E. Afr. Wildl. J. **8**: *105–121 (1970)*

AGE CRITERIA AND VITAL STATISTICS OF A BLACK RHINOCEROS POPULATION

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Summary

Tsavo National Park, in Kenya, probably contains the largest population of black rhinoceros (*Diceros bicornis* (L.)) left in existence. Large-scale damage of the vegetation initiated by elephants and aggravated by fire has changed considerable areas of the park. The ecology of the black rhinoceros in this changing environment has been studied: the present status and population structure is considered here, including the development of detailed ageing criteria for the species, an analysis of natural mortality and survivorship, and a record of the structure of the living populations within the major habitat types.

Crania and mandibles were collected from 506 rhinoceros found dead in all areas of the park. This material was divided into 20 relative age classes based on dental characteristics. Crude chronological ages, based on an estimate of the maximum expectation of life and the examination of seven known-age dental records of captive animals, were assigned to each age class. These crude ages were then refined by examination of 16 dental records of known-age wild rhinoceros, and a chronological age scale established.

A survivorship curve of the population was thus constructed. Annual mortality during the first and second year of life is about 16%, and the indicated mean annual mortality from 5-25 y is 9.8%. A theoretical model of the population structure is shown, and analysis of the annual mortality and recruitment at birth suggests that the population was stable during the 1960's. Assuming the data represent a stable population the mean expectation of life at birth is 8.4 y.

Thirteen major habitat types are described. The characteristics of the rhinoceros population within each habitat type were established both from ground studies and aerial observations. Nearly 700 rhinoceros were identified and catalogued on the ground, in sample areas selected for intensive study. Population structures, cow:calf ratios, and recruitment appear to be average in most habitat types. The analysis of recruitment at birth and mortality during the first year of life, both from computations from the survivorship curve and from the structure of the living populations, support the validity of the ageing criteria, and further suggest that the population was stable during the 1960's.

Finally, the relationship between the elephant and the rhinoceros in the changing environment is discussed with reference to recent findings in elephant ecology. In conclusion it is recommended that population reduction of the Tsavo elephants should be initiated.

Introduction

Tsavo National Park covers an area of some 23,500 km². Up until about 1950, large areas of the park were covered in *Commiphora* woodland. Under the large-scale destruction by elephant (*Loxodonta africana* (Blumenbach)) and fire the tree-bush complex has been reduced or destroyed in many areas, where it has been replaced by bush-grassland and grassland. Annual rainfall varies from 152—762 mm with a markedly seasonal pattern (Laws, 1969).

The total number of elephants using the entire ecological unit (an area of some 44,000 km² which includes the park and extends for a considerable distance beyond the park boundaries) has been established at 30-40.000 (Laws, 1969). The damage to the woodland partially caused by this population has been phenomenal. Thousands of trees and larger bushes have been knocked over and destroyed and many of the larger trees have been ring-barked and have fallen to the ground. With the large amount of dead and decaying woody material and debris present, hot ground fires have swept through and have changed the whole ecology of the region. Other prominent trees of the ecosystem, such as *Platycelyphium voense* (Engl.) Wild *Melia volkensii* Guerke. *Delonix elata* (L.) Gamble, and *Boscia coriacea* Pax. had remained virtually untouched by elephants up to the end of 1968.

In addition to its very large elephant population Tsavo is one of the last strongholds of the black rhinoceros. Concern has recently been shown by the government of Kenya, other African governments and international conservation organizations about the fate of this species throughout its entire range in Africa. Much concern has also been voiced about the possible effect that this changing environment in Tsavo may have on browsing species such as the black rhinoceros (Napier Bax and Sheldrick. 1963; Glover and Sheldrick. 1964).

Some observers felt that the large-scale devastation and damage initiated by elephant and aggravated by fire has been detrimental to the black rhinoceros; they believed that the rhinoceros were suffering severe competition from the elephant for the remaining food supplies and that the animals were slowly dying of malnutrition (Napier Bax and Sheldrick, 1963). This anxiety was heightened in the early part of this decade (between 1st August. 1960 and 30th September. 1961) when during a marked drought period at least 282 rhinoceros died along a 64-km section of the Athi river (Sheldrick. pers. comm.; Foster, 1965). The consensus of opinion among scientists who investigated this mortality was that these animals had died of nutritional anaemia (Tremlett, 1961).

In view of this problem, a major concern of the research in Tsavo was to ascertain the present status and population structure of the rhinoceros in the park. This necessitated the development of ageing criteria for specimens representing natural mortality, and a field study of the structure of the living populations within different major habitat types. The age criteria, an analysis of natural mortality and survivorship, and the status and present structure of the living populations are presented in this paper.

METHODS

Development of ageing criteria

During 1966—1968, at the request of the Tsavo Research Project and under the direction of the wardens of Tsavo, the park scouts collected crania and mandibles from rhinoceros found dead over the whole park. A reward was offered for each specimen recovered, and a collection representing 506 rhinoceros was made. The great majority of material in this collection probably represents natural mortality, but some poached animals were undoubtedly included, especially from the Rombo area (Goddard, 1969). As poaching of black rhinoceros in Tsavo appears to be essentially a non-selective activity (Sheldrick, pers. comm.), poaching has been assumed to be part of natural mortality, and the entire collection treated as such.

The following measurements and weights were made from each specimen depending on the material available. Measurements were made with calipers and recorded to the nearest mm (Tables 1, 2).

1. Basal length: The distance, in the midline of the maxilla, from a line connecting the most posterior border of the occipital condyles to a line connecting the most anterior processes of the premaxillary bone.

2. Zygomatic breadth: The greatest distance across the zygomatic arches of the cranium at right angles to the long axis of the skull.

3. Length of mandible: The greatest length of one ramus of the mandible.

4. Measure of wear: Recorded from both mandible and maxilla. The height of the anterior buccal crest of M2 above the gum line visible on the tooth. Taken from the tip of the crest to the point on the gum line directly below the crest.

5. Mandible weight: Dry weight of cleaned mandible to the nearest 25 g. Mandibles had been brushed, cleaned, and dried for >1 y before being weighed at the end of the dry season.

TABLE 1

Cranial and mandibular measurements(mm) of black rhinoceros from Tsavo National Park, Kenya

Age class	Basal length Mean	Basal length Range	Zygomatic breadth Mean	Zygomatic breadth Range	Mandible length Mean	Mandible length Range
I	221(2)	213–229	135(2)	130–141	192(1)	—
II	—		174(1)	—	248(1)	—
III	317(1)	–	191(2)	188–195	274(3)	266–280
IV	380(1)	—	216(1)	–	316(3)	307–323
V	435(1)	—	248(3)	225–264	354(6)	336–378
VI	465(1)	—	264(10)	253–276	380(18)	350–406
VII	477(14)	428–525	280(24)	260–301	403(35)	359–430
VIII	511(10)	473–535	306(12)	276–342	433(17)	409–453
IX	503(7)	476–530	297(7)	274–320	436(11)	404–464
X	516(9)	493–534	310(9)	295–317	441(18)	418–485
XI	529(6)	520–544	321(6)	306–340	450(22)	425–478
XII	532(9)	510–552	320(10)	305–345	450(19)	409–476
XIII	536(13)	517–560	326(15)	314–350	461(29)	425–484
XIV	549(24)	504–580	328(27)	312–347	454(55)	423–484
XV	550(29)	522–581	330(33)	305–377	458(51)	427–487
XVI	548(22)	504–585	328(22)	306–356	458(37)	426–516
XVII	550(19)	517–582	328(19)	311–350	463(34)	442–482
XVIII	557(17)	536–598	331(18)	303–354	464(28)	434–490
XIX	575(12)	545–618	340(14)	324–388	469(22)	448–502
XX	567(3)	546–592	330(3)	307–359	464(7)	444–496

(Figures in parentheses indicate the number in the sample)

Prior to measuring, the entire collection was grouped into 20 classes based on similar characteristics of eruption and wear patterns of the mandibular dentition. Tentative and approximate mean ages were then assigned to each class according to the procedure advocated by Laws (1966, 1968). In the assignment of these crude ages reference was made to the probable maximum life expectancy, i.e. c. 40 y (Table 5). By reference to this assumed approximate longevity, and dental records of seven known-age captive animals, time intervals were estimated between successive age classes based on the state of eruption and wear of the mandibular dentition. A more or less arbitrary time scale was thus established.

