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"Ivory Poaching and the Viability of African Elephant Populations"

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These are preliminary lecture notes, intended only for distribution to participants.

Ivory poaching and the viability of African elephant populations.

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ABSTRACT.

Three years ago, the African elephant, Loxodonta africana, was declared endangered and placed on Appendix I of CITES. In this paper we describe a demographic model for elephants that examines the effect that poaching has had on East African populations and the time that it would take exploited populations to recover under complete protection. All of the model's parameters are based on empirical data from a number of field studies. The analyses suggest that both social structure and reproductive physiology are crucial in understanding the demography of elephants and in determining the size and composition of viable elephant populations. In particular, inclusion of the elephant's social behaviour into the model creates a threshold below which the population will always collapse to extinction. The technique provides a framework which may be applied to studies of extinction in other endangered species.

Introduction.

The 1989 international ban on commercial trade in ivory was implemented by the international community because of very real concerns about the trend towards extinction of many African elephant populations. Between 1979 and 1989 poaching for ivory reduced the continental population from 1.3 million to 609,000 elephants (Douglas-Hamilton, 1988). In regions where poaching was severe individual populations declined by over 80 percent during the same period. During the 1980's the international ivory trade averaged some 800-1,000 tonnes per year, representing the deaths of up to 100,000 elephants annually. It has been estimated that up to 90% of the ivory traded originated from illegally killed elephants (Dobson & Poole, 1992). The offtake in many areas left elephant families fragmented and caused radical changes in grouping patterns (Poole, 1989a). A range of scientific and economic analyses conducted during 1988 and 1989 indicated that a continuation of the ivory trade would drive many elephant populations to extinction early in the next century (Beddington et al, 1989; Caughley et al, 1990). In this paper we examine the possible effect on already exploited populations of reopening the trade in ivory.

The African elephant, Loxodonta africana, has a complex social organization consisting of a network of alliances between matriarchal groups of related females (Moss, 1988). Adult males live essentially independent lives, alternating between periods of association with other adult males and extended periods of sexual activity during which they move between cow/calf groups in search of receptive females (Poole, 1987). Elephants are long-lived mammals; age determines dominance, leadership and calf survival among females and reproductive success through female choice and dominance among males (Poole, 1987, 1989b). Here we describe an age-structured model, based on the Leslie matrix (Leslie, 1945; Caswell, 1989), that includes functions describing both the decrease in female reproductive activity as population density approaches the carrying capacity and the decrease in the probability of conception as mature males become limiting through overexploitation. Empirical data from long term studies at Amboseli and surveys of age and sex structure in other African elephant populations are used to estimate the model's parameters and to illustrate the response of different populations to exploitation.

A model for elephant demography

Long term studies on elephants in Amboseli National Park in Kenya indicate that the occurrence of oestrus and conception are highly sensitive to resource availability (Moss, 1988; Poole, 1987; Laws 1969). Data from a number of different elephant populations studied by Laws (1969) suggest that both age at first reproduction and inter-birth interval increase with population density (Figure 1 a,b). However, since his data were gathered from elephants living in different habitats they compound density effects with variations in habitat quality. Under constant weather conditions, per capita resource availability should decline as population density approaches the carrying capacity. While we acknowledge that Laws's study may incorporate the effects of habitat and weather on reproduction, it does provide evidence from a sufficient range of populations to show that the reproductive activity of elephants is sensitive to population density. We have therefore used these data to describe rates of recruitment and set both age at first reproduction and interbirth interval as functions of density.

The model is constructed in the framework of a two-sex Leslie matrix with the population divided into five year age-cohorts. The natural survival rates of male and female elephants were estimated from the long term population data collected from the relatively unpoached elephant population at Amboseli (Moss, in press), these parameters form the off-diagonal of the matrix. The fecundity terms of the first row of a standard Leslie matrix are replaced by the density-dependent functions illustrated in Figure 1 (a,b), these expressions determine the birth rates of young (10-20 years) and mature (> 20 years) females. The effects of poaching were included by reducing the natural survival rate of any age or sex class by a term corresponding to the additional mortality due to poaching. The model was initially used to determine the effects of random exploitation on elephant populations, this essentailly corresponds to the case where family groups of elephants are culled for control purposes.

This initial analysis suggests that elephant populations are very susceptible to exploitation (Fig 2a,b). For example, a random annual offtake of 1.25% reduces the population to a new equlibrium at 50% of its initial size in about 100 years, while an annual removal of 7% is sufficient to drive a population to extinction in around 150 years. Present evidence suggests that annual levels of poaching averaged between 12 and 18% in some East African populations (Beddington et al, 1989; Milner-Gulland & Mace, 1991). Had harvesting continued at this level it would have driven many elephant populations to extinction early in the next century (Fig 2b).

However, as tusk size is dependent upon both the age and sex of an elephant (Fig 3), poaching is unlikely to operate in a random fashion. If we assume that poachers selectively remove elephants with tusks larger than a minimum size, we obtain a more complex relationship between ivory yield and population size (Fig 4a). Initially, the larger tusked adult males will be selected in preference to females and younger males. Selective poaching at lower tusk weights rapidly produces populations with distorted sex-ratio and age-structure (Fig 4b). Surveys conducted on East African elephants populations confirm these highly skewed sex-ratios, in some areas mature females outnumber mature males by a factor of over fifty to one (Poole, 1989a). Furthermore, the proportion of females showing signs of pregnancy or accompanied by recent offspring were diminished in these populations. To examine how these changes in social structure affect the ability of populations to recover, we have extended the model to ascertain the conditions when a paucity of mature males limits conception rates.

Social structure and population viability.

We model the social system of elephants by assuming that males searching for females have the dynamics of a simple predator prey system. We assume that M males search at a rate, α, in a population of F females, divided into G groups (the rate at which males find females in oestrus is thus $\alpha \epsilon F/G$, where ϵ is the proportion of time for which a female is receptive). Each male takes a constant period of time, h, to consort with each oestrous female. The number of females that any male succcesfully consorts with in a period of time T, equal to one oestrus cycle is given by the following equation;

$$\frac{N_e}{M_t} = \frac{\alpha T \epsilon F/G}{1+\alpha h \epsilon F/G} \qquad (1).$$

This expression for the instantaneous rate at which males encounter females may be used to estimate the probability that any individual female is not located by the available males during any one oestrus period. This probability is given by substituting Eqn 1 into the zero-th term of a Poisson distribution;

$$p_0 = e^{-(N_e/F_c)} \qquad (2).$$

The proportion of females who eventually conceive during the time equal to one inter-birth period is a function of the probabilty that she is not mated, p_0, the probability, c, that she conceives if mated and the number of times, τ, a female would come into oestrus every four years if not successfully mated. Thus the proportion of females who are pregnant or produce offspring in any four year time interval is given by

$$f(F,M) = 1 - [(1-c)(1-p_0) + p_0]^{\tau} \qquad (3).$$

Substitution of Eqn 2 into 3 allows us to obtain an expression for the proportion of females producing young in any four year interbirth interval

$$f(F,M) = 1 - [1 - c(1 - e^{-N_e/F})]^{\tau} \qquad (4).$$

This expression is a modification of one described by Dobson & Lyles (1989); it assumes that females who do not conceive, will continue cycling. Here we assume that males attain sexual maturity at age twenty and are sexually active for a proportion of time, s each year; they are promiscuous and will mate with several females during this period. The mating function suggests that the probability of a female conceiving during any one reproductive cycle is strongly dependent upon the numbers of males available and the number of groups into which the female population is divided (Fig 5a & b). As the sex ratio becomes more distorted towards females (as is the case in heavily poached elephant populations), or as the females become divided into many small groups, the proportion of females producing offspring declines (Figure 6).

