

the Board promulgates a policy which it thinks is in the best interests of the country, should approval be obtained from the Executive Branch before such a policy is announced?

Some Board members object to the constraints of this sort of administrative discipline, and at least in the past have felt that prior approval of this type should not be required. It might be reasoned that the director—who is a presidential appointee, who is on the federal payroll, and who is making a

career of federal service—is obviously subject to administrative discipline. But does the same reasoning apply to Board members? In fact, the question of giving testimony before a congressional committee itself has been raised. Must Board members offer only “approved” testimony? If so, this would seem to seriously weaken the Board’s voice in terms of the purposes for which it was established. In my opinion, the nation would best be served by making that voice stronger. Unless some provisions

are made to really strengthen the National Science Board, we are likely to witness a gradual shift of the control of national science policies and programs from the scientific community to the bureaucracy—with a consequent weakening and distortion of the whole scientific effort.

Reference and Note

1. V. Bush, *Science—The Endless Frontier*, 1945, reprinted by the National Science Foundation, Washington, D.C. (1960).
2. I have commented more fully on this matter in my letter to *Science* 155, 1489 (1967).

Extraordinary Sex Ratios

A sex-ratio theory for sex linkage and inbreeding has new implications in cytogenetics and entomology.

W. D. Hamilton

The two sexes are usually produced in approximately equal numbers. Fisher (1) was the first to explain why, under natural selection, this should be so, irrespective of the particular mechanism of sex determination. His rather tersely expressed argument has been clarified by subsequent writers (2) and seems to be widely accepted. In bare outline, the factor of parental care being ignored, it may be given as follows:

- 1) Suppose male births are less common than female.
- 2) A newborn male then has better mating prospects than a newborn female, and therefore can expect to have more offspring.
- 3) Therefore parents genetically disposed to produce males tend to have more than average numbers of grandchildren born to them.
- 4) Therefore the genes for male-producing tendencies spread, and male births become commoner.
- 5) As the 1:1 sex ratio is approached, the advantage associated with producing males dies away.
- 6) The same reasoning holds if females are substituted for males through-

out. Therefore 1:1 is the equilibrium ratio.

The argument is not affected by the occurrence or nonoccurrence of polygamy, or by any differential mortality of the sexes, provided this is uncorrelated with the sex-ratio genotypes.

More precisely, what has been called “Fisher’s principle” of the sex ratio states that the sex ratio is in equilibrium when, in the population as a whole, the totals of effort spent producing the two sexes are equal. If the totals are not equal, producers of the sex corresponding to the lesser total have an advantage.

This article is concerned with situations where certain underlying assumptions of Fisher’s argument do not hold. It will be seen that such situations must be quite widespread in nature. As regards ecological assumptions, for example, Fisher’s argument is restricted to the actually unusual case of population-wide competition for mates. A contrary case wherein the competition is local is discussed in some detail. In some features it has an unexpectedly close similarity to certain types of situations considered in the “theory of games.” Already the above outline seems to show that an individual supposedly able to choose the sexes of offspring would do best under natural

selection by selecting the extreme opposite to the current sex ratio of the population—that is, by producing a unisexual progeny of whichever sex was currently in the minority. This game-like feature, which has already led one writer (3) to refer to genetically determined sex ratios as “strategies,” in the sense of a play by the individual against the population, becomes accentuated as we proceed into circumstances of local competition.

Before considering local competition, however, it is convenient to discuss the consequences of failure of some of the genetic assumptions latent in Fisher’s argument.

Sex-Linked Drive under Random Mating

Fisher’s argument does apply to all cases where sex-ratio control is by genes acting in the homogametic sex, or in the female under the male-haploid system [contrary to some earlier statements of mine (4)], or by genes on the autosomes acting in the heterogametic sex. In all these cases the total number of the gene-bearer’s grandchildren is a true measure of the propagation of the gene. This is not so in the case of sex-linked genes acting in the heterogametic sex.

For simplicity of argument, suppose the male is heterogametic. Then grandchildren through daughters are obviously irrelevant to the fitness of a gene on the Y chromosome. This fitness is measurable entirely by the number of sons. Sex-ratio control in the male is effectively the same as genetic control over the relative success of the X-bearing and Y-bearing sperm in fertilization. Suppose the Y chromosome has mutated in a way which causes it always to win in the race to fertilize. A male with the Y mutant then produces nothing but sons. Provided these

The author is lecturer in genetics in the department of zoology and applied entomology, Imperial College, University of London, working at Imperial College Field Station, Silwood Park, Sunninghill, Berkshire, England.

sons, who also carry the mutant, cannot be in any way discriminated against in the unrestricted competition for mates (a situation which is implied if mating is random for the whole population), the Y mutant will have a constant selective advantage. As the mutant spreads, the population sex ratio will become more and more male-biased and the population itself will become smaller and smaller; finally the population will be extinguished, after the last

female has chanced to mate with a male carrying the mutant.