TABLE 2

Mandible weights (sexes combined) and heights of M2 in the maxilla and the mandible from a black rhinoceros population*

Age class	Mandible weight (kg) Mean	Mandible weight (kg) Range	Height of mandibular M2(mm) Mean	Height of mandibular M2(mm) Range	Height of maxillary M2(mm) Mean	Height of maxillary M2(mm) Range
I	0.210(1)	—	—		—	—
II	0.490(1)	—	—		—	—
III	0.706(3)	0.625–0.825	—	–	—	—
IV	1.185(1)	—		—	—	—
V	1.874(4)	1.550–2.475	-	—	—	—
VI	2.370(8)	2.025–2.650	—	—	—	—
VII	2.862(22)	2.200–3.775	—	—		—
VIII	3.877(10)	3.350–4.675	—	—		—
IX	3.900(10)	3.475–4.600	—	—		—
X	4.505(12)	3.725–5.870	—	—		—
XI	4.865(13)	4.450–5.550	40(23)	35–44	47(6)	33–54
XII	5.290(15)	3.950–6.175	36(23)	29–45	43(8)	31–55
XIII	5.160(16)	4.525–5.775	33(33)	27–40	39(15)	29–47
XIV	4.940(33)	3.800–6.200	29(60)	19–36	35(25)	20–47
XV	5.000(38)	3.975–6.250	24(55)	18–34	27(33)	15–42
XVI	4.905(26)	4.025–6.300	20(34)	16–25	23(22)	14–36
XVII	4.720(26)	3.850–5.975	16(33)	5–22	19(17)	11–32
XVIII	4.710(21)	3.675–5.725	15(28)	9–23	17(16)	11–27
XIX	5.160(15)	3.875–6.200	12(20)	8–20	13(10)	8–24
XX	4.450(7)	3.775–5.125	9(6)	7–15	10(2)	6–15

* See text

Refined ages were then determined for each age class by examination of the mandibular dentition of 17 specimens of known-age wild rhinoceros. The seven records of known-age captive animals were also examined. These animals varied in age from 0 y (birth) to 34 y (Table 3). Known-age wild rhinoceros up to 6 y old were immobilized, had their dentition examined, were measured and were marked with metal ear-tags (Table 3) stamped with the month and year of birth. The development of these rhinoceros had been followed closely since their birthdays (Goddard, 1967). Several of these animals were re-immobilized 2–3 y later and their dentition re-examined (see below). In some cases dental examination was facilitated by the use of an instrument which forced the buccal cavity wide open. With the aid of a pen-torch the entire dentition was examined. With rhinoceros under heavy anaesthesia this is a relatively simple procedure.

The dentition of known-age captive rhinoceros was examined directly, and by an X-ray of the entire mandibular tooth row (Plate 1a). I am indebted to Dr. L. R. Whittaker, Specialist Radiologist of the Kenyatta National Hospital, Nairobi, for his co-operation and enthusiasm in X-raying the captive animals and mandibles. Photographs of the entire tooth rows of a 34 y old captive male rhinoceros were also obtained.

Foster (1965) classified a series of 49 skulls from Tsavo into seven relative age-groups, but because of a lack of known-age data did not allocate precise ages to the material. He also reported dentine lines in the molariform teeth. External dentine rings were noted on some of the teeth in the material considered here. No correlation between the number of rings and the known-age specimens could be determined, probably because many external rings are vague and indefinite; just what constitutes a ring is not always clear. Anderson (1966) obtained some maxillae and mandibles from young black rhinoceros in the Hluhluwe Game Reserve, whose approximate dates of birth had been noted. Data from the present work were compared with the results of both these studies.

TABLE 3

Records of known-age black rhinoceros whose dental development was examined directly, by X-ray, or by photographs.

No.	Age (months)	Sex	Origin	Remarks
1(W)	Foetus	♀	Ngorongoro	39.04 kg and ready for presentation
2(W)	1	♂	Ngorongoro	Mutilated by hyaenas and shot at 30 d
3(W)	4½	♀	Ngorongoro	Birthday known within one week
4(W)	5, 29	♂	Ngorongoro	—
5(C)	5½, 12, 18, 24	♀	Tsavo East	"Stubs"—Birthday known within one week
6(W)	7½	♂	Ngorongoro	Birthday known within 5 d
7(W)	11	♀	Ngorongoro	—
8(W)	14, 36, 57	♀	Ngorongoro	Birthday known within 3 d
9(W)	17½, 39	♀	Ngorongoro	—
10(C)	19	♀	Tsavo West	"Tinkerbell"—Birthday known within a week
11(W)	29	[illegible]	Ngorongoro	—
12(W)	34, 72	♂	Ngorongoro	—
13(W)	38, 61	[illegible]	Ngorongoro	—
14(C)	81	♂	Tsavo East	"Rufus"—Birthday known within 2 d
15(C)	408	♂	Oldeani Mountain, Ngorongoro	"Pharaoh" in Chicago Zoo. Birthday known to within 6 months

(W)—Wild, (C)—captive; under column "Remarks", unless otherwise noted, the birthday of the rhinoceros was known to within one month. Under column "Age", two or more records indicate that the animal was examined at these ages.

Structure of the living population

Because of the sedentary nature of the rhinoceros in Tsavo it was quite feasible to establish the structure of the living population by direct field observation within the various habitats. Records and observations were made both from the ground and from the air.

On the ground certain areas were systematically covered on foot and by vehicle and each rhinoceros observed was recorded. The myopia of the rhinoceros permits a close approach on foot. Each animal was approached and identified using the procedure described by Goddard (1966), photographed if necessary, and catalogued. In this way, nearly 700 rhinoceros were catalogued by the author in several principal habitat types. This sample represents approximately 10 % of the Tsavo population (Goddard, 1969). Cataloguing was assumed to be random; in some small areas selected for intensive study the total population was known to the author. Rhinoceros were sexed, and aged as adult, immature, calf, and calf of the year (Table 10). An adult was considered to be a full-sized animal; an immature, an animal less than full size that had left its dam; a calf, an immature animal still in the company of its dam; whether a calf was under 1 y old was determined on the basis of body size and horn development. This study of field age-criteria will be the subject of a later paper.

Aerial observations were made of the ground study areas, and over vast areas of different habitat types. The same broad ageing criteria as used in the ground observations were used from the air. From the air rhinoceros were classified as adults (sex unknown), immatures (sex unknown), females with calves, and females with young of the year (Table 10). In the course of the aerial census of the Tsavo population random samples of the structure of the living populations were also obtained (Goddard, 1969).

RESULTS

Black rhinoceros dentition

The normal dental formula of the black rhinoceros is:—

Deciduous: $I\,\frac{0}{0};\ C\,\frac{0}{0};\ P\,\frac{4}{4} \times 2 = 16$

Permanent: $I\,\frac{0}{0};\ C\,\frac{0}{0};\ P\,\frac{4}{4}$ or $\frac{3}{3}$;

$M\,\frac{3}{3} \times 2 = 24\text{-}28$

The adult black rhinoceros normally has four premolars and three molars, the sequence of eruption being from anterior to posterior. Rudimentary incisors and canines do occur but are rare. The three molars are massive, ridged structures and are the principal teeth used in feeding. From known-age material collected from wild animals it was ascertained that M1—M3 erupt in an orderly sequence, each tooth taking longer than its predecessor to reach full development. Thus M1 starts to form as a tiny tooth bud at c. 2 months but is normally not fully developed until c. 36 months; M2 buds at c. 15 months and is fully erupted at c. 60 months; M3 buds at c. 48 months and is fully erupted at c. 96 months. A similar condition of increased progressive eruption has been noted in man (Geigy, 1956).

