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MS received 6 September 1988; revised 17 October 1988

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**Abstract.** Records of captive Asian elephants (*Elephas maximus*) were used to derive parameters of the von Bertalanffy function for growth in height, body weight and circumference of tusks with age. There was some evidence for a post-pubertal secondary growth spurt in both male and female elephants. Domestic elephants which were born in captivity or captured at a young age also showed a reduced growth in height in both the sexes and in body weight in males compared to wild elephants. Aspects of allometric growth such as height-body weight relationship are examined. The height was twice the circumference of front foot throughout the life span, indicating an isometric relationship.

**Keywords.** Asian elephant; *Elephas maximus*; growth; von Bertalanffy function.

## 1. Introduction

Aspects of growth in the Asian elephant *Elephas maximus* (Burne 1943; Rensch and Harde 1955; McKay 1973; Kurt 1974), have not been examined with the same rigour as in the African elephant *Loxodonta africana* (Hanks 1972; Laws *et al* 1975). This is ironical since a lot of data are available for Asian elephants in captivity. The present study was carried out to derive equations for growth in body length (in this case, the height at withers or shoulder height), body weight and tusk circumference at lip line with age, and also examine aspects of allometric growth. These relationships could be profitably used in various ecological studies, which may involve ageing wild elephants or estimating biomass of the population.

## 2. Methods

Hanks (1972) and Laws *et al* (1975) derived growth equations based on von Bertalanffy functions (von Bertalanffy 1938; Beverton and Holt 1957) for the African elephant. Their data base came from large samples of culled elephants, which were aged from their dentition (Laws 1966) and various body measurements. These studies were cross-sectional; that is, for each elephant the height or weight was known at only one instant in time. On the other hand, we collected data on elephants born in captivity or captured from the wild, which were kept for varying periods of time and measurements, particularly of shoulder height, taken every year. For some elephants records of growth were available for 40–50 successive years. All the elephants were captured in southern India and maintained by Forest Departments under semi-natural condition (in all cases inside the forest habitat itself, as opposed to those kept in temples in the towns). Records of nearly all elephants born in captivity (n = 165) or captured (n = 525) in the Madras Presidency and Tamil Nadu state during 1926–1984 were obtained. Some records (n = 74) also pertained to those captured during 1885–1925. Information on elephants born in captivity ($n=24$) or captured ($n=146$) in the Karnataka state was also obtained.

Most of the records pertain to only the shoulder height of elephants; much less information was available on circumference of front foot. Data on body weights have been recorded only in domestic elephants kept in the Mudumalai Sanctuary, where they have been weighed on a heavy-duty weighbridge from 1973 onwards. Practically no data were available on tusk growth. In Mudumalai Sanctuary 20–25 elephants were measured during 4 successive years (1981–1984). A number of elephant camps in Karnataka were visited during 1983 and measurements on 40 elephants were recorded. Measurement of tusks were also included in addition to height and circumference of front foot.

### 2.1 *Selection of elephants for use in the analysis*

For elephants born in captivity the available data could be used without any problem if their dates of birth were known. Captured elephants had to be aged as accurately as possible before the data could be included. We selected elephants for use in the analysis by the following procedure.

(i) Using the data on elephants born in captivity, von Bertalanffy growth equations were generated seperately for males and females aged 0–15 years. Since most of the elephants born in captivity were sold at an early age, the records were available for a sufficient number of them only up to age 15 years.

(ii) Of the elephants captured, only those kept in captivity for 5 or more years were selected. From this list, male elephants measuring below 205 cm (age 8 years) and female elephants below 198 cm (age 10 years) at the time of capture were reassigned ages based on the von Bertalanffy equations derived for elephants born in captivity. This reassignment was necessary since the age fixed at capture by the attending veterinarian would have been subjective. We noticed a distinct tendency to overestimate the age at capture. Records of elephants above these heights were eliminated since accurate ageing was not possible.

(iii) The data from elephants born in captivity and those reassigned ages were pooled together for further analysis on growth in height. Any slight inaccuracy in ageing captured elephants was unlikely to influence the final results since data on growth were included for at least 5 years (records for many of them were available for over 40 years). This was confirmed by a check later.

(iv) In addition, the heights of many wild adult elephants, which could be expected to have attained their maximum height, were determined by a photographic method described elsewhere (Douglas-Hamilton 1972; Jachmann 1980; Sukumar 1985).

### 2.2 *von Bertalanffy functions*

The functions derived by von Bertalanffy (1938) have been found suitable for studies on growth phenomena in vertebrates including fishes (Beverton and Holt 1957) and elephants (Hanks 1972; Laws *et al* 1975). The general form of the equation used is

$$S_t = S_\infty \{1-\exp[-K(t-t_0)]\}^M,$$

where $S_t$ = size (height, weight, etc.) at age $t$; $S_\infty$ = asymptotic size; $K$ = coefficient of catabolism, a fitted constant; $t$ = age of animal (years); $t_0$ = theoretical age at which the animal would have zero size (this constant is usually artificial) and $M$ = power of the function.

For growth in body weight the cubic form of the above equation can be used:

$$W_t = W_\infty \{1 - \exp[-K(t - t_0)]\}^3.$$

For growth in body length or height the equation used is:

$$L_t = L_\infty \{1 - \exp[-K(t - t_0)]\}.$$

### 2.3 *Computer analysis*

The parameters $S_\infty$, $K$ and $t_0$ of the von Bertalanffy function were determined using the non-linear least square method by an iterative procedure. For a set of starting values of these parameters, the sum of the squares of deviation between expected and observed size was computed, and also the derivative of this quantity with respect to $S_\infty$, $K$ and $t_0$. The Fletcher-Powel algorithm was used to modify the values of $S_\infty$, $K$ and $t_0$ at each stage, such that the sum of squares of deviates was minimized. The subroutine FMFP of the Scientific Subroutine Package developed by IBM was used for this purpose on a DEC 1090 computer at the Indian Institute of Science. The sensitivity of the method was tested by using different sets of initial values. It was seen that they all converged to the same final values of the parameters. A further check was carried out by the conjugate gradient method of minimization (subroutine FMCG of IBM SSP routine) which also yielded very similar results.

## 3. Results and Discussion

The results of all the growth equations presented here are based on the data set combining elephants born in captivity and those captured from the wild.

### 3.1 *Growth in height*

3.1.1 *Male elephants*: For male elephants the equation derived for age 0–15 years (507 measurements of 118 elephants) was

$$H_t = 236\{1 - \exp[-0{\cdot}182(t + 2{\cdot}82)]\}\ \text{cm}.$$

This gave a good fit to the data up to 15 years. But the observed heights of adult bulls above 15 years are much greater than the heights predicted by this equation. This suggests that a secondary growth spurt associated with puberty occurs in bulls, similar to that observed in African elephants by the same procedure (Laws *et al* 1975). Hanks (1972), however, did not find any evidence for a secondary growth spurt in the African elephant.

