removed by natural causes such as¹ diseases, accidents or predation.

The actual mating behaviour in the Hartmann zebra is relatively simple. As the dominant male and the females in the breeding unit are known to one another, courtship is peaceful with no elaborate ritualization. The first phase can be called the urination-flehmen sequence during which the male frequently exhibits flehmen behaviour as well as the tendency to urinate on the same spot as the female. During the second phase courtship takes place. This normally consist of the male rubbing the front part of his head against the female's vulva, when this is presented. This is followed by a placement of the male's head on the female's rump as a ritualized intention mounting movement (Walther, 1958). During intromission the male lays his head, with ears laid back, between the female's shoulder blades while he clamps her with his front legs. The female lowers her head with her ears also laid back and with lips pulled back. This facial expression in the Burchell zebra has been called "Rossigkeitsgesicht". Copulation normally only lasts a few seconds but is repeated almost at hourly intervals for a couple of days.

III AGE WHEN SEXUALLY MATURE

In the Hartmann zebra, as in the Burchell zebra (Klingel, 1965, and King, 1965) the age at which the male starts showing sexual activity is no indication of puberty. It is only when they are able to compete with older males and succeed in obtaining their own females that they show breeding activity. As can be seen in figure 1 the testis of the male starts increasing in weight from approximately two years of age. The testes however, only reach their maximum weight and size at about three and a half years of age. The average size of the testis (n = 24) of animals older than four years is 6.6×4.9 cm and the average weight 87.6 g. This is markedly smaller than the

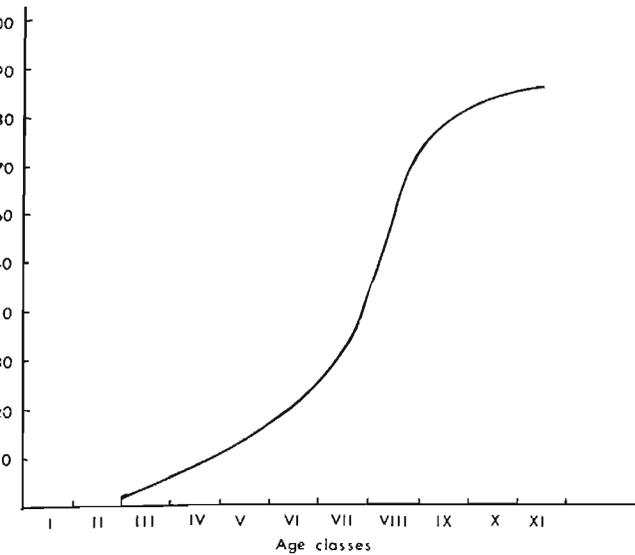


Figure 1. Increase in testis weight in the *Equus zebra hartmannae*.

size $10 \times 7 \times 5$ cm given by King (1965) for the Burchell zebra. From post mortems carried out in the field it looks as though the testes only descend into the scrotum after the animal has reached the age of two and a half years or more.

Klingel (1965) records that the first oestrus of a Burchell zebra mare takes place at 12 to 13 months. Although it might also occur at this age in the Hartmann zebra, no opportunity arose to record this in field observations. Several females of known age dropped their first foal at three years or shortly afterwards. A female collected in the field, at an age of three years, was on the point of giving birth. With a gestation period of approximately 12 months one can therefore assume that in the Hartmann zebra female sexual organs have normally reached their full development and function from about two years of age. The ovaries show a variety of shapes according to the stages of differentiation of the maturing follicles. Usually, however, they are kidney or pear shaped. The average weight of 26 pairs of ovaries obtained from breeding females is 47,3 g. (Maximum 141,53 g — minimum 19,64 g.) The average length of these ovaries (over the median) is 43,3 mm (maximum 63,6 mm — minimum 51,0 mm). Cross-section of ovaries of sexually immature females showed them to be brown on the inside as opposed to the whitish colour of sexually active ovaries.

IV REPRODUCTIVE CYCLES

To determine reproductive cycles of the male, testes of adult animals were collected. As already mentioned, a number were collected every month throughout one year. The testes were weighed and measured. Smears were made from the epididymis to determine the number of spermatozoa. As can be seen from figure 2 only a very slight variation in the mass of the testis is noticeable during the 12 months of the

year. The average mass of the testis shows a slight decline from a peak in January (99,4 g) to the lowest point during September (85,1 g). Semen counts by the SAIMR during January gave an average figure of 4 600 000 000 spermatozoa per ml, while during September the average figure obtained was 1 900 000 000 spermatozoa per ml. The number of abnormal spermatozoa remained at an average of 9 per cent throughout the year. From the above it would appear as though the testes are more active during the rainy months than during the dry months. Despite this however, there is still more than enough spermatozoa to fertilize a female during the drier months.