The development, eruption and consequent wear is similar in both the mandible and maxilla, but the maxillary dentition usually develops slightly ahead of the mandibular dentition. The first premolar is present at birth and at ages from about 12 y onwards it is permanently lost (see below). This tooth is not replaced by a permanent premolar. Foster (1965) states: "The first premolar is apparently shed and replaced at a very early age and may have disappeared entirely from older animals". Anderson (1966) refers to a "deciduous" and "first permanent premolar" and states that the first permanent premolar is erupting at 18 months. However, X-ray examination of living captive rhinoceros varying in age from 5-18 months, together with examination of 18 mandibles from wild animals (varying in age from birth to 3 y), both by X-ray and dissection, showed no evidence whatever of a "first permanent premolar". Laws (1968) reported the same condition in the hippopotamus (*Hippopotamus amphibius* L.) in which "only the deciduous premolars 2-4 are replaced by permanent premolars". It is suggested that in Anderson's specimen 1122 the "permanent first premolar", which was recorded as being in a state of eruption at 18 months, was in fact the original first premolar present from birth, which was retarded in development.

Description of the age classes

A description of the mandibular dentition within the 20 age classes follows. Chronological ages were assigned to these classes (Table 4) using the methods described below.

TABLE 4

Chronological ages allocated to the relative age classes

Age class	Mean age (y)	Probable range	Class	Mean age (y)	Probable range
I	0		XI	8	1
II	½	—	XII	9	1
III	1	—	XIII	10	1
IV	1½	—	XIV	12	1
V	2	½	XV	14	2
VI	3	½	XVI	17	2
VII	4	½	XVII	21	3
VIII	5	½	XVIII	25	3
IX	6	½	XIX	30	4
X	7	1	XX	35	4

Class I—P1 and deciduous P2 just erupting above bone level. Deciduous P3 and P4 not usually erupted above bone level. M1 alveolus open.

Class II—P1 erupted above bone level and has pierced gum. Deciduous P2 and P3 fully erupted and in slight wear, but exposed dentine between cusps of both teeth not joined. Deciduous P4 has pierced gum level; almost fully erupted. M1 bud formed, the anterior crest situated about 1 cm below bone level (Plate 2a).

Class III—P1 usually fully erupted but not in wear. Deciduous P2 and P3 in wear, and exposed dentine is usually continuous between the cusps of P2 but not of P3. Deciduous P4 fully erupted but has little or no wear. Alveoli of permanent P2—P4 not formed. Crests of M1 visible just below bone level. M2 alveolus not formed.

Class IV—P1 fully erupted and usually in slight wear. Deciduous P2 and P3 have marked wear; exposed dentine joined between cusps of P2 and almost joined in P3. Deciduous P4 has marked wear. Alveoli of permanent P2 and P3, together with tooth buds, usually forming. Alveolus of permanent P4 not formed. Anterior crest of M1 has erupted above bone level. M2 alveolus open and bud sometimes occupies $\frac{1}{4}$-$\frac{1}{2}$ of the alveolus.

Class V—P2 dentine broadly joined between cusps. Exposed dentine between cusps of deciduous P3 usually joined, but not joined in deciduous P4. Alveolus of permanent P4 just forming. M1 erupted above bone level, sometimes fully erupted, but not in wear. Bud of M2 fills approximately $\frac{1}{2}$-$\frac{2}{3}$ of the alveolus.

Class VI—Exposed dentine between cusps of deciduous P3 nearly always joined, and joined in P4 in 50% of the specimens. Sometimes marked constriction between cusps of P4. M1 invariably fully erupted and in slight to marked wear, especially on the anterior crest. Anterior buccal crest of M2 usually just below bone level. Alveolus of M3 not usually formed, but tiny alveolus sometimes forming (Plate 2b).

Class VII—Exposed dentine between cusps of deciduous P4 nearly always joined. Tooth bud of permanent P4 fills the alveolus. Permanent P2 and P3 erupted above bone level in one specimen. M1 fully erupted and in marked wear but marked constriction between two cusps. M2 usually erupted above bone level. M3 alveolus formed and tooth bud sometimes forming.

Class VIII—Exposed dentine of deciduous P2 and P3 broadly continuous between cusps and joined in P4. Permanent P2 and P3 usually erupted above bone level and have sometimes displaced their deciduous counterparts. Permanent P4 approaching bone level. Exposed dentine between cusps of M1 not usually joined. M2 fully erupted but not usually in wear, with a marked constriction between cusps. M3 bud usually fills approximately $\frac{1}{2}$-$\frac{2}{3}$ of the alveolus.

Class IX—Permanent P2 and P3 have invariably displaced their deciduous counterparts and are in wear. Permanent P4 has usually displaced its deciduous counterpart and sometimes in wear. Exposed dentine between cusps of M1 usually joined. Posterior crest of M2 has slight wear, and anterior crest has marked wear, but still a marked division between cusps. Cusps of M3 just above bone level.

Class X—Permanent P2—P4 all fully erupted and in wear. Exposed dentine between cusps of P2 joined, sometimes joined in P3, not joined in P4. Exposed dentine between cusps of M1 joined. M2 in marked wear but exposed dentine between cusps not joined. M3 is approximately $\frac{1}{4}$-$\frac{3}{4}$ erupted above bone level; not in wear.

Class XI—Permanent dentition complete but both P1 often (80% of specimens) lost. Exposed dentine between cusps of P3 joined; sometimes joined in P4 (50% of specimens). Exposed dentine sometimes joined between the cusps of M2. M3 fully erupted and sometimes in slight wear, but has marked constriction between cusps.

Class XII—Both P1 missing in 90% of specimens. Exposed dentine between cusps of P4 almost invariably (95% of specimens) joined. Anterior lingual infundibulum of M1 usually worn away. Exposed dentine often (60% of specimens) joined between cusps of M2. M3 in slight wear but marked constriction between cusps.

Class XIII—One or both P1 missing on all specimens. Exposed dentine between cusps of P4 joined. Exposed dentine between cusps of M1 broadly joined, with the anterior lingual infundibulum completely worn away,

but posterior lingual infundibulum still present. Exposed dentine between cusps of M2 joined. No marked constriction between cusps of M3, but exposed dentine not yet joined.

Class XIV—On this and subsequent classes both P1 were missing from all specimens. Posterior lingual infundibulum of M1 almost, and sometimes completely, worn away. Anterior lingual infundibulum of M2 completely worn away but posterior lingual infundibulum still present. Exposed dentine between the cusps of M3 rarely joined, anterior lingual infundibulum still present.

Class XV—Anterior and posterior lingual infundibula usually completely worn away in P2. Anterior lingual infundibulum of P3 worn away and posterior lingual infundibulum usually isolated or worn away. Anterior lingual infundibulum worn away in P4 but posterior lingual infundibulum still present. Posterior lingual infundibulum of M1 worn away and dentine is broadly continuous across entire width of occlusal surface. Posterior lingual infundibulum of M2 sometimes worn away. Exposed dentine between cusps of M3 joined and the anterior lingual infundibulum usually worn away, but posterior lingual infundibulum still present.

Class XVI—P2 sometimes missing. Posterior lingual infundibulum of P3 completely worn away, in P4 usually isolated or worn away. Occlusal surface of M1 often flat and tooth sometimes missing. Dentine between cusps of M2 broadly continuous and posterior lingual infundibulum usually isolated or worn away. Occlusal surface of M2 sometimes shows a marked concavity. Anterior lingual infundibulum of M3 worn completely away but posterior lingual infundibulum still present.

Class XVII—P2 and P3 sometimes missing. Posterior lingual infundibulum of P4 worn away. M1 sometimes worn to gum line and occlusal surface slopes markedly to the lingual edge. Posterior lingual infundibulum of M2 invariably worn away and exposed dentine very broadly continuous across width of tooth. Exposed dentine between cusps of M3 broadly continuous but posterior lingual infundibulum present.