Another set of parameters was derived for bulls aged 15–60 years (321 measurements, 34 elephants), which gave a good fit for this age range

$$H_t = 259\{1 - \exp[-0{\cdot}124(t + 2{\cdot}84)]\}\ \text{cm}.$$

A third equation was derived for bulls using the combined data for 0–60 years (816 measurements, 119 elephants), which gave a good fit only above 3 years (figure 1)

$$H_t = 256\{1 - \exp[-0{\cdot}133(t + 3{\cdot}58)]\}.$$

3.1.2 *Female elephants*: The equation fitted to data for age 0–15 years (376 measurements, 90 elephants) was

$$H_t = 215\{1 - \exp[-0{\cdot}193(t + 3{\cdot}02)]\}\ \text{cm}.$$

Once again the asymptotic height of 215 cm is much lower than the average maximum height attained by captive elephants. This suggests a secondary growth spurt in female Asian elephants. Laws *et al* (1975) did not observe such a growth spurt in female African elephants. This phenomenon has to be examined in more detail. Anyhow, a second equation was fitted for females aged 15–70 years (330

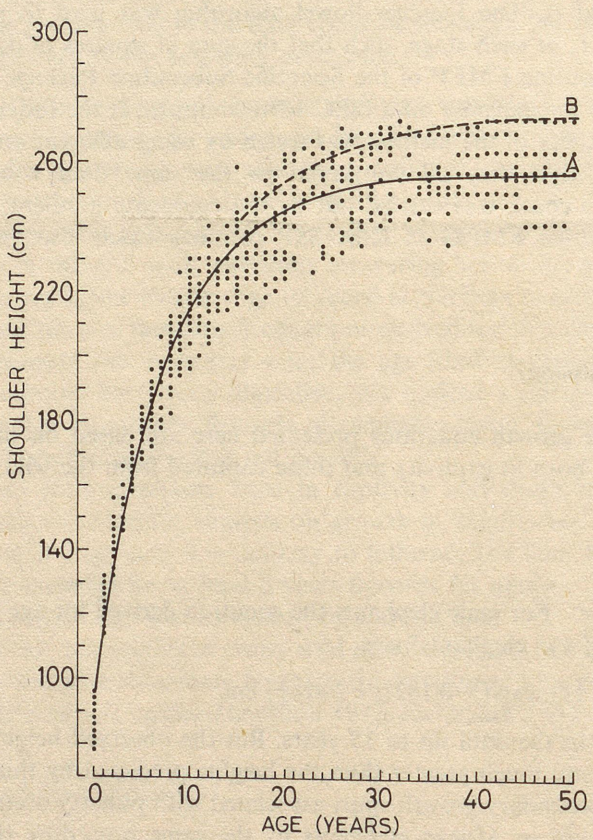

**Figure 1.** Growth in height in male elephants.
Plot of shoulder height (cm) against age (years). 816 measurements of 119 elephants, rounded off to the nearest 2 cm and 1 year. Data are given only up to 50 years for brevity.
**A.** Fitted von Bertalanffy equation (0–60 years) is $H_t = 256\{1 - \exp[-0{\cdot}133(t + 3{\cdot}58)]\}$ cm.
**B.** Presumed growth in wild bulls drawn by eye taking the higher asymptote of 274 cm (details in text).

measurements, 27 elephants), which gave a good fit for this age range

$$H_t = 232\,\{1 - \exp[-0{\cdot}266(t - 6{\cdot}13)]\}\ \text{cm}.$$

A third equation was derived for cows combining the data for 0–70 years (696 measurements, 93 elephants), which gave a good fit only above 3 years (figure 2)

$$H_t = 232\,\{1 - \exp[-0{\cdot}140(t + 3{\cdot}85)]\}$$

3.1.3 *Check on accuracy of ageing captured elephants*: To check the extent to which any slight inaccuracies in ageing captured elephants would influence the results, the following check was made. The parameters of the von Bertalanffy equation were derived for two modified sets of data, one in which the age at capture was uniformly increased by 2 years and the other in which it was lowered by 2 years for all elephants. The resulting values of the parameters could be hardly distinguished from the earlier values. Since a systematic error of over 2 years in ageing young captured elephants is highly unlikely, we conclude that the procedure adopted in ageing captive elephants was robust and hence acceptable.

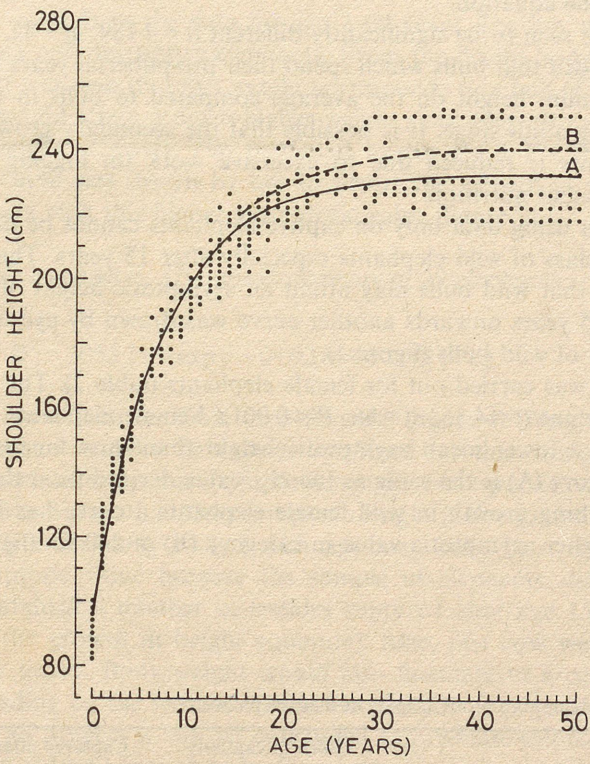

**Figure 2.** Growth in height in female elephants.
Plot of shoulder height (cm) against age (years). 696 measurements of 93 elephants, rounded off to the nearest 2 cm and 1 year. Data are given only up to 50 years for brevity.

**A.** Fitted von Bertalanffy equation (0–60 years) is $H_t = 232\,\{1 - \exp[-0{\cdot}140(t + 3{\cdot}85)]\}$ cm.

**B.** Presumed growth in wild cows drawn by eye taking the higher asymptote of 240 cm (details in text).

3.1.4 *Differences in growth rates of captive and wild elephants*: If these growth equations were to be used for ageing wild elephants it had to be confirmed that captive and wild elephants did not differ in their rates of growth. There were, in fact, reasons to believe that elephants in captivity were stunted in height compared to wild elephants. We carried out the following test to resolve this issue. The asymptotic heights of both males and female elephants were considered under these categories:

(A) Elephants born in captivity and those captured below age 10 years.

(B) Elephants which were above age 15 years when captured and wild adult elephants whose heights were estimated.

For captive elephants the criterion for determining asymptotic height was that they should have shown no increment in height for at least 4 successive years. Only such elephants were included in the analysis. The mean asymptotic heights grouped into two categories for male elephants are given in table 1.

An interesting observation is that the mean asymptotic height in category (A) is the same as the computer-fitted asymptotic height for bulls aged 15–60 years. This is not surprising since only bulls born in captivity or captured below age 8 years were used in fitting the equation.

The two means are seen to be significantly different ($t=4{\cdot}189$, $df=42$, $P<0{\cdot}001$). It can thus be concluded that bulls which spend their pre-pubertal years in captivity attain a lower maximum height on the average compared to bulls in the wild or those captured during adult stage. It is possible that the secondary growth spurt in such captive elephants is reduced due to excessive work (in logging and other activities) and insufficient nutrition.

The fitted equation using data only on captive elephants cannot be directly used to estimate the age class of wild elephants especially after 15 years. The data from category (B) suggest that wild bulls may attain an asymptotic height of 274 cm on the average. From 15 years onwards another curve was drawn by eye which could represent the growth of wild bulls (figure 1).

A similar exercise was carried out for female elephants (table 2). The two means are significantly different ($t=4{\cdot}36$, $df=86$, $P<0{\cdot}001$). Female elephants growing in captivity also attain a lower mean asymptotic height than those in the wild. The mean height in category (A) is the same as the $H_\infty$ value derived from the computer fit. For use in describing growth in wild female elephants a curve has been drawn by eye taking the higher asymptotic value in category (B) of 240 cm (figure 2).