Figure 1a represents such an episode, in which the starting condition is one mutant-bearing male in 1000 males. On the basis of the admittedly severe assumption that females produce only two offspring each, it was found that in the 15th generation the expected number of females is less than one.

A similar extreme mutation on the

differential X chromosome occasions a similar theoretical disaster but brings it about much more slowly. This is partly because in this case selection is intrinsically slower. Unlike the Y, the mutated X chromosome is not exposed to selection in every generation, and, overall, as might be expected from the proportion of its generations that an ordinary X chromosome spends in males, its spread is about one-third as fast. In Fig. 2 the two types of transience are compared, and the transience of an autosomal gene causing fully effective meiotic or gametic drive is also shown. As might be expected, the speed of the autosomal gene is intermediate. The progress toward extinction due to a driving X mutant is delayed by the occurrence of polygamy. Indeed, so long as the males remain sufficiently numerous to fertilize all the females, the population should show accelerating expansion (Fig. 1b).

Cases of X-linked "drive" are not uncommon in wild populations of some species of *Drosophila*, and their potential threat to the species has been recognized (5). Cases of autosomal drive have been under study and discussion for some time (6). With perhaps one exception, mentioned below, no equally striking cases of Y-linked drive have been reported. Perhaps, in view of the general inertness of the Y chromosome, this is not surprising. It is surprising, however, that the exceptional latent danger to the species presented by this form of drive has received so little comment; I suggest (and to the best of my knowledge this is the first time the suggestion has been made) that it may help to explain why the Y chromosome is so often inert. A population in which a driving Y mutant was spreading could be saved by another mutation,