Class XVIII—P2 and P3 sometimes missing. M1 sometimes missing and often worn to the gumline or below; this tooth frequently shows a distorted occlusal surface. Occlusal surface of M2 often slopes markedly toward lingual edge and is sometimes worn almost to the gum-line. Dentine of M3 very broadly continuous, and the posterior lingual infundibulum appears as a tiny recess on the lingual edge.

Class XIX—One or both P2 frequently missing. M1 often missing or nearly worn away. Lingual edge of M2 worn to gum line. Posterior lingual infundibulum of M3 usually worn away and dentine forms a broad figure-of-eight on occlusal surface.

Class XX—Several teeth often missing or reduced to stubs. M1 invariably missing or appears as a distorted stub. M2 almost completely worn away and frequently shows a distorted occlusal surface. M3 often slopes steeply towards the lingual edge, with centre worn to gum line or below.

Allocation of chronological ages

In the first instance crude chronological ages were assigned to the age classes using the method advocated by Laws (1966, 1968). Cranial and mandibular measurements (Table 1), and mandible weights and the rate of tooth wear (Table 2), suggest that the age-class series from I—XX does in fact represent an increasing age-scale. As Laws (1966, 1968), referring to the elephant and the hippopotamus, states "the age groups are a ranked series and while we can be confident that they represent a series of increasing ages the allocation of absolute ages presents difficulties. In spite of this an attempt has been made to allocate ages to the groups because even rough approximations to a true chronological age-scale, which can later be refined, are more useful than relative ages".

Firstly, a figure for probable maximum life expectancy was determined which would set the approximate age of the oldest wear class (XX). There is, as far as I know, no documented record for maximum longevity for the species attained under wild conditions. There are, however, several records from zoological gardens (Table 5). Considering these available records a maximum ecological longevity of about 40 y was assumed for the black rhinoceros. This, as will be seen later, is a fair estimate based on the established rate of wear of the teeth.

TABLE 5

Some longevity records of black rhinoceros in zoological gardens

Sex	Date received	Age at death	Locality	Author	Remarks
♀	?	22 y 7 months	London	Flower (1931)	
♂	25.5.06	25 y 5½ months	Chicago	Crandall (1964)	
—	31.12.14	27 y 10½ months	Pretoria	Crandall (1964)	
♂	19.5.35	34 y	Chicago	Rabb (pers. comm.)	"Pharaoh"
♀	19.5.35	Still living Jan. 1969, aged 36 y	Chicago	Rabb (pers. comm.)	"Mary"
—	—	49 y*	—	Flower (1931)	

* This was a Great Indian one-horned rhinoceros (*Rhinoceros unicornis* L.)

Next a more or less subjective time-scale was established, which estimated the elapsed time between the different age-classes by reference to the assumed potential longevity, and by examination of seven known-age dental records of captive rhinoceros. Dental development records (by X-ray and direct examination) were obtained for one female at the ages of 5½, 12, 18, and 24 months, on a 19-month female, an 81-month male, and a 408-month male. Crude ages were thus assigned to the age classes.

Finally, these crude ages were refined by reference to 17 dental records obtained from known-age wild rhinoceros. These 17 records were collected from immobilized animals which varied in age from birth (Class I) to 6 y; in several cases the birthday of the animal was known to within a few days (Table 3). Four animals were immobilized twice and one three times. Some of these were examined at intervals of approximately 2 y, and one 3½ y after its original immobilization (Table 3). Refined chronological mean ages were then assigned to the series up to age class XI (mean age 8 y) with the assessed degree of variation recorded in Table 4.

Mean chronological ages of later age-classes were established by reference to the dental development of the known-age animals which had been examined twice. From the known times of full eruption of the various teeth, and typical occlusal patterns which are shown two or three years later, it was possible to project subjective mean ages to older age classes.

In the final analysis, data from the captive animals were not used in the refinement of the crude chronological ages assigned. Thus all the captive or semi-captive rhinoceros examined showed retarded growth rates, all being relatively small for their age. "Rufus" for example, a semi-captive male rhinoceros in Tsavo raised from less than a week old, shows a retarded growth rate. His mandibular dentition was X-rayed when he was 6.8 y of age and he showed the exact dental development of a 5 y old wild animal (Plate 1a).

Laws (1968) has outlined the hypothetical effects of captivity and nutritional status on tooth wear of herbivorous species. In view of the diet of captive rhinoceros, including lucerne (*Medicago sativa* L.) and soft succulent plant material, one would expect the tooth wear to be less in captive rhinoceros compared with wild rhinoceros of similar age. Plate 1b shows the state of wear of the mandibular dentition of "Pharaoh", a captive male black rhinoceros which died in the Chicago Zoological Park at the known age of 34 y. I am indebted to the Chicago Zoological Park and the Field Museum of Natural History for providing this material. From the examination of the wear pattern and measurements of the teeth this animal would be placed in age class XVIII (25±3 y). Thus above the age of 25 y the relationship of the estimated age to the actual age of this single captive record agrees with expectation (i.e. the captive animal appears to be younger on the basis of the dental characters).

The two examples quoted above cast doubt on attempts to develop age criteria for black rhinoceros from known-age captive animals, and this is undoubtedly true for other species (Laws 1966, 1968). Because of the fairly large sample of precise known-age young wild animals available it is considered that up to age class XI (8±1 y) the ages assigned in Table 4 are very accurate, and that beyond this class the mean ages assigned to the material are probably accurate to within the limits shown in Table 4. Interesting

confirmation of the validity of the age scale constructed is provided later in this paper.

Finally, the age criteria developed were compared with those suggested by Foster (1965) and Anderson (1966). Because of a lack of known-age material Foster (1965) did not allocate precise ages to his material. However, all his broad subjective classes fit the age criteria developed from known-age wild animals in this study. Anderson (1966) presents data on tooth eruption of young wild black rhinoceros whose approximate date of birth had been noted in the Hluhluwe Game Reserve, Zululand. Specimen H30, a specimen of exact known age (7.25 y), was born earless and hence easily recognizable. This specimen fits the Tsavo ageing criteria exactly. Some of the younger animals from Hluhluwe fit the Tsavo age series well.

Some other specimens from Hluhluwe are apparently anomalous. Specimens H22 and H46 show that the permanent P4 has fully erupted while the deciduous P2 and P3 are still present. The normal sequence of eruption is from anterior to posterior, and none of the Tsavo specimens showed this anomaly. In specimen H11 from Hluhluwe (an animal recorded as 14 months old) M2 was in the process of eruption. Unfortunately Anderson does not indicate if the term "eruption" refers to eruption above bone level, gum level, or the actual formation of the tooth bud within the alveolus. He states, referring to P2 and P3, that "the remaining milk premolars are replaced at about two years of age" based on comparison with one specimen whose age was recorded as ± 2 y. In the Tsavo and Ngorongoro collection this event occurred, at the earliest, at 4 ± 0.5 y and on average at age class VIII (5±0.5 y). One wild female rhinoceros was examined at Ngorongoro at a known age of 5.08 y. The permanent P2 had displaced the deciduous P2 in the right ramus; in the left ramus the deciduous P2 was sitting loosely on top of the permanent P2. The other deciduous premolars were still present (Plate 1a). This rhinoceros was of average size for its age, and had also been examined at an age of 3.2 y.