The mating function (Eqn 4) is most sensitive to estimates of male search rate and the number of times a female enters oestrus. We assume that a female enters oestrus three times a year; the actual incidence may be less than this as females will fail to cycle if resources are limiting. Data collected from studies of bull elephants at Amboseli (Poole, 1989b) were used to quantify the rates at which males locate females (Figs 5 & 6 indicate the sensitivity of the results to variation in this parameter). Since females find mature males more attractive than younger, inexperienced males (Poole, 1989b), these data may overestimate the success rate of males in populations where poaching will have reduced the numbers of older males. Both these effects may cause the model to overestimate expected conception rates in heavily exploited populations.

Inclusion of the mating function (Eqn 2) into the fecundity terms of the demographic model described above considerably increases the susceptibility of exploited elephant populations to extinction. Essentially, the elephant's social behaviour determines a threshold population size where successful mating becomes limiting and below which the population always collapses to extinction. The presence of such a threshold means that the viability of elephant populations is dependent not only on past and present levels of poaching, but also upon the sex-ratio and group structure of the exploited populations.

Empirical data from surveys of East African elephant populations provide support for this model of mate limitation (Poole 1989a). In Mikumi, Tanzania, where the surveyed elephants were widely dispersed in many small groups, only 39% of the adult females had developed breasts (and were, therefore, either pregnant or lactating). In contrast, in Queen Elizabeth, Uganda, most of the elephants had grouped together to form a single permanent large aggregation, and 87% of the adult females had developed breasts. The number of mature females to mature males in the two parks was 74:1 and 26:1, respectively. Using the observed numbers of males of breeding age and female group size structures observed in these populations (the mean number of females per group for Mikumi is 3, while mean number of females per group in Queen Elizabeth is 67), our model predicts 40% and 95%, of females pregnant or lactating for Mikumi and Queen Elizabeth Park respectively (14).

To further illustrate this point we have run simulations using the model and the observed age structure, group and sex composition for Mikumi NP, Tanzania, Queen Elizabeth National Park, Uganda and Amboseli and Tsavo NP's, Kenya (Figure 7). In the first case we have assumed an "effective" ban on the ivory trade, in the second case we have looked at the situation where a limited ivory trade creates an incentive for poaching and 3% of the elephant population is killed each year. In the case of a complete ban, three of the populations take thirty to fifty years to attain equilibrium density and considerably longer (50-100 years) to establish stable age structure. The population at Mikumi never recovers from its present condition and in the absence of migration declines to extinction. In the situation where a limited trade in ivory encourages poaching, the populations at both Mikumi and Queen Elizabeth Park are driven to extinction; those at Tsavo and Amboseli show pronounced declines. These results suggest that even a slight increase in poaching may be sufficient to cause the presently disrupted elephant populations in many parts of East Africa to collapse to extinction. All our calculations suggest that as populations become fragmented their recovery rates become increasingly sluggish.

The model can also be used to estimate the length of time it will take different elephant populations to recover. This relationship may be calculated for populations for which information is available about the mean weight of the tusks being removed from the population. The rate at which the population recovers will be a function of whether the individuals have been selectively or randomly poached with respect to tusk size. We have calculated the recovery times for both random and selectively poached populations and assume the actual recovery time for any elephant population will lie somewhere between the two extreme values. We have also calculated the recovery times to two different population densities: 50% of carrying capacity, the density at which maximum ivory yield is obtained from a randomly culled population; and 98% carrying capacity, the density at which total ivory yield is maximized (Figure 8). In each case the recovery times of selective poached populations is longer for a similar mean tusk weight, while the time for heavily poached populations to recover to levels where they will maximize ivory production is of the order a century. Milner-Gulland and Mace (1991) have published estimates of the average tusk weights for a number of African countries in the mid-1980's, these data can be used to estimate the recovery times of the elephant stocks in these countries (Fig 9a & b). These data suggest that while the populations in Southern African countries, such as South Africa and Zimbabwe, are still relatively healthy, the populations in East Africa will take at least thirty to fouty years to recover, and may take as long as one hundred years to reach levels where they will maximize ivory productivity.

Conclusions

The work outlined in this article has important implications for elephant conservation and ivory trade policy. The first section of the paper suggests that elephants are highly susceptible to overexploitation. Although the maximum growth rate of an elephant population may be as much as 7% per year (Hall-Martin, 1970), the non-linear relationship between population density and recruitment for elephants (Figure 1) means that exploitation at a level in excess of 1% per year is sufficient to ultimately reduce a population at carrying capacity by 50%. Once overexploited, elephant populations may take at least 50 years to recover from the effects of poaching. The analysis of selective poaching of the larger tusked individuals suggests a complex interaction between ivory offtake and elephant population size. In particular, selective poaching distorts the sex and age structure of the population and can lead to rapid declines once poachers include females and immature males in their harvest.

Non-linear effects are also important in determining the time scale at which elephant populations respond to exploitation; selective culling can rapidly remove the largest tusked individuals from a population, but it will then take thirty to fourty years for a cohort of older males to regenerate. In contrast, random culling at low levels may provide a steady supply of tusks for a long time, but attempts to increase yields by raising the culling level quickly leads to diminished returns from a population which subsequently takes longer to recover. These calculations underlie many of the paradoxes of elephant conservation and the ivory trade. As was originally pointed out by Pilgrim & Western (1987), both honest ivory dealers and conservationists receive maximum value from elephant populations kept as close as possible to carrying capacity. In contrast, where elephant populations are culled to prevent habitat damage by excessive elephant use, the long-term yield of ivory diminishes rapidly with the efficacy of control. Consequently, conservation projects that are paid for with ivory from culled elephants will receive diminishing revenues through time. Indeed the maximum yield of ivory from a culled elephant population is usually an order of magnitude less than the yield from a selectively managed population. Under these criteria, fencing, and potentially fertility control, may present alternatives to culling that are both economically and ethically more sound.

