

Evolution of sex ratios in social hymenoptera: consequences of finite brood size

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MS received 30 May 1986

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Reprinted from

Journal of Genetics



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Abstract. Evolutionarily stable sex ratios are determined for social hymenoptera under local mate competition (LMC) and when the brood size is finite. LMC is modelled by the parameter d . Of the reproductive progeny from a single foundress nest, a fraction d disperses (outbreeding), while $(1-d)$ mate amongst themselves (sibmating). When the brood size is finite, d is taken to be the probability of an offspring dispersing, and similarly, r , the proportion of male offspring, the probability of a haploid egg being laid. Under the joint influence of these two stochastic processes, there is a nonzero probability that some females remain unmated in the nest. As a result, the optimal proportion of males (corresponding to the evolutionarily stable strategy, ESS) is higher than that obtained when the brood size is infinite. When the queen controls the sex ratio, the ESS becomes more female biased under increased inbreeding (lower d). However, the ESS under worker control shows an unexpected pattern, including an *increase* in the proportion of *males* with *increased inbreeding*. This effect is traced to the complex interaction between inbreeding and local mate competition.

Keywords. Sex ratios; local mate competition; social hymenoptera; evolutionarily stable strategies; mathematical modelling.

1. Introduction

How best—in an evolutionary sense—should sexual organisms allocate their resources between their male and female progeny? Sex ratio theory, which attempts to answer this question, has been a very active area of evolutionary biology (Charnov 1982). Especially interesting are the applications to social insects (Trivers and Hare 1976; Alexander and Sherman 1977), where predictions made on this basis have proved invaluable in testing the various competing theories for the evolution of social behaviour (Craig 1980; for a review, see Gadagkar 1985). Beginning with the classic work of Hamilton (1967), theoretical investigations have encompassed a variety of factors which govern the sex ratio (defined as the proportion of males in the brood)—local mate competition (Taylor and Bulmer 1980), worker control of sex ratio (Trivers and Hare 1976), workers laying male eggs (Benford 1978), multilocus control (Pamilo 1982) and inbreeding (Herre 1985)—either separately, or jointly (Joshi and Gadagkar 1985).

Almost all these studies assume an infinite population and an infinite brood size, and determine the evolutionarily stable sex ratio, i.e. the value of the genetically controlled sex ratio, which, if prevalent in the population, would prohibit the spread of any other sex ratio mutant.

Real life systems, to which these theories have to be applied have, of course, finite populations and finite brood sizes, and it is desirable to investigate the extent to which this would alter the optimal sex ratios. Moreover, even before one applies the sex ratio theory to any specific system, several questions of theoretical interest arise: will the evolutionarily stable strategy (ESS) always be obtained from any arbitrary starting

composition of gene frequencies? If so, how long will it take? To what extent will the sex ratio in a finite population fluctuate in response to stochastic effects? The technique of Monte Carlo simulation is an ideal one for answering these questions. As a prelude to undertaking such an investigation, the present work reports the consequences of finite brood size on the optimal (evolutionarily stable) sex ratio.

Such investigations have been carried out earlier for the special case of highly inbred (though not social) wasps. When there is complete inbreeding, LMC theory predicts the proportion of males to be zero; which implies production of "just enough males (ideally one) to inseminate all the females" (Hamilton 1967). Hartl (1971) was the first to point out that if fertilization of the egg were a binomial process (like the tossing of a highly biased coin), the optimal proportion of males would be higher than that corresponding to only one male. The process of sex determination is more precise than binomial in such highly inbred systems (Green *et al* 1982; Putters and Van der Assem 1985). Green *et al* (1982) have developed an elaborate model for determining optimal sex ratios, which takes into account the effect of such enhanced precision.

The present work extends these studies to cover the entire spectrum from complete inbreeding to complete outbreeding. It also examines the situation where the workers in the nest control the sex ratio. Consequences of polyandry are also explored.

2. The model

An outline of the model is presented below. The detailed model, except for the effects of the finite brood size, has been described at length in an earlier publication (Joshi and Gadagkar 1985).

2.1 The breeding system

The model assumes an infinite population of nests, each founded by an inseminated female (the queen). After reproduction, the queen dies. A fraction d of the brood (both males and females) disperses from the nest to join the mating pool where the females are inseminated (outbreeding). In the fraction $1-d$ remaining at the nest, sibmating takes place. The inseminated females emerging from the nest, as well as those from the pool, establish new nests to begin the next generation.

The sex ratio trait is modelled by a one-locus two-allele (A and B) system. When the queen controls the sex ratio, the proportion of males produced by the genotype AA is r_A and by BB is r_B . The two alleles are assumed to be co-dominant, and the proportion for AB is $(r_A + r_B)/2$. Under worker control, the sex ratio is taken to be the weighted average of the sex ratios specified by the genotypes of the workers.

2.2 A probabilistic approach when the brood size is finite

Let N be the total number of eggs laid in a nest. If r is the sex ratio for the nest then the probability that a male (haploid, unfertilized) egg is laid is also taken to be r . Assuming a binomial distribution, the probability that exactly K fertilized eggs are laid (K females are produced) is

$$P(K) = [N!/(N-K)!K!] (1-r)^K r^{N-K}. \quad (1)$$

Similarly, $1-d$, the fraction of offspring which remain at the nest, is also taken to be the probability that an offspring remains at the nest. Under binomial distribution, the probability that n out of K females remain at the nest is

$$P(n, K) = [K!/(K-n)!n!] (1-d)^n d^{K-n}. \quad (2)$$

For these females to be inseminated, at least one of the $N-K$ males produced in the nest should remain at the nest, and the associated probability is $1-d^{N-K}$.