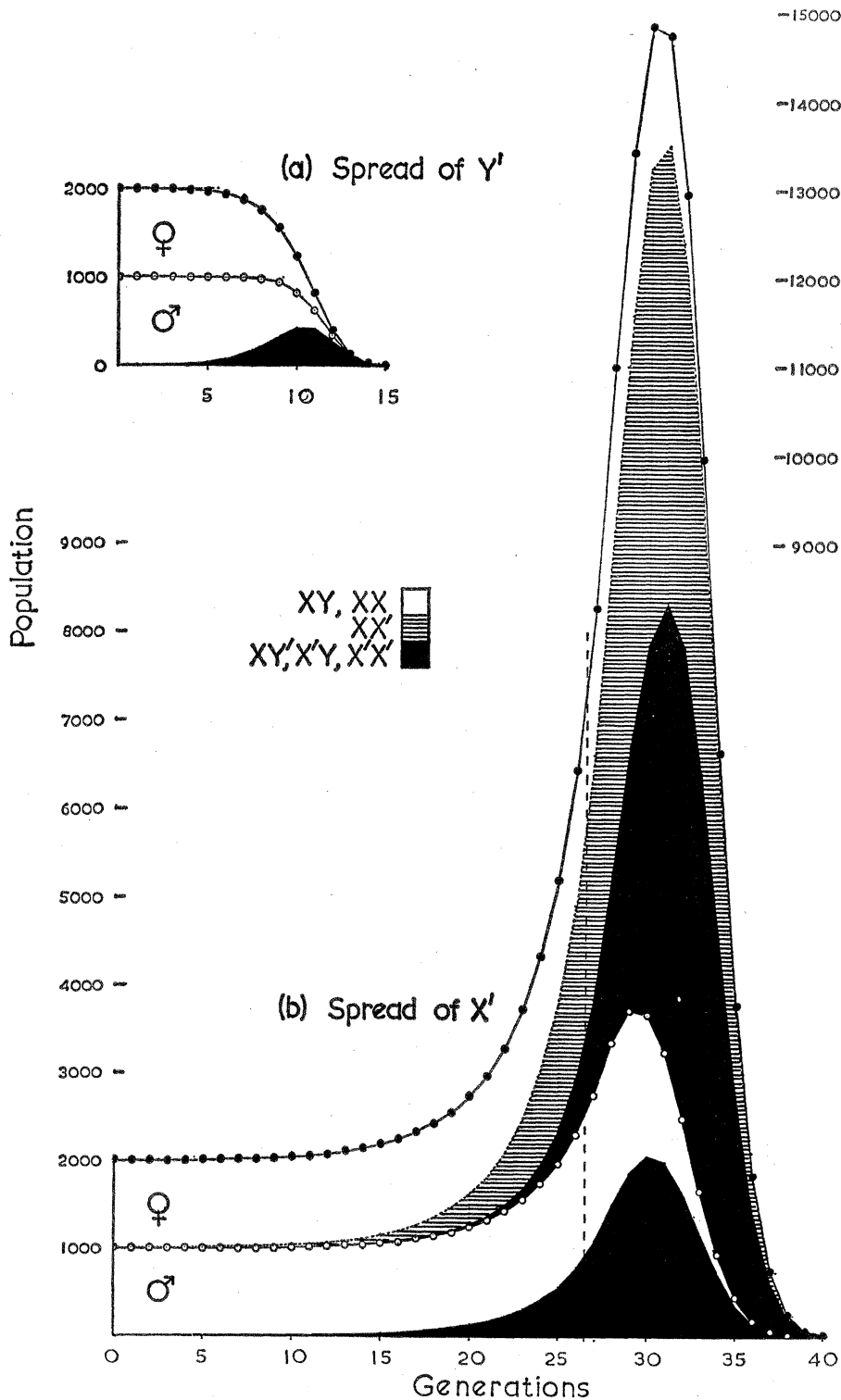


Fig. 1. Population and its distribution by sex and genotype in the course of natural selection of (a) a Y chromosome and (b) an X chromosome, having complete drive in spermatogenesis. Mating is random, and normal males give a sex ratio of $\frac{1}{2}$. It is assumed (i) that mated females have two offspring each, so that, before mutation produces the driving chromosome, the population is stationary, and (ii) that males can fertilize only two females each, so that, in (b), from the first generation in which the sex ratio is less than $\frac{1}{3}$ (generation 27), some females have no offspring because they are unmated. Both populations start with one chromosome of the driving type in 1000 chromosomes. Extinction is considered to occur after the first generation in which the expected number of females is less than one.

on an autosome or on the X chromosome, which was capable of inactivating the relevant region of the Y mutant. That such a mutation would spread follows from Fisher's principle. In doing so it would slow down (although it would never arrest) the spread of the Y mutant and, at the same time, would cover up its effect.

It seems probable that something like this has happened in the mosquito *Aedes aegypti*, if the genetic situation inferred by Hickey and Craig (7) is correct. In this case the "Y" is apparently a male-determining gene, certainly not a whole chromosome, and it seems that, in the strains where the driving Y mutant exists, there may be several different "X" alleles which restrain the action of the Y mutant in differing degrees. It is hybrid males from outcrosses of such strains that often give extreme male-biased sex ratios. All-male progenies were sometimes recorded.

Hickey and Craig have pointed out the potentiality of their effect for biological control. They did not attempt to demonstrate the capability for spread of their driving Y gene but did show in some experiments that it could maintain itself at high frequency, with consequent detriment to the experimental population. Some other experiments showed, however, a rapid masking of the sex-ratio effect. This may have been due to reconstitution of the restraining mechanism which operated in the paternal population. Clearly, if the view presented here is valid, a principle of application in biological control will involve repeated backcrossing of the hybrid male-producing males to females of the susceptible population. Unless this is done prior to liberation of male-producing males, some part of the genetic mechanism on other chromosomes which previously masked the sex-ratio effect (for example, a recessive gene) is likely to be introduced at the same time. It should be worthwhile to look for male-producing effects in racially hybrid males in other outbreeding species with male heterogamy, and also perhaps for genetical devices by which the Y chromosome could be freed from the inhibitory action of the rest of the genome. The implied method of biological control is in theory very powerful, since the mere seeding of a population with a few prepared males could cause its extermination or at least its reduction to a density where mating was no longer effectively random.

The fact that no other case like that of *Aedes aegypti* has yet been reported, in contrast to several cases of X-linked drive, accords with the drastic rapidity of spread of the driving Y mutant and its immediately adverse effect on reproductive potential. Presumably an outbreeding species cannot long continue to exist if it has a Y chromosome likely to mutate in this way. The same does not apply if the female is heterogametic. An extreme sex-ratio swing which is very suggestive of the spread of a driving Y chromosome has recently been reported in a butterfly population (8). As with the driving X chromosome under male heterogamy, such an event would be advantageous to the population at first. The frequent discovery of driving X chromosomes

in wild populations of *Drosophila* is not very surprising, although, in order properly to understand their existence in a permanent polymorphism, there has to be postulated either a severe disadvantage to females homozygous for the driving chromosome (9) or some basis of interpopulation competition, as Novitski (5) suggested and as is shown in the model given below.