The second half of the paper considers how disruptions to the social system of elephants affect their population dynamics. The simulations in this section use data gathered from East African populations to compare the theoretical fate of populations with known age and sex structure. As with any non-linear ecological model the projections are dependent upon the assumptions of the model. Thus the results for Mikumi are pessimistic as they exclude the effects of immigration from the adjoining Selous Reserve, while the results for all the parks may be optimistic as they ignore any detrimental interaction between the elephants and their food resources, this may lead to increased mortality if the elephants severely degrade the habitat. The results we have presented are most sensitive to our estimate of male searching rate α. The figure we have used is based on a study of mature bulls at Amboseli (Poole, 1989b). Older bulls are more attractive to females, who tend to run away from younger, inexperienced males. This means it is likely that we have overestimated the success rate of the younger males present in a heavily exploited population and in essence our calculations may underestimate the effects of male limitation in a heavily exploited population.

The inclusion of other features of elephant social behaviour, such as the effect of allomothering on infant survival (Lee, 1987) further increases the propensity for fragmented populations to collapse (O'Connell & Sutton, 1990). All of this analysis suggests we should be more cautious in the way we manage populations of elephants and that more research is needed to fully understand the relative importance of the different processes that determine viability in different areas and habitats. While it has been argued that some elephant populations are not endangered and could sustain a limited harvest, the inability of both exporting and importing countries to regulate the trade in ivory would again lead to illegal exploitation of endangered populations elsewhere in Africa. The numbers of deaths in East African elephant populations has steadily decreased since the 1989 ban and elephants have begun to leave the protection of the smaller parks and recolonize parts of their former range. The evidence presented in this paper suggests that lifting the ban on international trade in ivory in the immediate future could still be catastrophic for many African elephant populations.

FIGURE LEGENDS.

Figure 1. (A) & (B) The influence of population density on age at first reproduction and interbirth interval in elephant populations surveyed by Laws (1969). The fitted curves are functions of the form $p = 1/(1+(aN)^b)$, where p is the proportion of females producing offspring and N is population density; we assume density determines a significant component of <u>per capita</u> resource availability. The parameter estimates are (A - age at first reproduction) $b = 3.04$ (± 0.38), $a = 1/2.00$ ($\pm$ 1/0.10), $r^2 = 0.98$ and (B -inter birth interval) $b = 1.54$ (± 0.51) and $a = 1/1.97$ ($\pm 1/0.31$), $r^2 = 0.84$. These two functions are used to determine the proportions of females producing offspring in each four year time interval. The resultant figures are multiplied by 1.25 to give the birth rate in each five year interval of the Leslie matrix model described in the main text.

Figure 2 (A) The effect of exploitation on an elephant population is illustrated in the form commonly used by fisheries biologists: population size on the horizontal axis is expressed as a proportion of carrying capacity. The amount of ivory harvested from the population is expressed on the vertical axis as a proportion of the maximum amount that could be obtained (the "MSY" level); the numbers superimposed on the figure correspond to the annual percentage of the population required to produce these yields. (B) An indication of the time scale over which different rates of poaching lead to changes in population size:

the time taken to reduce the population to 50% of its size prior to exploitation and the time taken to drive a population to extinction. In both cases the starting population was set at an equilibrium value of 1000 elephants, extinction was defined as a population of less than one individual.

Figure 3. The relationship between age and tusk size for male and female elephants; the two arrows indicate the age at sexual maturity.

Figure 4. (A) The effect of selective poaching for large tusks on ivory yield and elephant population size. Here we assume that poachers select elephants with tusks larger than a certain size. As males have substantially larger tusks than females, they will be more heavily exploited in the early years. As mature males become rare, poachers include females and immature males in the harvest producing a more complex relationship between yield and population size. It is particularly important to note that once females have been included in the harvest, small decreases in average tusk weight produce large decreases in population size. The irregularity that occurs in the recruitment function close to carrying capacity reflects the switching point when poachers begin to include females into their harvest. (B) The effect of selective poaching on the sex ratio of elephants in the population (mature females per mature male).

Figure 5. The effect of population size and grouping pattern on the rate at which oestrous female elephants are located by mature males. The probability that an oestrous female will be mated is assumed to have the dynamics of a simple predator-prey system; the numbers of females located is dependent upon encounter rate, α, female group size, F/G, and the proportion of females in oestrus, e. Each oestrous female is fertile for two days, and if she does not conceive, she will cycle three time a year (thus $e = 6/360$). The duration of oestrus also determines the period of time, h, that a male spends consorting with any individual female and is unavailable to others. The observed pregnancy rates at Amboseli may be used to obtain a conservative estimate for encounter rate α ($\alpha = 3$). The dotted lines on either side of the line for five groups illustrate the sensitivity of the mating function to this parameter (upper line $\alpha = 2$, lower line $\alpha = 4.5$). When either sex is limiting encounter rate is likely to be a function of habitat size. We have therefore estimated α for other parks by modifying the Amboseli estimate by the relative area of each park (we assume α is a function of distance travelled and that this will scale with the square root of habitat area, thus $\alpha \approx 1.2$ for Queen Elizabeth and $\alpha \approx 1.8$ for Mikumi).

Figure 6. The effect of variation in sex ratio on expected proportion of females pregnant or lactating in a population containing two hundred sexually mature female elephants. The

figure assumes that males search for females with a success rate determined by the functional response depicted in Figure 5. Successfully mated females have only a 50% chance of conceiving (Moss, 1988). The expected proportions pregnant or lactating are drawn for populations split into 2, 5, 10 and 50 groups. The lines are discontinued below densities where it would be impossible to subdivide the population to the given extent. The dashed lines on either side of the 5 group contour illustrate the sensitivity of the function to α, it is again allowed to vary by a factor of 2. Included in the figure are the data from surveys of pregnant or lactating females in Queen Elizabeth National Park, Uganda (QENP), Mikumi National Park, Tanzania (MNP) and the relatively unpoached population at Amboseli National Park, Kenya (ANP).

Figure 7. Projections of the populations at (A) Amboseli, (B) Tsavo, (C) Mikumi and (D) Queen Elizabeth National Parks assuming a complete cessation of poaching and an ineffectual ivory ban. Each simulation was performed using the estimates of age and sex-structure recorded in the surveys by Poole (1989a) as the starting conditions. In each figure the model is run to compare effective poaching control (upper line in each figure) with one in which poachers are able to take 3% of the population in any year (lower line).

Figure 8. The relationship between average tusk size weight and

recovery time for African elephant populations. Two different recovery contours are illustrated, the shorter recovery times are the time it takes for populations to return to fifty percent of carrying capacity; the longer times are the time it takes for populations to recover to 98% of carrying capacity. In each case a band of recovery times is delineated by the extreme values determined by whether the population had been exploited randomly or selectively, in both cases the longer recovery times represent populations that have been selectively poached.

Figure 9. (A) The observed mean tusk sizes exported from a number of African countries in the mid-1980's. The data for Singapore represent pooled ivory from a variety of populations all over Africa (12). (B) The estimated recovery times of the elephant populations for which tusk size data are available. In each case data are given for the recovery time to 50% of carrying capacity (assuming the population has been poached at random) and to 98% of carrying capacity (assuming it has been selectively poached).

