population dynamics of large mammals

A.R.E. Sinclair and J.J.R. Grimsdell

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POPULATION DYNAMICS OF LARGE MAMMALS

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SECTION 1 INTRODUCTION

1.1 General

A population is a collection of individuals of one species in a particular environment. These individuals are all different from one another because each has a unique genetic and developmental background. As a result individuals respond to the environment in which they live in slightly different ways.

The features of a population can therefore be represented by the mean and the range of all these individual characteristics. For example, one can talk about a mean birth rate or a mean survival rate. Other features of a population include the sex ratio and the age structure (or distribution), which, although they vary over time, are absolute features at any particular moment. Both the sex ratio and the age distribution influence the means noted above. Added to all this, some individuals may leave the population and go elsewhere (emigrants) while others may join the population from other places (immigrants).

Whether a population increases, decreases, or remains constant, is determined by the relative rates of birth and immigration versus death and emigration. If, for example, the former two have higher rates than the latter then the population will increase. The study of population dynamics, then, is concerned with :

(1) The particular characteristics of sex ratio and age distribution, and the rates of input and output of the population.

(2) The causes that alter these rates. Causes can be, for example, lack of food or some other resource, predation or crowding resulting in conflict.

Caughley presents two analyses of population dynamics to which the reader should refer for a more advanced treatment.[7,10] Our aim in this short handbook is to put across the essence of the subject with the minimum of mathematics.

1.2 Population dynamics and management

Before going on to describe how the study of population dynamics is carried out, we must consider why such studies are necessary. Caughley[10] notes that there are essentially only three potential problems that require management of populations :

(1) Conservation

This is concerned with the manipulation of declining populations to reverse the trend, or to prevent a small population from declining further. Conservation is particularly relevant to national parks and reserves. As often as not the reasons for a decline are due to changes in the environment or habitat of a population induced by man-made disturbances. These may be obvious, and simple habitat protection is all that may be necessary. Comparison with a healthy population in another area is a useful approach in this situation.

If such treatment is unsuccessful then a detailed study of the population is necessary.[10] This requires a study of birth rates and death rates in order to discover reasons for the population decline. In large mammals the chief reason for a population decline is normally a high rate of mortality, either of adults, juveniles or both. If adult mortality is abnormally high while juvenile mortality is normal then excessive hunting is implicated as a cause of the decline (on the assumption that hunters select adults). If juvenile mortality is high, then low food supply, unsuitable habitat or some other environmental feature is implicated, as they act heavily on juveniles.

(2) Harvesting

In areas outside of national parks, mammal populations are often harvested either for meat, skins or trophies of some kind. In this case the aim is to obtain a proportion of the population on a long-term basis, the sustained yield. Naturally this proportion must be such that the population does not become extinct, or become so low that it is unprofitable to harvest.

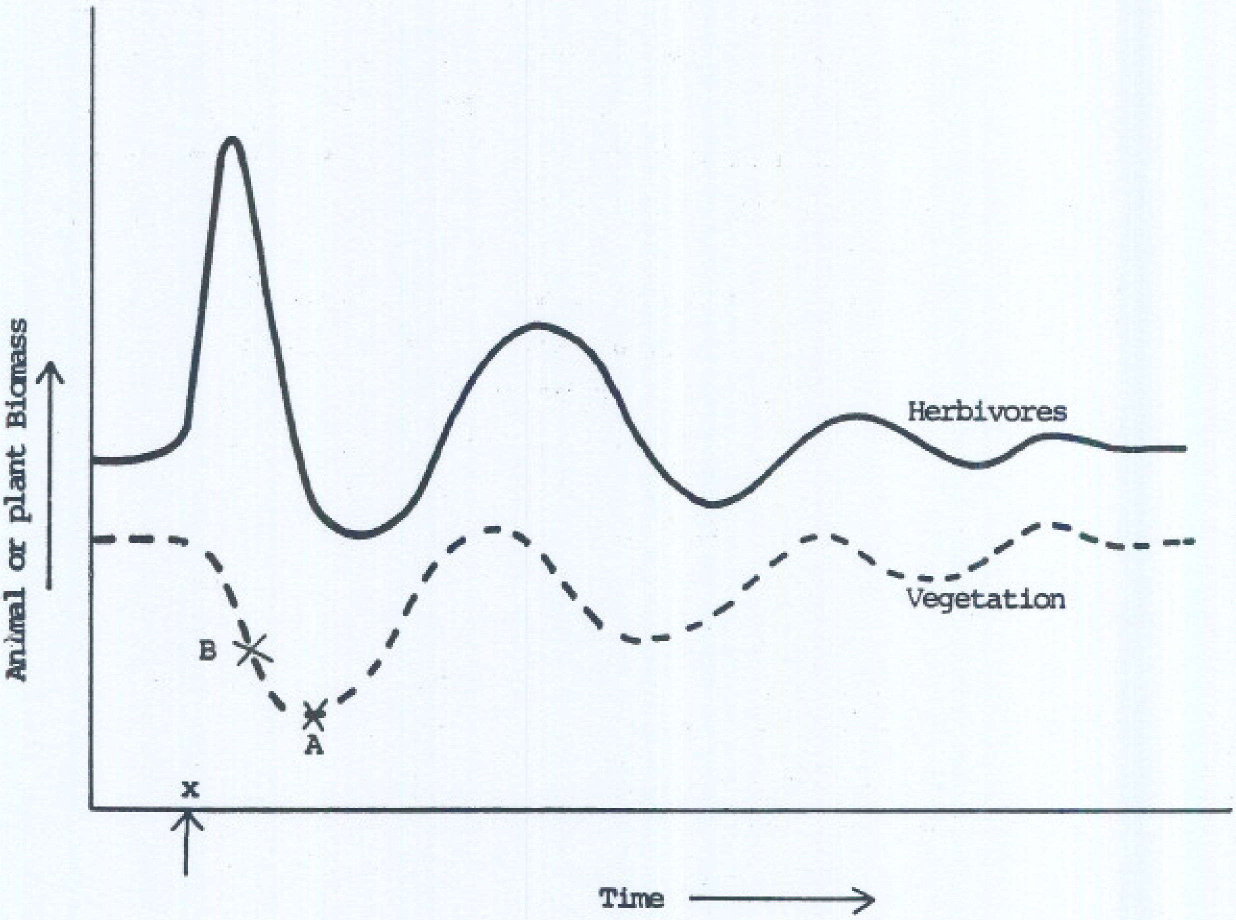
To achieve a suitable sustained yield requires a knowledge of birth rates, death rates, rates of increase and the sex ratio, at different densities of animals. Furthermore if harvesting is to be conducted in semi-natural areas where predators are also present, the effect of predators on the prey which is being harvested for human use should be measured and taken into account.

(3) Control

This is concerned with a situation where too many animals occur in an area. This may arise in a national park if animals are pushed in by encroaching cultivation outside. It may also arise if there is a substantial change in environment, such as weather or habitat. Weather is unlikely to change in one direction consistently, though dry or wet spells can cover 5 or even 10 years. Habitat changes are more common: the progressive desertification on the southern edge of the Sahara is a case in point. The flooding of an area, as occurred in the Zambezi valley to create Lake Kariba, considerably reduced the dry season habitat of many ungulates, leaving them stranded in unsuitable habitat along the valley sides.[35]

In these cases the populations will decline and the habitat will change so that some sort of balance will arise eventually.[7,10] Perfect balance is never attained, of course, because climatic fluctuations will disturb the system but, within reasonable limits, accommodation between plants, herbivores and their predators will probably come about. In reaching this equilibrium, there may be some initial fluctuations (Fig. 1) in both animals and plants which appear excessive. This may be

Figure 1 A sudden increase of animals at time *x* will lead to disturbances in the plant-herbivore interaction that dampen with time.



unsatisfactory for a number of reasons. For example, removal of plant cover by large numbers of herbivores may be scenically displeasing, and control by removal of some of the animals could be carried out to dampen the initial fluctuation. The timing of this control is important, for it could lead to an intensification of disturbance rather than alleviate it. Control is often a reaction by managers to habitat change and takes place when near its extreme (A in Fig. 1). Removal of animals at this stage will only exaggerate the next fluctuation. The sensible strategy would be control at a time B before the habitat has been changed too much.

Control is also adopted to prevent the spread of diseases. In the earlier part of this century rinderpest was stopped in southern Tanzania by a belt from which nearly all ungulates had been removed. In other areas tsetse fly control was attempted by removal of wild mammals.[15,26]

A management problem exists only in the context of the aims of management for the species in a given area. Most problems can be classified as either conservation, control or harvesting. In order to manage the population according to these aims requires a knowledge of population characteristics. In the following sections we shall discuss how some of these can be measured.

SECTION 2 METHODS OF AGE AND SEX DETERMINATION

2.1 General

Before describing the various techniques it should be pointed out that the accuracy required for age-determination depends entirely on the uses to which it is to be put. For example, if one is interested in the average birth rate and recruitment only, then one need determine only those ages of animals younger than the age of maturity and all those older can be classed as "adult". This is still a perfectly valid method of age-determination. Therefore, the methods used will depend on the purpose of the investigation.

2.2 Age-determination from live animals

Obviously before any measurements can be made on the population, the different classes of animals must be identified. The age of young animals of all species can be recognised by merely comparing the young animal with the adults in the field. The characteristics that can be used are

a) body size
b) colouration
c) horn shape.

The number of age groups that can be identified depends on the rate of growth of the animal. Thus for elephant a large number of juvenile classes can be distinguished,[38] whereas only one or two may be found for small antelopes such as dik-dik. Difficulties in measuring age from a continuously changing characteristic, such as body size or horn shape, occur when the birth season covers a relatively large part of the year. Then one finds a continuum of sizes and it becomes difficult to make natural divisions and categorize animals into different age classes, especially when the comparison with adults is done rather subjectively by eye.

These difficulties were overcome in elephants by taking vertical photographs of herds, subsequently measuring the size of the animals from the photographic prints.[19,22] In warthog, the ratio of tusk length to snout width was taken from a series of photographs to calculate age.[2] It was found that the measurements conveniently fell into four categories because there was a distinct period of births.

Where such objective methods are not possible, the subjective estimate of size as an indicator of age must be checked with some other method. The variability in the estimates can also be checked by recording the same sample of animals several times over and comparing the results. If there is a large variation in the proportions of the different age categories, then it would be advisable to lump these categories. Examples of more continuous breeding can be found in the Serengeti Thomson's gazelle which produce young the year round but with two rather shallow peaks, and with impala in the same region where young are produced in most months with one shallow peak.

For species that have a clear-cut birth season these difficulties do not arise for there is a division in time between the different ages, so the animals can be easily identified as belonging to one or other of the age classes. Examples of this type are the wildebeest and buffalo in the Serengeti, both of which have a single birth season covering only a few months each year. In the buffalo it is possible to categorize animals by body size and horn shape into those in their first, second and third year of life[28,52] whereas for wildebeest it is possible for the first and second year of life only.