Mortality and survivorship

Of the 506 specimens collected in the Tsavo National Park, 477 were assigned to the age classes. Specimens were collected from all areas of the park and for purposes of analysis are considered to represent one population. Adult and immature black rhinoceros skulls can survive for a considerable period in an arid environment (Goddard, 1967), and the collection is assumed to represent the mortality occurring between 1958 and 1968, on average 1963

A survivorship curve, representing both sexes, was constructed in the usual manner. Thus all animals in the sample have reached the age of 0 (birth). Because all are this age or older the numbers progressively dying in each age-class are subtracted to give the survival to the next class (Table 6). The raw

TABLE 6

Survival table for the black rhinoceros population in Tsavo compiled from the raw data

Age class	Age (y)	Deaths	Survivors
I	0	0	477
II	½	1	477
III	1	3	476
IV	1½	4	473
V	2	8	469
VI	3	21	461
VII	4	39	440
VIII	5	23	401
IX	6	14	378
X	7	22	364
XI	8	26	342
XII	9	26	316
XIII	10	35	290
XIV	12	63	255
XV	14	58	192
XVI	17	38	134
XVII	21	35	96
XVIII	25	29	61
XIX	30	24	32
XX	35	8	8

data from Table 6 were plotted on a semi-logarithmic scale showing the survivors to each age class (Figure 1). In this type of plot a straight line represents a constant mortality rate (Laws 1966, 1968).

It seems certain that young rhinoceros (up to c. 2½ y) are under-represented in the collection. Rhinoceros crania and mandibles from young animals are quite fragile, and are dragged away by scavengers and demolished in a short time. This considerably lessens the chance of attention being drawn to the carcass. However, adult and immature crania and mandibles are massive structures and survive for many years (Goddard, 1967).

Because of the under-representation of young animals, the curve was completed

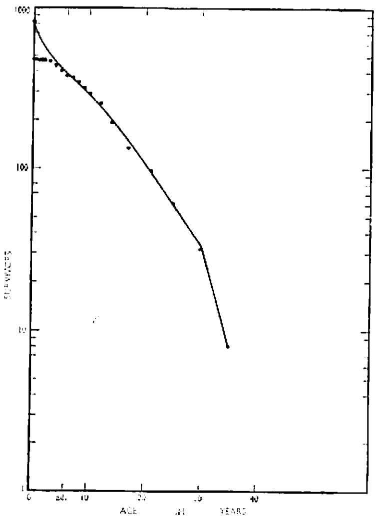

Figure 1
Survivorship curve for black rhinoceros in Tsavo National Park.

by estimating recruitment at birth according to the method used by Laws (1966), interpolating up to the age of 3 y, and assuming that the data represent female survivorship. It was also assumed that the population was stable; this assumption is supported by the field observations and is probably correct (see below).

Recruitment at birth was estimated by assuming a mean age of "recruitment" maturity of 5.5 y, and a mean calving interval of 2.5 y (Goddard, 1967 and unpublished data). There is evidence that reproduction in the black rhinoceros continues into very old age. One very old female at Olduvai (age class XIX) was found to be pregnant. From the survivorship curve the survivors are summed from 6 to 35 y. This gives a hypothetical population of 4120 adult females which should produce 1648 calves per year. Assuming a sex ratio of 1:1 at birth, 824 of these calves should be female. Summing the rest of the females from the curve this gives a total hypothetical population of 7545 females. Estimated recruitment at birth is thus 10.9%.

TABLE 7

Model life table of the Tsavo black rhinoceros population

Age class (x)	d^1_x	d_x	l_x	q_x	L_x	e_x
0	130	160	1000	160	920	8.40
1	114	141	840	168	770	8.90
2	75	93	699	133	652	9.60
3	55	68	606	112	572	10.00
4	40	50	538	93	513	10.19
5	27	33	488	68	471	10.18
6	25	31	455	68	439	9.89
7	25	31	424	73	408	9.58
8	25	31	393	79	377	9.30
9	20	25	362	69	350	9.04
10	20	25	337	74	324	8.68
11	21	26	312	83	299	8.33
12	20	25	286	87	273	8.06
13	20	25	261	96	248	7.78
14	20	25	236	106	223	7.55
15	20	25	211	118	198	7.38
16	17	21	186	113	175	7.32
17	14	17	165	103	156	7.20
18	13	16	148	108	140	6.97
19	11	14	132	106	125	6.74
20	10	12	118	101	112	6.49
21	9	11	106	104	100	6.16
22	9	11	95	116	90	5.82
23	8	10	84	119	79	5.51
24	8	10	74	135	69	5.19
25	7	9	64	140	59	4.92
26	6	7	55	127	51	4.65
27	5	6	48	125	45	4.28
28	5	6	42	143	39	3.81
29	5	6	36	166	33	3.36
30	5	6	30	200	27	2.93
31	5	6	24	250	21	2.54
32	4	5	18	280	15	2.22
33	3	4	13	308	11	1.94
34	3	4	9	445	7	1.56
35	2	2	5	400	4	1.4
36	2	2	3	660	2	1.0
37	1	1	1	1000	1	1.0
38	1	0	0	—	0	—
Total:	810				8398	

Table 7 shows a model life table for the Tsavo black rhinoceros population based on the above data with the l_x values calculated to show the survival of a cohort of 1000. The d^1_x, d_x, q_x, L_x and e_x values are also shown. Annual mortality in the first and second year of life is about 16 % and the indicated mean annual mortality from 5 to 25 y is 9.8%. From c. 26 y onwards the mortality rate rises slowly.

Table 8 shows a theoretical model of the Tsavo black rhinoceros population. The L_x values from Table 7 were summed and each L_x value converted to a percentage of the total to show a theoretical percentage age structure of the living population (Table 8). These percentages were converted to the

TABLE 8

Theoretical structure of the Tsavo black rhinoceros population and loss through mortality per year

Age class	Structure of population (%)	Structure of a cohort of 1000	Mortality from life table (%)	Actual number of animals lost through mortality in cohort of 1000
0	10.9	109	16.0	17.4
1	9.2	92	16.8	15.4
2	7.8	78	13.3	10.4
3	6.8	68	11.2	7.6
4	6.1	61	9.3	5.7
5	5.6	56	6.8	3.8
6	5.2	52	6.8	3.5
7	4.9	49	7.3	3.6
8	4.5	45	7.9	3.5
9	4.2	42	6.9	2.9
10	3.8	38	7.4	2.8
11	3.6	36	8.3	2.9
12	3.2	32	8.7	2.8
13	3.0	30	9.6	2.8
14	2.7	27	10.6	2.8
15	2.4	24	11.8	2.8
16	2.1	21	11.3	2.4
17	1.8	18	10.3	1.8
18	1.6	16	10.8	1.7
19	1.5	15	10.6	1.6
20	1.3	13	10.1	1.3
21	1.2	12	10.4	1.3
22	1.1	11	11.6	1.3
23	1.0	10	11.9	1.2
24	0.8	8	13.5	1.1
25	0.7	7	14.0	1.0
26	0.6	6	12.7	0.8
27	0.5	5	12.5	0.6
28	0.5	5	14.3	0.7
29	0.4	4	16.6	0.7
30	0.3	3	20.0	0.6
31	0.2	2	25.0	0.5
32	0.2	2	28.0	0.6
33	0.1	1	30.8	0.3
34	0.1	1	44.5	0.4
35	0.1	1	40.0	0.4
36	—	—	66.0	—
37	—	—	100.0	—
Total:	100.0	1000	—	111

theoretical structure of a living cohort of 1000. The q_x values in Table 7 were used to calculate the theoretical numbers of rhinoceros actually lost each year in each age class of the cohort (column 5, Table 8).

This theoretical model shows a total loss of 111 rhinoceros each year over the entire age scale in a cohort of 1000. Estimated recruitment at birth was 10.9% (i.e. 109 rhinoceros were recruited to a cohort of 1000 each year). Assuming male and female survivorship to be similar (they may be different) it is suggested that this is strong evidence of a stable population, and supports the validity of the age-scale constructed. Further confirmation of this is demonstrated in an analysis of the living populations presented below.

Assuming that the population is stable, the mean expectation of life at birth is 8.4 y rising to 10.2 y at age 4 y and then falling.