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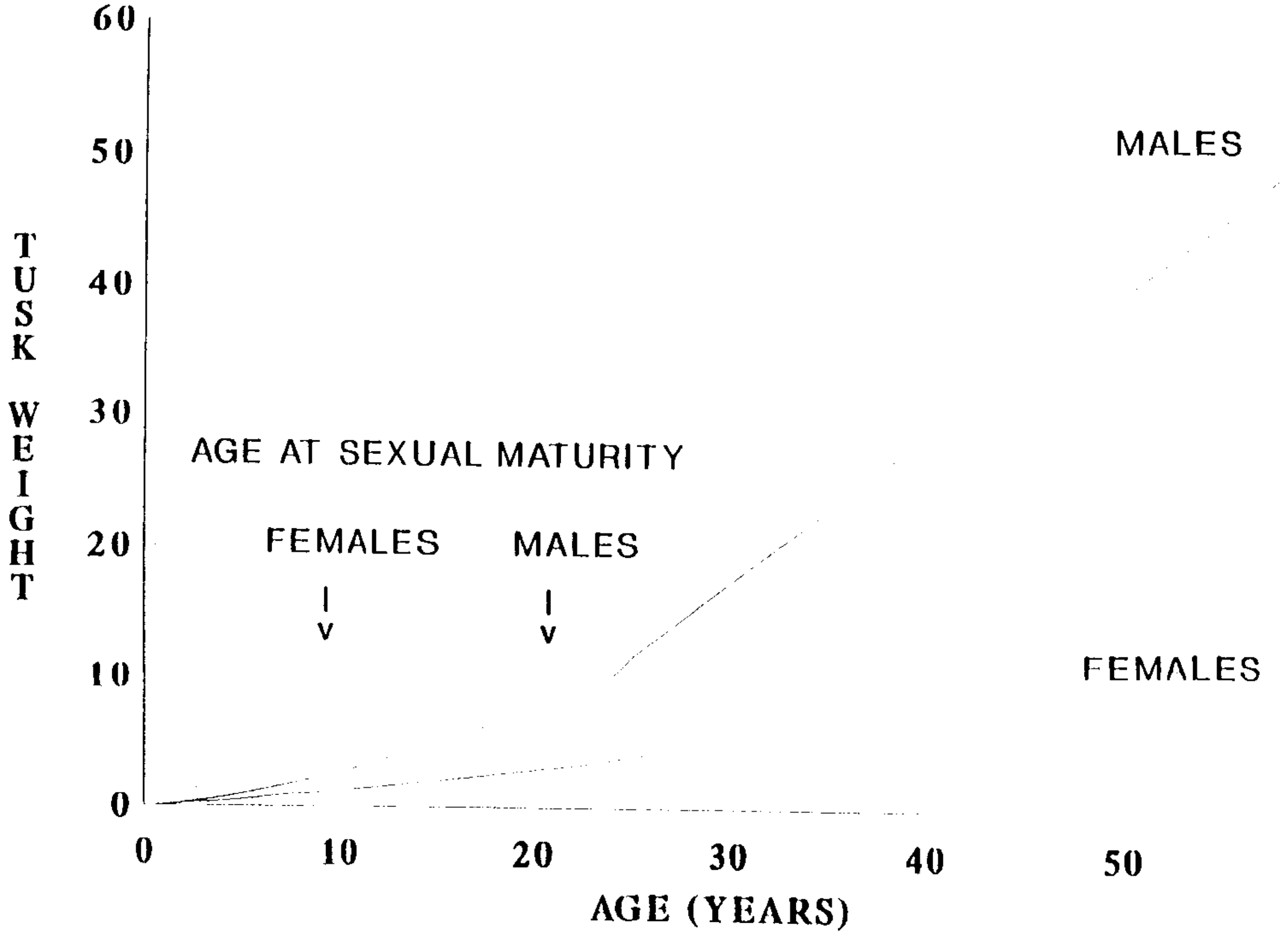
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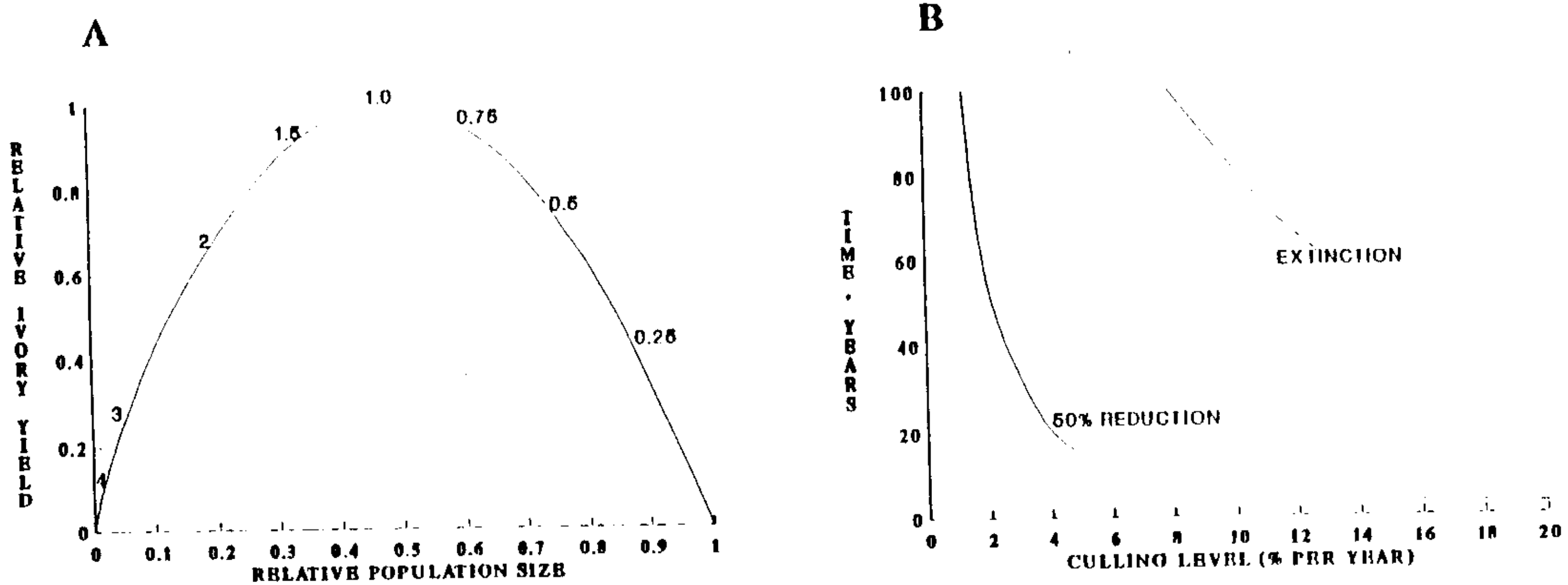
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TIME - YEARS
100
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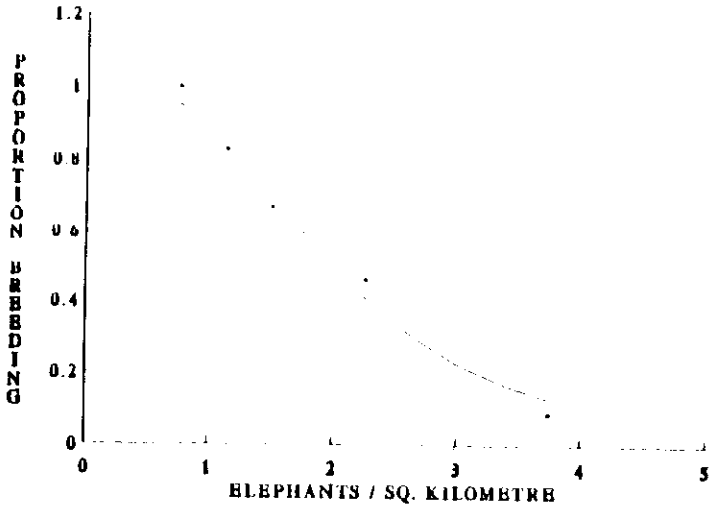
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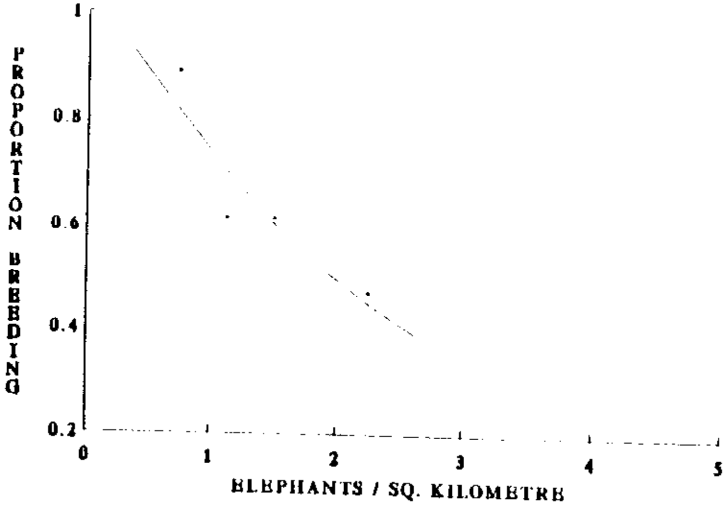
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ELEPHANTS / SQ. KILOMETRE