Hence, the expected number of inseminated females emerging from the nest is given by

$$\begin{aligned} F_{\text{nest}} &= \sum_{K=0}^N P(K) \sum_{n=0}^K P(n, K) n (1-d^{N-K}) \\ &= \sum_{K=0}^N P(K) (1-d^{N-K}) \left[\sum_{n=0}^K n P(n, K) \right]. \end{aligned}$$

The term in the square brackets is just $(1-d)K$. Thus, using (1)

$$F_{\text{nest}} = (1-d) \sum_{K=0}^N [N!/(N-K)!K!] (1-r)^K r^{N-K} K (1-d^{N-K}).$$

This summation can be evaluated to yield

$$F_{\text{nest}} = N(1-d)(1-r) \{1 - [1-r(1-d)]^{N-1}\}. \quad (3)$$

The term $[1-r(1-d)]^{N-1}$ thus represents a correction due to the finite brood size, and tends to zero as N tends to infinity, as expected.

2.3 Stability analysis

Each nest is characterized by the genotype of the foundress, and the genotype of the male(s) she has mated with. Social hymenoptera being haplodiploid, the genotype of the male is either A or B . Under single insemination, there are six types of females: $AA.A$, $AA.B$, $AB.A$, $AB.B$, $BB.A$ and $BB.B$. If the frequencies P_1, \dots, P_6 of each of these six classes in the n th generation are known, then for given values of d , r_A and r_B , the contributions from each of the above classes to the next generation, via inseminated females from the nests, and via the males and females joining the mating pool, can be evaluated, and the frequencies, $P_1 \dots P_6$ for the next $(n+1)$ th generation can be determined. When a population consisting entirely of the genotype A is invaded by a small proportion of the competing allele B , the dynamics is expressed by

$$[P_1(n+1), \dots, P_5(n+1)]^T = G[P_1(n), \dots, P_5(n)]^T, \quad (4)$$

where G is a 5×5 matrix (since the frequencies add up to 1, only 5 variables need be considered) whose elements are functions of r_A , r_B and d . If the dominant eigenvalue λ of the matrix is greater than unity, this implies that B can invade the population of A ; if it is less than unity, A is uninvadable. The optimal sex ratio \hat{r} corresponding to the ESS is obtained from the condition (Maynard Smith 1982),

$$\partial\lambda/\partial r_B = 0 \quad |_{r_A=r_B=\hat{r}}.$$

The calculations were done numerically on the DEC-1090 computer system at the Indian Institute of Science.

Generalization of the above procedure to cases where a female mates with more than one male is straightforward.

2.4 Optimal sex ratios using the Hamiltonian approximation

The contribution of a female to the next generation (fitness) is given by the sum of the number of daughters produced by her and the number of inseminations which her sons have performed (Hamilton 1967). If the sons and daughters are not equally related to the mother, the corresponding terms should be weighted by the appropriate coefficients of relatedness. Hence, in the present model, the fitness f_2 of a mutant female (sex ratio r_2) in a population with sex ratio r_1 is given by

$$f_2 = (1 - r_2) \cdot R_f + (1 - r_2) \cdot (1 - d) \cdot R_m + [d(1 - r_1)r_2/r_1] \cdot R_m, \quad (5)$$

where R_f and R_m denote her relatedness to the daughter and the son, respectively. The second term corresponds to the inseminations by the sons at the nest, while the third one to those in the mating pool. The ESS \hat{r} is obtained from the conditions $\partial f_2 / \partial r_2 = 0$, $r_1 = r_2$, and is seen to be

$$\hat{r} = dR_m / (R_m + R_f). \quad (6)$$

A slight departure from outbreeding ($d = 1 - \varepsilon$) leads to the expression (neglecting terms in ε^2 and beyond)

$$\hat{r} = [(1 - \varepsilon)R_m] / (R_m + R_f). \quad (7)$$

On the other hand, when the brood size is finite (N), the fitness is given by

$$f_2 = (1 - r_2) [1 - (1 - d)(1 - r_2(1 - d))^{N-1}] R_f \\ + (1 - r_2)(1 - d) \{1 - [1 - r_2(1 - d)]^{N-1}\} R_m + [d(1 - r_1)r_2/r_1] R_m.$$

The expression for \hat{r} turns out to be too involved to be expressed as a convenient formula. However, under a slight departure from outbreeding ($d = 1 - \varepsilon$), it can be shown that

$$\hat{r} = R_m / (R_m + R_f). \quad (8)$$

When workers control the sex ratio, R_m and R_f denote the relatedness with brother and sister respectively. As will be discussed in the last section, the differences in (7) and (8) have an important bearing on the differences in the optimal sex ratios under queen control and worker control.

3. Results

3.1 Queen control of the sex ratio

Optimal sex ratios (OSR) under queen control were determined for the entire range of d ($d = 0$, complete inbreeding, to $d = 1$, complete outbreeding), for brood sizes ranging from 5 to infinity. The results are summarized in figure 1. The OSR is always female biased for $d < 1$. As expected, for a fixed value of d , an increase in the brood size leads to a decrease in the proportion of males. For moderate to high values of d , and

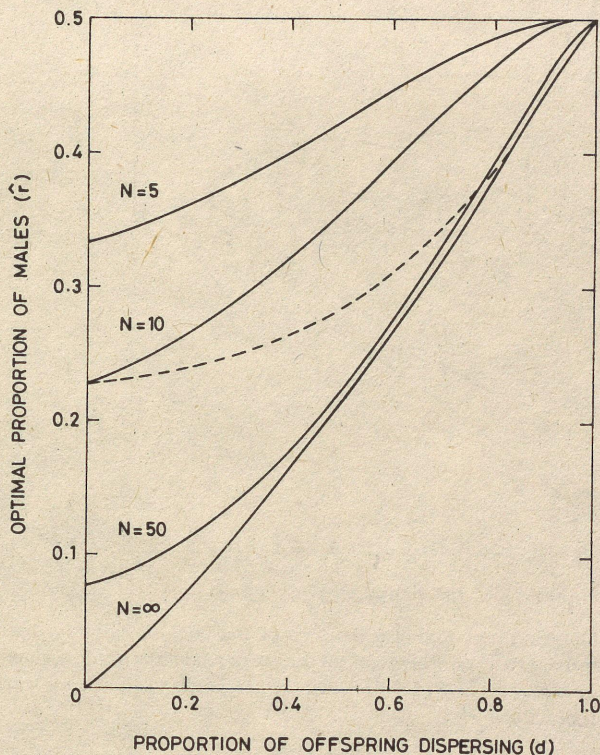


Figure 1. Optimal proportion of males (\hat{r}) is plotted as a function of d , the proportion of offspring dispersing when the queen controls the sex ratio. The brood size is denoted by N . The broken line corresponds to \hat{r} for $N = 10$ under the density dependent dispersal model.