2.3 Sex determination from live animals

Virtually the same criteria and qualifications apply in the identification of the sexes. Whereas the youngest animals are the most easily identified with respect to age, the adults are the easiest to segregate into sexes; in fact for newborn ungulates the different sexes are very hard to identify in the field at birth. For adults the presence or absence of male genitalia can be used for some species, but often other characteristics are more easily observed. For example, body size can be used for elephant, giraffe and eland; the shape of the perineal skin in Burchell's zebra;[53] the presence or absence of horns in waterbuck, bushbuck and impala; and the shape and size of horns in buffalo, wildebeest and other hartebeests and gazelles. Examples of specific age and sex determination methods can be found for wildebeest,[60] for gazelle,[57] for waterbuck[54] and for greater kudu.[50]

2.4 Age determination from teeth[56]

(1) Immature animals

In young animals the sequence of tooth eruption provides one of the best methods of age-determination and should be used in the first place to check the field method for live animals. The age at which the different teeth erupt should be determined from known-age captive animals. In captive animals the eruption of molars can be checked by the use of an impression tray filled with some soft material such as 'plasticine'; the mouth is held open with a gag, while the tray is pressed upon the tooth row. In buffalo, for instance, the timing of the eruption of a tooth can vary by 6 months on either side of the mean.[28] This degree of variation is reasonably small for age determination purposes, but can be corrected for if there is a marked season of births because it should be possible to place into distinct age groups.

(2) Adult animals

In adult animals after the full set of teeth has erupted, the number of cementum or dentine lines deposited in the tooth root, and the rate of wear on the crown have been used as methods of age determination. In the tooth root there is an outer layer of cementum, an inner layer of dentine and a central space called the pulp cavity. Both cementum and dentine are deposited throughout life but the rates of deposition vary with season so that on staining a series of light and dark bands appear.[32,58]

Depending on the ease with which internal layers in the tooth can be seen, three methods of tooth sectioning are possible. In increasing levels of fineness, they are :

a) Bisected whole teeth[42]
b) Rapid freeze sectioning[46]
c) Fine histological sectioning.[59]

It is advisable to test the methods in the order listed, since the first takes a few minutes, the second a few days, the third several weeks. Method b) and c) depend on decalcification and sectioning with a microtome, both laborious and time-consuming processes.

The identification of the lines in the sections requires practise and in some sections lines cannot be seen at all. If cementum lines can be seen these should be used in preference to the dentine lines, for there are other lines in the dentine with which the seasonal deposition lines can be confused. Cementum may be better seen in the incisor than the molar, and at the tip and base than at the side of the root, but it varies from species to species. The best tooth and part of root should be determined by inspection. Longitudinal sections are essential for correct counting of lines.

Again, the number of lines in relation to the age of the animal is best calculated from known-age animals. Preferably teeth from older known-age animals should be used, but if all else fails, teeth from young animals whose age can be found by the eruption sequence can be used. In any case the decision to be made is relatively simple: whether there are one or two cementum lines deposited each year. This probably comes about from there being one or two dry seasons depending upon from which area of Africa the specimens are obtained. For example buffalo molar roots from Uganda show single cementum lines, two of which are laid down each year,[28] but in the Serengeti region the lines come in close pairs, sometimes fused into one very dark line, one pair being laid down each year.[52] The above refers to ungulates but in carnivores the lines are probably more related to factors other than season, and one has to be more careful in determining the relationship of lines to age.

Once this relationship is found, one can determine the age of the animal from which the section was obtained. However, the method of using cementum lines, although the most accurate, is long and tedious and the equipment for it difficult to obtain. Hence it has usually been found advisable to forfeit accuracy for a quicker method so that larger samples can be obtained.

One of the more rapid methods of estimating the age of adult herbivores is the measurement of rate of wear on the molar crowns. The measurement is on the height of enamel on the buccal side (outside) of the cusps of the first molar. The first molar is used because it is the centre of the tooth row, receiving more even wear than the other teeth. The only difficulty comes in very old animals when all the enamel is worn away; in this case one can switch to making the same measurement on the third molar, which is rarely worn down to the roots. The measurements, using a pair of simple callipers, are taken from the base of the enamel at the top of the root to the cusp tip (making sure the cusp tip has not been broken off). The two cusps on the two upper first molars are measured and the average of the four measurements used. The lower first molars are worn away at a different rate, and this relation to age must be determined separately. The base of the enamel in old animals is often obscured by an overgrowth of calcium and this has to be chipped away first. One advantage of measuring crown height is that it can be done without taking the tooth out of the skull.

The relationship of crown height to the number of cementum lines (and hence age) is found simply by sectioning a sample covering all stages of wear. Usually the relationship is represented by a shallow curve as seen in measurements of wildebeest teeth (Fig. 2). For buffalo it has been found that the error for young adults was within one year, and for old adults about two years.[28] Other methods of measuring either the whole tooth or the ratio of cusp width to cusp height, are less accurate for they incorporate extra errors from the growth of the root and from the extra measurements of cusp width.

For some purposes it is not necessary to determine the age of adults as accurately as this so that a quicker method can be employed. This involves recording the state of wear of each tooth, which can be done in the field merely by inspection of the tooth row. In herbivores the teeth have a number of cusps and ridges which wear down and disappear as the animal grows older. It is possible to record the sequence of disappearance of these ridges and relate this to the age of the animal using one of the methods mentioned above. Because of variation in wear, only broad categories can usually be discerned with any confidence. However, these are quite sufficient to distinguish, for example, between old adults, middle aged adults, and young adults.[28,31,54] The subjective estimate of wear has also been used in carnivores.[37]

2.5 Sex determination from skulls

The determination of sex from skulls can be found by:

(1) presence or absence of horns (in impala) or teeth (canines in zebra)

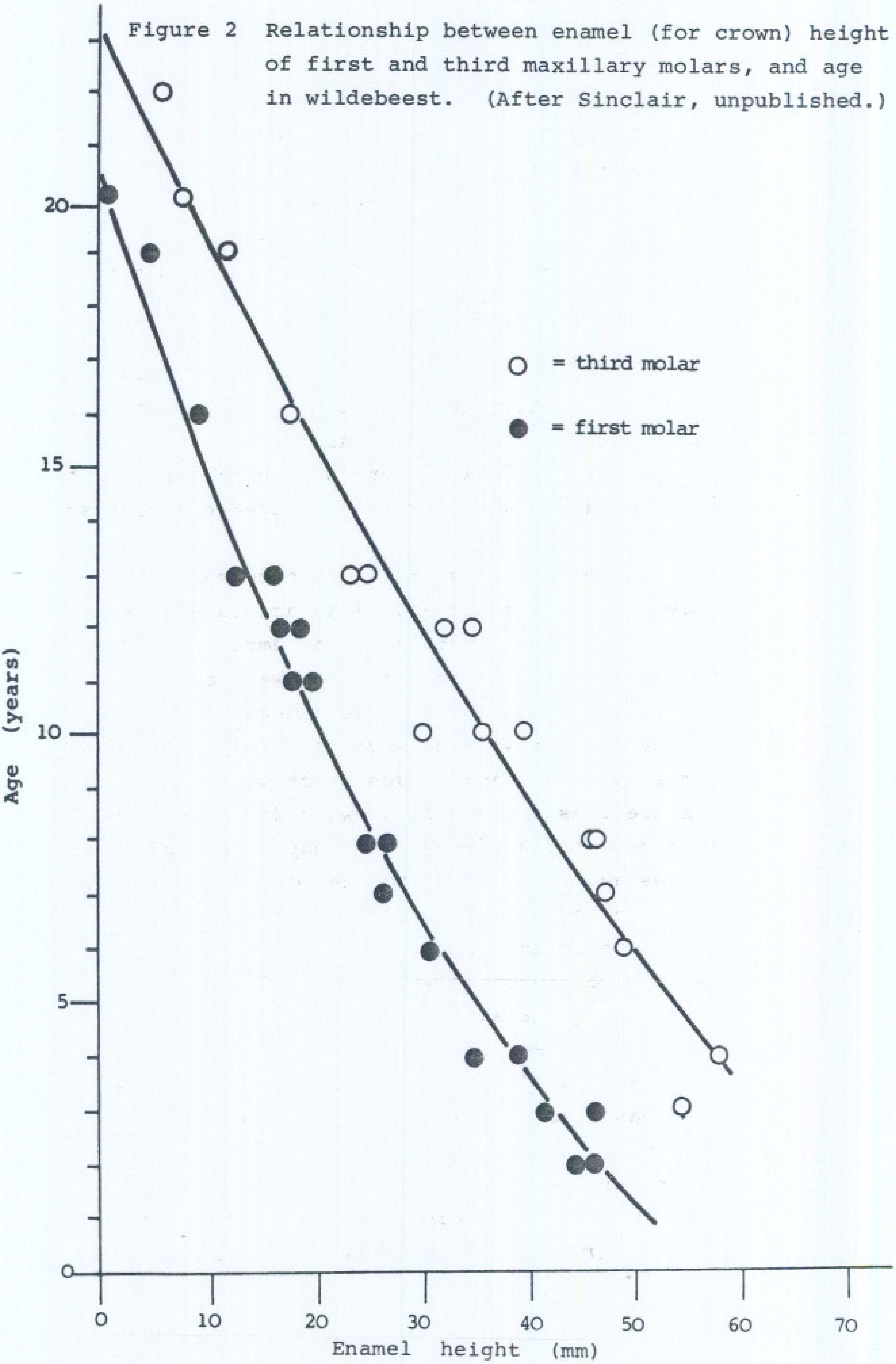


Figure 2 Relationship between enamel (for crown) height of first and third maxillary molars, and age in wildebeest. (After Sinclair, unpublished.)

(2) the shape and size of horns (buffalo, wildebeest) or teeth (elephant) or

(3) if these are not applicable, by some measurement of the skull.

In the last case a collection of specimens of known sex must be made first. The measurements used must be determined according to the species under study. For some species the length of the lower jaw differs between the sexes, but other skull measurements can also be used. In other cases, the degree of closure of the cranial sutures gives an indication of the animal's sex.