**Table 1.** Mean asymptotic heights of male elephants.

| | Born in captivity or captured below age 10 years (A) | Captured after age 15 years or photographed in the wild (B) |
|---|---|---|
| Mean asymptotic height (cm) | 258·2 | 273·7 |
| Standard deviation | 10·60 | 13·95 |
| Sample size (n) | 26 | 18 |

**Table 2.** Mean asymptotic heights of female elephants.

| | Born in captivity or captured below age 10 years (A) | Captured after age 15 years or photographed in the wild (B) |
|---|---|---|
| Mean asymptotic height (cm) | 231·4 | 239·5 |
| Standard deviation | 9·83 | 6·40 |
| Sample size (n) | 20 | 68 |

### 3.2 *Growth in body weight*

The computer-fitted parameters of the von Bertalanffy equation for growth in body weight with age in captive elephants are as follows.

3.2.1 *Male elephants*: (130 measurements of 22 elephants in the age range 0–60 years)

$$W_t = 3255\,\{1 - \exp[-0{\cdot}149\,(t + 3{\cdot}16)]\}^3 \text{ kg.}$$

This gave a good fit to the data for age 2–60 years. The low asymptotic weight of 3255 kg refers only to captive elephants. From the height-body weight relationship (see below) it was seen that this weight corresponds to a bull of 258 cm height. Bulls in the wild would attain a much higher weight since they also attain a higher mean maximum height (274 cm). The predicted weight for a 274 cm tall bull is about 4000 kg. A curve was drawn by eye to depict the growth in weight of wild bulls above 15 years with this higher asymptotic value (figure 3).

3.2.2 *Female elephants*: (100 measurements of 29 elephants in the age range 0–70 years)

$$W_t = 3055\,\{1 - \exp[-0{\cdot}092\,(t + 6{\cdot}15)]\}^3 \text{ kg.}$$

This gave a good fit to the data for 2–70 years (figure 4). Weights of both pregnant and non-pregnant females have been combined for this fitting. From the height-body weight relationship this asymptotic weight corresponds to a female of 247 cm height, which is higher than the asymptotic height (240 cm) attained by these in the wild. The curve for body weight with age may have been influenced towards a higher asymptotic value because the sample of elephants used for deriving the equation contained a number of females captured after age 15 years (which were omitted for the growth in height equation). Also, one cow weighing 3750 kg was exceptionally heavy. Body weight would also fluctuate to a certain extent (unlike height) depending on the season, on whether the cow is pregnant or not and so on. Considering all aspects it can be concluded that female elephants in captivity do not show any reduced growth in body weight.

### 3.3 *Tusk growth in bulls*

The length of exposed tusks in a male elephant may be a poor indicator of age partly due to the high variation in degree of wear, but the circumference of the tusk

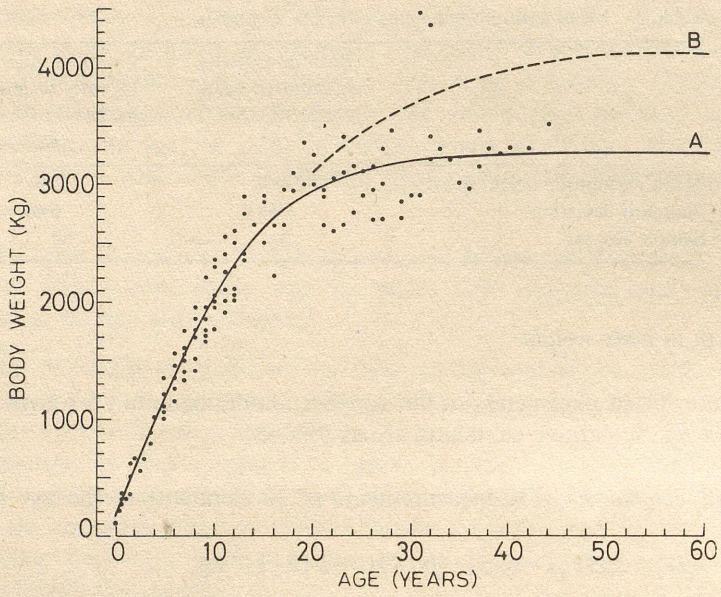

**Figure 3.** Growth in body weight in male elephants.

Plot of body weight (kg) against age (years). 130 measurements of 22 elephants, rounded off to the nearest 50 kg (for those above age 2) and 1 year.

**A.** Fitted von Bertalanffy equation is $W_t = 3255\,\{1-\exp[-0{\cdot}149\,(t+3{\cdot}16)]\}^3$ kg.

**B.** Presumed growth in wild bulls drawn by eye taking a higher asymptote of 4000 kg.

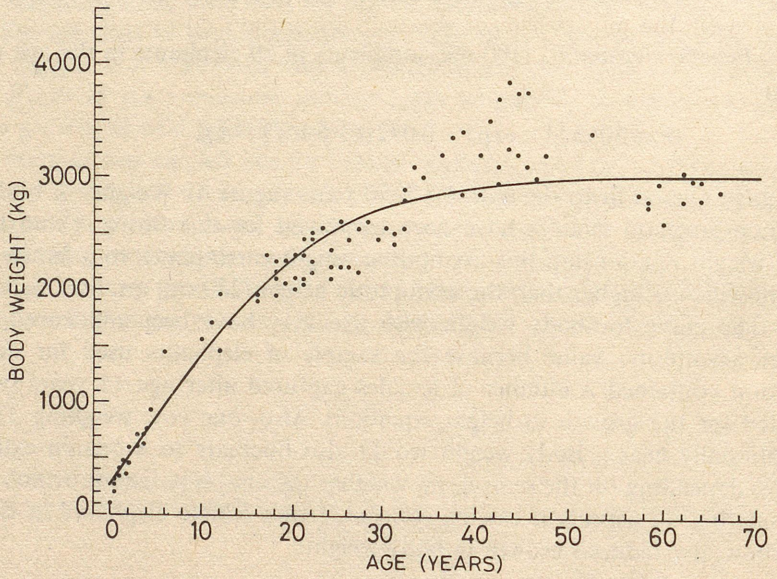

**Figure 4.** Growth in body weight in female elephants.

Plot of body weight (kg) against age (years). 100 measurements of 29 elephants, rounded off to the nearest 50 kg (for those above age 2) and 1 year.

Fitted von Bertalanffy equation is

$$W_t = 3055\,\{1-\exp[-0{\cdot}092\,(t+6{\cdot}15)]\}^3 \text{ kg.}$$

at lip line (CTLL) is not affected (Hanks 1972). We examined the records (and some tusks) of 247 pairs of tusks obtained from wild bulls and also measured tusk size in 30 captive bulls which could be aged reasonably accurately. Although the sample sizes are small it was seen that the maximum CTLL (below 40 cm) in captive bulls was much lower than that attained in the wild (48 cm). After fitting von Bertalanffy equations for various age ranges it was found that the equation for age 2–25 years gave a good fit for captive bulls in this age range and could also be extrapolated for wild bulls above this age. The parameter $t_0$ was set to zero since no measurable tusks are seen at birth. The derived equation for CTLL with age is

$$\mathrm{CTLL}_t = 43{\cdot}4\,\{1 - \exp[-0{\cdot}064\ t]\}\ \mathrm{cm}.$$

From 211 pairs of tusks the CTLL and the weight were obtained. Since there is a distinct tendency in elephants to wear out one tusk faster than another, we took the weight of only the intact tusk in each pair. The cube-root of tusk weight when plotted against CTLL gave a linear relationship and a regression was fitted

$$\sqrt[3]{\text{tusk weight}} = (0{\cdot}0715 \times \mathrm{CTLL}) - 0{\cdot}0888\ \mathrm{kg}$$

$$\text{i.e. tusk weight} = \{(0{\cdot}0715 \times \mathrm{CTLL}) - 0{\cdot}0888\}^3\ \mathrm{kg}.$$

Using the tusk circumference–tusk weight relationship and the von Bertalanffy equation for growth in tusk circumference with age, a curve was drawn to describe the growth in tusk weight with age (figure 5). The result was a sigmoid growth in weight curve, which is exponential during 0–10 years, linear during 10–30 years and later shows a declining rate. In contrast, Laws (1966) described an exponential growth rate in tusk weight throughout the life-span of male African elephants. He has not given any basis for how an exponential increase in tusk weight could be sustained by the metabolism of an elephant during old age. It is more logical to believe that growth rate of tusks would decrease as of any other organ due to increased catabolism.