brood sizes beyond 50, the OSR for finite and infinite broods are almost indistinguishable. However, for low d (high inbreeding) there are marked differences between the two.

For the special case of complete inbreeding ($d = 0$), the OSR is the one which maximizes the number of inseminated females emerging from the nest (Hartl 1971; Green *et al* 1982). This can be readily obtained from (3) to be

$$\hat{r} = 1 - (1/N)^{1/(N-1)}, \quad (9)$$

which agrees very well with the results shown in figure 1, obtained from stability analysis described in §2.3.

When the queen mates with more than one male, the OSR are, as expected, indistinguishable from those under single insemination.

3.2 Worker control of the sex ratio

The variation of OSR with the extent of inbreeding under worker control of the sex ratio is shown in figure 2 for various brood sizes. The pattern is qualitatively different from that under queen control. For a fixed brood size, the optimal proportion of males first increases with d , attains a maximum, and then decreases with increasing d . In particular,

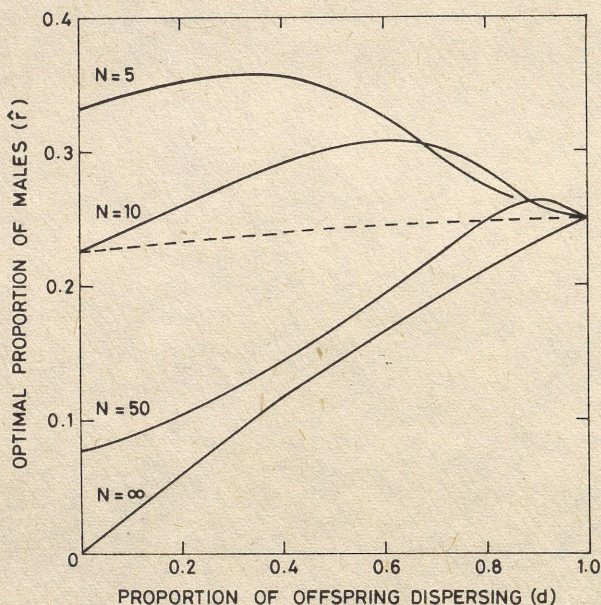


Figure 2. Optimal proportion of males (\hat{f}) is plotted as a function of d , the proportion of offspring dispersing, when workers control the sex ratio and the queen is singly inseminated. The brood size is denoted by N . The broken line corresponds to \hat{f} for $N = 10$ under the density dependent dispersal model.

near $d = 1$, for a small increase in inbreeding (small decrease in d), there is an *increase* in the proportion of males. The variation of OSR with brood size (figure 3) for a fixed value of d is also not monotonic, unlike that under queen control. The pattern of variation also seems to depend on the value of d . The anomalous increase in the proportion of males with brood size is very small in magnitude, however, and is restricted to low values of brood size. The OSR for $d = 0$ are identical to those under queen control, as expected, since under conditions of complete inbreeding, the females are equally related to their sisters and daughters and to their brothers and sons.

Optimal sex ratios obtained when a female mates with two males are shown in figure 4. The pattern is similar to that in figure 2. The differences between the patterns under queen control and worker control are seen to diminish with polyandry, as expected.

4. Discussion

A major impetus for sex ratio theory was provided by the observation (Trivers and Hare 1976) that its predictions could be useful in evaluating the competing theories for the evolution of sociality on the basis of field data. Subsequent rigorous analyses (Oster *et al* 1977; Taylor and Bulmer 1980; Uyenoyama and Bengtsson 1981; for a review, see Charnov 1982) have highlighted the influence of factors like local mate competition, queen-worker conflict etc. on the OSR. The present work demonstrates that the brood size is also likely to affect the OSR to a significant extent, and for empirical tests of sex ratio theory, data on brood size should also be taken into account. For most of the species of ants, the reproductive brood sizes are of the order of several hundreds and the

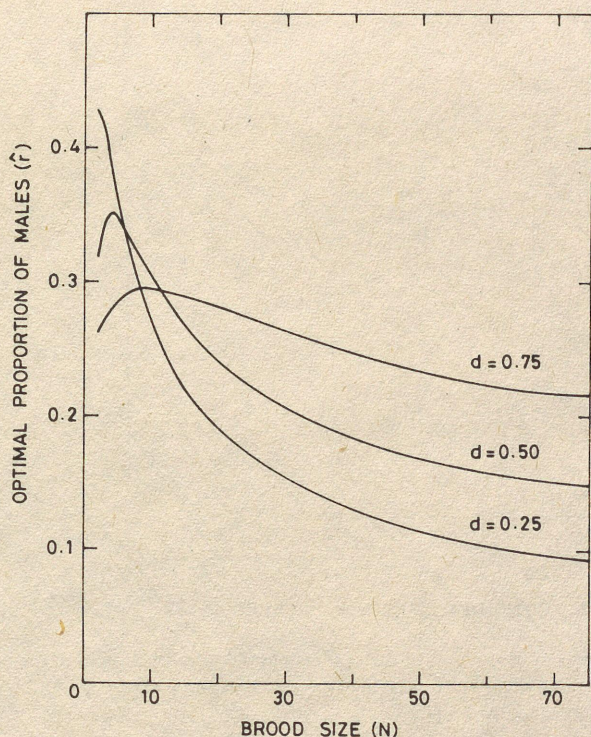


Figure 3. Optimal proportion of males (\hat{r}) is plotted as a function of N , the brood size, for different values of d , the proportion of offspring dispersing.

infinite brood size approximation is adequate. However, individual nests of some primitively eusocial wasps (e.g. *Polistes*, *Vespula*) produce 5–50 reproductives and the results presented here would be relevant to these (see Brian 1965).

