A REVIEW OF SOME LIFE HISTORY FEATURES OF THE LARGE HERBIVORES OF AFRICA*

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INTRODUCTION

In wildlife management there is a need for ready access to knowledge of the biologies of species. Available data are unfortunately widely scattered throughout the literature, and an annotated bibliography would assist the wildlife manager to find and apply what is already known.

In this review the large herbivores indigenous to Africa are dealt with species by species according to the systematic treatment of the Smithsonian Institute's Preliminary Identification Manual for African Mammals (Ansell, 1968; and Gentry, 1968). Known information on the reproductive performances of each species is summarised.

In considering these reproductive performances relevant life history features are individually reviewed, and, by way of introduction, these features are briefly discussed below.

LIFE HISTORY FEATURES

African large herbivores are iteroparous (reproduce more than once in a life-time) and, with few exceptions, are monotocous (produce one young per birth). Regarding reproduction, the particular life history features whose values affect each species' power of increase are:

    (i)   age at which females first give birth;
    (ii)   annual birth rate of females;
    (iii) age at which birth of last offspring occurs.

It has been suggested (Cole, 1954) that these life history features are as much a product of natural selection as the morphology of behaviour of a species. To what extent each one of these life history features, and to what extent change in them may contribute in affecting the productivity of a population is important. This review deals with the values which these various life history features in African large herbivores have been reported to take, with emphasis on what may be realistic potentials in the wild.

Before discussing each of the life history features enumerated above, it may be emphasized that it is the performance of females rather than it may be which is of primary concern. For as long as there are fertile males males to cover females it is the latters' productivity which determines the population's reproductive performance. Nevertheless, details of ages of males at sexual maturity and at first participation in breeding, and details of seasonal activity in male reproductive organs are included.

Age at first parturition

In the species, and amongst the life history features discussed in this review, it is age at which reproduction begins in which change most sensitively affects a population's power of increase. In establishing the age at first parturition knowledge of supplementary life history features is of assistance. For this reason details of age at sexual maturity and length of gestation period have been included in the review.

The age at attainment of puberty and sexual maturity may be respectively defined as the age at which reproduction first becomes possible and the age when full reproductive power is acquired. In this review attention is focused on the age when the ability to conceive (or fertilize) becomes a likely probability in the wild, and the terms "puberty" and "sexual maturity" have been used loosely.

It is well known that the age at puberty in domestic animals is related to the rate of growth, the attainment of a certain degree of physiological development, and the plane of nutrition (Joubert, 1963). In contrast to domestic mammals, wild herbivores have not yet been subjected to specific experiment to investigate factors affecting puberty. Nevertheless, nutritional differences and other factors have been invoked to explain differences in age of attainment of puberty (see, for example, Skinner & van Zyl, 1969; Daniel, 1963; and Laws, 1969).

Annual birth rate of females

The life history features pertinent here are:
  (i)   litter size;
  (ii)   time interval between successive litters to the same female;
  (iii) sex ratios at birth.

Reliable quantitative information on litter size in African herbivores has mostly only recently become available, and many earlier reports of multiple births are suspect. Despite the prominence given by Asdell (1964) and Walker (1964) to multiple births, the data at hand (Zuckerman, 1953; Brand, 1963; and others) suggest that, except for members of the Suidae and Caprinae, African large herbivores are monotocous, multiple births occurring infrequently.

In estimating time intervals between successive births the occurrence and degree of restricted breeding is clearly of importance; furthermore, for many species there is no detailed information on *post-partum* anoestrus. It is for these reasons that seasonal breeding patterns have been reviewed. Documentation of seasonal breeding of large herbivores in Africa started relatively early, hunters and explorers incidentally noting rutting and calving times in their wanderings in Africa. These early notes were followed by such accounts as those of Stevenson-Hamilton (1912) and Shortridge (1934) which were based on personal experience and reference to earlier writings. Subsequently there have been analyses of breeding in captivity (Flower, 1932; Zuckerman, 1953; and Brand, 1963), and analyses of records of sightings of mating behaviour and of new born young (Ansell, 1960; Fairall, 1968). In the past 15 years detailed studies have been published, based on sizeable samples of culled animals collected over fairly restricted time intervals. These latter studies have not only produced a respectable body of evidence, but they have also emphasized a number of deficiencies in earlier methods.

