J. Genet. Vol. 67, No. 3, December 1988, pp. 161–171. © Printed in India.

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

N V JOSHI
Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India

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), 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 α and β, can take a variety of shapes (figure 1) and thus makes the model widely applicable. If μ and σ^2 denote the desired mean and variance of the distribution of S, the corresponding values of α and β 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 μ 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,

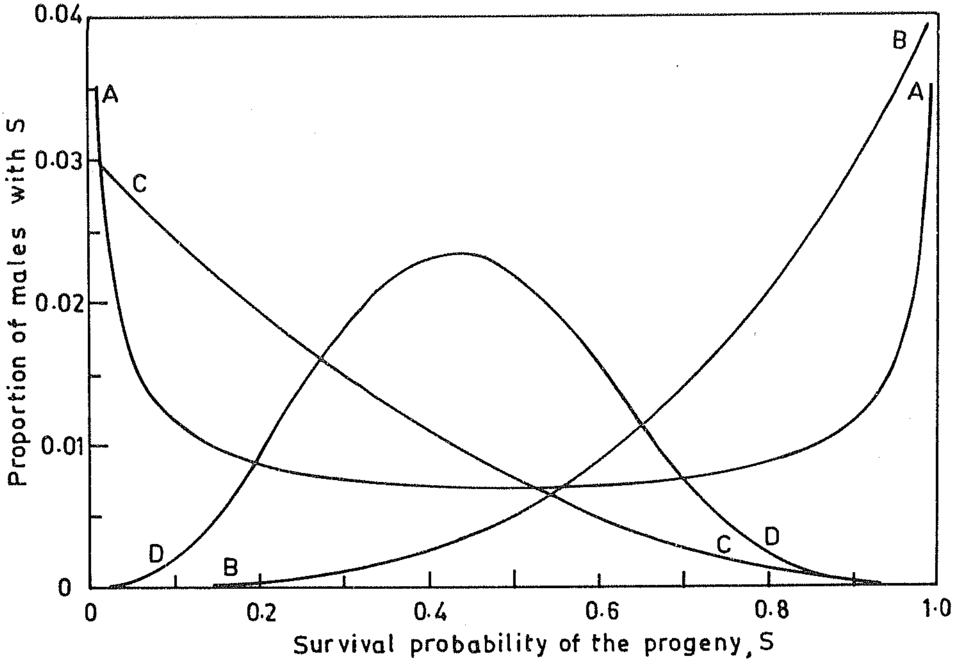

Figure 1. The probability density curves corresponding to the distribution of male quality (survival probability of the offspring fathered by the male) characterized by the beta distribution. A – Bimodal distribution, $\alpha=0{\cdot}50$ and $\beta=0{\cdot}50$; B – unimodal, mode at 1, $\alpha=4{\cdot}00$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