The two stochastic processes which influence OSR, when the brood size is finite, are sex determination and dispersal. Unlike the binomial distribution assumed here, brood sex ratios (at least in highly inbred species) are known to be determined with a better than binomial precision (Green *et al* 1982; Putters and van der Assem 1985). Even if it were so for less inbred species, the random component due to dispersal would still maintain the differences between the OSR under finite and infinite brood sizes. Yet another factor, not considered in the present work, is brood mortality (Green *et al* 1982); if all the offspring do not survive to adulthood, some females in the nest may remain unmated due to the absence of males, and shifts in the OSR similar to the present model would be expected.

One of the important consequences of finite brood size is the possible dependence of OSR on the dispersing characteristics of the males, which may be different from those of the females (Hamilton 1979). When the brood size is infinite, as long as the proportion of males dispersing is different from zero or unity, the OSR is determined exclusively by the d corresponding to the females. An examination of (3) shows that if the proportions of males and females dispersing from the nest are d_m and d_f , respectively, then the number of inseminated females leaving the nest would be given by

$$F_{\text{nest}} = N(1 - d_f)(1 - r) \{1 - [1 - r(1 - d_m)]^{N-1}\},$$

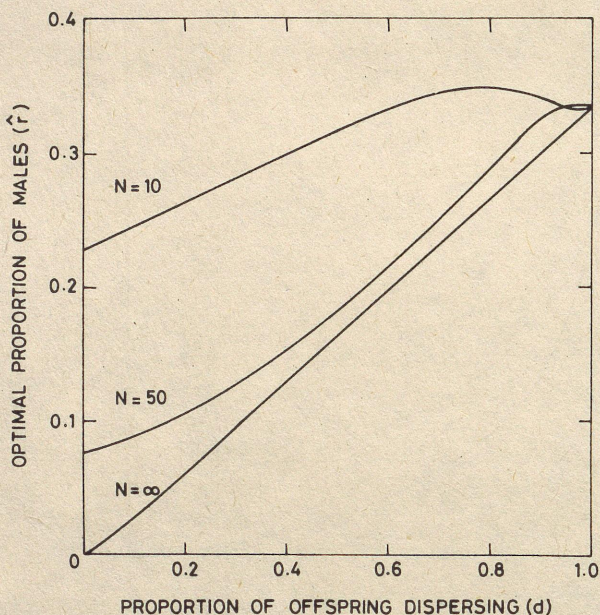


Figure 4. Optimal proportion of males (\hat{f}) is plotted as a function of d , the proportion of offspring dispersing when workers control the sex ratio, and the queen is doubly inseminated. The brood size is denoted by N .

indicating an explicit dependence on d_f and d_m . The consequences of the differential dispersal of male and female offspring on OSR are being investigated.

Another possibility to be examined is the density dependent dispersal of males. The probability of a male dispersing may be a function of the number of males present in the nest; the lower the number, the lower the probability of dispersal. This would lead to a decrease in the number of uninseminated females and consequently a reduction in the optimal proportion of males. In a simplified version of this model, it is assumed that at least one male remains in the nest. In this case, only an all-female brood leads to some of the females remaining uninseminated. The optimal sex ratios obtained for such a model are shown by the broken lines in figures 1 and 2. When there is complete inbreeding ($d = 0$), none of the males disperse; under complete outbreeding ($d = 1$) all of them disperse and the two models lead to identical values of \hat{f} . For intermediate values of d , the density dependent dispersal model leads to a reduction in the proportion of males (figures 1 and 2).

The higher proportion of males, predicted under worker control in an almost outbreeding population compared to the completely outbreeding one, is intriguing at first sight. This effect can be understood when one looks at the two factors determining the OSR which are often compounded—local mate competition and inbreeding. Herre (1985) has emphasized the distinction between the two, and has very elegantly demonstrated how their effects can be separately examined. It can be seen from (7) that the optimal sex ratio is determined by the product of d which denotes the extent of local mate competition, and $R_m/(R_m + R_f)$ which reflects the effect of inbreeding. A decrease in d , implies more local mate competition, and hence a reduction in the proportion of males.

Under complete outbreeding, the queen is related to both her sons and daughters by $1/2$, while under complete inbreeding, these values change to $1/2$ and 1 respectively, and the ratio $R_m/(R_m + R_f)$ decreases from $1/2$ to $1/3$. Thus, inbreeding also leads to a reduction in the proportion of males.

On the other hand, under complete outbreeding, a worker is related to her brother by $1/4$ and sister by $3/4$; and under complete inbreeding, by $1/2$ and 1 respectively. The ratio $R_m/(R_m + R_f)$ thus increases from $1/4$ to $1/3$. Since the increase (and consequently, the rate of increase) is small, the term corresponding to $LMC(1 - \epsilon)$ dominates in (7), and for infinite brood size, near $d = 1$, a reduction in the proportion of males with d is observed. When the brood size is finite, however, as seen from (8), near $d = 1$, only the inbreeding term influences the sex ratio, and an increase in the proportion of males is expected, as seen in figure 2. In fact, even under queen control, when the brood size is finite, near $d = 1$, only the inbreeding term contributes to the OSR, and the decrease in the proportion of males (figure 1) is slower than when the brood size is infinite.