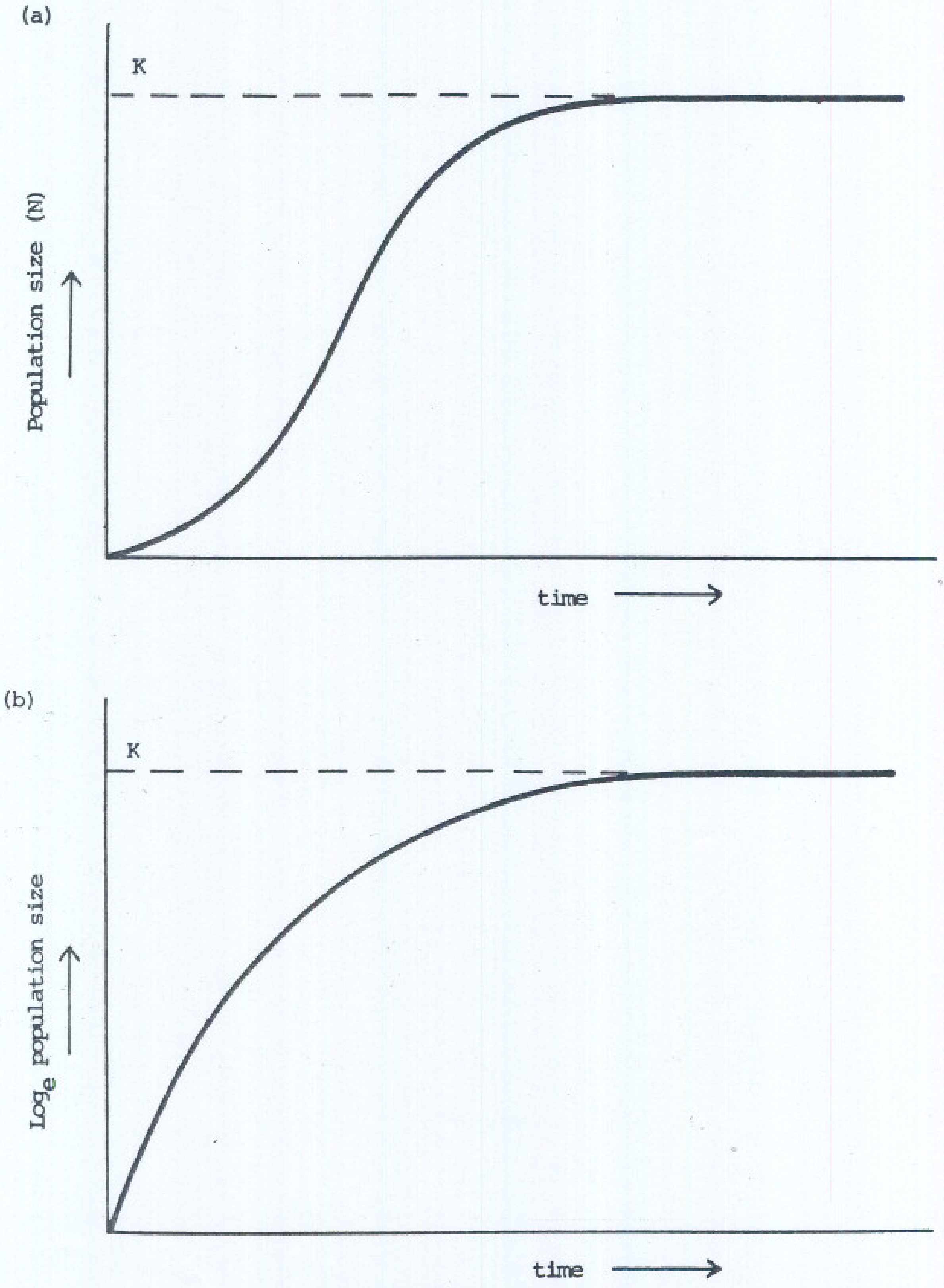
SECTION 3 RATE OF INCREASE

3.1 The logistic curve

Many large mammal populations fluctuate about an equilibrium level; when they are too high they are depressed by lack of resources, too much predation or disease; when low they have excess resources so the populations increase (unless predators hold them down). A simple description of population growth is given by the logistic curve as shown in Fig. 3. A population of N individuals grows with an S-shaped curve (Fig. 3(a)). The line K shows the population size at the carrying capacity of the area; that is, the maximum number of animals that a particular area can hold in terms of food supply, places to live, etc. At very low density, population growth is greatest, but as the population size approaches K so the rate of increase declines progressively until at K the rate of increase is zero. The second figure shows this best (Fig. 3(b)). This is a log plot - used for showing *rates* of change - and demonstrates this point more clearly than the ordinary plot of straight numbers. In effect, what this shows is that as the population increases, so also does the 'environmental resistance'; for example, the food supply gets scarcer.

In reality, this is an oversimplification of how populations grow. From the above it might be supposed that the food supply is an inert resource, that is depleted in a regular way as the population increases. For herbivores, there is an interaction between the animal population and its plant food supply, the latter changing in character and structure as the size of the animal population changes.[9] Consequently, there is not a straightforward relationship between population size and available food, so we would not expect an animal population to follow a logistic curve very closely. Also, K is not a constant but may be modified by many factors, e.g. climate, abundance of other herbivores. Nonetheless, the logistic curve does provide a useful, generalised concept of population growth.[62]

Figure 3 The logistic curve :
(a) Population size against time
(b) Log_e population size against time.
K = population size at the ecological carrying capacity of the area.[11]



As we have said above, many populations of animals will tend to remain stationary in the long term. This means that the population is regulated by the equilibrium level dictated by K in the logistic curve. However, various permutations on this theme are possible, some of which are indicated in Fig. 4.

3.2 Finite and exponential rates of increase[10]

The finite rate of increase of a population is simply the ratio of population size in one year to that a year later.

$$\text{Finite Rate} = \frac{N_{t+1}}{N_t}$$

where N is the number of animals and t is time. The finite rate is simply the number of times N_t has to be multiplied to arrive at N_{t+1}. If this rate is greater than 1 the population increases, if less it decreases. Thus a population of 100 in one year reaches 120 in the next, and so has a finite rate of increase of 1.2. The increase is often described as a proportion of the first year, i.e. $\frac{20}{100} \times 100 = 20\%$. This can lead to confusion and is not a good way of expressing the increase; it is better to say the population multiplied itself 1.2 times.

Because of the way populations grow we can say that the finite rate is equal to e^{rt}. This comprises a constant e which is the base of natural logs; it is raised to the power of r, the exponential rate of increase; and t is the time period used. In simpler terms r is the amount of increase each individual contributes to the population over the unit of time, in this case a year. Units for r are therefore individuals/individual/year. The exponential rate, r, is often termed the infinitesimal rate of increase.

Although r appears less understandable than the finite rate, it is of greater use in the analysis of populations.

Figure 4 Models of population regulation

K = carrying capacity of the environment
N = population size
t = time (years)

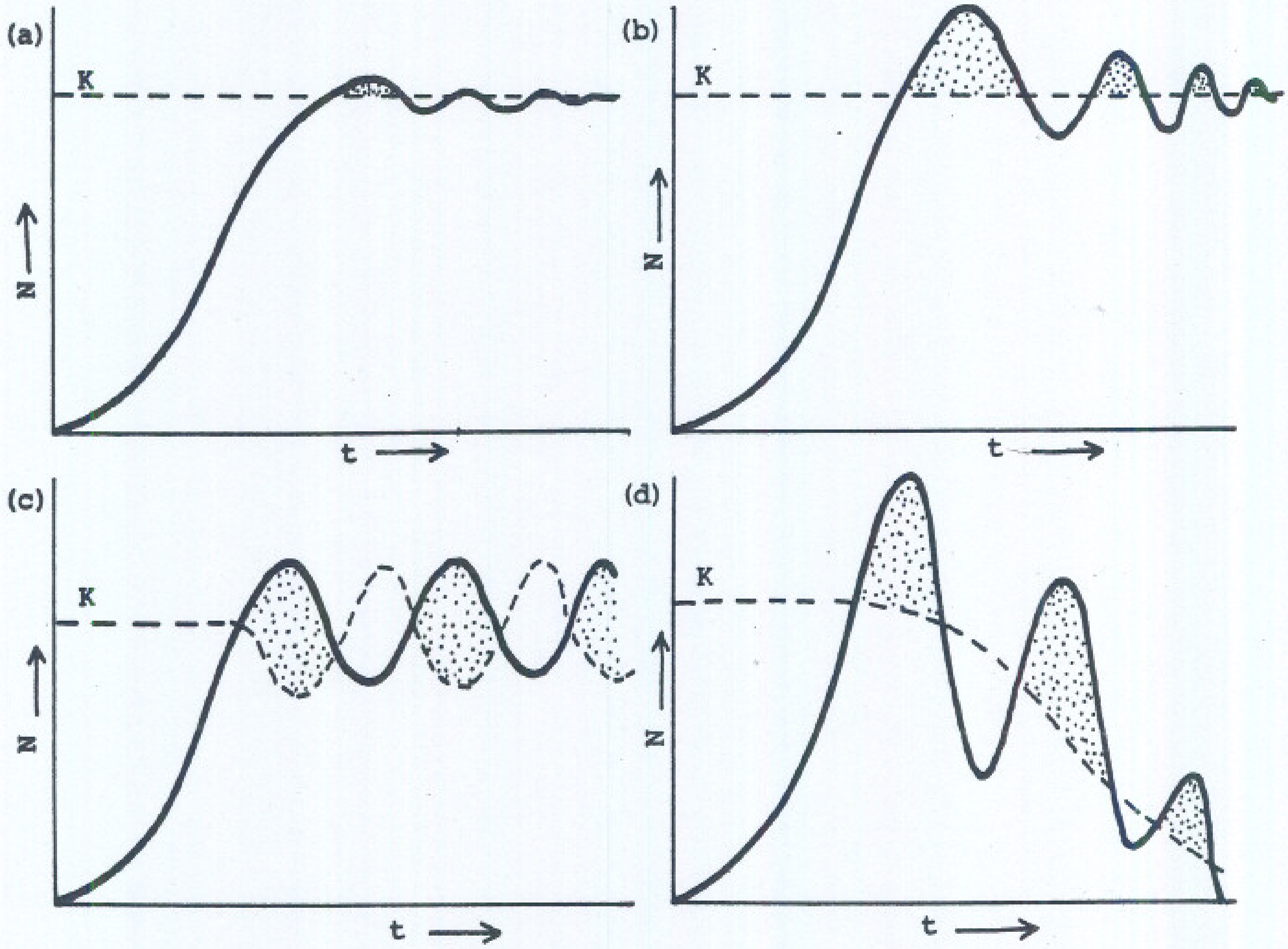


Fig. 4(a) shows almost perfect regulation to the equilibrium level with only minor fluctuations about *K*.

Fig. 4(b) shows less accurate regulation at first but gradually the equilibrium level is reached and then maintained.

Fig. 4(c) shows that perfect regulation is never achieved; instead the population shows a constant cycle of change, oscillating with *K* in a regular way. (This is called a 'stable limit cycle'[8].)

Fig. 4(d) Shows an extreme case of failure to regulate; the population overshoots *K* so much that *K* itself is reduced and eventually the population plunges to extinction.

(Stippled areas in the Figures show when *K* is exceeded.)

Since the finite rate = e^{rt}

then $$\frac{N_{t + 1}}{Nt} = e^{rt}$$

or $$N_{t + 1} = N_t e^{rt}$$

If we take the natural logs of this, e drops out and we get

$$\log_e N_{t + 1} = \log_e N_t + rt$$

It can be shown that the above term reduces to the formula for a straight line, $y = a + bx$. Therefore, if a population is growing at a constant rate, a graph of the natural logarithms of numbers against time will produce a straight line, the slope of which is r (Fig. 5). An example of this type of analysis has been published for a lechwe population in Zambia.[30]

We can also find r by taking the natural log of the finite rate of increase over one year ($t = 1$)

i.e. $\log_e$ finite rate $= r$

The exponential rate of increase r is affected by all the factors limiting a population, for example food, space, predators, etc. When resources are abundant and predation and disease insignificant, the population will increase as fast as it is genetically capable, a situation that normally occurs when the population is small in size. This maximum rate, $r_{\max}$, is called the intrinsic rate of increase. As the population becomes larger, resources become more restricting, and the rate of increase declines to zero when the equilibrium population is reached at K (Fig. 6). Later on we will need to obtain a measurement of $r_{\max}$ to calculate a harvest from a population.