Description of habitat types

Brief descriptions of the various habitat types in the ecosystem and their current black rhinoceros densities are given below: these refer to conditions during 1967-1968. The position of the habitat types is shown in Figure 2; relative densities are shown in Table 9 and refer to Goddard (1969). Structures of the living rhinoceros populations are shown in Table 10. More detailed descriptions of some of the habitat types will be presented in a paper on food preferences.

TABLE 9

Mean densities of black rhinoceros within each density stratum of Tsavo in 1968 (Goddard, 1969)

Stratum	Mean density (rhinoceros/km^2)
Very high	1.4
High	0.9
Medium	0.4
Low	0.1
Very low	0.04

Habitat 1. Low rhinoceros density. Aruba-Buchuma grasslands: open grassland dominated by *Chloris roxburghiana* Schult. *Sericocomopsis pallida* (S. Moore) Schinz is a very common shrub. Ground herbs sparse, with *Heliotropium* sp. locally common. Scattered and sparse growths of *Cordia gharaf* (Forsk.) Ehrenb., *Grewia* sp. and *Anisotes ukambensis* Lindau. *Commiphora* destruction almost complete, but patches of *Commiphora* scrub present in south-eastern corner. Tree cover very sparse with *Platycelyphium voense* (Engl.) Wild, *Melia volkensii* Guerke and *Delonix elata* (L.) Gamble. Part of block appears to be burnt regularly, by fires started from the railway.

Habitat 2. Low rhinoceros density. Murka grasslands: Open grassland dominated by *Chloris* sp. and *Cenchrus* sp. Scattered *Grewia* sp., *Cordia gharaf*, *Acacia* sp., and *Platycelyphium voense*. Ground herbs such

TABLE 10

Population structure of some black rhinoceros populations in Tsavo National Park 1967-1969

Hab-itat	Density stratum	Date	Method	(n)	Adult (? sex)	Adult ♂♂	Adult ♀♀	Imm. (? sex)	Imm. ♂♂	Imm. ♀♀	Calves (? sex)	Calves ♂♂	Calves ♀♀	Cow: calf ratio	% yearling calves*	Cow: yearling calf ratio
1	Low	22.7.67	S.A.C.	102	33	—	30	11 (10.8)	—	—	28 (27.4)	—	—	100:72	8.8 (67)	0.30
1	Low	1.12.67-31.12.67	R.G.C.	67	—	22 (32.8)	24 (35.8)	—	0 (0.0)	4 (6.0)	2 (—)	9 (13.4)	6 (9.0)	100:71	10.4 (67)	0.29
1	Low	30.11.68	S.A.C.	84	32	—	21	12 (14.3)	—	—	19 (22.6)	—	—	100:56	8.3 (68)	0.33
2	Low	15.5.68	S.A.C.	91	27	—	26	15 (16.5)	—	—	23 (25.3)	—	—	100:70	6.6 (67)	0.23
3	Low	6.7.68	S.A.C.	45	11	—	12	11 (24.4)	—	—	11 (24.4)	—	—	100:100	15.5 (67)	0.58
4	Medium	22.8.67	S.A.C.	86	29	—	23	11 (12.8)	—	—	23 (26.8)	—	—	100:70	7.0 (67)	0.26
4	Medium	18.6.68-27.6.68	R.G.C.	53	—	17 (32.0)	18 (34.0)	—	1 (1.9)	4 (7.5)	1 (—)	6 (11.3)	6 (11.3)	100:72	11.3 (67)	0.33
4	Medium	28.11.68	S.A.C.	74	18	—	26	5 (6.8)	—	—	25 (33.8)	—	—	100:87	13.5 (68)	0.38
—	Medium	22.3.68-27.3.68	R.A.C.	85	28	—	26	6 (7.1)	—	—	25 (29.4)	—	—	100:73	11.8 (67)	0.38
5	High	6.2.68-19.2.68	R.G.C.	124	—	32 (25.7)	41 (33.1)	—	9 (7.3)	10 (8.1)	—	20 (16.1)	12 (9.7)	100:75	8.1 (67)	0.24
5	High	25.11.68	S.A.C.	112	29	—	37	13 (11.6)	—	—	33 (29.4)	—	—	100:80	6.2 (68)	0.19
6	High	8.9.67	S.A.C.	86	22	—	26	12 (14.0)	—	—	26 (30.2)	—	—	100:84	7.0 (67)	0.23
6	High	9.10.67-17.10.67	R.G.C.	89	—	30 (33.7)	25 (28.1)	—	9 (10.1)	6 (6.8)	—	10 (11.2)	9 (10.1)	100:76	7.9 (67)	0.28
6	High	21.11.68	S.A.C.	105	33	—	28 (26.6)	16 (15.2)	—	—	28 (26.6)	—	—	100:74	8.6 (68)	0.32
7	High	1.9.68-31.10.68	R.G.C.	119	—	41 (34.4)	37 (31.1)	—	4 (3.4)	13 (10.9)	—	13 (10.9)	11 (9.2)	100:65	10.9 (67)	0.35
7	High	24.11.68	S.A.C.	105	34	—	26	21 (20.0)	—	—	24 (22.8)	—	—	100:63	9.5 (68)	0.39
8	High	14.5.68	S.A.C.	71	20	—	20	13 (18.3)	—	—	18 (25.4)	—	—	100:69	7.0 (67)	0.25
8	High	2.10.68-13.10.68	R.G.C.	79	—	25 (31.6)	26 (33.0)	—	4 (5.1)	5 (6.3)	2 (—)	9 (11.4)	8 (10.1)	100:73	11.4 (67)	0.35
—	High	6.3.68-15.3.68	R.A.C.	207	74	—	59	21 (10.1)	—	—	53 (25.6)	—	—	100:68	5.8 (67)	0.20
9	High	26.2.69	S.A.C.	55	16	—	17	5 (9.1)	—	—	17 (30.9)	—	—	100:77	12.7 (68)	0.41
10	High	27.2.69	S.A.C.	79	25	—	20	15 (19.0)	—	—	19 (24.0)	—	—	100:66	6.3 (68)	0.25
11	V. High	7.12.67	S.A.C.	77	30	—	19	10 (13.0)	—	—	18 (23.4)	—	—	100:58	9.1 (67)	0.37
11	V. High	25.3.68	R.A.C.	79	18	—	27	7 (8.9)	—	—	27 (34.2)	—	—	100:93	7.6 (67)	0.22
11	V. High	29.11.68	S.A.C.	94	22	—	31	15 (16.0)	—	—	26 (27.6)	—	—	100:76	7.5 (68)	0.23
12	V. High	21.5.68	S.A.C.	76	30	—	18	12 (15.8)	—	—	16 (21.0)	—	—	100:52	6.6 (67)	0.28
13	V. High	11.5.68	S.A.C.	51	17	—	14	8 (15.7)	—	—	12 (23.5)	—	—	100:57	6.0 (67)	0.21

Under "Method" —
S.A.C. = systematic aerial census
R.G.C. = random ground cataloguing
R.A.C. = aerial census (random sample)
* % of calves in the sample which were born in the year shown in parentheses
(Density strata refer to Goddard, 1969)