In fact, a more general prediction can be made in the light of this analysis. If, in an experimental situation, the effects of LMC and inbreeding are separately examined (see Herre 1985), then when the workers control the sex ratio, an increase in the proportion of males with increasing inbreeding would be observed.

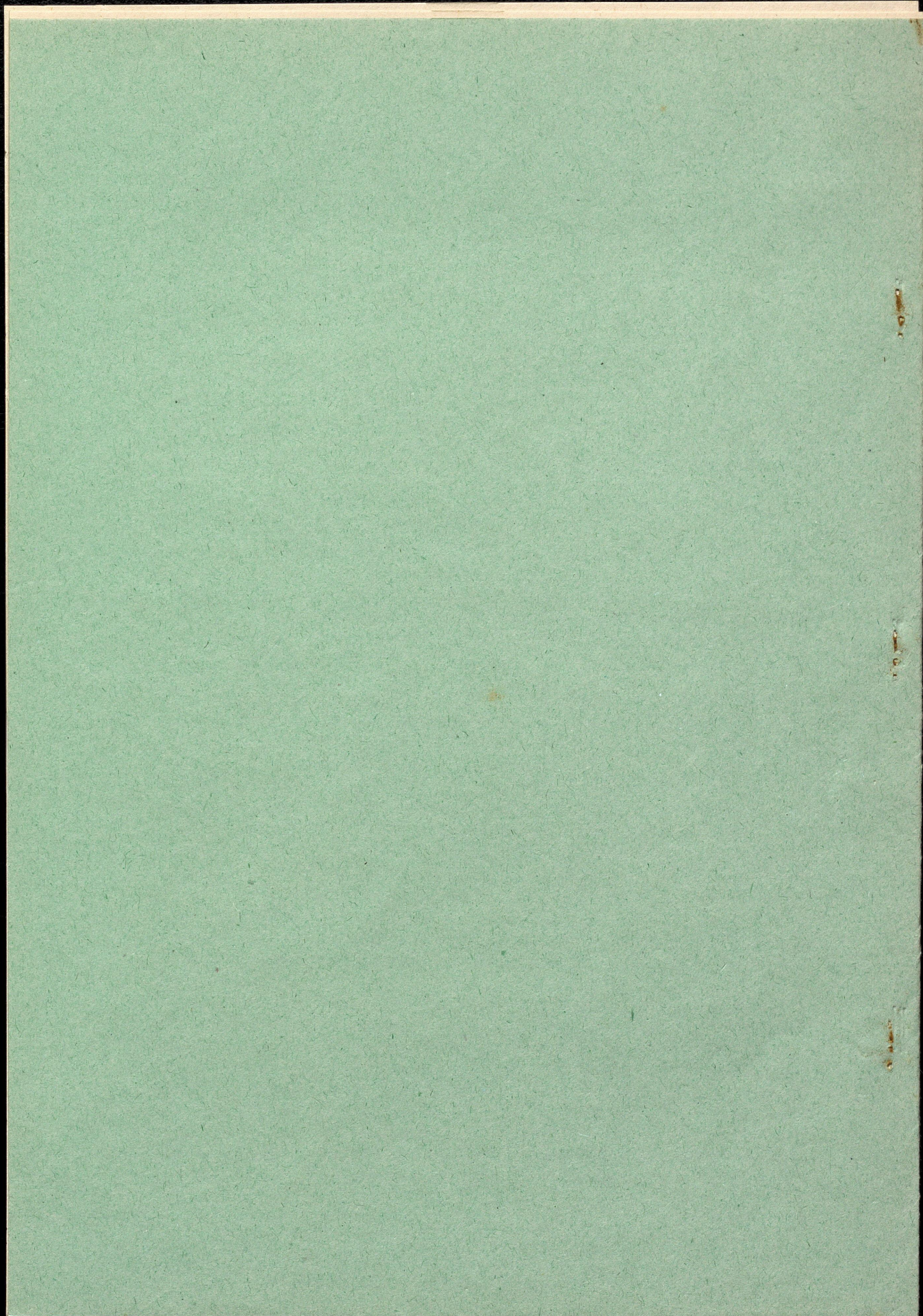
Acknowledgement

I thank Professors Madhav Gadgil and H Sharat Chandra, and Dr Raghavendra Gadagkar for critically reading the manuscript and for helpful suggestions.

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Reprinted from
The Journal of the Indian Institute of Science

BOOK REVIEWS

The ancient tradition of geometric problems by Wilbur Richard Knorr. Birkhauser Verlag, P.O. Box 133, CH-4010, Basel, Switzerland, 1986, pp. 420, S. Fr. 128.

For the ancient Greeks, mathematics meant geometry. The problem of cube duplication, angle trisection, and circle quadrature have attracted major interest among scholars of ancient Greek geometry. The search for solutions to these problems profoundly influenced Greek geometry and led to many important discoveries. The literature on ancient Greek geometry is inextricably bound up with these problems and a variety of solutions which the ancients produced from the pre-Euclidean period through the generation of Euclid and Archimedes to the time of Apollonius. No significant progress was made by the ancient geometers after Apollonius except of course by way of producing a few excellent treatises on geometry. The impossibility of solving these famous problems of antiquity with Euclidean tools was not realized until the nineteenth century. Proofs of these facts are essentially algebraic in nature and not amenable to attack by the geometric methods of the ancients.

The admirable book under review written by Wilbur Richard Knorr undertakes a survey of the ancient Greek geometric tradition. It makes a notable contribution to the field of history of ancient Greek mathematics. The basic difference between the many existing books on this subject and the book under review is one of emphasis and general philosophy rather than content. Wilbur Richard Knorr's book has made an attempt to trace the movement of ideas which accompanied the ancient Greek masters and to give a more coherent development of the subject. The book is well motivated and well documented.