Figure 5 The relationship of $\log_e$ population size plotted against time for a population growing at a constant rate. The slope of the regression line is an estimate of *r*.

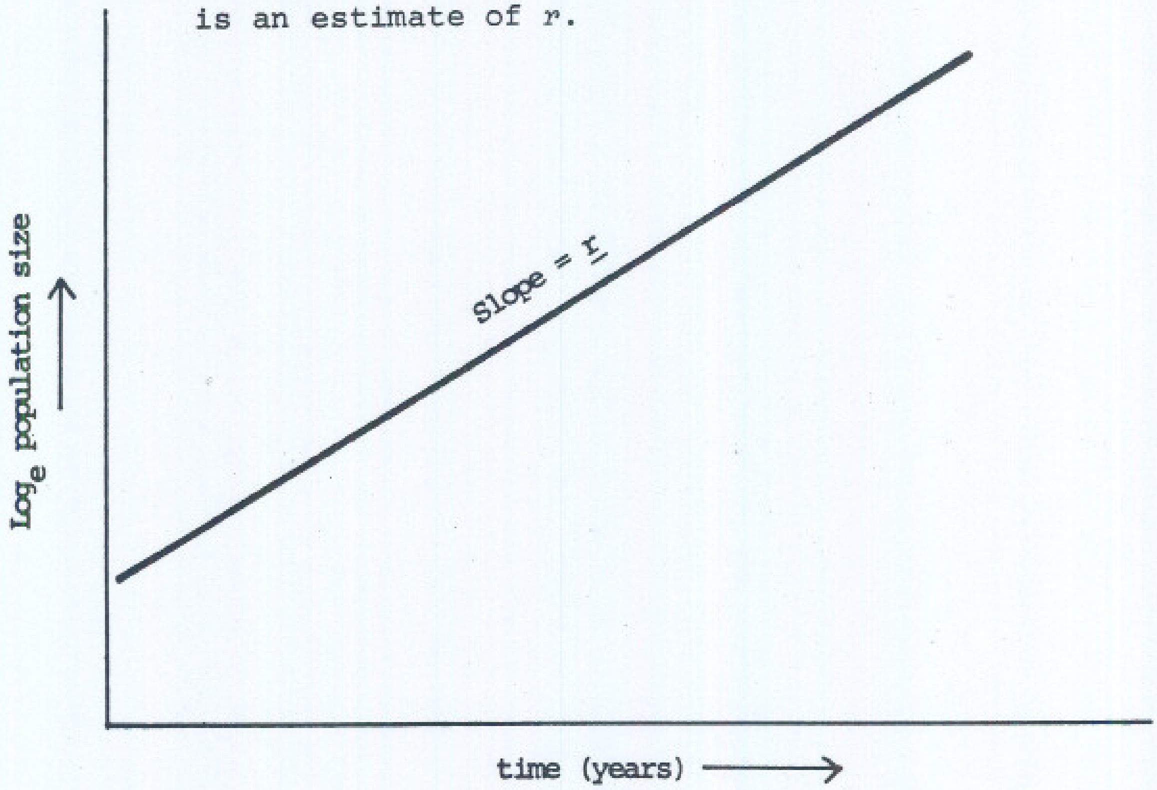
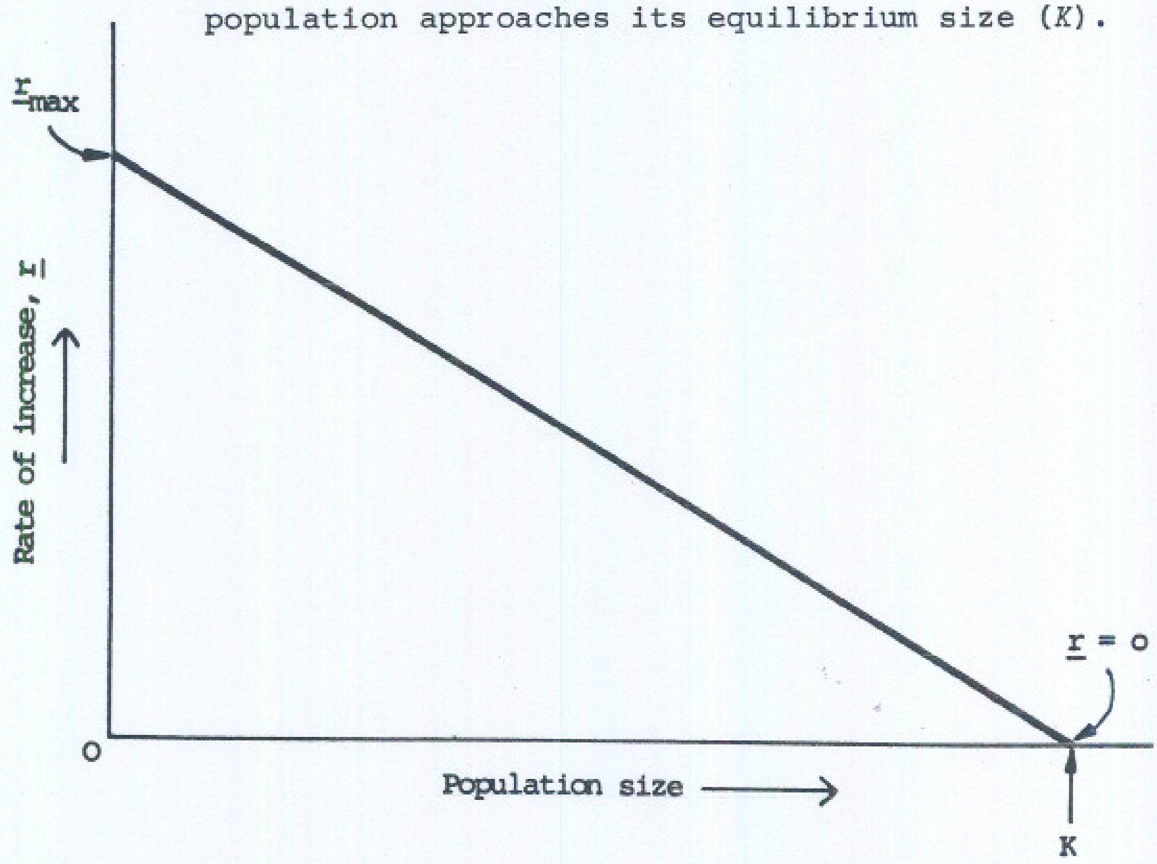


Figure 6 The rate of increase (*r*) declines to zero as the population approaches its equilibrium size (*K*).



SECTION 4 THE MEASUREMENT OF BIRTH RATES

4.1 General

The birth rate of the population is derived from the proportion of mature females that give birth during the year. If the number of mature females in the population is known (from censuses of the population, estimates of the proportion of mature animals and the sex ratio of adults) then the number of animals born to the population can be calculated, and further, if this is done over several years, then the variation in this number can be observed.

Four methods have been used on large mammals for measuring the birth rate. These are :

(1) by the collection and *post mortem* examination of a random sample of mature females;

(2) by pregnancy diagnosis of a random sample of live females;

(3) by a backward extrapolation of the mortality rate of newborn animals;

(4) by recording the reproductive histories of individually known females.

4.2 Measurements from collected samples

This method has usually been carried out on ungulates when it is practical to collect animals specifically for the purpose, or in conjunction with cropping schemes. It should be mentioned that in the collection, which is usually by shooting the animals, care must be taken to make the sample random with respect to the adult females. This is because classes of adults such as old animals may be more easily collected but at the same time have a lower than average birth rate. Similarly females with suckling young may have a different birth rate to those without young, yet the former group are more timid and difficult to collect. For animals that live in herds, a simple method of randomizing the collection is to pick on one animal as a reference point and then to count a certain number of animals to right or left of this reference, the number being determined by a random series previously written down. The animal arrived at should be the one collected.

Unless births take place uniformly throughout the year - and this almost never occurs - the collection of one sample at one time is not sufficient to give an estimate of the mean birth rate. Consequently samples have to be collected at intervals throughout the year, or over a number of years in the very large mammals, such as the elephant, which have long gestation periods and intervals between births of several years. In general, if the species has a short gestation period with multiple breeding in the year, then the sampling should be at a higher frequency than with a species of long gestation and one birth peak. In the elephant, the mean birth rate may be estimated from counts of placental scars.[39]

After the random samples throughout the year have been collected, the following calculations should be carried out on each sample separately, and the mean of these computations found in order to take account of differing sample size.[21]

The *Prevalence of Pregnancy* (Pp) for each sample is the number of pregnant adults divided by the total number of mature females. The mean Pp over all samples should be found, with its standard error given by

$$\text{S.E. of } Pp = \sqrt{Pp\ (1 - Pp)/N}$$

where N is the total number of females in all samples. This calculation is needed to measure the *Incidence of Pregnancy* (Ip), which is the number of pregnancies that an average female has each year, this being virtually equivalent to the mean birth rate in animals that produce one young at a time (i.e. the majority of large mammals).

$$Ip = Pp.t/\text{Gestation time in days}$$

where t = 365 days, and

$$\text{S.E. of } Ip = (\text{S.E. of } Pp).t/\text{Gestation time in days.}$$

A worked example of these calculations is shown in Table 1.

4.3 Measurements from live animals

As it is not always possible to conduct *post mortem* examinations, other methods have to be used. This can be done very simply by observing external signs of pregnancy in live animals.[24] Because this is a subjective method there are unknown errors involved, so it is not very suitable for year to year comparisons. By capturing animals and carrying out pregnancy diagnosis - a more reliable and objective method - the above difficulties can be overcome, but in their place are the practical problems of obtaining large enough samples. Pregnancy diagnosis can be conducted in various ways: for large ungulates this can be done on immobilized animals by standard veterinary techniques of manipulation through the rectum. Some training on cattle with a practised veterinarian is required first. For other animals chemical tests of urine and blood will detect pregnancy. A third method is to use a foetal ultrasonic pulse detector, a small, portable instrument that can detect the heart beat of the foetus.[27,31] However, none of these can give information on the number of foetuses present, and this information must be obtained from other sources.