### 3.4 *Height-weight relationship*

Hanks (1972) showed that in African elephants above 30 years of age the height increases much less than weight (allometric growth). He suggested that the relationship between these two body measurements would be best expressed by a semilog plot, log body weight on shoulder height. We found that a linear regression of cube root of body weight on shoulder height gave a better fit than the semilog plot. The height-weight relationship derived for both male and female elephants were very similar.

Male elephants (130 height-weight measurements from 22 elephants)

$$\sqrt[3]{\text{weight}} = (0{\cdot}057\ \text{height in cm}) + 0{\cdot}114\ \mathrm{kg}$$

$$\text{i.e. weight} = \{(0{\cdot}057\ \text{height in cm}) + 0{\cdot}114\}^3\ \mathrm{kg}.$$

Female elephants (100 height-weight measurements from 29 elephants)

$$\sqrt[3]{\text{weight}} = (0{\cdot}060\ \text{height in cm}) - 0{\cdot}335\ \mathrm{kg}$$

$$\text{i.e. weight} = \{(0{\cdot}060\ \text{height in cm}) - 0{\cdot}335\}^3\ \mathrm{kg}.$$

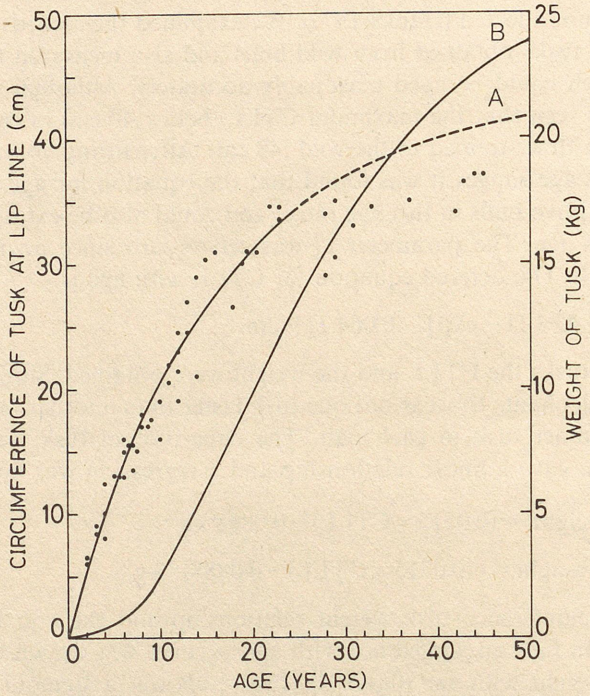

**Figure 5.** Tusk growth in male elephants.
Plot of circumference of tusk at lip line (CTLL in cm) against age.
**A.** Fitted von Bertalanffy equation for growth in CTLL using data for 2–25 years. $\mathrm{CTLL}_t = 43{\cdot}4\,\{1 - \exp[-0{\cdot}064t]\}$ cm.
**B.** Growth in tusk weight (kg), based on the relationship between CTLL and tusk weight (see text for details).

### 3.5 *Height-circumference of front foot relationship*

It has been the standard practice in Asia to take the height of an elephant as twice the circumference of front foot (CFF) measured at the sole. To see whether this relationship holds good over the entire lifespan of the animal, the height/CFF ratios were plotted against the CFF and a linear regression fitted. There was practically no difference between male and female elephants and therefore the equation for the combined data is given below (353 height-CFF measurements from 111 elephants).

$$\frac{\text{Height}}{\text{CFF}} = 2{\cdot}03 - (0{\cdot}0004)\ \text{CFF}.$$

This is the same as saying that

$$\text{Height} = 2{\cdot}03\ \text{CFF}.$$

For practical purposes twice the CFF can be taken as the height, which confirms the traditional estimate although the range of height/CFF ratio went from 1·74

2·18. The slope of the regression is also practically zero, strongly suggesting that the relationship is isometric, that is, the shoulder height and CFF increase at the same rate throughout the lifespan of the animal. The CFF provides another criterion by which to estimate the age of an elephant.

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# volution of polyandry by reduction in progeny number variance in tructured populations

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MS received 11 November 1988

**Abstract.** When there is a variation in the quality of males in a population, multiple mating can lead to an increase in the genetic fitness of a female by reducing the variance of the progeny number. The extent of selective advantage obtainable by this process is investigated for a population subdivided into structured demes. It is seen that for a wide range of model parameters (deme size, distribution of male quality, local resource level),

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# Evolution of polyandry by reduction in progeny number variance in structured populations

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**Abstract.** When there is a variation in the quality of males in a population, multiple mating can lead to an increase in the genetic fitness of a female by reducing the variance of the progeny number. The extent of selective advantage obtainable by this process is investigated for a population subdivided into structured demes. It is seen that for a wide range of model parameters (deme size, distribution of male quality, local resource level), multiple mating leads to a considerable increase in the fitness. Frequency-dependent selection or a stable coexistence between polyandry and monandry can also result when the possible costs involved in multiple mating are taken into account.

**Keywords.** Evolution of polyandry; multiple mating; structured demes; variance reduction; sexual selection.

## 1. Introduction

Identification of factors which confer selective advantage upon a polyandrous female over a monandrous one has been the object of many investigations (Parker 1970; Cole 1983; Smith 1984; Crozier and Page 1985). The most obvious consequence of polyandry is an increase in the genetic diversity of the progeny, and this by itself has been believed to be selectively advantageous, e.g. in variable environments (Williams 1975), due to increased disease resistance (Sherman *et al* 1988), etc. If there is some variability in the quality of males (Parker 1984), then another consequence of multiple mating is a reduction in variance in the quality of the progeny. A more general version of this scenario has recently been investigated by Loman *et al* (1988), where males differ in the survival probability of the progeny fathered by them. This in turn implies a reduction in the variance in clutch size. As Gillespie (1974, 1977) has pointed out, this by itself confers a selective advantage. By means of numerical examples, Loman *et al* (1988) have shown that the polyandrous females would have significant selective advantage, especially in small populations.

This paper describes a generalization of the above model, and also extends it to explore its consequences for a structured population. To estimate the minimal advantage secured by the polyandrous female, the analysis is restricted to a comparison between singly and doubly mated females. Effects of variation in the clutch size, distribution of male quality, spatial aggregation and local resource limitations are explored. It is seen that for a wide range of model parameters, the polyandrous females exhibit higher fitness than the monandrous ones.