In evaluating writings of early natural historians the following points may be borne in mind:
  (i)   in seasonally breeding animals some variation may occur in the time of breeding at a single locality from one year to the next (Talbot & Talbot, 1963; Fairall, 1968; Watson, 1969; Hanks, 1970; Bigalke, 1970). This means that observation over one season may not be a reliable guide to breeding patterns in a given locality;
  (ii) in seasonally breeding species there may be considerable spatial variations in the time of breeding (Ansell, 1960; Dasmann & Mossman, 1962a; Laws, 1969; Bigalke, 1970). Awareness of this fact may well avoid the sort of generalisation where it was concluded that there is apparently no fixed season in greater kudu *Tragelaphus strepsiceros* "as authorities disagree about the season of birth" (Asdell, 1964: 579). It has since been found that at least in some areas kudu are seasonal breeders (Wilson, 1965; Fairall, 1968; Simpson, 1968; and Skinner & Huntley, in press a);
  (iii) for some seasonally breeding herbivores such as wildebeest *Connochaetes taurinus* and hartebeest *Alcelaphus buselaphus* it seems that timing of calving is at least partly related to producing calves in the presence of good grazing (Watson, 1969; and Gosling, 1969), while in elephant *Loxodonta africana* conception peaks have been correlated with rainfall and quality of range (Laws, 1969; Hanks, 1969). Thus, species with gestation periods longer than a year (e.g. elephant, rhinoceros, giraffe) may superficially appear to have no or irregular calving seasons, but, on closer examination, the degree and nature of restricted breeding may be affected by rainfall peaks and the quality of the range. In addition, the degree to which arid zone species are opportunistic in being able to respond to irregular rainfall and its effect on range condition might, short of detailed study, preclude reliable general statements on seasonality of breeding.

Up to now and in this review the emphasis in study of seasonal breeding has been placed on females. It is, however, noteworthy that it has been recently shown that in at least some seasonally breeding species there occur distinct morphological, chemical and histological cycles in the male reproductive organs whose peaks in activity coincide with rutting times (Skinner, 1971). Nevertheless, it appears that there are always some fertile males throughout the year.

On the basis of available data sex ratios at birth mostly approximate to 1 : 1. However, there are some notable exceptions *(Giraffa camelopardalis, Raphicerus campestris* and *R. sharpei).* Lowe (1969) showed that sex ratio of progeny was affected by age of dam in *Cervus elaphus.* Some information on secondary sex ratios is also provided in the present review.

Age at which birth of last offspring occurs

There is little information on the reproductive longevities of African large herbivores in the wild. However, most species have been kept in

captivity and particularly the papers of Flower (1931), Jarvis & Morris (1960), and Crandall (1965) have yielded valuable data.

How helpful longevities in captivity might be for estimating potentials in the wild will be revealed only after widespread use of refined ageing techniques on wild animals. Comparative data at hand show some agreement between longevity in captivity and potentials in the wild. In any case, small errors in equating potential ecological longevity with longevity in captivity are of very minor population consequence, for, with increasing age, breeding females contribute progressively less and less to the population's power of increase (Cole, 1954).

In the body of this review omission of species, and omission of some life history features may be taken to imply an absence of known, useful details.

ACKNOWLEDGMENTS

Loxodonta africana   African elephant

Age at sexual maturity

Mean age of about 10 years with a range of from 8 to 12 years of age (Perry, 1953); but using Laws' ageing criteria Perry's data indicate age at puberty 11—12 years, and Savidge's data 14—15 years (Laws, 1966).

Possibly earlier attainment of puberty in forest elephant, i.e. about 8 years (Laws, 1966).

Mean ages at attainment of sexual maturity in East Africa from 11 to 20 years with a range from 9 to 33 years of age. Potential mean age at puberty about 10 to 11 years (Laws, 1969).

While Perry (1953) suggested sexual maturity in both sexes attained at 8 to 12 years of age, Laws & Parker (1968) indicated males mature 1—2 years later than females, but collection of further data and re-examination of evidence point to ages at attainment of puberty not significantly different between sexes (Laws, et al, 1970).

Age at puberty 13—15 years in females in Zambia (Hanks, 1970). In the Kruger National Park three of four 12-year old females were pregnant, and indications are that puberty is reached before 12 years, perhaps as early as about 9 years (Smuts, pers. comm.).

Gestation period

600—690 days (Kenneth & Ritchie, 1953)
649—661 days (Lang, 1967).

Age at first parturition

Assuming potential mean age at puberty about 10 to 11 years, and gestation period about 22 months, then potential mean age at first parturition about 12—13 years.

Mating, calving and calving interval

Widely reported that elephant calve in every month of the year, or that there is no apparent calving season (Perry, 1953; Ansell, 1960; Pienaar, 1963; Buss & Smith, 1966; Fairall, 1968), but recently peaks have been demonstrated (Laws & Parker, 1968; Laws, 1969; Hanks, 1969 and 1970; Laws, et al, 1970), and rainfall, by its influence on habitat, has been invoked as the proximate environmental factor determining conception peaks. In Kruger Park not only do conception peaks coincide with rainfall peaks, but conception rate also fluctuates in proportion to yearly rainfall (Smuts, pers. comm.).