4.4 The birth rate from measurements of newborn mortality

In species in which the season of births is restricted to part of the year, the rate of mortality of newborn young can be used to calculate the number born to the population. This takes into account both the proportion of females that are pregnant and the number of young per female (litter

Table 1. Example of calculation of birth rate in a buffalo population in Uganda.[29]

	Subsamples by seasons	Number Pregnant	Total mature females	*Pp*
1.	December - February	17	22	0.77
2.	March - May	16	30	0.53
3.	June - August	15	30	0.50
4.	September - November	19	27	0.70
	Totals	67	109	Mean over the 4 subsamples = 0.63

Standard error of $Pp = \pm\sqrt{0.63\ (0.37)/109} = \pm 0.046$

95% confidence limits of $Pp = \pm 0.092$

Incidence of Pregnancy $(IP) = \dfrac{0.63 \times 365 \text{ days}}{340} = 0.68$

(gestation time for buffalo)

Standard error of $Ip = \dfrac{\pm 0.046 \times 365}{340} = \pm 0.049$

As female buffalo only produce one young at a time, the mean birth rate for mature females in the buffalo population is estimated from the sample to be 0.68 ±0.049 (S.E.)

size). The method is as follows: the proportion of young in the population (or the number of young per adult female if this is more accurate) is assessed at frequent intervals after the peak of births. This peak must be known but can be found simply by starting the sampling well before the peak has occurred. The proportion of newborn will decline after the peak for a certain period and then will level off (Fig. 7). The initial decline is a reflection of the mortality taking place over the whole birth season. This is an assumption, but any potential errors are likely to be small.[52]

Another assumption is that the early mortality rate of those born remains fairly constant. This assumption is unlikely to be true because several studies on the mortality rate of young ungulates have suggested that the rate is not steady. The usual pattern is a high rate of mortality soon after birth followed by a declining rate in the subsequent months of early life.[1,17,55] This factor will probably introduce a bias into the calculation of the birth rate by the method described below. In order to assess the degree of bias, an independent check should be made of the birth rate by one of the methods given above (4.2 and 4.3). This was done for the buffalo of Serengeti National Park and in this case little difference was found between the birth rates measured by the newborn mortality method and by the pregnancy rate from a shot sample.[52] However, this relationship must be checked for other species, because the agreement between methods might not always be so good.

The proportions of newborn in the samples collected during the period of the initial decline after the peak, are transformed to logarithms, and these are plotted graphically against time (Fig. 8). The regression line of log newborn proportion against time is calculated and drawn in on the graph. This line is then extrapolated backwards until the time when the first newborn of that season were recorded (effectively the start of the birth season, w in Fig. 8). The reading on the y axis at this time is the

Figure 7 The number of young per 100 adult females in a buffalo population, showing the mid-year peak of births.[52]

w = time when first young of the year observed

x = point where deaths begin to exceed births

y = time when the mortality rate of the young lessens.

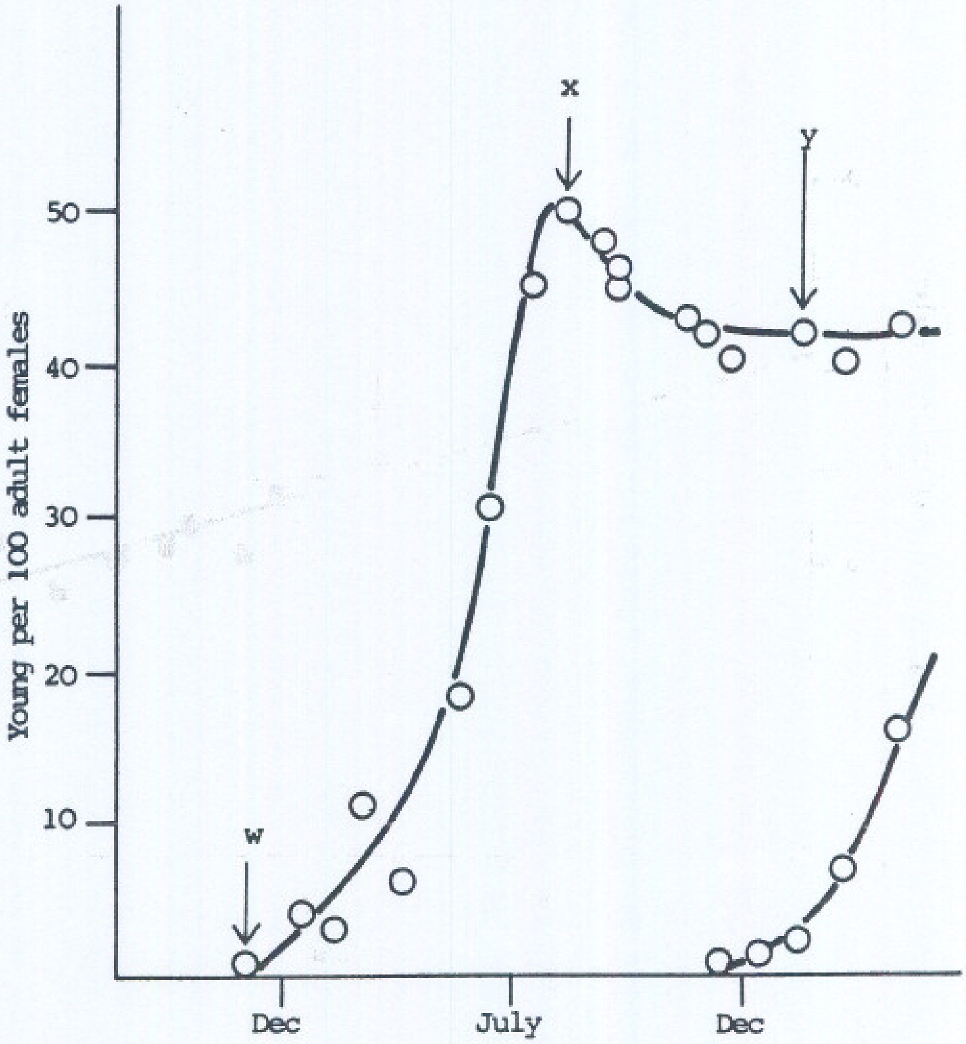


Table 2 Estimated age-specific birth rate (of female young) (m_x) for two populations (R and G) of thar in New Zealand.[5]

Age	Number		Breeding		Non-breeding		m_x	
(yr)	R	G	R	G	R	G	R	G
1	25	94	0	1	25	93	0.000	0.005
2	18	97	12	26	6	71	0.333*	0.135*
3	18	107	14	94	4	13	0.389	0.440
4	19	68	19	57	0	11	0.500	0.420
5	11	70	11	65	0	5	0.500	0.465
6	12	47	11	40	1	7	0.458	0.425
7	8	37	7	34	1	3	0.437	0.460
8	2	35	2	34	0	1	0.500	0.486
9	3	24	3	24	0	0	0.500	0.500
10	4	16	2	16	2	0	0.250	0.500
>10	5	28	5	23	0	5	0.250	0.411

* Significant difference found between the populations for the birth rate of this age group.

SECTION 5 AGE GROUPS AND RECRUITMENT

5.1 The use of age ratios

The methods described below depend on measuring the proportion of particular age groups in the population. As has been discussed,[6] age ratios or proportions can give ambiguous results. For example, supposing that the proportion of yearlings in an ungulate population was to change from 10% in one year to 15% in the next. This might mean that (a) the rate of recruitment had increased owing to increased birth rate, improved first year survival, or both, and that the rate of population increase had gone up; or (b) the survival in adults had been lowered compared to that in yearlings, so that the relative proportion of yearlings had increased; in this case the rate of population increase might have been lowered.

The only reliable way of interpreting age proportions is to know the population rate of increase as derived from census data. However, if the relationship between population growth and age proportions can be established for a particular population, then it may be found that age proportions can be used as a useful index of recruitment and of changes in population growth.

5.2 Immature age groups and recruitment

The recruitment to the population is the proportion of the population at the age when the animals are first capable of reproduction. This age must be ascertained first by studies of the species' reproduction; as in the buffalo or the elephant for example.[29,39]

For most species the age group when recruitment occurs can be identified in the field and sometimes even on aerial photographs. However, if this is not possible then a younger age group should be measured and a correction made for the mortality occurring between this age and the age at recruitment. In practice this mortality is usually small for the animals have grown past the stage of early juvenile mortality.

The determination of the proportion of the recruitment age group, or younger age groups, usually requires taking a random sample unless the population under study is so small that all the animals can be counted. Sampling depends on the distribution of the species in question. For resident species that can be easily observed in the field, sampling can be carried out by randomly selecting groups of animals, and recording the number of animals at each identifiable age. From this the proportion at each age in the total can be calculated.

Another way of calculating the proportion is to record the number of animals in each age group per adult female. This is advantageous when a section of the population, such as non-breeding males, is highly mobile, sometimes segregating out and sometimes mixing with the females. When this happens the clumping effect of the segregation creates a large variance in the estimates of recruitment and hence makes it difficult to compare consecutive estimates for changes. By relating each immature age group to adult females, one avoids this problem and smaller samples can be used. To obtain the proportion in the population a second calculation for the proportion of adult females also has to be obtained by a large sample, but this need only be done a few times as it is unlikely to change very much even over a period of years. The samples for recruitment, however, have to be collected relatively frequently so that large samples would become impractical.

If the population under study is widespread and the sampling is done on the ground it may be impractical to take a random sample from the whole population and subsamples must be used. Alternatively a few selected areas can be studied intensively whilst comparing rather less frequently with the rest of the population. This comparison is necessary to check that the selected areas are representing the processes taking place in the population.

If the population is highly mobile then selected areas cannot be used and it is necessary to sample the whole population. If the population is also widespread then ground sampling becomes impractical. An example of this situation is found with the Serengeti migratory wildebeest population which covers an area of up to 5000 km^2 at any one time but which completely alters its location in as short a time as one week. The problem in this case was solved by taking random aerial photographs. Animals from newborn to nearly one year old can be distinguished from the rest so that the proportion of yearlings in the population can be calculated. As conception can take place at 16 months, this is effectively the recruitment.

Another problem is found when the animals behave in such a way that they cannot be counted from the ground. Such a problem is encountered with buffalo which form compact groups and which are often so timid that ground counting becomes impossible. Again the problem can be overcome by the use of aerial photographs. In this case animals up to two years old can be readily distinguished. First conceptions occur at three years old but the mortality between two and three years old, estimated from random collections of the live population, is almost negligible so that the correction to obtain the recruitment is very small. It has been found that if two-year-old animals comprise 11% of the population, in the following year the same group, then three years old, would not be less than 10%. Hence there is less than 1% change, and so the error is less than 10%.[52]

When the proportion of recruitment age, or any other proportion of the population, is estimated from samples, an estimate of the sampling error must be obtained. This is best done for each occasion when samples are collected, by treating each group of animals in a ground count as a separate sample (or each transect if this is used as a technique). Similarly when photographs are used, each photograph is treated as a separate sample. With these data the formula given in the Appendix can be used to calculate the confidence limits. These confidence limits are essential when one wants to compare estimates from consecutive time periods for measurements of change.

5.3 Measurement of adult age groups in the population

If the proportion of adults as a whole is to be considered or the sex ratio of all adults is needed, then the estimates can be obtained in the same way as those for immature animals. However, if the proportion of age groups within the adult class is needed then field identification methods cannot be used and a random sample of the population has to be obtained. The age of the collected animals is determined by methods mentioned above (Section 2).

The proportion of each group in the adult population can be calculated but the sample sizes will be very small for the older age classes in which changes from year to year will be hard to detect. However, it is usually not necessary to obtain this sort of information and large samples of the population are rarely needed.