## 2. The model

### 2.1 *Population characteristics*

An infinite population with nonoverlapping generations is assumed to be distributed over a number of patches, and consists of two life-history phases. In the colonization phase, inseminated females colonize the habitat patches with $K$ females per patch. The carrying capacity of each patch is denoted by $C$, which is the maximum number of individuals that it can support. Each female lays $N$ eggs (fecundity $= N$) and dies. Only a fraction of them hatch successfully, and the offspring compete amongst themselves such that $C$ (or fewer, depending on the number of survivors) grow to maturity. In the mixing phase, individuals from all the patches join a common mating pool where random mating takes place, and inseminated females start the colonizing phase of the next generation.

### 2.2 *Variability between males*

The males are assumed to differ from each other (in a non-inheritable manner) in the survival probability $S$ of their progeny. The females are assumed to be unable to discern the quality of the males. If a female mates with a male characterized by $S_j$, then the probability of any of her $N$ eggs successfully hatching is $S_j$. The number of eggs hatching successfully follows a binomial distribution with mean $NS_j$.

The proportion of males in the population who are characterized by $S$ is assumed to be described by the beta distribution.

$$f(S) = [1/B(\alpha,\beta)] \cdot S^{(\alpha-1)} . (1-S)^{(\beta-1)}, \tag{1}$$

$$\text{where } B(\alpha,\beta) = \int_0^1 X^{(\alpha-1)} (1-X)^{(\beta-1)} \, \mathrm{d}X,$$

$$\text{mean}(S) = \alpha/(\alpha+\beta), \text{ and } \text{var}(S) = \alpha\beta/[(\alpha+\beta)^2(\alpha+\beta+1)].$$

This family of distributions, characterized by the two parameters $\alpha$ and $\beta$, can take a variety of shapes (figure 1) and thus makes the model widely applicable. If $\mu$ and $\sigma^2$ denote the desired mean and variance of the distribution of $S$, the corresponding values of $\alpha$ and $\beta$ are given by

$$\alpha = (\mu/\sigma^2)\,[\mu(1-\mu) - \sigma^2],$$
$$\beta = [(1-\mu)/\sigma^2]\,[\mu(1-\mu) - \sigma^2].$$

Since the values of $S$ lie between 0 and 1, variance cannot increase indefinitely, and the maximum possible value of the variance for a distribution with mean $\mu$ is $\mu \cdot (1-\mu)$. This property is, in fact, independent of the distribution of $S$.

### 2.3 *Computation of clutch size*

For a female who mates with a single male (of quality characterized by progeny survival probability $S$), the probability that $i$ of the $N$ eggs hatch successfully is given by the binomial distribution

$$P1_s(i) = \{N!/[i!(N-i)!]\}\, S^i (1-S)^{(N-i)}, \tag{2}$$

and the mean is $N.S$. Since the variance of the distribution is given by $NS(1-S)$, the mean square is $NS(1-S) - N^2S^2$. Since the probability that the female mates with such a male is $f(S)$ from (1), the probability that $i$ eggs hatch is obtained by integrating over $S$,

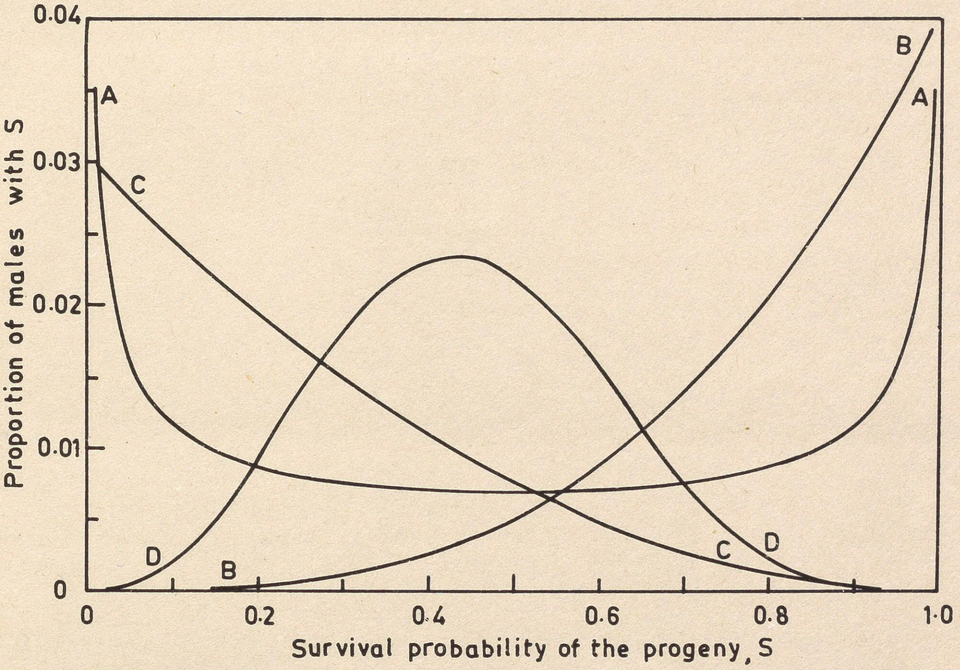

**Figure 1.** The probability density curves corresponding to the distribution of male quality (survival probability of the offspring fathered by the male) characterized by the beta distribution. A – Bimodal distribution, $\alpha = 0{\cdot}50$ and $\beta = 0{\cdot}50$; B – unimodal, mode at 1, $\alpha = 4{\cdot}00$ and $\beta = 1{\cdot}00$; C – unimodal, mode at 0, $\alpha = 1{\cdot}00$ and $\beta = 3{\cdot}00$; D – unimodal, mode at 0·44 $\alpha = 4{\cdot}00$ and $\beta = 5{\cdot}00$.

$$P1(i) = \{N!/[i!(N-i)!]\}\int_0^1 f(S)S^i(1-S)^{(N-i)}$$

$$= \{N!/[i!(N-i)!]\}\,[B(\alpha+i,\beta+N-i)/B(\alpha,\beta)].$$

The mean and variance of the distribution can be similarly calculated as

$$\text{mean} = N\int_0^1 S\cdot f(S)\cdot \mathrm{d}S = N\cdot\mu,$$

$$\text{variance} = \int_0^1 [NS(1-S) + N^2S^2]f(S)\,\mathrm{d}S - N^2\mu^2$$

$$= N\mu(1-\mu) + N(N-1)\sigma^2.$$

For a female who mates with two males characterized by $S_1$ and $S_2$, the number of eggs hatching successfully will be binomially distributed with mean $N(S_1+S_2)/2$, since the sperms are assumed to mix completely. The probability $P2(i)$ of the number of eggs hatching successfully being $i$, as well as the variance, can be obtained from (2). Since the probability of mating with such males is $f(S_1)f(S_2)$, the population average is computed by double integration. Since the males are assumed to be independently chosen, this reduces to a product of single integrals to yield

$$P2(i) = \frac{N!}{i!(N-i)!} \sum_{z=0}^{i} \frac{i!}{z!(i-z)!} \sum_{y=0}^{N-i} \frac{(N-i)!}{y!(N-i-y)!} \times$$
$$\times \frac{B(\alpha+z, \beta+N-i-y)}{B(\alpha,\beta)} \frac{B(\alpha+i-z, \beta+y)}{B(\alpha,\beta)}.$$

The mean number of eggs successfully hatched

$$= N\,[\int_0^1 f(S_1)S_1\,\mathrm{d}S_1 + \int_0^1 f(S_2)S_2\,\mathrm{d}S_2]/2 = N\mu \text{ as earlier.}$$