Twenty-six pairs of ovaries were collected during the study-period. No differentiation in the activities of the ovaries could be detected. Follicles of Graaff were found maturing either in the left or right, or more often in both ovaries. Before rupturing, the follicle normally became so large that it projected beyond the surface of the ovary. Sometimes several of these large follicles would be found in one ovary at the same time. Even the number of developing follicles in each ovary showed a marked similarity. The outer walls of these follicles are thin and care had to be taken not to rupture them while working with the ovaries. The average diameter of these maturing follicles was 25,5 mm.

Kupfer (1928) found that donkey and horse mares show a definite periodicity of ovarian activity. Kupfer states that in South Africa, in the animals mentioned above, ovulation takes place only during the months October (second half), November, December, January, February, March and April (first half). Ovulations are thus confined to a season of six or seven months. King (1965) and Klingel (1965) detected no breeding season in Burchell and Grevi's zebra in East Africa. Klingel (1965) however, reports a main foaling season from January to March for the Burchell zebra. In the Hartmann zebra newborn foals have been recorded throughout the year, but a distinct breeding peak is noticeable. This is a

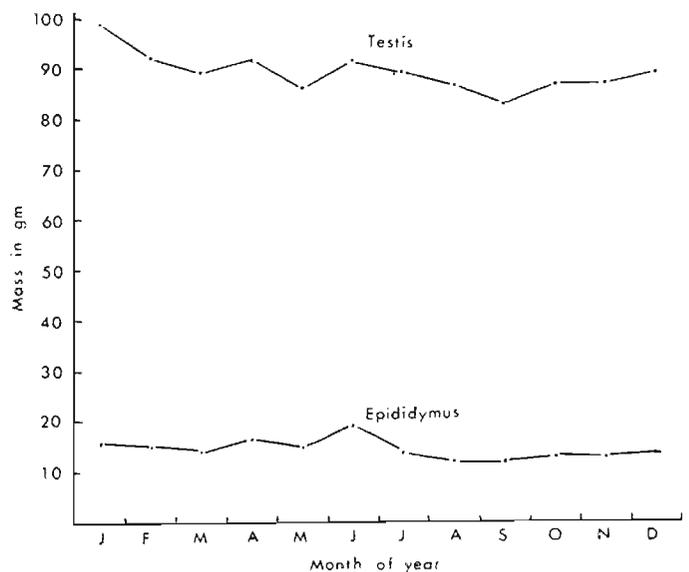


Figure 2. Seasonal changes in the mass of testis and epididymis in adult *Equus zebra hartmannae*.

clear indication that conception can take place throughout the year. During the three years of study, however, mating activities were only seen from September to April the following year, with a peak in February (for three years of observation). This indicates that mating activity during the rest of the year is very rare, which agrees to some extent with the work done by Kupfer (1928) on the donkey and horse.

One of the marked characteristics found in the ovaries investigated was the presence of a large corpus luteum even at an advanced state of pregnancy of up to five months. King (1965) found the same in the Burchell zebra.

Kupfer (1928, 1245) reports the same:

“the whole process of transformation from the ruptured follicle to the yellow body and its reduction, takes a very long time in South African donkeys (and in South African equines — horses — altogether) when compared with other animals. A rapid development and reduction of the corpus luteum, such as found in a concentrated ovulation cycle with intervals of three weeks only (for instance cattle) does not take place here.”

The average size of the corpus luteum before reduction takes place is similar to that in Burchell zebra as found by King (1965) viz. 25 mm. The colour changes of the corpora lutea were also found to be the same as described by Kupfer (1928) and King (1965). The active corpus luteum has a red-brown colour before changing to yellow. King (1965) found in ovaries three to six weeks post-partum ($n=4$) remnants of a corpus luteum which appeared to be slightly larger than that seen at full term. This was found in one animal's ovaries in Hartmann zebra and suggests oestrus a week after parturition. Oestrus eight to ten days post-partum has been observed in both captive (Wackernagel, 1965) and free animals (Klingel, 1965). From observations at the Daan Viljoen Game Reserve the foaling-conception interval varied between three to seven weeks. It appears as though conception does not take place during the first oestrus following parturition.