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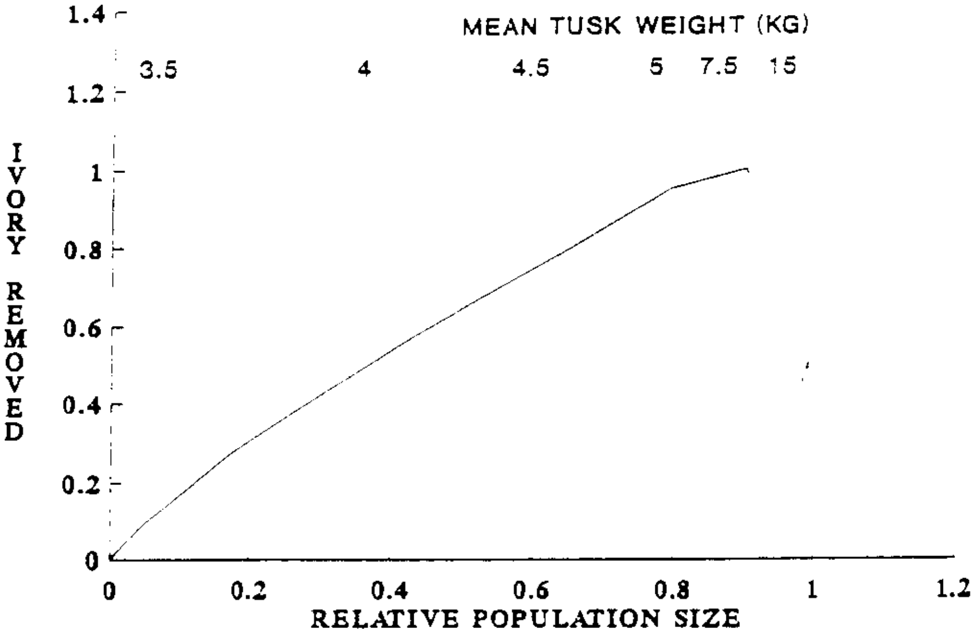
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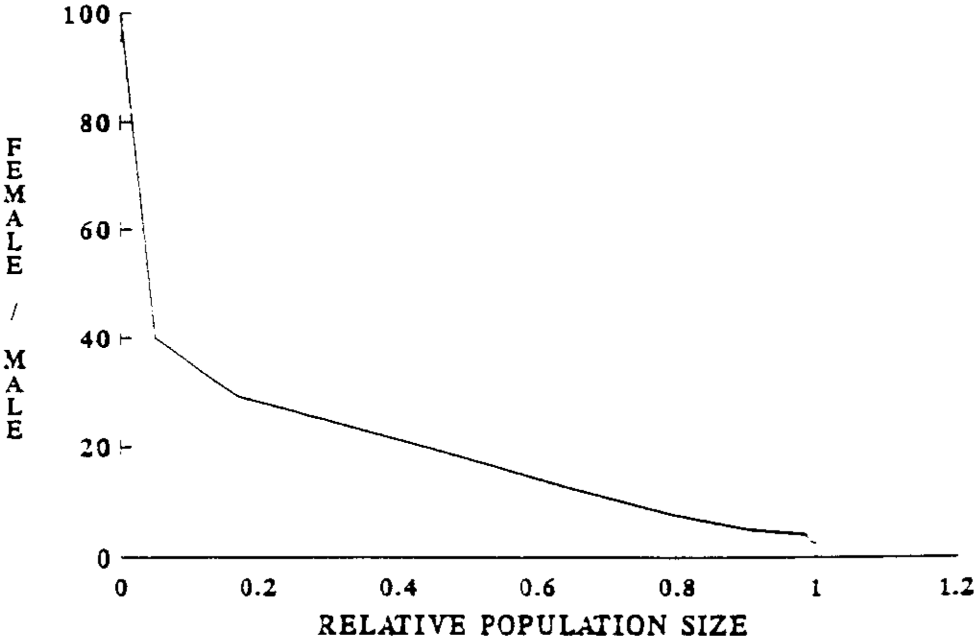
RELATIVE POPULATION SIZE