Shortest recorded individual calving interval appears to be about 2½ years; maximum individual calving interval may be as high as 13 years. Field studies in East Africa indicate mean calving intervals ranging

from 4—5 years to 8—9 years (Laws, 1969; Hanks, 1970). Laws, *et al*, (1970) find a peak fertility in the 31—40 year age group of a sample of females taken from Murchison Falls Park, South.

In Kruger National Park indications are that there is a 4-year calving interval (Smuts, pers. comm.).

Twinning

3 out of 222 embryos and foetuses i.e. 1,35± 1,55% (Laws, 1969).

In Kruger National Park twinning observed in 1,2% of pregnancies examined (Smuts, pers. comm.), and one confirmed case of twin births in a population of 6 000 or so elephants (Fairall, pers. comm.).

Sex ratios

Foetal sex ratio: n = 171 93 (54,39%) male : 78 (45,61%) female insignificantly different from 1 : 1 (P > 0,05)(Laws, 1969).

n = 109 foetuses: 53 males : 56 females (Smuts, pers. comm.).Up to 2 years of age: n = 290 54,66% male which is significantly different from 1 : 1 (P > 0,05). Secondary sex ratio: 55,7% female (Laws, 1969).

Longevity

Only two cases exceeding 30 years reported by Flower (1931 and 1947): female 35 years 4 months 16 days, 39 – 39½ years.

2 females 40 years and 43 years respecrively (Bourlière & Verschuren, 1960, vide Laws, 1966),male in Addo Park 56 years (Anon., 1968a).

Upper age limit about 60 years (Laws, 1966).

Laws, et al (1970 observed an increasing proportion of reproductive inactivity amongst females estimated 51—60 years of age, and the possibility of this "menopause" being density- or habitat-dependent is indicated.

Ceratotherium simum   square-lipped or white rhinoceros   455

Age at sexual maturity

Appear to be no substantiated observations, but Vaughan-Kirby (1920) and Lang (1920) estimated 4—5 years.

Gestation period

548—578 days (Kenneth & Ritchie, 1953)
614 days (Anon., 1968b)
584 days (Wilson, 1969a)
476 days)
482 days) (Vincent, 1969)

Age at first parturition

From above may be 5½ — 6½ years.
6—7 years in Umfolozi Game Reserve (Owen-Smith, 1971).

Mating, calving and calving interval

Data indicate a wide spread of births (Fairall, 1968; Natal Parks Boards unpubl. records). However, Owen-Smith (1971) reports the onset of oestrus apparently stimulated by a flush of green grass, so that there is a mating peak in spring and subsequent calving peak in autumn nearly a year and a half later.

2½ years   )
2¾ years   ) Kruger Park, vide Vincent, 1969
2½—3 years   )
4,33 years at Loskop Dam (Anon., 1968b).

However, Owen-Smith (pers. comm.) has observed in Umfolozi Game Reserve oestrus at 6—7 months *post partum* indicating that calving interval may be as little as 21—22 months.

Sex ratios

Population sex ratios:
n = 409   213 males   : 188 females   Chi² = 1,557
n = 226   116 males   : 110 females   Chi² = 0,164
Conclude sex ratio 1 : 1 (Vincent, 1969).

Longevity

Female 21 years (Huntley, 1967)
Female 36 years old still bearing calves (Player & Feely, 1960).

Diceros bicornis   black rhinoceros

Age at sexual maturity

Captive rhinoceros:

	Dittrich (1967a)	Greed (1967)	Hays (1967)
First mating	Male 7 years Female 9 years	Male & female 4,5 years	Female 7 years
First successful mating	—	Male & female 6 years	Female 8 years

Wild rhinoceros:
The following are observations of Goddard (1970b) at Ngorongoro:

Sex	Birthday	Age at sex maturity	Remarks
Female	1961	4,7 – 5,7 years*	Produced female calf Dec. 1967
Female	1961	3,8 – 5,0 " *	Produced male calf Jan-March 1967
Male	Oct. 1962	4,3 "	Mating 17.2.67
Female	Aug. 1963	4,5 "	Mating 3.2.68 and produced male calf June 1969.

* Assuming a gestation period of 15—18 months.