Altogether, the evidence for the workability of the suggested differential evolution of the Y chromosome is good. There is evidence that genes and other chromosomes can suppress the "sex ratio" trait in *Drosophila* (10), that heteropycnosis may be a cytological manifestation of such inactivation (11), and that heteropycnotic regions sometimes do cause disturbed segregations

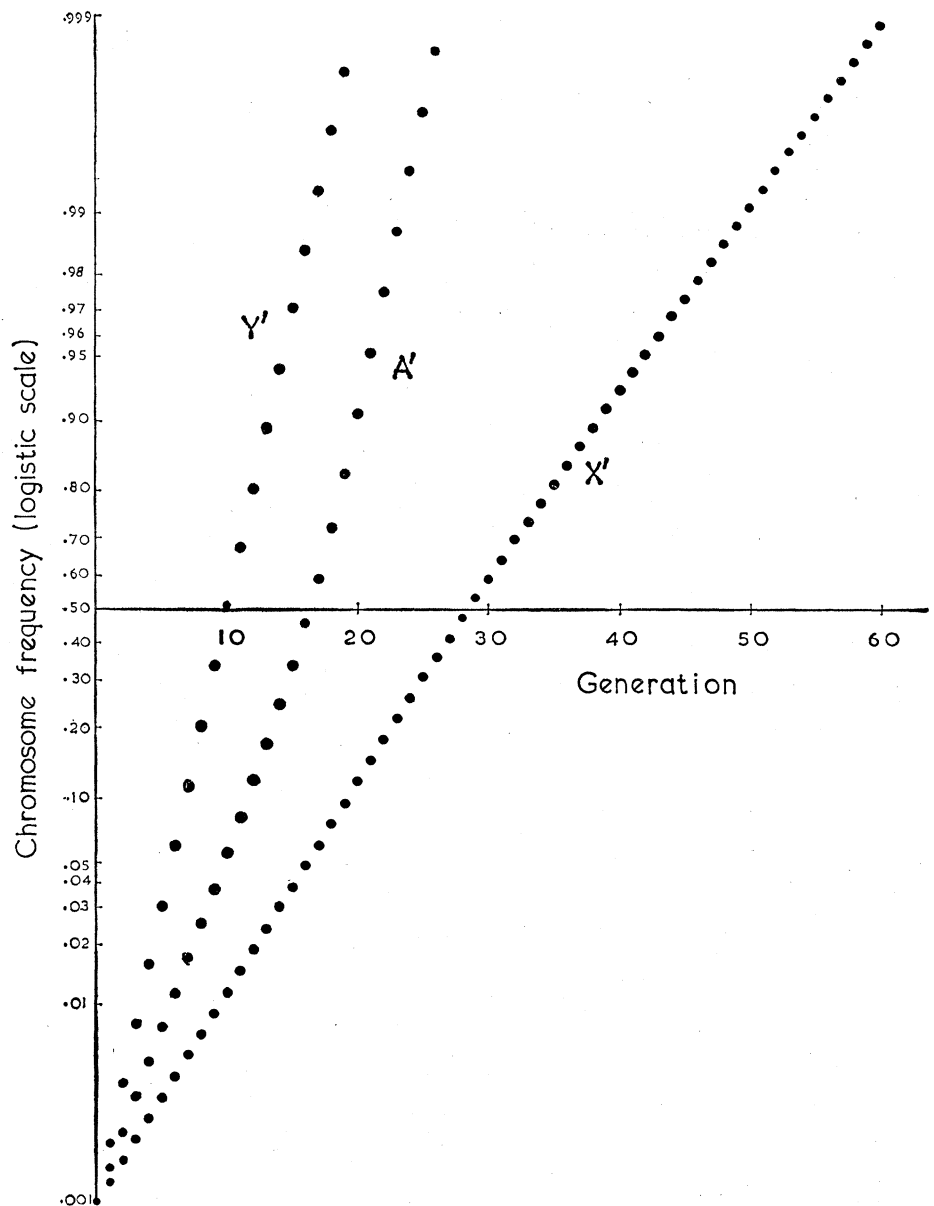


Fig. 2. Logistic plots showing the progress in frequency of occurrence of sex chromosomes (X' , Y') and an autosome (A') having complete drive in spermatogenesis. Each course starts with one chromosome of the mutated type in 1000 chromosomes.