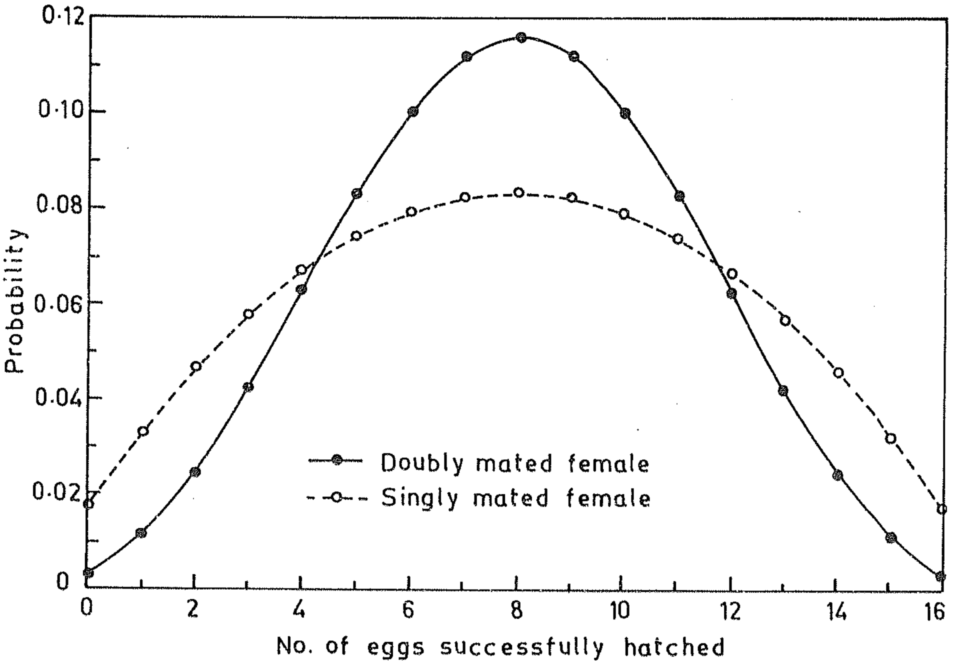

Figure 2. The probability density curves for the number of eggs that are successfully hatched by singly and doubly mated females. Note the reduction in the variance for the doubly mated female. $N=16$, $\mu=0{\cdot}50$, $\sigma^2=0{\cdot}05$.

$P1(i)$ 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 (F2/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(F122/F11) and the selective advantage by 2(F122/F11) − 1. Alternatively, if a rare monandrous mutant invades a pure polyandrous population, its rate of loss is 2(F121/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 [F22/(2 F121)] − 1.

3. Results and discussion

There are five independent parameters in the model: the two parameters α and β characterizing the distribution of male quality (alternatively, μ and σ^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

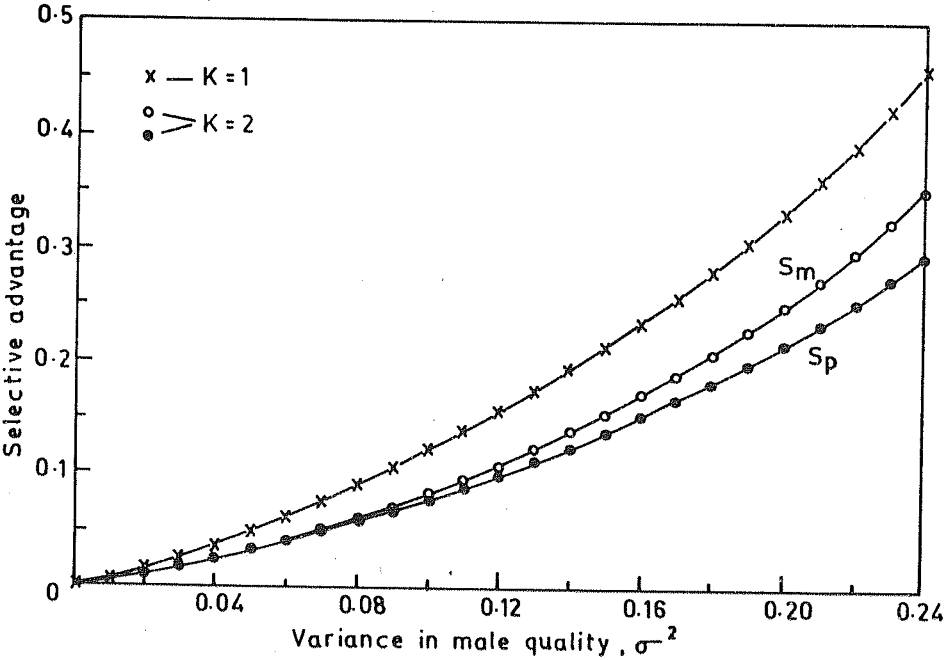

Figure 3. Selective advantage for polyandry as a function of the variance in male quality. $N=16$, $C=4$, $\mu=0{\cdot}50$.