Gestation period
469 days (Dittrich, 1967a)
446, 478 days (Goddard, 1967)
457 days (Gowda, 1967)
438, 419, 438 days (Greed, 1967)

4 observations of slightly greater than 17 months and another observation of 15 months (Hallstrom, 1967)

  463, 454, 457 days (Hays, 1967)
  465, 462 days (Yamamoto, 1967)
  Mean length of gestation period about 454 days.

Age at first parturition

Captive rhinoceros:
7 + years (Greed, 1967); 8 + years twice reported (Dittrich, 1967a, and Yamamoto vide Goddard, 1967).
  9 + years (Hays, 1967).

Wild rhinoceros:
From data of Goddard (1970b) quoted above under "Age at sexual maturity" from 5 + years to about 7 years with one definite case of age at first parturition at about 5,75 years.

Mating, calving and calving interval

No good evidence to indicate any seasonal peaks of reproductive activity (Ansell, 1960). However, Joubert (1969, von Richter, pers. comm.) recorded the following birth dates in the Kaokoveld: December 1967, January 1967, March 1966(2), March 1967, March 1968, April 1967, May 1966, May 1967, June 1967 and August 1967. In view of the black rhino's long gestation period Joubert's (Op.cit.) suggestion of photoperiod being implicated in apparent seasonal breeding is not entirely acceptable, but the alternative flushing of trees and shrubs (on which the rhino feed) in the rainy season may stimulate oestrus and result in a peak of conceptions.

Observations of time intervals between successive births to same female as follows:
  40+ months, 32+ months (Greed, 1967)
  2 observations of 30 months (Hays, 1967)
  23½ months (Yamamoto, 1967)
  2 observations of 24 months; 35½ months (Goddard, 1967)
  25 months, 28 months, 29 months (Goddard, 1967).

Roth & Child (1968) deduce from data from zoos (15½—16 month gestation period, and a 12 day period before the first oestrus *post partum* a theoretical potential birth rate of 72—75 calves per 100 sexually mature females per year i.e. 1 calf per adult female every 16—16½ months). These workers observed in the Kariba Lake basin what they estimate a birth rate of about 50 calves to every 100 adult females (i.e. 1 calf every 2 years for each adult female).

Goddard, (1967) says: ". . . a normal healthy female could be expected to produce a calf approximately every 27 months". This may be accepted as a realistic potential. Moreover, from the calculations given below and using Goddard's (1970a) theoretical age structure for the Tsavo rhinoceros population it is evident that at least in the Tsavo population the calving interval must average about 27 months, assuming age at first parturition is 6 years.

(In cohort of 1 000 animals there are 536 adult animals, 6 years and older, (see Goddard, 1970a) of which 268 are females on the assumption of a 1 : 1 adult sex ratio. One calf per adult female every 27

months (or 4/9 calves per adult female per annum), as suggested by Goddard (1967), corresponds to 119,1 calves per annum for the cohort of 1 000 animals. This recruitment is just greater than Goddard's (1970a) calculated theoretical of 109 calves which Goddard shows is approximated closely by his Tsavo field counts).

Sex ratios

The following figures show little departure from a sex ratio of 1 : 1.

	Males	Females	Source	Chi²	P
Adults	37	29	(Goddard,	0,97	> 0,5
	22	19	1967)	0,22	> 0,5
	87	81	(Hitchins, 1968)	0,203	> 0,5
	167	170	(Goddard, 1970a)	0,013	> 0,5
Immatures & juveniles	19	21	(Goddard,	0,1	> 0,5
	18	14	1967)	0,2	> 0,5
	16	15	(Hitchins, 1968)	0,032	> 0,5
Immatures	27	42	(Goddard, 1970a)	1,6	> 0,5
Calves	67	52	(Goddard, 1970a)	0,97	> 0,5
Population	29	28	(Roth & Child 1968)	0,18	> 0,5

Population sex ratio in Joubert's (1969, von Richter, pers. comm.) study area in the Kaokoveld was 1 : 0,87. Elsewhere the ratio deviates even further from parity, the explanation given being that females with calves at foot are particualrly aggressive and therefore persecuted by the local inhabitants.

Longevity

Records of longevity in captivity reviewed by Reynolds (1962) and Goddard (1970a). There are numerous instances of captive animals exceeding 20 years of age, and the following three exceeding 30 years of age:
Male 34 years 14 days in Johannesburg Municipal Gardens (Reynolds, 1962).

Male 34 years in Chicago)
Female 36 years in Chicago and still) (cited by Goddard, 1970a)
living)

In addition Goddard (1970a) found an old female, estimated 30 ± 4 years of age and from a wild population at Olduvai, to be pregnant. In his consideration of the vital statistics of the Tsavo population, Goddard (op. cit.) has assumed a maximum ecological longevity of about 40 years.