SECTION 6 MORTALITY AND POPULATION REDUCTIONS

Estimates of mortality and the reduction of the potential birth rate, can be calculated from year to year in a population if the following information has been obtained:

(1) annual census of the population;
(2) the proportion of all immature age groups in the population, and
(3) the remainder after (2) has been calculated, gives the proportion of adults;
(4) the sex ratio of adults;
(5) from (1), (3) and (4) the actual number of adult females can be calculated;
(6) average litter size for that year;
(7) from (5) and (6) the potential number of young born to the population can be calculated;
(8) the proportion of pregnant females in that year;
(9) from (5), (6) and (8) the actual number of young born to the population can be calculated;
(10) the difference between (7) and (9) gives the loss of potential births (i.e. the pre-natal deaths);
(11) from (1) and (2) the actual number of one-year-olds, two-year-olds, etc. to the age of recruitment, or as old as is needed can be calculated.
(12) the difference between (9) and the number at one year old in (11) a year later gives the *mortality in the first year*, the difference between the number at one year old in one year and the number at two years old in the following year gives the *mortality in the second year*, and the process is repeated for as many age classes as data are available. Similarly if adults are lumped as one age group then *adult mortality* can be assessed simply by the difference between the adults plus recruitment in one year and the adults in the following year.

Therefore it is possible to obtain measurements of reductions of the potential birth rate and of the reductions due to mortality that take place each year in a particular population. These methods have been used to study a buffalo population in the Serengeti National Park.[52] It should be repeated at this point that these measurements are based upon samples each of which has a sampling error. Unless these errors are measured and kept small, it is not possible to measure mortality in this way.

Occasionally in populations of ungulates it is possible to count carcasses of dead animals, obtaining a direct and independent measure of mortality. The counting can be done by using transects or by complete searching of blocks. In the former case transects have to be calibrated for visibility and in the latter case some measure of searching efficiency must be made. At the same time it is necessary to calculate both the density of live animals in the study area and also for how long the mortality has been taking place. From this information it is possible to obtain a rate of mortality. These measurements can be made when either a large population inhabits a small area as does, for example, the Serengeti wildebeest or white-eared kob in Sudan, or a large and obvious mortality takes place, as was seen in the Tsavo elephants in 1971.[18,43]

SECTION 7 LIFE TABLES

Once the proportions of different age groups in the population have been estimated, it may be useful to construct a life table showing the survivorship of animals at different ages from birth to the oldest age group. It is usually started with 1000 newborn animals (a cohort). If this group could be followed through to old age recording the number still alive at each age then a time-specific survival curve could be produced. However, to do this for a large mammal would take from ten to fifty years and would be of no practical use. If, however, the rate of survival (or death) at each age is the same for succeeding cohorts born in successive years and the population stays stationary in size, then the proportion of each age group in the population would reflect its survivorship. In other words if one found year after year that in the population newborn animals comprised 30%, yearlings 15%, two-year-olds 10%, and so on, with decreasing percentages for the other age groups, then one could say that with a start of 1000 newborn, half would survive the first year (15%/30%)100 = 50%, resulting in 500, and two thirds of those would survive the next year (10%/15%)100 = 66.6%, resulting in 333, and these calculations could be continued throughout the age groups until none survive. An age-specific life table would be the result.

This type of life table construction relies on the fact that survival at the same age in successive cohorts remains the same. This constant age-specific survival can only occur if the rate of increase (r) of the population is constant. This rate of increase can be positive (in an expanding population), negative (in a declining population) or zero (stationary population). The last represents the simplest situation of a population of constant size with a constant age distribution - sometimes referred to as a stationary age distribution.

If a population has remained more or less constant in size for a long time then a stationary age distribution will be found. The calculations require a knowledge of the proportion of each age group within the population. Having obtained this information the life table (called a *klx* series with *k* = 1000 animals and the *lx* the proportions of that 1000 which survive at each age *x*) can be calculated starting with the 1000 newborn as demonstrated above. These figures can be plotted as in Fig. 9 to show a survivorship curve.

The proportion of each age group in the population is best calculated by obtaining a random sample of live animals from the population at the time of the birth peak. However, these samples of living animals are often impractical to obtain. But the life table can also be calculated from a random sample of animals that have died; for example, skull and jaw material collected in the field. This assumes that of 1000 newborn all have died by the oldest age group. A *kdx* series can be constructed as shown in Table 3. Normally the first age group is under-represented in samples of dead animals, so the mortality at this age must be calculated as mentioned in Section 6, or by other methods; for example, based on the lactation state of pregnant females[55] or by entering a value at the top of the life table of the probable number of young born to the female segment of the life table.[3] In Table 3 it was estimated by independent methods[29] that 50% died in the first year of life, i.e. 500 of the 1000 died leaving 500 in the *kdx* series. In the second age group, 10 out of a total of 435 animals over one year old were found dead and this represents 12 of the remaining 500 animals that would eventually die, leaving 488 animals. In the third age group 5 animals were found dead which represents 6 of the original 500. The 6 is subtracted from 488 to leave 482 alive. This process is continued until the last age group.

One drawback of these calculations is that any sampling error in one age group of the original sample of 435 dead animals is incorporated into all subsequent calculations of animals in older age groups. Hence the errors are cumulative. In the examination of age-specific survival or mortality one way of avoiding this problem is to calculate

Figure 9 The survivorship curve for the two sexes of a buffalo population assumed to have a stable age distribution. A semi-logarithmic plot is used to show rates of change of survivorship.

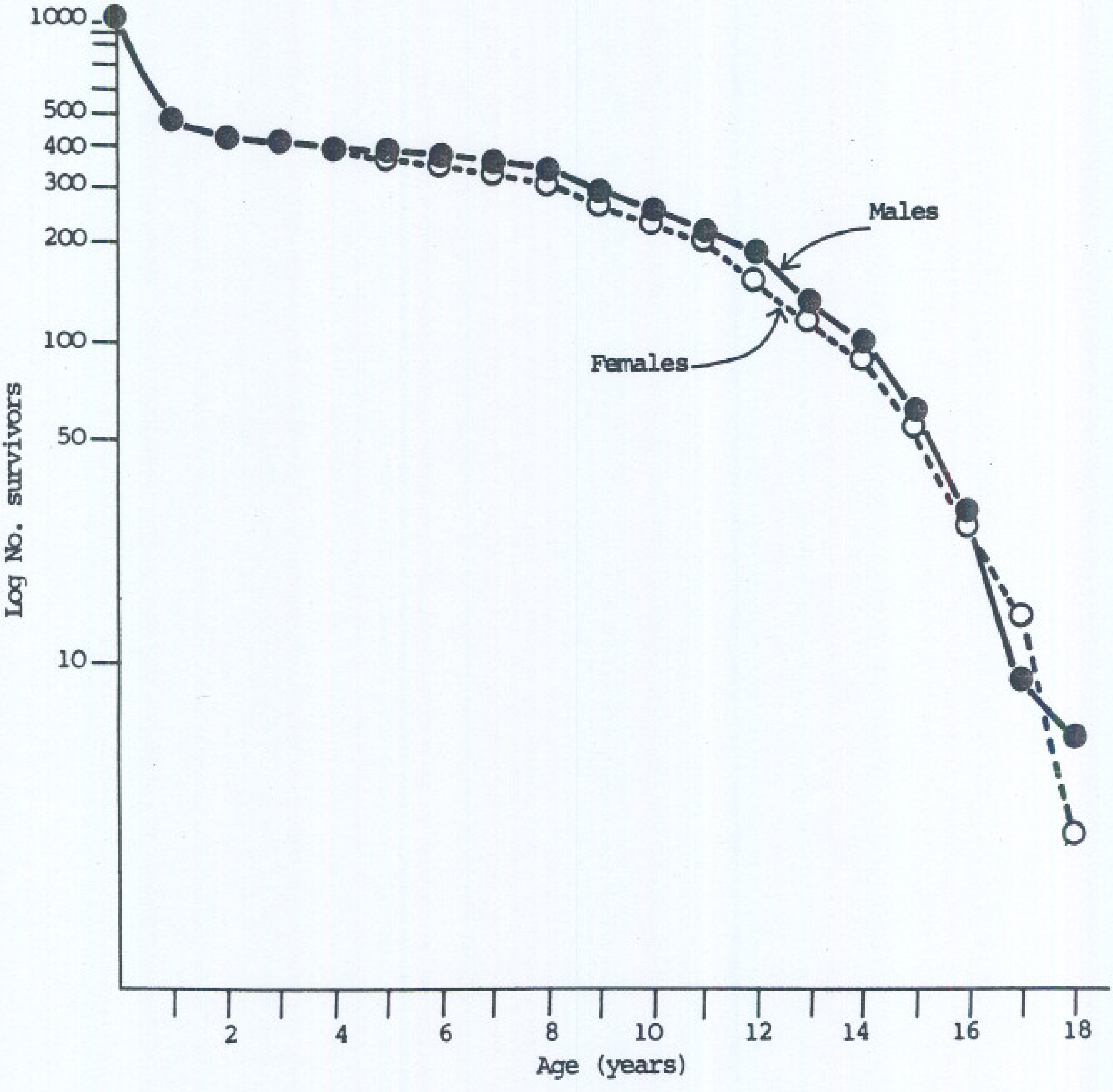


Table 3 Life table for a buffalo population (both sexes combined); the population was stationary in size and the age distribution was assumed to be stable (Grimsdell, unpublished data).

Age (x) years	No. skulls collected	kdx	klx	kqx
0	(6)*	500	1,000	500
1	10	12	500	24
2	5	6	488	12
3	16	18	482	37
4	19	22	464	47
5	28	32	442	72
6	44	51	410	124
7	35	40	359	111
8	46	53	319	166
9	35	40	266	150
10	34	39	226	172
11	39	45	187	241
12	37	43	142	303
13	25	29	99	293
14	14	16	70	229
15	16	18	54	333
16	13	15	36	417
17	7	8	21	381
18	2	2	13	154
19	4	5	11	454
20	2	2	6	333
21+	3	4	4	1,000
Total :	435 over one year of age			

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*The first age group is greatly under-represented in the collection of skulls and an independent estimate is needed of first year mortality.[29]

a kqx series. This age-specific mortality is measured as the number dying per 1000 alive at the beginning of each age group. For example, in Table 3, during the first year 500 animals die per 1000 animals alive at the beginning, during the second year 12/500 die which is 24 per 1000 in the kqx column. This enables one to examine each age group separately. If these figures are plotted against age, a typical "fish-hook"-shaped curve often results with high mortality in the young and old age groups and low mortality in the intermediate age groups.[3]

So far we have considered only those populations with zero rate of increase. If a population has been increasing steadily for some time a different constant age distribution results. In order to find this the lx series is calculated as described above, and then each age group is multiplied by e^{rx}, where e is the base of the natural logarithms, x is the age, and r is the infinitesimal rate of increase.[5] An example of this procedure is shown in Table 4. The rate of increase is measured as the increase per animal per year and can be found simply from a series of censuses as described in Section 3.

Of course the same multiplication in theory applies when r is zero. In this case the term e^{rx} is unity, so that the lx series remains the same. If the population is changing either from one that is stationary to one that is increasing or decreasing, or vice versa (i.e. the rate of increase is changing), then an accurate lx series cannot be calculated.