The book is divided into eight chapters. Each of these chapters, except the first and the last, is structured around the ideas and techniques developed in solving these three famous problems by Greek geometers and this is accompanied by some sort of a commentary by the author whose purpose seems to place the findings of these geometers in a proper historical perspective.

In chapter one the author formulates the principal objective of this project and explains at length the difficulties that one faces in such an endeavour and makes certain recommendations bearing on the present study to overcome these difficulties.

In chapter two, the author after surveying the various historical sources tries to clarify the way in which the cube duplication and the quadrature of the circle were first articulated as problems. The contributions of Hippocrates of Chios to the study of these geometric problems which lay the foundation for later researches is given.

Chapter three is devoted to the contributions made by the group of geometers affiliated to Plato's Academy in Athens which was the centre for geometric studies during the fourth century B.C. It is learnt that the technical methods in geometry experienced significant advances at the hands of Archytas, Eudoxus, and Menaechmus. The most significant among these are the techniques of limits and the theory of proportions by Eudoxus. It is a view often held that the later theory resolved the first foundational crises. It is of interest to know the author's reaction: "one hypothesized a paralysis of research, a renunciation of the use of proportions in geometry, and so on, until this impasse was finally broken through the efforts of Eudoxus. One seemed not to care that the extant evidence, fragmentary as it is, indicates no signs of such paralysis or renunciation, but rather a remarkable degree of continuity in the development of technical methods".

Chapter four is concerned with the contributions of Euclid an effective teacher and a compiler. His contributions were seminal for the development of problem solving in the third century.

Chapter five is devoted to the work of Archimedes who is considered to be the greatest mathematician of antiquity. Even though he was more or less a contemporary of Euclid, than of Eudoxus, it is the work of the latter that had a profound influence on Archimedes.

The estimation of π , effective rules of estimating square and cube roots, quantitative measurements of geometric figures, for instance, the areas and volumes and the centre of gravity of circular figures dominate the work of Archimedes.

Chapter six is devoted to the work of Eratosthenes, Nicomedes, Hippias and many others in the third century whose research efforts are strongly guided by the Archimedian methods.

Chapter seven is all about the work of Apollonius who is famous for his contributions to the theory of conics. The major concern of Apollonius was to recast, extend, and reorganize the results of his predecessors.

The final chapter is primarily concerned with the mathematical and philosophical reflections of the author on various questions that confront scholars of ancient Greek geometry.

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B. S. PANDURANGA RAO

Quantum theory of finite systems by Jean-Paul Blaizot and Georges Ripka. The MIT Press, 28, Carleton Street, Cambridge, Massachusetts 02142, 1986, pp. 657, \$51.75 (Indian orders to Affiliated East-West Press Pvt. Ltd, Madras 600 010).

The volume is an advanced text on the quantum theory of many-body problems. It contains 18 chapters spanning 649 pages. Each chapter beginning with a brief

introduction, ends with a set of problems and is complete with its own bibliography. The main emphasis is on finite systems with most topics such as the spontaneous symmetry breaking are treated in some mean-field approximation and as such there is no explicit treatment of the thermodynamic limit. While there already exists a number of very good but highly specialized texts on the quantum many-body theory, what sets the book under review apart from the rest is its somewhat unconventional selection of topics from the current contents that should have a much wider appeal today. Thus, for example, the discussion of the Fermionic coherent states in terms of the Grassmann algebra, and that of the Bosonic coherent states in terms of the Bargmann representation in chapter I, is very apt and welcome. These mathematical objects have shown up unexpectedly in many areas of active research in recent years and a working knowledge of the related mathematical tools is very desirable. Perhaps, this book lays too much emphasis on the coherent state representation in that the entire scheme of semi-classical approximation is based on the path integral representation of the coherent states, Bosonic as well as Fermionic. There is a powerful discussion of the self-consistent Fermion pairing field and of the Hartree-Fock-Bogoliubov equation in chapter 7. Also, there is a very readable account of the spontaneously broken symmetry and the symmetry restoring collective modes in chapter 8. Standard diagrammatic perturbation theory is discussed in chapters 12–14. Chapter 16 deals with renormalization (amplitude and vertex) while chapters 17 and 18 deal with the advanced topics of correlated wave functions.

From the pedagogic point of view, chapters 1 through 15 can form a text for a graduate course in many-body theory. But on the whole, the book is addressed to research workers. Strongly recommended for libraries attached to Physics departments.

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Maxwell on molecules and gases edited by Elizabeth Garber, Stephen G. Brush and C. W. F. Everitt. The MIT Press, Cambridge, Massachusetts, 1986, Hardbound, pp. 565, \$62.25.

The volume is about the scientific works and philosophical thoughts of the “leading molecular scientist” of the 19th century—James Clerk Maxwell. More specially, it brings out Maxwell’s wide-ranging contributions to the dynamical theory of gases and his ideas on the nature of atoms and molecules. The dynamical theory developed by Maxwell between 1860 and 1875 led to the first successful application of the Laplacean method of probability and statistics to the many-body problem of gases, and provided a kinetic theory of transport properties of gases—viscosity diffusion and thermal conductivity. Through 92 original documents reproduced without change and one comprehensive introduction to Maxwell’s kinetic theory and numerous annotated cross-references, the authors have presented a perspective on Maxwell the physicist in the context of the 19th century science, which should be of great interest both to a student of history of science as well as to an active researcher in the field of statistical mechanics. Several fundamental ideas, *e.g.*, that of pressure as being due to molecular impacts rather than intermolecular

repulsion, the idea of meanfree path and finally the idea of equipartition of energy are seen to evolve as a discursive formation of thought. This is seen clearly in his frank correspondence with and reference to his great contemporaries—Tait, Stokes, Spencer, Clausius and Boltzmann. The authors also bring out very clearly the main preoccupation of Maxwell namely, the atomic structure of matter and not a theory of heat. The book is more than a collected works or an original sourcebook on Maxwell meant for an archive. It *analyses* Maxwell the physicist and the philosopher who is very much relevant to-day. The book, of course, has no prosopographical details but has adequate bibliography on this aspect. Also, the later more mature contributions of Maxwell on 'Statistical Mechanics' have been reserved for a separate companion volume. (The two will have to be read together for completeness). The book is highly recommended for libraries attracting physicists, philosophers and scholars of history of science.