B.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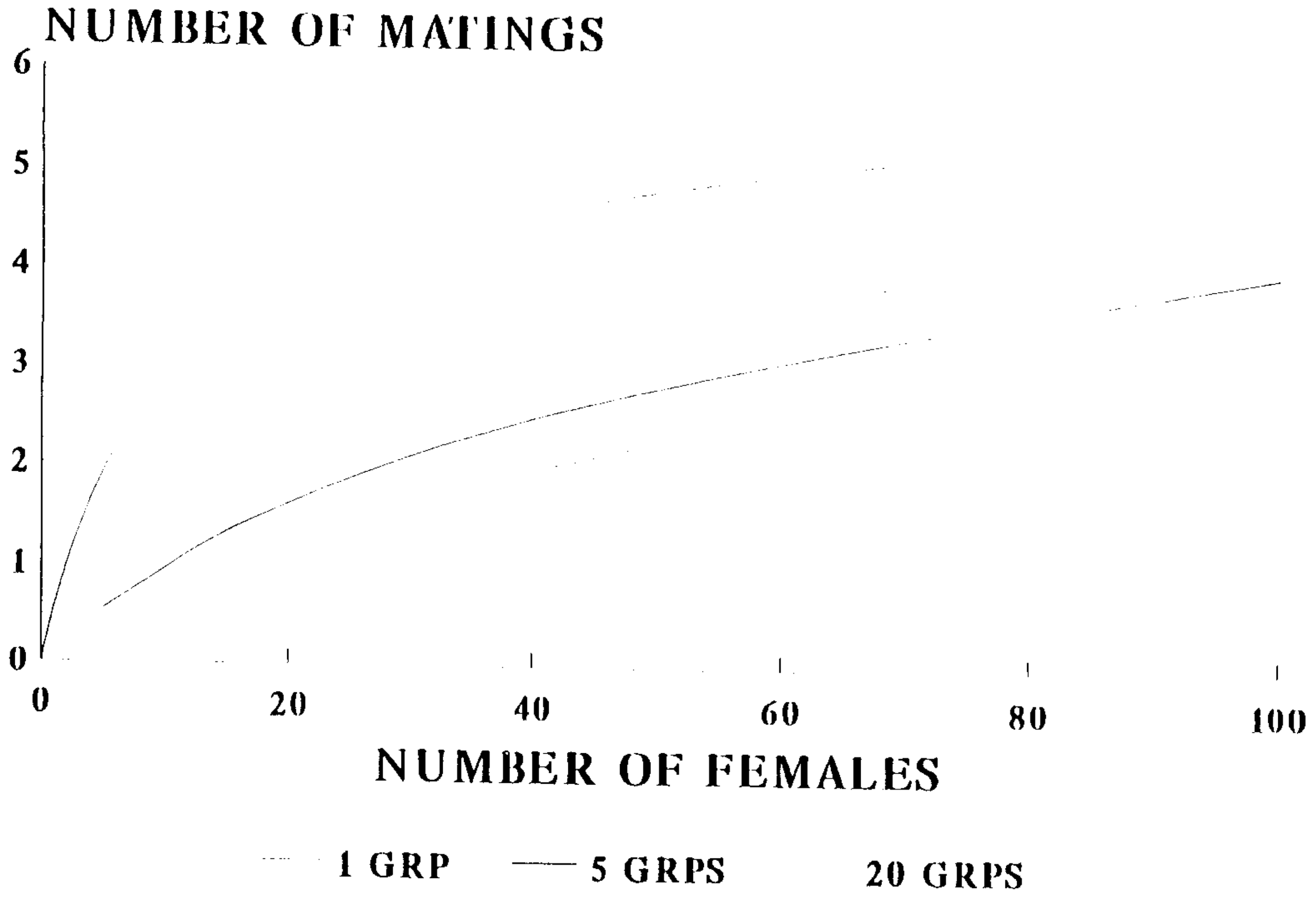
RELATIVE POPULATION SIZE