In recent years some misconceptions have crept into the literature concerning the use of these life tables. A number of workers have tried to estimate the rate of increase directly from the klx series. This is, of course, logical nonsense because one must know what the rate of increase (r) is before the lx series can be constructed. Hence r cannot be calculated from such a series. If r is calculated from a klx series, based either on the age distribution of the living population or of dead animals, an answer close to zero will always be obtained.[12] This is

Table 4 Life table for female Serengeti buffalo.[52]

Age (x) yrs	N	Kdx'	$Kdx'e^{rx}$	kdx	klx	kqx	mx
0	-	485	465	330	1,000	330	0
1	-	129	139	94	670	140	0
2	9	14	16	11	576	19	0
3	9	14	18	12	565	21	0.06
4	15	23	31	21	553	38	0.14
5	10	16	24	16	532	30	0.41
6	17	27	43	29	516	56	0.41
7	11	17	29	20	487	41	0.41
8	18	28	52	35	467	75	0.41
9	24	38	76	52	432	120	0.41
10	19	30	65	44	380	116	0.41
11	29	46	107	73	336	217	0.33
12	25	39	98	67	263	255	0.33
13	19	30	82	56	196	286	0.33
14	16	25	73	49	140	350	0.33
15	13	20	63	43	91	473	0.33
16	7	11	38	26	48	542	0.33
17	4	6	22	15	22	682	0.33
18	1	2	10	7	7	1000	0.33
	246	1,000	1,471	1,000			

N = no. skulls collected

kdx' = deaths per 1000, assuming a stationary population

$kdx'e^{rx}$ = adjustment for the population rate of increase, as obtained from census dat

kdx = adjusted deaths per 1000

$kl\,x$ = adjusted survival per 1000 born

kqx = adjusted age specific mortality

mx = no. female offspring produced per female per year not surprising since the life table data are forced into a model in which the number of deaths (1000) equals the number of births (1000).

In view of the labour involved in the collection of the information, workers should first seriously consider what their main objectives are, and whether life tables will be useful. On the whole, the main advantage of life tables is in standardizing the description of age-specific survival and mortality in different species. However, life tables with hypothetical lx series can be useful in determining the probable range of population increase or decrease of which a particular species is capable.[31,34] This information can be used in the calculation of sustained yields (Section 9.2). Life table data can also be used to calculate an index of demographic vigour (Section 8.3).

SECTION 8 POPULATION CONDITION

8.1 Description of population condition

Two main concepts have been put forward in order to describe population condition, namely, physiological condition and demographic vigour.[33] Ideally, both of these approaches should be used until such time as the relationships between the two are better understood. When suitable calibration has been carried out for particular species, it may be possible to simplify the description of population condition quite considerably. Measurements of population condition are useful in many aspects of population analysis, whether for conservation, harvesting or control.

8.2 Physiological condition

Physiological condition refers to the general body condition of individuals in a population, and would be expected to be related to the potential rate of population increase. In Himalayan thar, for example, it was found that the kidney fat index (see below) was highest in increasing populations, lower in stable populations, and lower still in declining populations.[4]

Some methods of assessing physiological condition are as follows:

(1) Live animals: The field technique developed by Riney[47] has been used by several workers in Africa. Animals can be classified visually into three or four grades depending on the characteristics of the lumbar region.

(2) Captured animals: If a sample of animals can be caught and examined by hand, a less subjective method of condition scoring can be used, for example, based on criteria developed for sheep.[48] These criteria were modified for scoring lechwe antelope and are based on manual palpation of the *longissimus dorsi* muscles in the region of the anterior lumbar vertebrae.[31] Such an index of

muscle volume may reflect physiological condition quite accurately in antelopes, in which subcutaneous fat is either absent or very scanty. Captured animals can also be weighed and measured. An index of physiological condition is body weight divided by body length, the latter being a useful measure of skeletal frame size.[31]

(3) Shot animals: In a recent review,[33] five broad methods of assessing physiological condition are described, based on deposited fat reserves, adrenocortical hypertrophy, blood chemistry and hematology, urinary excretion of hydroxyproline and body weight. One of the more widely used methods is the kidney fat index, being calculated as a hundred times the weight of fat surrounding the kidney, divided by the weight of the kidney. A kidney fat index of 80 or above indicates that an antelope is in 'good' condition; below an index of about 40, bone marrow fat is mobilized and the animal moves into the 'poor' condition category.[33] Apart from fat, muscle can also be measured. Muscle weights, standardized against a skeletal measurement (e.g. the length or weight of a limb bone) appear to provide a useful index of physiological condition, as found in topi antelope for instance.[23] Perhaps the most convenient index of physiological condition is dressed body weight divided by body length. This is a slightly more refined method than that mentioned under (2) above.[61]

8.3 Demographic vigour

Caughley[10] has suggested that demographic vigour can be summed up neatly by a single statistic, r_s; that is, the rate at which a population would increase if it had a stable age distribution appropriate to its current schedules of age-specific survival and birth rate. The stable age distribution refers to the age-distribution that would result if these age-specific schedules do not change over time; the rate of increase then becomes constant and any imbalances in the original age distribution are eliminated. A computer program for calculating r_s is given by Caughley.[10]

When sufficient data are available for a particular species, it will be possible to correlate different values of r_s with some of the indices physiological condition mentioned above. However, this has not yet been done for any African mammal.

A more easily obtained measure of demographic vigour, though not as satisfactory as r_s, is the birth rate of the first mature age group as this seems to be a sensitive indicator of population condition.[36] For example, the following pregnancy rates were recorded for three lechwe populations in Zambia:

	Pregnancy rate
(1) Stable population (Kafue Flats)[49]	0.36
(2) Increasing population (Bangweulu flood plains)[31]	0.67
(3) Rapidly increasing population (small captive herd)[31]	1.00

Other measures of demographic vigour could be based on foetal development, first-year mortality, adult mortality, sex ratio and the birth rate in adult females - all being various components of the overall statistic r_s.

Measurements of demographic vigour may have to be evaluated according to whether a species is more of an *r*- or more of a *K*-strategist. An *r*-strategist will be characterized by rapid development, early reproduction, short life span, small body size and high rates of $r_{\max}$; while a *K*-strategist will have the opposite characteristics.[44] It might be expected that a small antelope, such as an impala, would show a different pattern of demographic vigour than, say, a buffalo. In the absence of hunting and heavy predation, an impala population might display high values of r_s until the carrying capacity, K, was exceeded and then undergo a marked population crash. On the other hand, a buffalo population would show lower values of r_s and, as suggested by the Serengeti buffalo population,[50] show declining values of r_s as K is approached.

SECTION 9 THE ANALYSIS OF POPULATION DYNAMICS

So far in this handbook we have been concerned with the methods by which it is possible to estimate the characteristics (or parameters) of a population.

Having obtained this kind of informtion it must then be used to investigate the dynamics of the population. As we have said in Section 1, the study of population dynamics can be useful if three types of situation; namely, conservation, harvesting and control.

Therefore in the remainder of this handbook we will discuss how the analysis of population dynamics can help in solving problems - either in conservation, harvesting or control.

9.1 Conservation

The problems of conservation concern the protection of rare species - possibly encouraging them to increase - and discovering the reasons for the decline of certain populations with a view to halting or reversing the trend.

The usual reasons for the decline of a population are:

(1) adverse habitat change;
(2) competition from another animal species;
(3) excessive hunting or predation;
(4) disease;
(5) some combination of the above factors.

As has been discussed by Caughley,[10] the investigation of the problem can be tackled in two stages. Firstly, a simple investigation can be carried out in order to discover any obvious reason for the decline of a population. Such an investigation can take the form of a comparison between the declining population and a healthy population of the same species living in a different area. Any obvious differences between the two areas, as regards habitat, competing species, predation or disease can be investigated further. If, for instance, there is much more human settlement in or near the area of the declining population, one might make a closer study of the level of human hunting to see if this might be causing the decline. Perhaps a disease - such as tuberculosis or rinderpest - might be present in the area occupied by the declining population but absent in the area used by the healthy, 'control' population. Again, this would be a factor requiring further study.

If no obvious reasons for a population decline emerge from the initial investigation, then a more detailed study is needed. One of the aims of the study will be to determine age specific birth rates and death rates of the population, as already described. This will help to isolate the cause of the decline. Of course, information on birth and death rates must be available from a healthy population in order to make comparisons. If the cause of the decline is adverse habitat change then one would expect to find a high rate of juvenile mortality coupled with a low birth rate in the first mature age group; in fact, the age at first reproduction might even be delayed by a year or more. If, on the other hand, birth rates are not depressed but mortality is high, we might suspect that a high level of hunting or predation is causing the decline.

An example of the latter situation is provided by the black lechwe antelope of Zambia.[31] This population had declined from a level of around half a million at the beginning of the century to some 17,000 in 1970. Although there had been some change in the flood plain habitat used by the black lechwe, the chief cause of the decline seemed to be excessive hunting by man. A detailed investigation showed that age specific birth rates and body condition values were high in comparison with other lechwe populations, but that survival rates were low. The conclusion seemed clear enough: that heavy hunting had reduced the population to a level well below the carrying capacity of the flood plain habitat, and if the amount of hunting could be reduced then the population would begin to increase.

The situation of the black lechwe may be compared with another lechwe population living along the Chobi river in Botswana. A study of this lechwe population indicated that juvenile survival was low and that the physical condition of the lechwe was poor, suggesting unfavourable habitat conditions with limited food resources. The available evidence suggested that the population had declined considerably in recent years.[14] In a case such as this further investigation would be needed, particularly with regards to possible habitat change. The habitat of lechwe is affected by the depth and duration of flooding and if these had altered in any way, then it could explain the population decline.

In some cases the habitat change can be predicted in advance, a good example being the Kafue Flats in Zambia where the construction of two dams will completely alter the natural flood regime. A large population of lechwe occupied the Kafue Flats before the installation of the dams, but once both dams are operational the population is expected to decline on account of habitat changes brought about by the changes in flooding.[45,49]

As lechwe are comparatively numerous animals living in open habitat, they are relatively easy to study. However, other species present much more of a problem; for example, rare species living in wooded or forested habitats. Examples of such species in Africa are roan and sable antelopes, the forest antelopes and some of the cat family. In these cases the investigations are hampered by the difficulty of collecting sufficient data, making it much more of a problem to isolate causes of population decline, even if the latter can be measured.

9.2 Sustained yield harvesting

Provided that the growth form of a population is logistic (see Section 3), then it is possible to estimate the sustained yield (SY) that a population of a particular size can withstand. The SY is given by the same formula as for the logistic curve, as follows:

$$SY = r_{max}\frac{N\ K - N}{K}$$

where r_{max} = the maximum rate of increase of a population, under stated conditions, at a very low density

N = population size at which the SY is to be taken

K = the maximum population size that a particular area can hold, i.e. the population size at the ecological carrying capacity of the area.[11]

From the above, it can be shown that the maximum sustained yield (MSY) is $\frac{1}{2}r_{max}.\frac{1}{2}K$, this representing the optimum trade off between rate of population increase and population size (Fig. 10).