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Polymer science by V. R. Gowariker, N. V. Viswanathan and Jayadeva Sreedhar. Wiley Eastern Limited, New Delhi 110 002, 1986, pp. 505, Rs. 50.

Synthetic polymers which started out as a discovery from Baekeland's laboratory in 1909 soon became, in the following decades, a focal point of study in the various disciplines of science and engineering. Polymers as we know today have come out of these long and perserving studies. Today the overall insight into polymer science and technology is so deep that a material scientist can create an almost limitless range of new materials—materials which can be used to bear loads, bond objects, seal joints, fill cavities—in fact, anything from clothing the body to powering a space vehicle to even replacing a worn-out human organ! The annual production of plastics has increased several fold in recent years having surpassed, on a volume basis, even the production of steel in some of the advanced countries.

One consequence of this widening use of polymers is that a large fraction of chemists and chemical engineers, to say nothing of those in other disciplines, is employed in jobs related in some way to polymers. In fact, a science student entering a science-based industry has today a better than 30 per cent chance of being involved with work relating to polymers in one form or another. No wonder, very often we encounter people who have no formal training in polymers, but now due to their job requirement want to learn about polymers in a short time. Education in polymer science, it appears, has not kept pace with the growth of polymer industry.

The need for polymer education has to be filled, however, by teaching at several levels in several disciplines. At the post-graduate level, polymers are now taught under various titles like polymer chemistry, polymer science, polymer technology, polymer processing, and industrial polymers. In addition, more specialised polymer courses are offered in curricula leading to degrees in polymer disciplines. Polymer science, as a discipline is no longer confined to post-graduate curricula and has expanded to the levels of graduation

and diverse industrial courses, creating need for simpler polymer texts for beginners. While many specialised books have been published over the last 30 years on each of the various facets of polymers, their science and technology, there are only very few introductory level books on polymer science. The only three such books, to this reviewer's knowledge, are Billmeyer's *Textbook of polymer science*, Rudin's *The elements of polymer science and engineering* and Cowie's *Polymers: Chemistry and physics of modern materials*. Viewed against this background, *Polymer science* by Gowariker, Viswanathan and Sreedhar is a welcome addition.

The book features separate chapters dealing with the chemistry of polymerisation, molecular weight and size, kinetics of polymerisation, chemical and geometrical structure of polymer molecules, glass-transition temperature, crystallinity of polymers, and copolymerisation. The authors have done well to devote one full chapter to glass-transition temperature and another to polymer crystallinity alone as these are very important factors influencing polymer behavior and properties. Polymer rheology and polymer solution properties are also presented in two separate chapters. Most of the commercially important polymers are described individually in one chapter giving, though very briefly, their properties, uses and method of production. The functional groups present in polymer molecules can, depending on their chemical nature, undergo a variety of chemical reactions leading to polymer structures with interesting new properties. Polymers have thus been put to many novel uses and new applications are continually being developed. It is to the credit of the authors that they have recognised their importance and devoted one whole chapter to polymer reactions. Other distinctive features of the book are the special treatment given to polymer degradation and experimental techniques for polymers.

None of the chapters, however, has been provided with problems or exercises at the end. This would be a drawback if the book is to serve as a text for polymer science courses.

The book, written in a very lucid style, uses simple analogies and illustrations to explain some of the most abstract concepts in polymer science. The text is eminently suitable for self-study. The authors and publishers should be complimented for producing this fine volume.

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Structural stability of columns and plates by N. G. R. Iyengar. Affiliated East-West Press Pvt. Ltd., 104, Nirmal Tower, 26, Barakhamba Road, New Delhi 110 001, 1986, pp. 316, Rs. 75.

This book contains a lucid presentation of elastic and inelastic buckling behaviour of columns and plates, buckling of frames, torsional and torsional-flexural buckling of open sections, and postbuckling behaviour of plates. Buckling of laminated composite columns is briefly introduced. A chapter is devoted to buckling of composite plates

covering author's contributions in this area. The text is supplemented by an Appendix on constitutive equations for anisotropic materials and, in particular, orthotropic laminates.

Chapter 1 deals with elastic buckling of columns, in which stability criteria from four different approaches, *viz.*, equilibrium approach, energy approach, imperfection approach, and dynamic (vibration) approach are clearly presented. Applications of Timoshenko's method, Rayleigh-Ritz method, Galerkin method, finite difference techniques, and finite element techniques are given in great detail through several illustrative examples. Columns with open cross-sections, pinjointed triangulated frames, rigid jointed frames, and multi-storeyed-multibay frames are dealt in chapters 3 and 4.

In chapter 2, inelastic buckling of columns is treated through double modulus theory and tangent modulus theory. Eccentrically loaded columns are also considered. Various empirical relations for evaluation of critical stresses for short columns are included in this chapter. Inelastic buckling of plates dealt in chapter 7 covers Stowell's theory and Bleich's theory. Both approaches are illustrated through application to rectangular plates subjected to uniaxial as well as biaxial loads.

Chapters 5 and 6 deal with elastic buckling of isotropic rectangular and circular plates, tapered plates, stiffened plates, polar orthotropic circular plates, thick rectangular plates and composite plates.

Postbuckling behaviour of plates is treated in chapter 8. Derivation of von Kármán's large deflection equations is presented in great detail. This final chapter ends up with two useful sections, one on ultimate compressive strength and the other on ultimate shear strength of flat sheets.