NUMBER OF MATINGS
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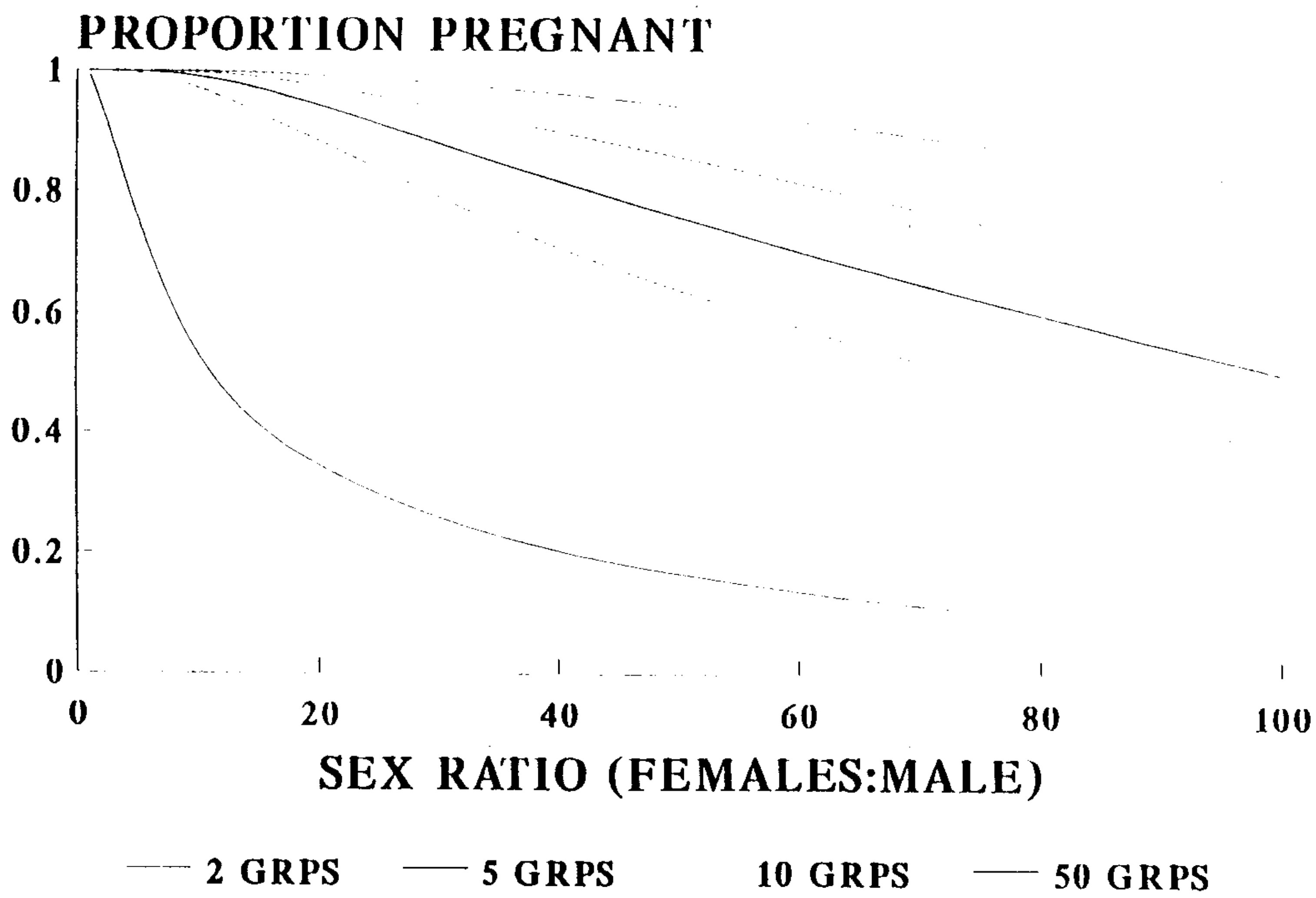
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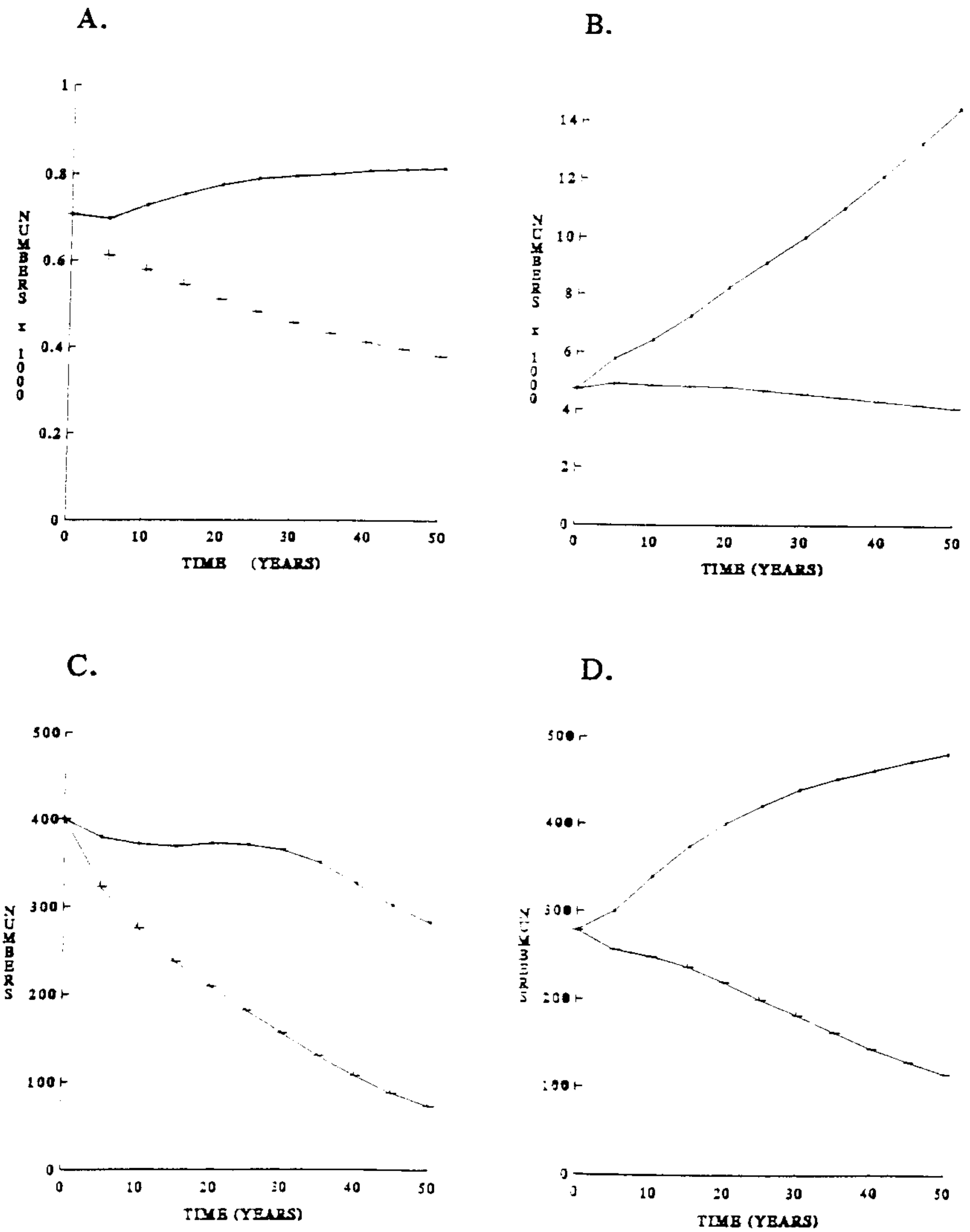
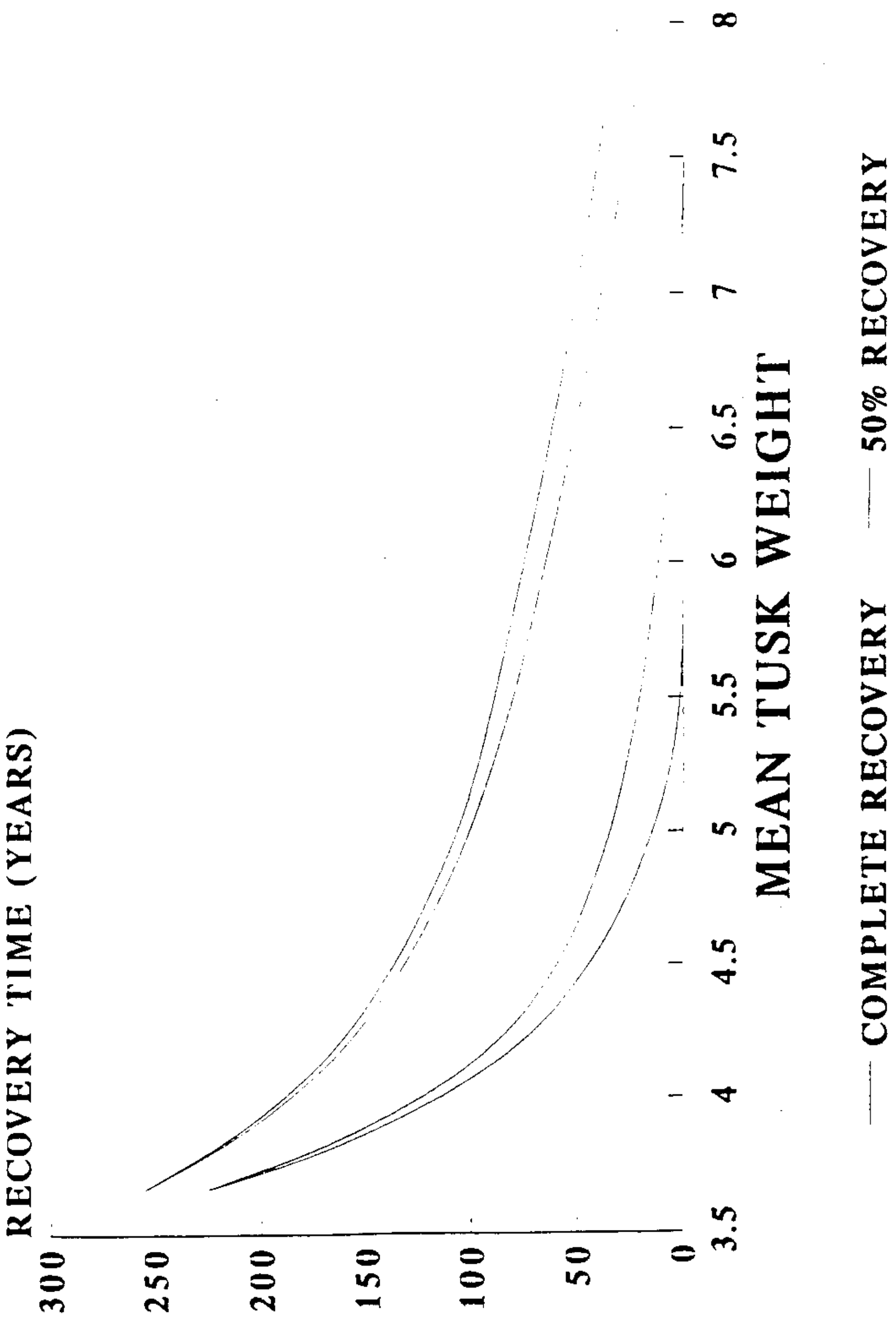
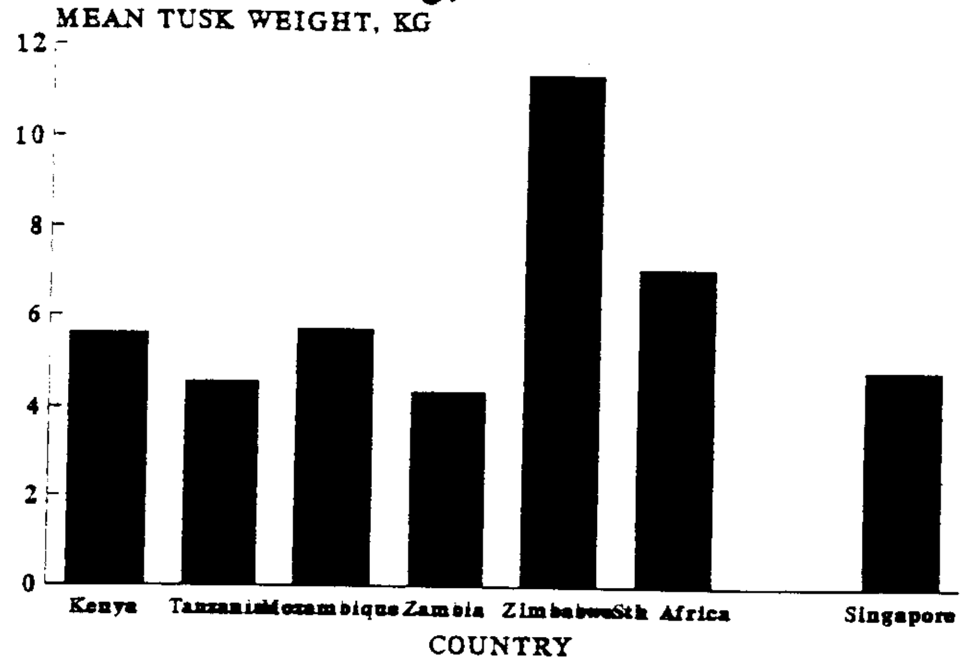
0
20
40
60
80
100
SEX RATIO (FEMALES:MALE)
2 GRPS
5 GRPS
10 GRPS
50 GRPS