V SEASON OF BREEDING

As already mentioned new-born Hartmann zebra foals have been recorded throughout the year. But as Klingel (1965) found in the Burchell zebra a clear peak is noticeable. In the Hartmann zebra this peak is from November to April — thus commencing a month later and ending a month later than what Klingel found in Burchell zebra. This might be attributed to the rainfall season in South West Africa (see figure 3). Newly born foals recorded over the three year study were distributed as follows. During November to the end of April 86 per cent of all foals were born (Burchell zebra, October to March = 85.5 per cent), with 68 per cent during the main foaling season January to April (Burchell zebra, January to March = 61 per cent).

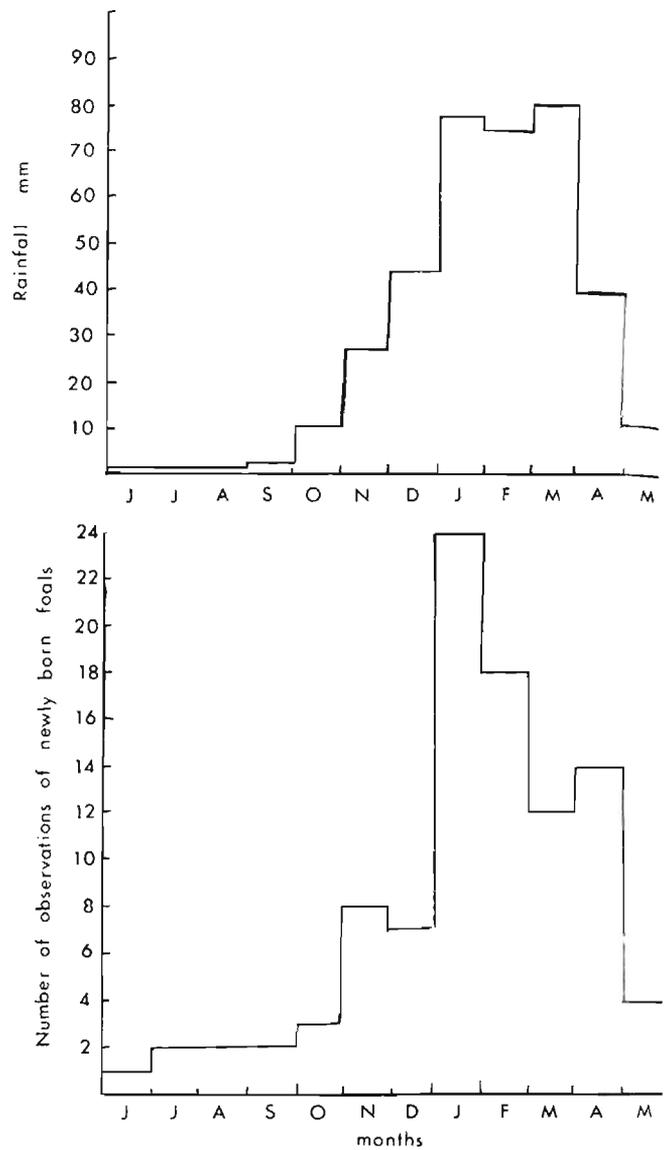


Figure 3. The correlation between rainfall and foaling in *Equus zebra hartmanniae*.

VI GESTATION PERIOD

Wackernagel (1964) gives the gestation period of Burchell zebra as 371 days. This was determined in a zoo. Only one accurate gestation period could be recorded from the Hartmann zebra. A pair was kept in an enclosure of 14 ha next to the Legislative Building in Windhoek. On the 25th July, 1967, Mr Holtzhausen saw the pair mating and on the 25th July, 1968 the female gave birth to a foal. This gives a gestation period of 362 days.

VII ACKNOWLEDGEMENTS

During the initial stages I received valuable advice and assistance from Messrs D. Visser and P. Brand. A special word of thanks is due Mr C. G. Coetzee,

Director, State Museum for his advice and guidance and for making facilities available, Mr Boshoff, Officer in charge of the Meteorological station, Windhoek, for his friendly assistance in providing meteorological data. Dr S. S. Grové and his staff, especially Mrs Lang, from the South African Institute for Medical Research is thanked for their assistance with the semen samples, as is Mr H. Böhme for preparing the figures.

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