The text is well-organised and is designed for the undergraduate/graduate in aeronautical, civil, and mechanical engineering. It contains numerous worked-out examples and results are presented in non-dimensional form so as to be useful to the practising engineer. Several problems and references are included at the end of each chapter.

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Computer environments for children by Cynthia Solomon. The MIT Press, Cambridge, Massachusetts 02142, 1986, pp. 183, \$25.88

It is not the title *Computer environments for children* but the subtitle *Reflections on theories of learning and education* that more accurately reflects the contents of this book. There are no recipes for setting up ideal computer environments for children (to prepare them for the twenty-first century). There are instead some thought-provoking questions about computers in education, especially for children; questions which sometimes reach beyond the computer issue and force us to examine the very policies about education.

It was in the early sixties, with the advent of time-sharing computers, that it became

possible to think about introducing children to computers. Within a short span of two decades, due to the spectacular technological advances in the field of microelectronics, one finds millions of children interacting with computers today. That the computer can be a powerful and exciting educational aid has been widely recognised. How best can we use it?

The author, Dr. Cynthia Solomon, describes four different approaches in as many chapters. In fact, she discusses "an individual or a team, in each case considering the intellectual origins, the approach to using the computer and the extent to which this approach has penetrated school practice and has been evaluated". These four approaches have been further divided into two broader categories: Computer as an interactive textbook and Computer as an expressive medium.

In the first category, Patrick Suppes' work with the Computer Curriculum Corporation deals with the use of computers for drill, practice and rote learning. The author gives a detailed description of the project (the way mathematics curriculum was divided into blocks, the way the exercises were presented, etc.), its successes (increased scores of the students who underwent the course) and its shortcomings (only the students whose performance had earlier been below average were seen to have been benefitted the most). Though methodically prepared and extensively tested, one is left with a feeling that such a package of programs seems to put the computer to a most pedestrian use—simulating a very patient, untiring but unimaginative teacher. On the other hand, the approach adopted by R. B. Davis for the Madison Project (described as "Socratic Interactions and Discovery Learning" by the author) draws on the reality and uses the computer to bring the children's everyday experiences into the classroom. For example, while teaching about fractions, the child is asked to divide a handful of beans equally amongst their friends—except that the beans as well as the friends are present only on the computer screen! Undoubtedly the children would find this more fun than rote learning and because of that, they may learn the fractions much faster. The author gives examples of several attractive games (torpedo, car race, darts, etc.) to illustrate other concepts in mathematics (arithmetic operations, the number line, etc.). The goals of the project, as outlined, go far deeper than creation of pretty programs, however. The potential of the computer as a "flexible medium to create sets of materials for children to do mathematics in a creative manner" is to be exploited to help the student to acquire a wide range of abilities—from "discovering patterns in abstract situations" to "appreciating pure mathematics for its own sake". The students of education should find this part fascinating.

In the second category, Tom Dwyer ("Eclectism and Heuristic Learning"!) teaches the children about the computers, about programming and leaves them to carry out their own explorations. The metaphor of flying an aeroplane is very apt—the child should be instructed in the use of computers and programming till he can "fly solo". The language of choice has been BASIC, due to reasons mainly of availability and ease of learning. The children did seem to pick up the language quite fast and seemed to enjoy the programming projects. The author's criticism of this approach is on philosophical grounds. It is generally agreed that BASIC is not the best of the programming languages,

since it is not structured. As the author convincingly demonstrates, the program for a decision tree, written in BASIC, works perfectly, but the source code gives no clue whatsoever about the inherent hierarchical organization of such a tree. Should one, then, go all out to teach BASIC to the young children?

Perhaps the most radical of all is the approach by Seymour Papert. It is so broad in outlook and calls for so fundamental a change that it is impossible to capture its essence in this short review. To quote, "Papert ... sees most of present-day school mathematics as denatured and alienating and outside of child's concerns. He sees the computer as a way to create new learning conditions and new things to learn. He envisions the computer as a 'mathland', in which the computer becomes an instrument for children to talk in mathematics about their everyday life experiences and in which children learn mathematics as naturally as they learn to speak". The author has brought out the important aspects of Papert's work—LOGO, importance of debugging, use of the powerful ideas like procedures and recursions, etc—very clearly. Dr. Solomon's constant comparisons of the four approaches, though repetitious, helps the reader to understand the fundamental similarities as well as the differences from a proper perspective.

The last two chapters—Trends in practise and Computer educators—deal with more concrete matters. Based as they are on the author's detailed research as well as on the two decades of experience in teaching children about computers, they provide a very realistic picture of the way things are. One of the points which comes out very strongly is the inadequacy of the infrastructure—even in the United States, the average amount of computer time available per student is about 15–20 minutes per week! Such information will be crucial for a realistic planning of computer education in the Indian context. The perceptiveness and sensitivity shown by the author when describing the way children react to computers and programming is truly remarkable. Even the brief description of her experiences gives valuable hints for computer educators.

This book grew out of Dr. Solomon's doctoral thesis. This is quite evident from the style, especially of the first five chapters. These are written by an academician for academicians and the balance is more in favour of the terse and the esoteric rather than the simple. The last two chapters, on the other hand, have a more human touch and are considerably easier to understand, and yet as informative.

This is not a book for light reading. Only those seriously interested in the deeper issues of computer education for children would find it worthwhile to read through this thesis. For others who would like to give some thought to this topic, the last two chapters give a lucid account of how things are and what could be done to integrate the computer into the children's everyday learning environment. It is interesting to note that the excerpts from several reviews of the book (printed on the jacket) by scientists with impressive credentials are unanimous in their praise of the author for raising the deeper issues in this otherwise fashionable and trendy subject. Perhaps the most important contribution of the book is that it clearly outlines the areas of research in the field of computer education

for children, and emphatically brings out the need for such research for exploiting the full potential of the computer.

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