Clearly, good estimates of r_{max} and K are needed in order to calculate an SY or the MSY. The calculation of K is often difficult and beyond the scope of this handbook. It requirs a knowledge of the food requirements of a particular species and the amount available during the most critical period of the year; for example, the dry season food and water supply. In Africa, estimates of K have been made by comparison with the density of a population believed to be at or near that level,[31] or on calculations based on available food in different ecological zones.[41] A value for r_{max} can sometimes be obtained from the observed rate of increase of a population at very low density, although well documented cases for African mammals are extremely rare. An alternative method is to estimate r_{max} from a hypothetical population with maximum birth reproduction and minimum mortality.[31,34] A fair idea of maximum birth rates and minimum age at sexual maturity can often be obtained; but we are less certain about minimum death rates, so that an informed guess may have to be made. A few rough estimates of r_{max} have been calculated for African large mammals; for example:

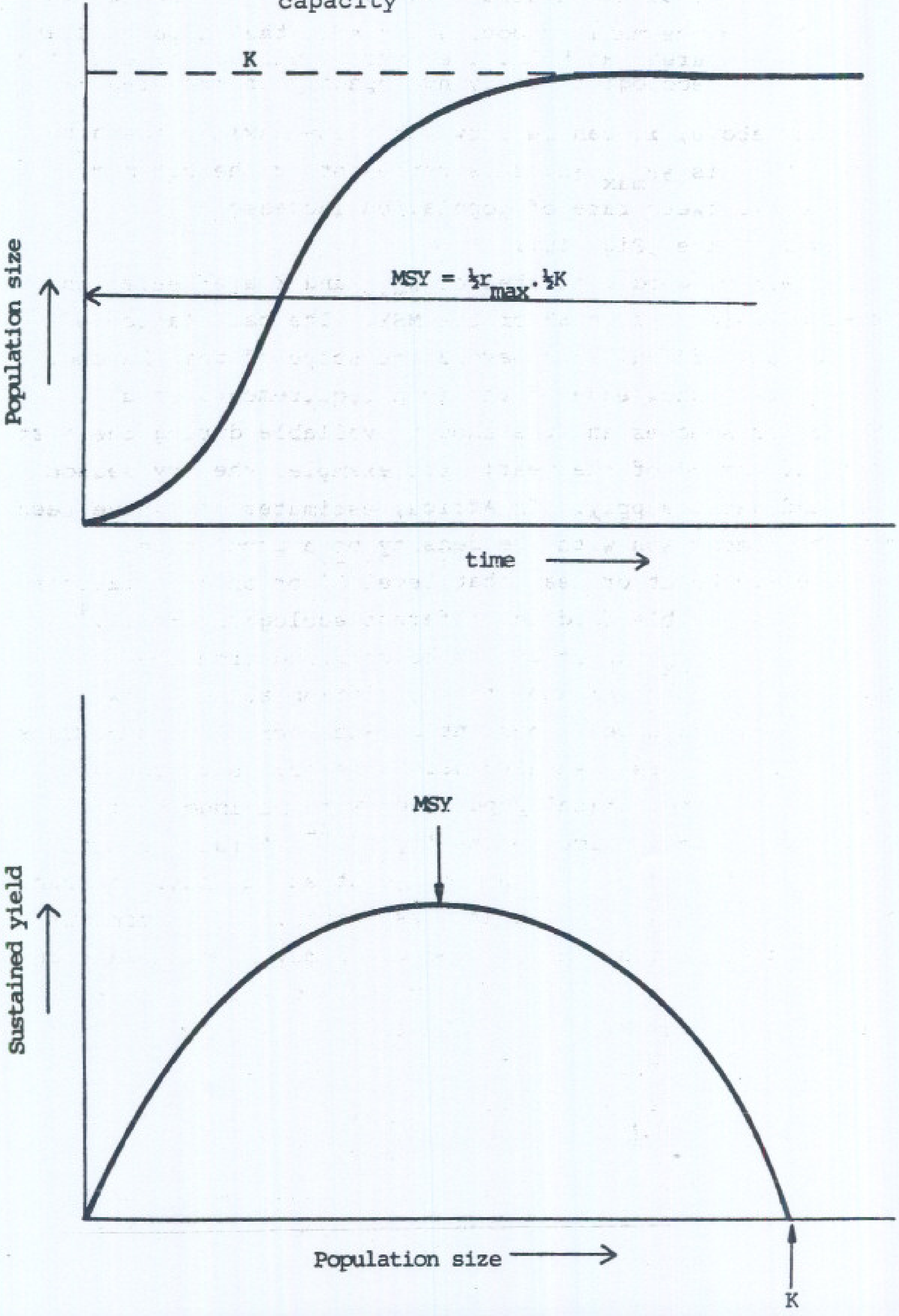
African buffalo $r_{max} = 0.23$
Lechwe antelope $r_{max} = 0.27$
Hippo $r_{max} = 0.22$

The r_{max} values are, in fact, infinitesimal values; when converted to finite values they come out somewhat

Figure 10 Sustained yield harvesting based on the logistic curve.

MSY = maximum sustained yield

K = population size at ecological carrying capacity[11]



higher. Thus, the lechwe value of $r_{\max} = 0.27$ is equivalent to a finite rate of increase of about 1.3, or 30% per year.

Recently it has been shown[13] that $r_{\max}$ is a simple function of body weight and can be calculated approximately as follows:

$$r_{\max} = 1.5W^{-0.36}$$

where W = weight in kg
and $r_{\max}$ is calculated on a yearly basis

In polygamous species, the rate of increase will be even higher if the population is biased towards females. This can make a large difference to the MSY. Hence, sex-selective harvesting - that is, selective harvesting of males in a polygamous species - can considerably increase the MSY. In contrast, it can be shown by computer simulation that age-selective harvesting is of no advantage; in fact, the most productive harvest is random with respect to age.[10]

As there are no well-documented examples of MSY harvesting of African large mammals, it is impossible to go further than this theoretical treatment. In practice, an estimate of the MSY would be useful to have as an upper limit to exploitation; but, to be on the safe side, one would be wise to exploit at a lower level until such time as MSY harvesting is better understood. Furthermore, the MSY may not necessarily be the same as the optimum economic yield,[40] so clearly economic factors have to be examined as well. An essential adjunct to harvesting are regular population counts to make sure that the population is not over-exploited and reduced to an unproductive size.

A full treatment of harvesting is given by Caughley.[10]

9.3 Control

Control implies the adjustment of an animal population to some predetermined level, according to specific management objectives; while in some cases control can mean complete elimination of a particular species.

Control operations can either be conducted directly against the animals themselves, often by shooting them, or indirectly by manipulation of the animals' habitat. Again, the reader should refer to Caughley's book[10] for a discussion of this topic.

In direct control operations, the animal population responds in the same way as a harvested one, in that the rate of population increase becomes greater the further the population is reduced below its size at K (see Fig. 6). This makes complete elimination of an animal population very hard to achieve by hunting, as was discovered, for example, in tsetse control operations against large mammals in northern Botswana.[15]

If the aim is to stabilize the population at some arbitrary level, then this can be achieved by removing a constant proportion of the population each year, provided that the proportion does not exceed r_{max}. As we have mentioned in Section 1, control measures can be taken to help prevent undue habitat change, provided action is taken at an early stage (see Fig. 1). Action of this kind is known as reduction cropping and is not necessarily aimed at stabilizing the population at a particular level, although this is often an additional objective. Some examples of this form of control come from Uganda, where reduction cropping was applied to populations of hippopotamus and elephant.[25,39]

Undoubtedly, the most sophisticated means of controlling an animal population is by manipulation of its habitat; that is, by alteration of key components of the food supply or of the animal's cover. In order to carry out this type of indirect control, a detailed knowledge is required of the animal's ecology, particularly its feeding ecology. Very few examples of this type of manipulation seem to be available from Africa, and those that are available have been aimed at encouraging population growth rather than depressing it.

One of the most useful tools for habitat manipulation is probably fire; for example, controlled burning operations can be used to encourage either woodland or grassland, and to alter the growth stage of the herb layer. Other techniques that could be experimented with are artificial cutting of vegetation, application of fertilizers, fencing or ditching off key areas of habitat, and by favouring the growth of a competing animal species.

The analysis of population dynamics can help to provide an answer as to whether a control operation is needed or not. If sufficient data of the right kind have been collected for a particular population, then it is possible to construct mathematical models which simulate the dynamics of the population. Such models can be used to predict whether a population is likely to reach an equilibrium level and what the population size would be at that level.

A model of this kind has been constructed for a buffalo population in the Serengeti National Park.[51,52] By a detailed study of birth rates and death rates, it was possible to discover how these were changing as the population increased (and as food resources became more limited). The death rate of adult buffaloes was found to be especially sensitive to changes in population size; that is, as the population increased so the survival rate of adults decreased. This is known as a density dependent response, or a negative feed-back mechanism to population growth. By modelling the growth of the buffalo population it was shown that the density dependent response of adult mortality was by itself sufficient to regulate population size and bring it to an equilibrium point.

Therefore, by this type of simulation modelling it was possible to demonstrate that regulation of population size was occurring, and it was also possible to predict the population size at equilibrium (i.e. at K). In this case, no management action would be necessary or desirable because the buffalo population would eventually stabilize at a level set by the resources of the environment.

Given adequate data, predictive models can be made for other large mammal populations. The models can help to show whether a population is likely to reach a stable equilibrium level, or to oscillate predictably (the stable limit cycle),[8] or to be inherently unstable. Models can also be used to see how well a population responds to a change in environment. A model of this kind has been used to explore the response of elephant populations to changes of their habitat.[20]

Unfortunately, predictive models have their drawbacks. This is because they are usually based on the assumption that environmental conditions are stable or that they change in a regular way. In certain environments these assumptions may be accurate enough, but in others the assumptions will be invalid (e.g. in many semi-arid areas). As has been pointed out,[20] the usefulness of population models is limited by their ability to accommodate and cope with unpredictable events. Rainfall and human actions are good examples of such events.

Population analysis and modelling can certainly be useful in solving problems in wildlife management, but must be combined with ecological monitoring in order that unforseen changes are noticed and taken into account as soon as possible.

APPENDIX

Method of measuring the standard error of proportions[16]

Using the actual numbers of animals obtained in each sample of the population (herds, transects, aerial photographs, etc.), let y be the number of animals in the class being investigated (e.g. yearlings, adult females, pregnant females) in a sample and let x be the number of all other animals in the same sample. Then the ratio R over all samples is:

$$R = \frac{\Sigma y}{\Sigma x}$$

and the Standard Error is

$$s(R) = \frac{1}{\sqrt{n}.x} \cdot \sqrt{\frac{y^2 - 2R.\ \Sigma yx + R^2.\ \Sigma x^2}{n - 1}}$$

where n is the number of samples.
If p is the proportion of y in the whole population of $\Sigma(y + x)$, then p (as a percentage) is

$$p\ \% = 100/(1 + \frac{1}{R})$$

The confidence interval can be transformed in the same way.

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