However, the variance

$$= N\int_0^1\int_0^1 \left(\frac{S_1+S_2}{2}\right)\left(1-\frac{S_1+S_2}{2}\right) + N^2\left(\frac{S_1+S_2}{2}\right)^2 \mathrm{d}S_1\,\mathrm{d}S_2 - N^2\mu^2$$
$$= N\mu(1-\mu) + N(N-1)\sigma^2/2,$$

which is smaller than the variance in the number of eggs hatching successfully for the singly mated female. In fact, it can be shown that the value of this variance for a female mating with $n$ males is given by $N\mu(1-\mu)+N(N-1)\sigma^2/n$. Figure 2 shows

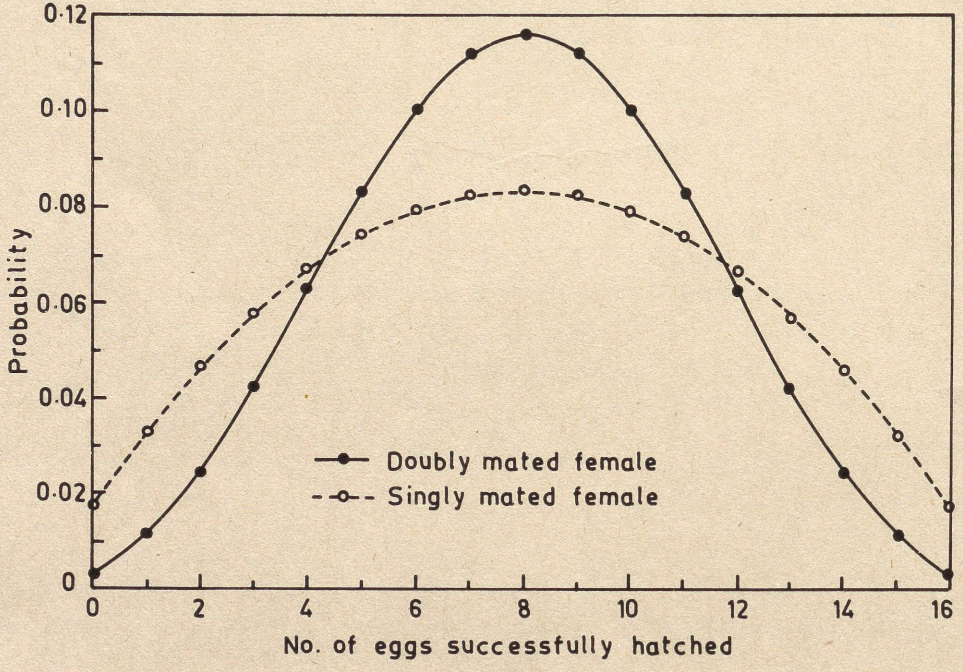

**Figure 2.** The probability density curves for the number of eggs that are successfully hatched by singly and doubly mated females. Note the reduction in the variance for the doubly mated female. $N = 16$, $\mu = 0{\cdot}50$, $\sigma^2 = 0{\cdot}05$.

$P1(i)$ and $P2(i)$ for a typical set of the parameters of the model. A reduction in the variance for a doubly mated female is clearly seen in the figure.

### 2.4 *Computation of fitness*

The trait of monandry or polyandry is assumed to be genetically determined. Considering a population where an allele coding for monandry has gone to fixation, we wish to explore whether an invading rare mutant allele coding for double mating would increase in frequency.

$P1(i)$ and $P2(i)$, respectively, denote the probabilities of monandrous and polyandrous females successfully hatching $i$ eggs. $C$ is the carrying capacity of the patch colonized by the females, i.e. the maximum number of adults emerging from the patch joining the mating pool.

When only one female colonizes a patch, the average contribution to the mating pool from a monandrous female is given by

$$\mathrm{F1} = \sum_{i=0}^{C} P1(i)\cdot i + C \sum_{i=C+1}^{N} P1(i).$$

Similarly, F2 can be computed, and the relative fitness of the polyandrous female is given by F2/F1 and the selective advantage is given by $(\mathrm{F2}/\mathrm{F1}) - 1$.

When two females colonize a site, there are three types of sites: both monandrous, both polyandrous and one of each type. If $i$ and $k$ denote the number of eggs successfully hatched by the two females in a patch, we define

$$\begin{aligned} Ei &= i, \text{ if } i+k \leqslant C, \\ &= Ci/(i+k), \text{ if } i+k > C. \end{aligned}$$

The contributions to the pool from the monandrous females then are

$$\mathrm{F11} = \sum_{i=0}^{N} \sum_{k=0}^{N} P1(i)\,P1(k)\,(Ei + Ek),$$

for the patch with both females monandrous, and

$$\mathrm{F121} = \sum_{i=0}^{N} \sum_{k=0}^{N} P1(i)\,P2(k)\,Ei,$$

for the patch where only one of the females is monandrous.

When a rare mutant for polyandry invades a pure monandrous population, the rate of spread is given by $2(\mathrm{F122}/\mathrm{F11})$ and the selective advantage by $2(\mathrm{F122}/\mathrm{F11}) - 1$. Alternatively, if a rare monandrous mutant invades a pure polyandrous population, its rate of loss is $2(\mathrm{F121}/\mathrm{F22})$. To make this value comparable to the previous one, it is expressed as a reciprocal, i.e. the selective advantage to a polyandrous female is given by $[\mathrm{F22}/(2\,\mathrm{F121})] - 1$.

## 3. Results and discussion

There are five independent parameters in the model: the two parameters $\alpha$ and $\beta$ characterizing the distribution of male quality (alternatively, $\mu$ and $\sigma^2$, the mean and variance of the distribution); the fecundity of the female $N$; the carrying capacity of a patch $C$; and finally, $K$, the number of females colonizing each patch. When $K = 1$, there is no local competition between the two genotypes (specifying monandry and polyandry) whereas for $K > 2$, they compete for resources on the patch. The analysis here is restricted to $K = 1$ and $K = 2$ to cover these two possibilities, since higher values of $K$ are unlikely to lead to qualitatively different outcomes.

### 3.1 *Selective advantage and the distribution of male quality*

As seen from figure 3, the selective advantage for polyandry increases with increasing variance in the male quality. This is as expected, since the larger the initial variance, the larger is the reduction in it due to multiple mating. The values of selection coefficients are also seen to be quite high, indicating a very rapid fixation of this trait in the population.

For constant variance, the selective advantage seems to decrease with increasing mean male quality (survival of the progeny); however, the dependence is in general rather complex (figures 4a, b). This is a consequence of the beta distribution used for characterizing the variability in male quality. For constant variance, as the mean increases, the shape of the distribution changes from bimodal (with the modes at the extremes) to a unimodal one with the mode at 0. As the mean increases further, the mode shifts to a value between 0 and 1 and then to 1. For still higher values of the mean, the distribution again becomes bimodal, with the modes at the extremes. Since the clutch size, and ultimately the fitness, depends on the shape of the