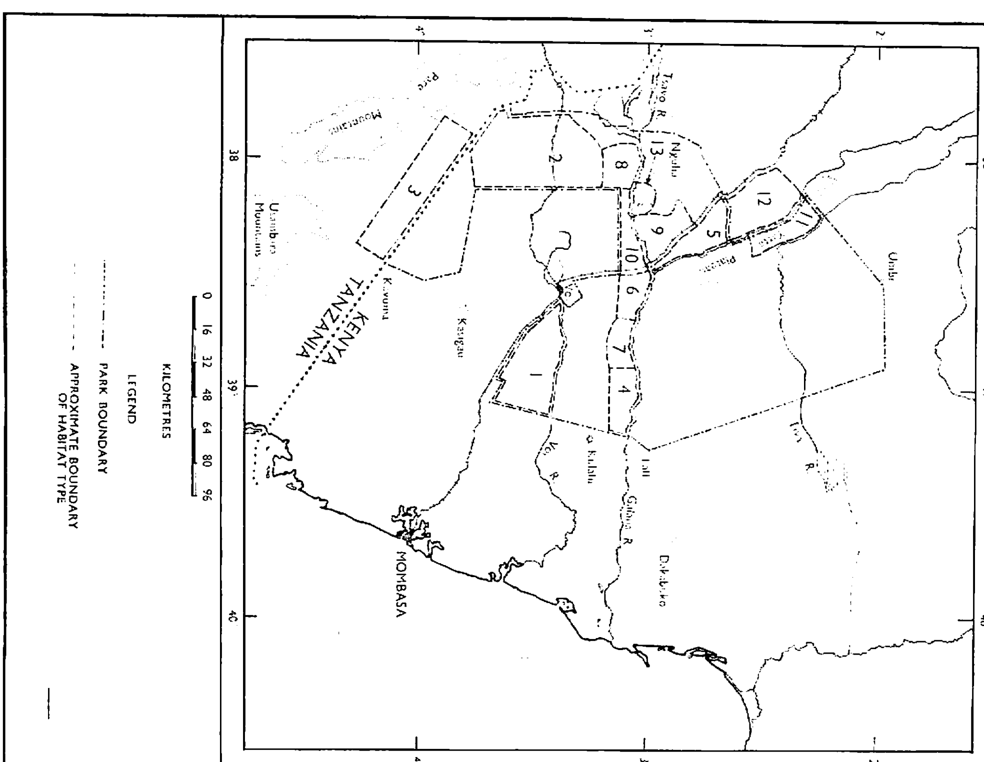

Figure 2

The Tsavo ecological unit showing position of habitat types (see text).

as *Heliotropium* sp. and *Cassia mimosoides* L. locally common. *Commiphora* scrub in sparse widely scattered patches. Tree cover sparse with *Sericocomopsis pallida* locally common.

Habitat 3. Low rhinoceros density. Mkomazi Game Reserve: essentially *Acacia-Commiphora* scrub over large areas. *Sericocomopsis* sp. colonizing open areas. *Grewia* sp. and *Cordia* sp. are common shrubs.

Habitat 4. Medium rhinoceros density. Open bush-grassland with *Chloris* sp. locally common. *Commiphora* destruction complete, and very sparse regeneration of this genus. *Indigofera spinosa* Forsk. and *Blepharis linearifolia* Pers. form a mat throughout, together with *Pupalia lappacea* (L.) Juss. *Grewia* sp., *Cordia* sp., and *Caucanthus albidus* (Nied.) Nied.. widely scattered. *Caesalpinia trothae* Harms and *Sericocomopsis pallida* locally common in a few areas. Tree cover very sparse with *Dobera glabra* (Forsk.) Poir. and *Boscia coriacea* Pax scattered throughout. *Lawsonia inermis* L. common on banks of seasonal stream beds.

Habitat 5. High rhinoceros density. Scrub-bush grassland. *Commiphora* destruction complete in southern part, and very little regeneration of this genus. Grasses such as *Schmidtia pappophoroides* Steud. and *Hyparrhenia* scattered throughout, *Indigofera spinosa* and several species of *Tephrosia* abundant. Both species of *Sericocomopsis* present but not common. *Indigofera vohemarensis* Baill. very common in sand ravines with *Lawsonia inermis* along the banks. *Grewia forbesii* Mast., *Grewia lilacina* K. Schum., *Grewia villosa*, *Cordia* sp., and *Caesalpinia trothae* scattered throughout. Regeneration of *Boswellia hildebrandtii* locally common. Tree cover sparse with *Boscia coriacea* common, and *Acacia* and *Delonix elata* scattered throughout.

Habitat 6. High rhinoceros density. Bush-scrub. About 90% of *Commiphora* totally destroyed. *Pupalia lappacea*, *Indigofera spinosa*, *Tephrosia villosa* (L.) Pers. and other *Tephrosia* are common with *Helinus integrifolius* (Lam.) Kuntze scattered throughout. *Bauhinia taitensis* Taub., *Dirichletia glaucescens* Hiern and *Grewia villosa* are common shrubs with *Cassia longiracemosa* Vatke, *Grewia forbesii*, *Grewia lilacina*, and *Premna resinosa* (Hochst.) Shauer locally common. *Indigofera vohemarensis* common in sand ravines. Common trees are *Boscia coriacea* with *Acacia tortilis* (Forsk.) Hayne and *Acacia mellifera* (Vahl) Benth, scattered throughout. Grasses such as *Schmidtia pappophoroides* colonizing some open areas. *Lawsonia inermis* common on bank fringes of dry stream beds.

Habitat 7. High rhinoceros density. Open bush-grassland characterized by *Hyparrhenia* and *Schmidtia pappophoroides*. *Commiphora* destruction virtually complete. Very little regeneration of this genus. Perennial grasses common. *Indigofera spinosa* is very common throughout with *Indigofera schimperi* Jaub. & Spach locally common. *Caucanthus albidus*, *Premna resinosa*, and *Sericocomopsis pallida* are common shrubs with *Dirichletia glaucescens*, *Caesalpinia trothae* and *Bauhinia taitensis* scattered throughout. *Boscia coriacea* and *Salvadora persica* L. are common trees. Some regeneration of *Acacia*. *Lawsonia inermis* common on banks of dry stream beds.

Habitat 8. High rhinoceros density. Large areas of climax *Commiphora* woodland. In a few areas damage to *Commiphora* and *Sterculia* considerable, and regeneration of former is abundant in open areas. *Grewia lilacina*, *Premna resinosa*, *Bauhinia taitensis*, *Grewia* sp. and *Cordia* sp. common. *Blepharis linearifolia* forms a dense mat with an abundance of *Tephrosia villosa* and patches of *Indigofera arrecta* A. Rich. scattered throughout. *Indigofera vohemarensis* common in sand ravines. *Boscia coriacea*, *Acacia tortilis*, and *Commiphora* sp. are common trees.

Habitats 9 and 10. High rhinoceros density. These habitat types closely resemble habitat 8 described above.

Habitat 11. Very high rhinoceros density. Very thick bush and scattered woodland. Common trees are *Adansonia digitata* L., *Acacia* sp., and *Delonix elata*. *Erythrochlamys spectabilis* Guerke, *Bauhinia taitensis* and *Premna* sp. are common shrubs. Succulent herbs are abundant and ground legumes of several species of *Indigofera*, *Tephrosia*, and *Crotalaria* occur widely.

Habitat 12. Very high rhinoceros density. Very thick bush and open woodland. *Adansonia digitata*, *Acacia* sp., *Commiphora* sp., *Platycelyphium voense* and *Sterculia* sp. are common trees. *Erythrochlamys spectabilis*, *Bauhinia taitensis* and *Premna resinosa* with *Hibiscus vitifolius* L., *Pavonia patens*

(Andr.) Chiov., *Grewia bicolor* Juss. and *Grewia villosa* form a dense undergrowth. Ground legumes including *Indigofera schimperi*, *Cassia mimosoides*, *Indigofera* sp., *Tephrosia* sp., and *Crotalaria* sp. are abundant and widespread.

Habitat 13. Very high rhinoceros density. Thick bushland. *Adansonia digitata*, *Delonix elata*, *Sterculia* sp., *Strychnos decussata* (Pappe) Gilg and several species of *Acacia* are common trees, with *Bauhinia taitensis* and *Premna* sp. abundant. *Triumfetta flavescens* A. Rich. is a very common shrub. Ground herbs and ground legumes such as *Tephrosia villosa*, *Indigofera arrecta* and *Crotalaria* sp. are abundant. *Indigofera vohemarensis*, *Pavonia* sp., *Hibiscus* sp., and *Hemizygia fischeri* (Guerke) Greenway locally common.

Random samples of the populations in the medium, high and very high density strata were obtained during the census of 1967—1968 (Goddard, 1969). These samples have been included in Table 10.