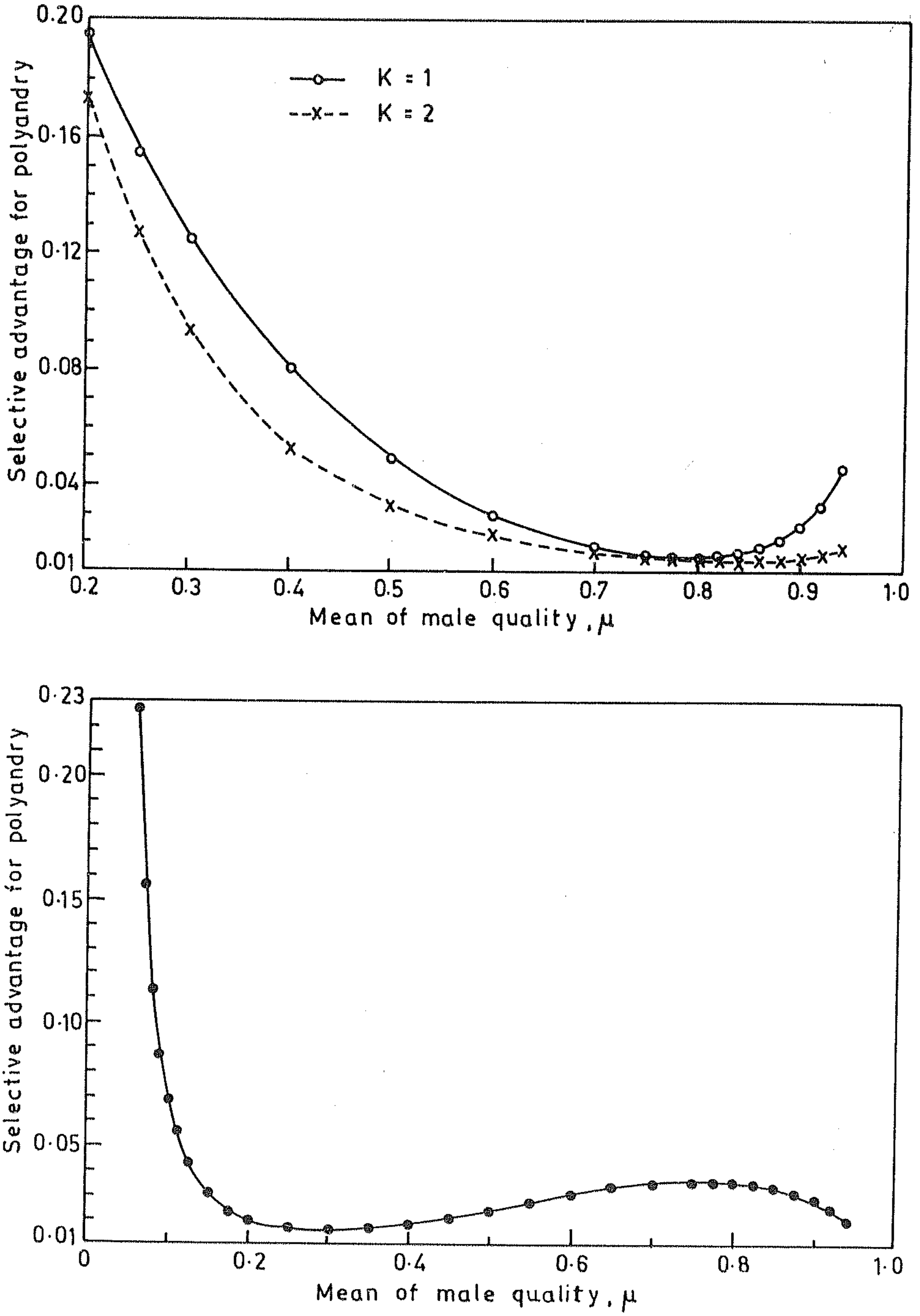

Figure 4. Selective advantage for polyandry as a function of the mean of male quality, (a) $N=16$, $C=4$, $\sigma^2=0{\cdot}05$, (b) $N=16$, $C=12$, $\sigma^2=0{\cdot}05$.