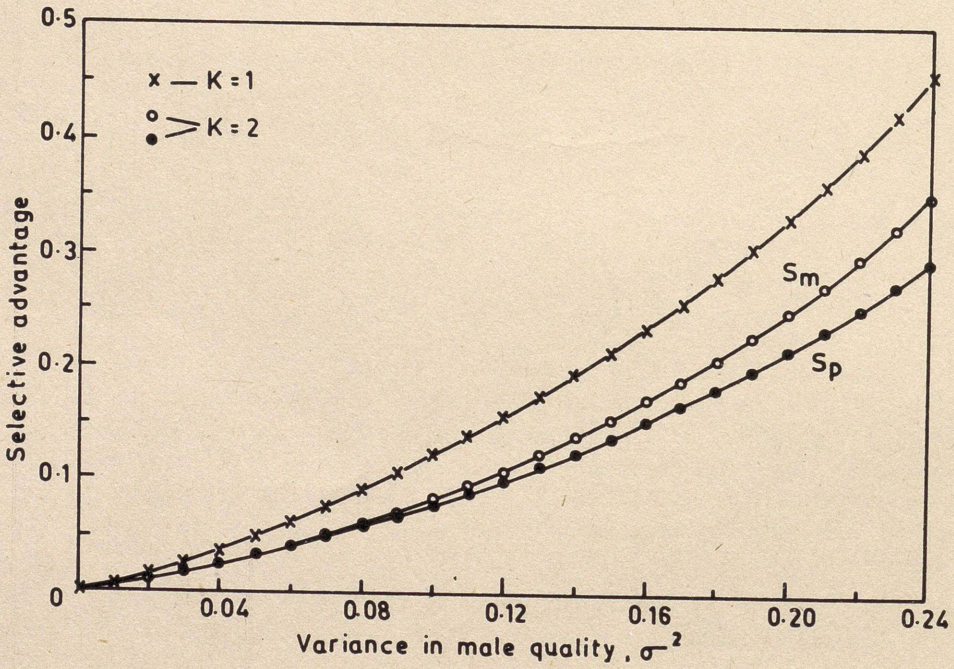

**Figure 3.** Selective advantage for polyandry as a function of the variance in male quality. $N = 16$, $C = 4$, $\mu = 0{\cdot}50$.

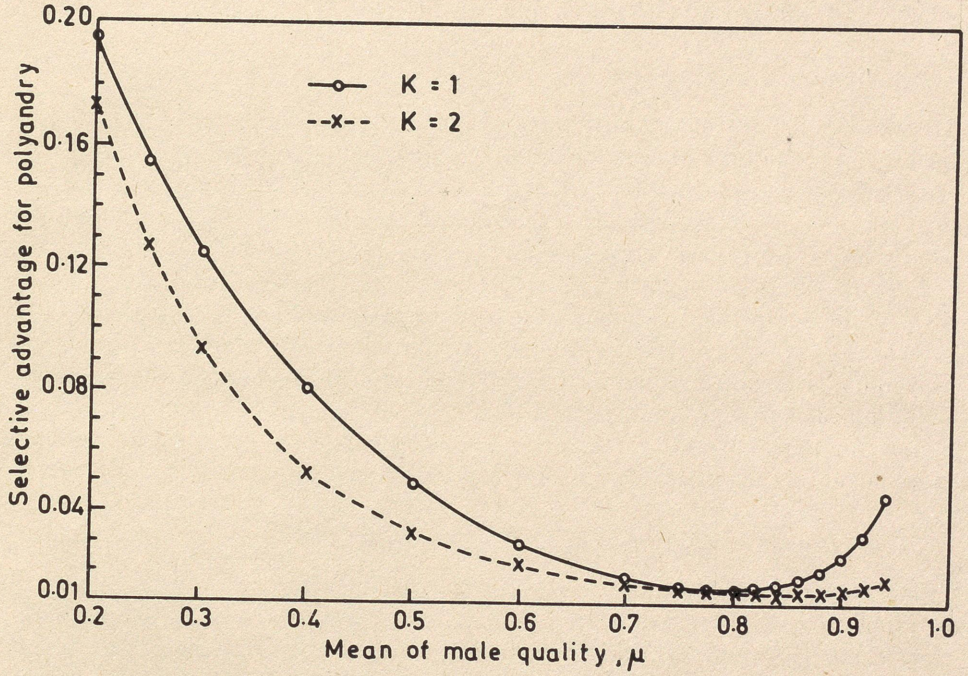

**Figure 4.** Selective advantage for polyandry as a function of the mean of male quality, **(a)** $N = 16$, $C = 4$, $\sigma^2 = 0{\cdot}05$, **(b)** $N = 16$, $C = 12$, $\sigma^2 = 0{\cdot}05$.

distribution, it is not surprising that we observe a complex dependence of the selective advantage on the mean of male quality.

### 3.2 *Selective advantage and fecundity*

The change in the selective advantage of polyandry as a function of fecundity ($N$, the maximum number of eggs that can be laid) is shown in figure 5. The two traits are selectively equivalent when $N.K$ is less than $C$, the local carrying capacity. As $N$ increases, the advantage initially increases and then decreases to a constant value. This is more clearly seen when there are two females per patch.

For low values of $N$, there is less competition for the local resources, while for high $N$, the competition is intense. Figure 5 brings out an interesting aspect of the presence of an optimal level of competition for which the selective advantage for polyandry is maximal. A comparison of the selective advantages for $K=1$ and $K=2$ indicates that at low as well as high values of $N$, a higher selective advantage is seen for polyandry for $K=2$, while for intermediate values of $N$, polyandry is more advantageous when there is only one female per patch.

### 3.3 *Selective advantage and local carrying capacity*

Figure 6 depicts the variation in selective advantage for polyandry with $C$, the carrying capacity of the patch. Here too an initial increase is seen to be followed by a decrease. However, the selective advantage vanishes when $C$ increases beyond $N.K$. When $C$ is greater than $N$ but less than $2N$, polyandry is favoured when there are two females per site but *not favoured when* there *is only one female per site*. This

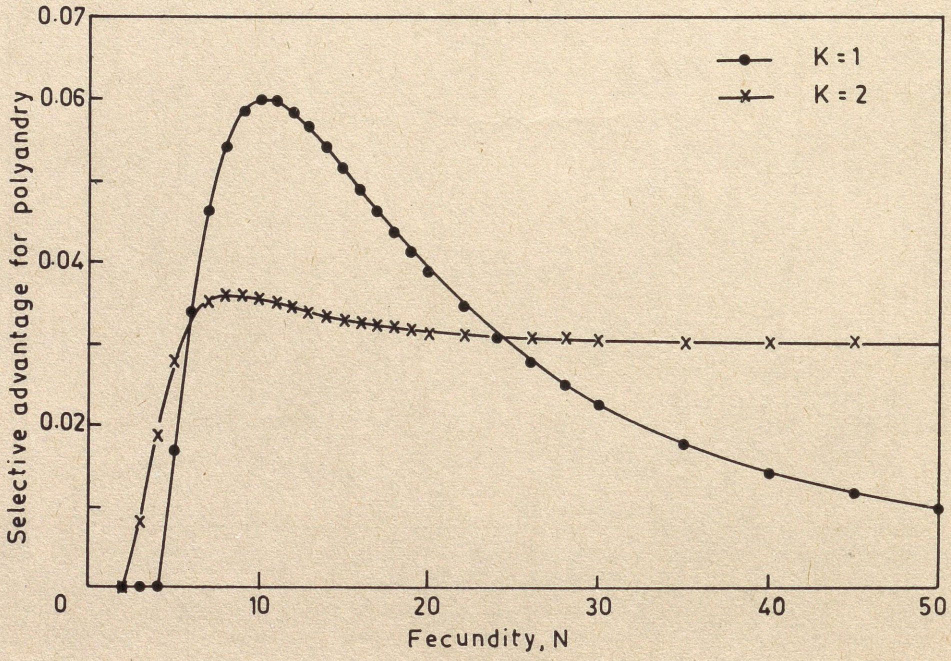

**Figure 5.** Selective advantage for polyandry as a function of fecundity $N$, $N=16$, $\mu=0{\cdot}50$, $\sigma^2=0{\cdot}05$, $C=4$.