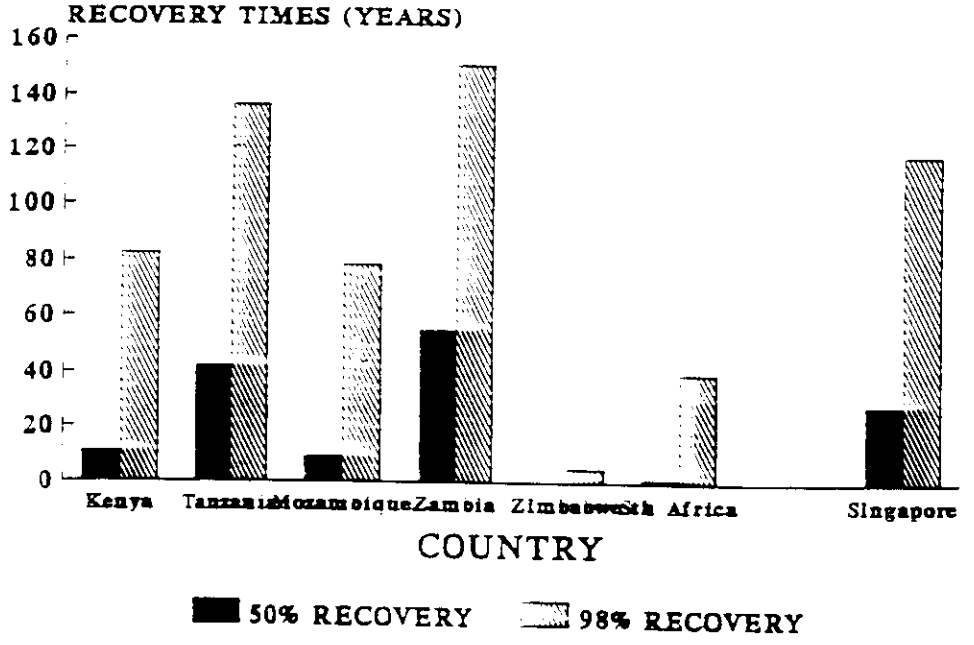

A.
1
0.8
0.6
0.4
0.2
0
NUMBERS x 1000
0
10
20
30
40
50
TIME (YEARS)
B.
14
12
10
8
6
4
2
0
NUMBERS x 1000
0
10
20
30
40
50
TIME (YEARS)
C.
500
400
300
200
100
0
NUMBERS
0
10
20
30
40
50
TIME (YEARS)
D.
500
400
300
200
100
0
NUMBERS
0
10
20
30
40
50
TIME (YEARS)


RECOVERY TIME (YEARS)
300
250
200
150
100
50
0
3.5
4
4.5
5
5.5
6
6.5
7
7.5
8
MEAN TUSK WEIGHT
COMPLETE RECOVERY
50% RECOVERY

A


MEAN TUSK WEIGHT, KG
12
10
8
6
4
2
0
Kenya
Tanzania
Mozambique
Zambia
Zimbabwe
Sth Africa
Singapore
COUNTRY

B


RECOVERY TIMES (YEARS)
160
140
120
100
80
60
40
20
0
Kenya
Tanzania
Mozambique
Zambia
Zimbabwe
Sth Africa
Singapore
COUNTRY
50% RECOVERY
98% RECOVERY