Structure of the living rhinoceros populations

The structure of the living populations within the various habitat types and density strata is shown in Table 10. In the ground studies cow:calf ratios were calculated from the actual field observations (Table 10). In order to calculate cow:calf ratios from the aerial data all adults in the sample were totalled and a sex ratio of unity assumed among the adult population. Fiducial intervals were computed for the probable adult female population after calculating "a" in the normal approximation test (p at the 0.05 level, $n>30$, $z=1.96$; Steel and Torrie (1960)), and probable cow:calf ratios determined. The upper fiducial limit of the probable adult female population was used in calculating ratios, so cow:calf ratios calculated in this manner are minimum ones (Table 10).

The percentage of yearling calves represents the number of calves born either in the year the count was made or the year previous to the count. Figures in parentheses after these percentages indicate the year concerned. Determination of calves of the year was based on body size and will be the subject of a later paper. Ratios of yearling calves to adult females were calculated from the actual ground observations and from the aerial observations. In the latter case lone adults could not be sexed so that the true ratio may have contained a higher proportion of adult females.

Table 10 shows that the population structures, cow:calf ratios and recruitment are very similar in the various habitats of the changing ecosystem. In most cases there is also close agreement between ground observations and aerial calculations in the same areas. It is interesting to note the low cow:calf ratios and low recruitment in some areas of the very high density strata suggesting that the populations may be adjusting to high densities. Recruitment in most cases appears to be as expected for stable populations and the population structures closely resemble the structures of the populations at Ngorongoro and Olduvai: these were considered to represent stable populations (Goddard, 1967). As mentioned earlier, the theoretical structure of the total population based on an analysis of natural mortality and survivorship suggests a stable population.

Finally, one of the strongest arguments to support the validity of the ageing criteria is shown from an analysis of recruitment and first year mortality of the living populations. Records from Table 10 show that the mean percentage of 1967 calves (calculated mainly from ground and aerial observations made towards the end of, or shortly after, the end of the calendar year 1967) for 11 areas (18 samples) was 8.82%. The corresponding mean calf percentage for 1968 for 8 areas (8 samples) was 9.07%.

The theoretical recruitment at birth was estimated at 10.9%, i.e. 109 rhinoceros born in a stable hypothetical cohort of 1000 each year (see above and Table 8). From the model life table (Table 7) the estimated mortality during the first year of life was 16%, i.e. of the 109 animals born at the beginning of the year, 16% (c. 17) will die during the year leaving c. 92 rhinoceros (c. 9.2% of a stable cohort of 1000) alive at the end of the year. This figure represents the theoretical percentage of yearling calves in the population at the end of the year and is in close agreement with the estimated percentages from field observations.

It is considered that such close agreement is good evidence of the validity of the age criteria. It is argued that unless the chronological ages assigned to the age classes were not reasonably precise such close agreement would not be demonstrated. Because of the possibility of differential rates of tooth wear depending on diet it is suggested that the same relative age-classes could be used for rhinoceros in other regions, but different absolute ages may have to be allocated to the series as Laws (1968) has suggested.

DISCUSSION

From the data presented it is suggested that the black rhinoceros population in Tsavo during the 1960's was stable, in spite of the large-scale destruction and devastation of the *Commiphora* woodland by elephant. This is probably because the elephants have been remarkably selective in destroying *Acacia* spp., *Commiphora* spp. and *Sterculia* sp. (Agnew, 1968), which are not important foods of the black rhinoceros (Goddard, 1968). High densities of black rhinoceros are still present in some of the areas showing the most total and complete destruction of former *Commiphora* woodland.

Buss (1961) in Murchison Falls National Park in Uganda, Napier Bax and Sheldrick (1963) in Tsavo, and Laws and Parker (1968) in Tsavo have demonstrated that a relatively high percentage of the diet of the African elephant is grass, and Buss (1961) showed in a study in Uganda that this was the preferred diet, even where woody vegetation was available. He also suggested that large areas of grassland are important for supporting high densities of elephant. Wing and Buss (1970) reiterate the importance of grass as the preferred diet of the African elephant in several areas of Uganda.

Conversely, Laws and Parker (1968) present evidence that the elephant populations in Murchison are declining, and they associate this decline partly with the disappearance of large areas of former woody vegetation. They also postulate that one population in Tsavo is probably in the preliminary phase of a crash or a slow decline, and associate this particularly with the massive destruction of the woody vegetation by elephant.

At certain periods elephant do compete with black rhinoceros for food in Tsavo and there is overlap in the foods selected (Napier Bax & Sheldrick, 1963; Goddard, unpublished). However grass is unimportant in the diet of the black rhinoceros and in Tsavo this species shows a marked preference for legumes. It is possible that the rhinoceros in Tsavo could survive in the present bush-grassland, or even grassland, by utilizing the abundant ground legumes present or by utilising shrubs such as *Sericocomopsis* which exist in abundance in the present grassland areas. The absence of shade did not appear to be a limiting factor during the present study.

According to Agnew (1968) destruction of the woody vegetation has "apparently now ceased and regeneration is in progress over sections of the park where a marked increase in shrub cover has been recorded in the past year". However, this marked increase in shrub cover has resulted partly from the relatively heavy and atypical rainfall during the last few years. Whether or not this will be a permanent condition is not known. Moreover, destruction of the habitat has not ceased. During early 1969 the elephant began destroying *Delonix elata* and *Platycelyphium voense*; both these species were rarely touched by elephants in former years.

If Laws and Parker (1968) are correct in their suggestion that healthy, stable elephant populations can only be maintained in areas with extensive browse, then in drier years the competition between elephant and rhinoceros will increase in Tsavo. Competition will probably reach crisis proportions in drought or very dry periods, when more browse is consumed as the grasses reach the nutritive value of a poor quality standing hay, or wither completely. In the long term (possibly over a period of 50 y or more) this could result in a reduced carrying capacity for the black rhinoceros.

Scientific evidence for a true and real decline in a black rhinoceros population would take many years to accumulate and demonstrate. The present paper suggests that the population of rhinoceros in Tsavo during the 1960's was stable and the recruitment adequate to maintain it. Laws and Parker (1968) have postulated that unless population management (i.e. reduction cropping) and habitat management is initiated in Murchison Falls Park South this could lead to the virtual extinction of the elephant in this area by the year 2020.

If large areas of Tsavo continue to be converted from thick bushland to grassland by elephant activity and by the effect of fire, and if Laws and Parker (1968) are correct in their hypothesis that healthy stable populations of elephant can only be maintained in areas with extensive woody vegetation, then in an area of such low and erratic rainfall (and in the absence of population management or emigration of the elephants) the quantity of available and palatable browse will inevitably decrease. Viewed in this way, this can only be regarded as a deteriorating environment for browsing mammals including the black rhinoceros.

The elephant and the rhinoceros, being late-maturing, relatively long-lived species, are not likely to undergo sudden and spectacular population crashes in response to a deteriorating environment. The mechanism of population control of such large mammals is undoubtedly exceedingly complex and would take many years of research to comprehend fully. However, on the preliminary evidence presented by Laws and Parker (1968), and as a safety precaution, management of the elephant populations, involving reduction cropping, should be initiated in Tsavo. The possible survival of one of the largest and most spectacular populations of elephant and black rhinoceros left in existence may be at stake.

ACKNOWLEDGEMENTS

I should like to thank Dr. R. M. Laws for his helpful suggestions on ageing criteria and Dr. L. R. Whittaker, Specialist Radiologist, Kenyatta National Hospital, Nairobi for X-raying captive rhinoceros and known-age mandibles.

I should also like to thank the East African Wild Life Society, the New York Zoological Society, the Canadian Federal Government, the Ontario Provincial Government, and the Ford Foundation for financial support of the rhinoceros research in Tsavo.

A special word of thanks is extended to the wardens of Tsavo, Messrs. D. L. W. Sheldrick and C. W. Marshall, for organizing the collection of rhinoceros specimens, and to the park scouts who actually made the collection.

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(Received for publication February, 1969)