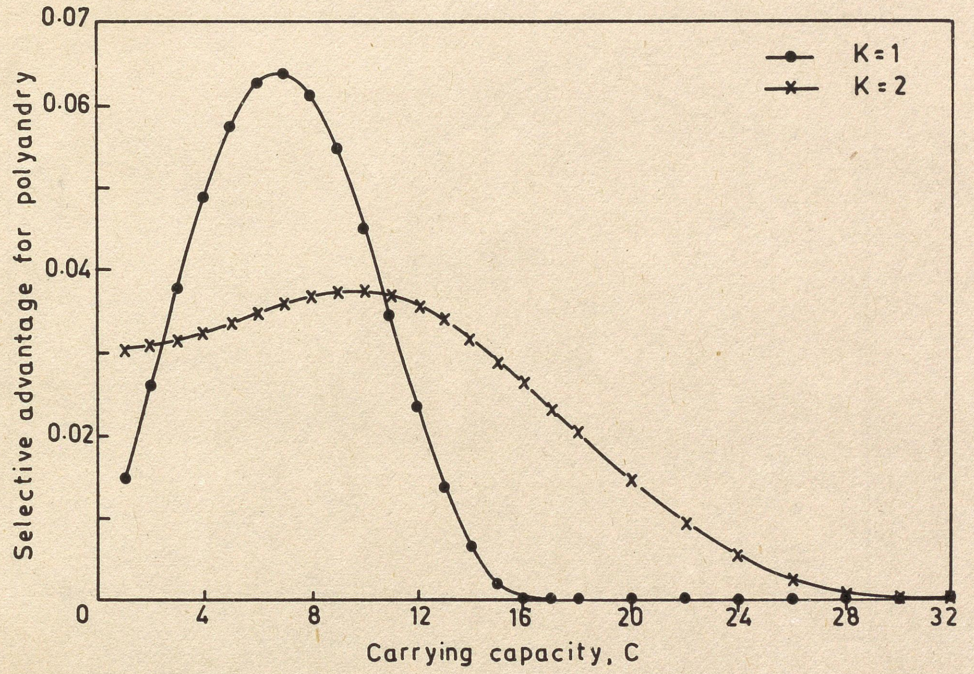

**Figure 6.** Selective advantage for polyandry as a function of the local carrying capacity $C$, $N=16$, $\mu=0{\cdot}50$, $\sigma^2=0{\cdot}05$.

is in contrast with the earlier results (Loman *et al* 1988), where the advantage declined with increasing number of competing females. In fact, if $(K-1)N<C<KN$, polyandry is favoured only when there are $K$ or *more* females per patch.

### 3.4 *Cost of multiple mating and stability analysis*

So far, the polyandrous female was assumed to incur no costs from the additional matings. The cost can be modelled by introducing a cost factor which reduces the fitness of the polyandrous female by a fixed amount $c$. If $S$ is the selective advantage, then polyandry (monandry) is favoured when $S>c\,(S<c)$.

Let $S_m$ denote the selective advantage for polyandry when a pure monandrous population is invaded by a mutant allele specifying the polyandrous trait, and $S_p$ the selective advantage when a pure polyandrous population is invaded by a mutant allele specifying monandry. Then, if the cost $c$ is greater than both of these, monandry is the evolutionarily stable strategy (ESS) and if $c$ is less than both $S_m$ and $S_p$, then polyandry is ESS. When the value of $c$ is intermediate between the two, there are two other possibilities. If $S_m$ is less than $S_p$, then neither of these strategies can invade the other. Else, a stable coexistence between polyandry and monandry is predicted.

Figure 7 shows the variation of $S_m$ and $S_p$ with local carrying capacity when there are two females per patch. Both the cases (i.e. $S_m<S_p$ and $S_m>S_p$) are seen in the figure. Thus, depending on the value of $c$, the cost of multiple mating, a varied range of outcomes is predicted.

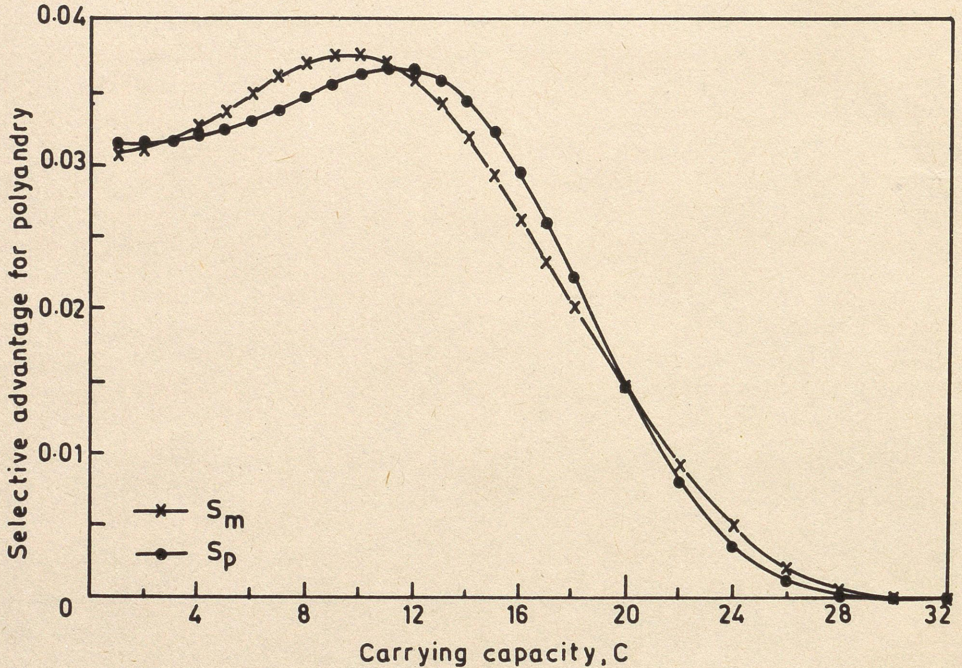

**Figure 7.** The selective advantage for polyandry when the monandrous allele is rare ($S_p$) and when the polyandrous allele is rare ($S_m$).

### 3.5 *Concluding remarks*

The selective advantage of multiple mating for males is much more obvious than that for females, and this was believed to be a major factor responsible for a female having to mate more than once (Smith 1984). In fact, it has been suggested (Halliday and Arnold 1987) that polyandry is a nonadaptive consequence of the genetic correlation between the sexes and the selection favouring multiple mating in males. The advantages from the viewpoint of the female (Knowlton and Greenwell 1984) range from "achieving adequate sperm supply" to "minimizing the loss of time and energy required to resist insistent males" (Drummond 1984). Polyandry can also serve to protect against the possibility of some of the males being functionally impotent, as suggested by Gibson and Jewel (1982). In social hymenoptera, diploid individuals homozygous at certain loci develop into males, and thus there is a reduction in the worker force in the colony (Crozier 1977). Polyandry confers an advantage by reducing the proportion of homozygous individuals (Crozier and Page 1985).

That a reduction in the variance of the progeny number is selectively advantageous was first pointed out by Gillespie (1974). He later obtained the result from very general arguments (Gillespie 1977) and called it a new evolutionary principle. The magnitude of the advantage, however, was inversely proportional to the population size, and hence expected to be small for large populations. Loman *et al* (1988) have given a concrete instance where such a mechanism operates very effectively. They too have emphasized the role of small and founding populations.

The present investigation, on the other hand, considers a large but spatially structured population (structured demes, Wilson 1982), and obtains high selective advantage for multiply mated females under a very general set of conditions. It has also brought out an intriguing aspect, that of an optimal level of local competition which would confer maximum advantage on a polyandrous female as compared to a monandrous one. When the cost of multiple mating is included, the model also brings out the possibility of frequency-dependent selection, or of a stable polymorphism between monandry and polyandry.

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