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

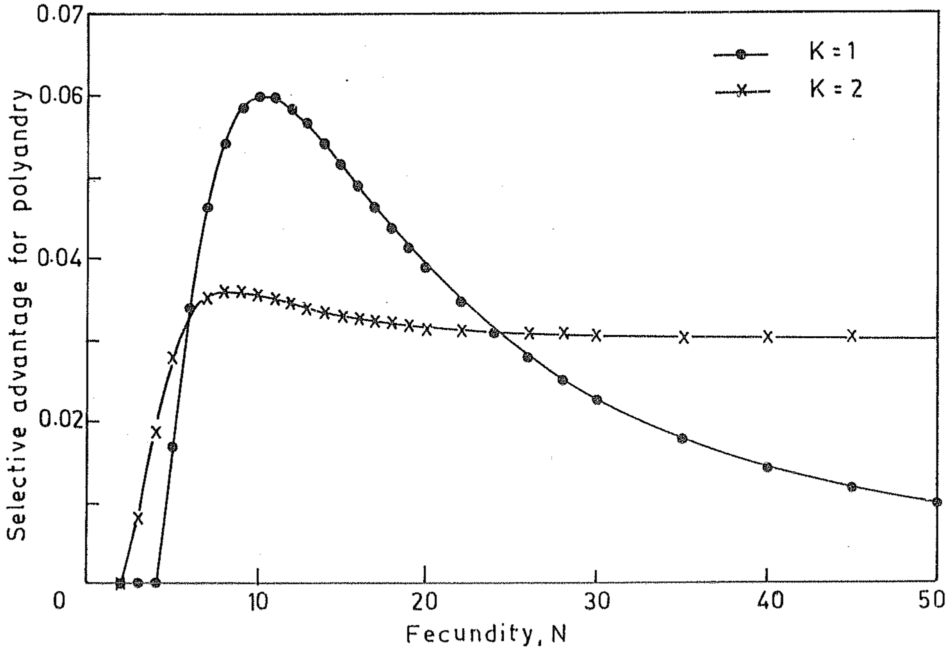

Figure 5. Selective advantage for polyandry as a function of fecundity N, $N=16$, $\mu=0{\cdot}50$, $\sigma^2=0{\cdot}05$, $C=4$.

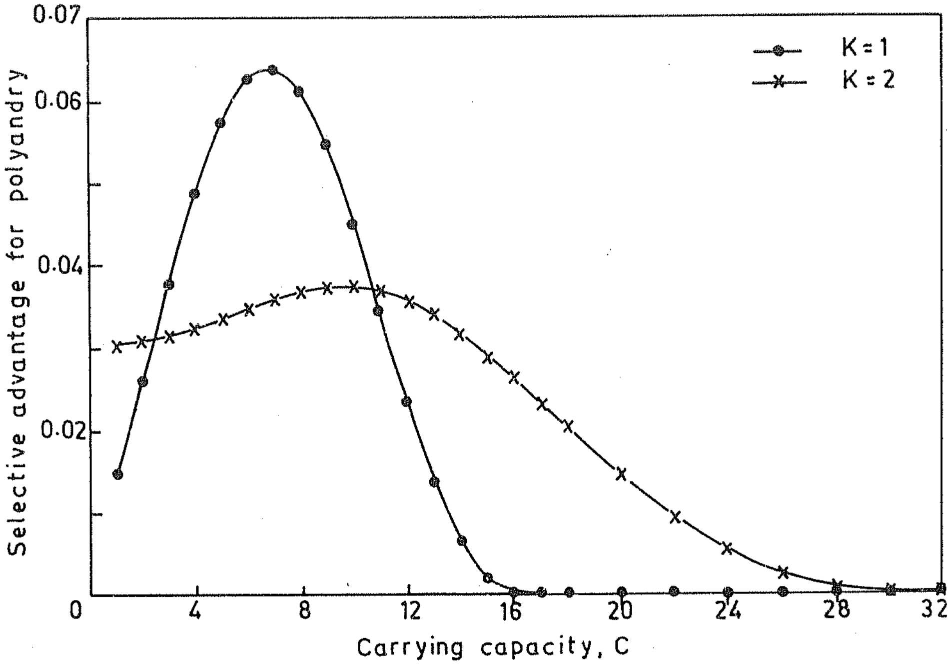

Figure 6. Selective advantage for polyandry as a function of the local carrying capacity C, $N = 16$, $\mu = 0{\cdot}50$, $\sigma^2 = 0{\cdot}05$.

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.

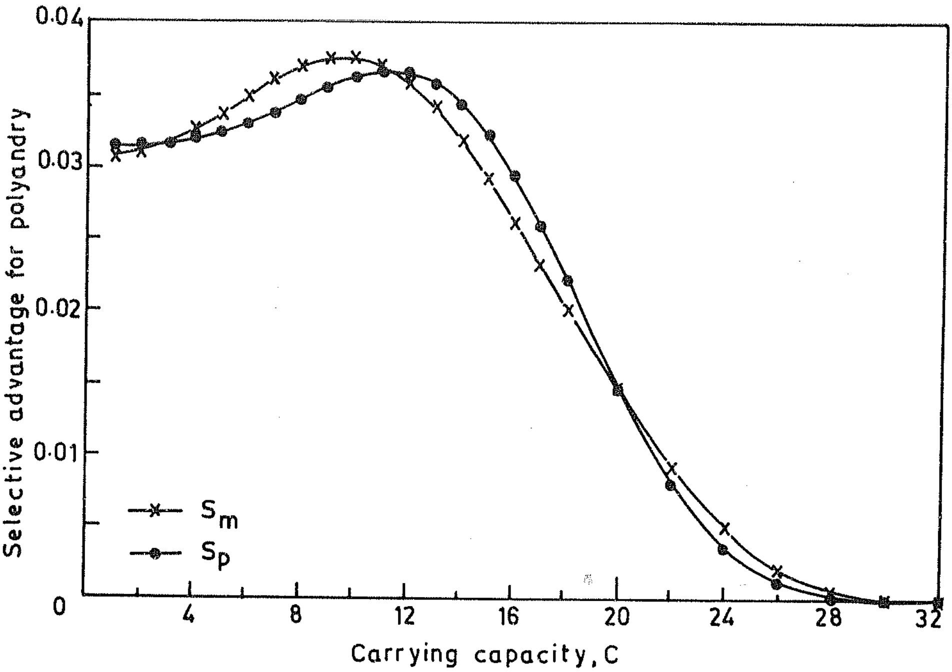

Figure 7. The selective advantage for polyandry when the monandrous allele is rare (S_p) and when the polyandrous allele is rare (S_m).

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.

Acknowledgements

I thank Arun Venkatraman and particularly K Chandrasekhar for bringing many relevant references to my attention.

References

Cole B J 1983 Multiple mating and the evolution of social behaviour in Hymenoptera. *Behav. Ecol. Sociobiol.* 12: 191–201

Crozier R H 1977 Evolutionary genetics of the Hymenoptera. *Annu. Rev. Entomol.* 22: 263–288

Crozier R H and Page R E 1985 On being the right size: male contributions and multiple mating in social Hymenoptera. *Behav. Ecol. Sociobiol.* 18: 105–115

Drummond B A III 1984 Multiple mating and sperm competition in lepidoptera. In *Sperm competition and the evolution of animal mating systems* (ed.) R L Smith (Orlando, Fl: Academic Press) pp. 291–370

Gibson R M and Jewel P A 1982 Semen quality, female choice and multiple mating in domestic sheep: A test of Triver's sexual competence hypothesis. *Behaviour* 80: 9–31

Gillespie J H 1974 Natural selection for within generation variance in offspring number. *Genetics* 76: 601–606

Gillespie J H 1977 Natural selection for variance in offspring numbers: A new evolutionary principle. *Am. Nat.* 110: 1010–1014

Halliday T and Arnold S J 1987 Multiple mating by females: a perspective from quantitive genetics. *Anim. Behav.* 35: 939–941

Knowlton N and Greenwell R 1984 Male sperm competition avoidance mechanisms: the influence of female interests. In *Sperm competition and the evolution of animal mating systems* (ed.) R L Smith (Orlando, Fl: Academic Press) pp. 61–84

Loman J, Madsen T and Hakansson T 1988 Increased fitness from multiple matings, and genetic heterogeneity: a model of a possible mechanism. *Oikos* 52: 69–72

Parker G A 1970 Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.* 45: 525–567

Parker G A 1984 Sperm competition and the evolution of animal mating systems. In *Sperm competition and the evolution of animal mating systems* (ed.) R L Smith (Orlando, Fl: Academic Press) pp. 1–60

Sherman P W, Seeley Thomas D and Reeve Hudson K 1988 Parasites, pathogens and polyandry in social hymenoptera. *Am. Nat.* 131: 602–610

Smith R L (ed.) 1984 *Sperm competition and the evolution of animal mating systems* (Orlando, Fl: Academic Press)

Williams G C 1975 *Sex and evolution* (New Jersey: Princeton University Press)

Wilson D S 1982 *The natural selection of populations and communities* (Menlo Park, CA: Benjamin-Cummings)