(12). In general it is gametogenesis rather than fertilization that is the likely arena of the dysgenic effects that have been considered. Hickey and Craig show that their effect is probably due to events that either suppress production of X-bearing sperm or cause such sperm to degenerate, and McCloskey (13) has recently emphasized the extreme scarcity of evidence of gene activity in animal gametes in general. However, McCloskey admitted that his experiments with *Drosophila* could not exclude the possibility, significant for the present hypothesis, that genes in the main heterochromatic regions might be active in the sperm, and he also noted some hints that mammalian sperm may not be so inert genetically as the sperm of *Drosophila*. Therefore, just possibly the indications of high primary sex ratios in some mammals (14), and of higher activity of Y-bearing sperm in rabbits and cattle (15), are relevant evidence of a stronger tendency of the Y chromosome to evolve spermatid drive. Somewhat against this possibility, however, is the evidence, for plants (in which gene activity in the penetrating pollen tubes is well known), that it is the X-bearing pollen that tends to win under competitive conditions (16). This is understandable on the basis of Fisherian theory only if it is the genotype of the style that controls the race, for, as Lewis has pointed out, abundant pollination will usually imply that males are common in the neighborhood, so that to favor the production of females is the correct policy. With occasional pollination the sex ratio produced tends to be 1:1. This is, no doubt, the sex ratio of the pollen grains, but that a male-biased ratio is not in some way brought about from sparse pollination may be partly due to the factor of local competition, now to be considered.

Sex-Linked Drive with Local Competition for Mates

In a "viscous" population—that is to say, one where the individual can mate only with a rather permanent set of neighbors who tend also to be his relatives—it is clear that the initial spread of a driving Y mutant from the point where the mutation occurred will bring about a local collapse of population due to the lack of females, and vacant space will tend to be filled

by normal immigrants from surrounding areas. Thus some sort of equilibrium could occur.

Another biological situation in which the spread of the aggressive Y mutant is eventually checked is as follows. Free-moving females search for isolated food objects, or "hosts." Each host is colonized by a certain number and is eventually exhausted through feeding of the progenies. The subpopulation of adults reared on a host mates randomly *within itself*; no males successfully mate outside their own group. Inseminated females emigrate to take part in population-wide competition to discover new hosts. In this system, matings will be a mixture of sibmatings and outcrosses, the former becoming common when the number of females settling on a host is small. It is at once obvious that the driving Y mutant cannot supervene completely in such a population, provided the population is large and the females are fecund, for the grouping sets a limit to the extent to which a female's brothers can be outnumbered by the mutants among her suitors, and there always remains a finite chance that she will mate with a brother.

To facilitate further analysis of such a situation, let us suppose that always exactly n females settle on a host and that the progenies reared are equal. Suppose that there exist two types of Y chromosome, Y^a and Y^b .

Females accept only one insemination, so the host-seeking females will be of two types, according to the contents of their spermathecae: XY^a -bearing and XY^b -bearing, or, more briefly, type-a and type-b. Suppose these two types are constrained to give progenies in which males form fractions x_a and x_b of the totals. Such fractions are convenient measures of the sex ratio, and hereafter in this article all sex ratios are given in this form.

Consider the set of hosts which happen to be shared by r type-a females and by $n-r$ type-b females. The sex ratio, X_r , in the progeny of this set will be

$$X_r = [rx_a + (n-r)x_b]/n$$

Through fair competition for mates, a particular type-a female may be expected to be responsible for the spermathecal contents of a number of emigrant females proportional to

$$\frac{x_a}{X_r} (1 - X_r)$$

This may be called the Y-chromosome fitness in such a female in such a group. It is required to know whether the average for type a, taken over all such sets, is above or below the whole-population average for Y-chromosome fitnesses. This will indicate whether the Y^a chromosome is gaining or losing in frequency.

Consider therefore the $n-1$ associates of a type-a female selected at random from the whole set of those that have succeeded in finding hosts. Let F_r represent the probability distribution of the number ($r-1$) of type-a females among these associates. The average Y^a -chromosome fitness, W_a , is then seen to be

$$W_a = \sum_1^n F_r \frac{x_a}{X_r} (1 - X_r)$$

The general average for Y-chromosome fitness must be

$$W = 1 - X$$

where X is the sex ratio of the whole population. Explicitly,

$$X = px_a + (1-p)x_b$$

where p is the frequency of Y^a .

The selective advantage, E_a , of the Y^a chromosome with respect to the population average is

$$\begin{aligned} E_a &= W_a - W = \sum_1^n F_r \frac{x_a}{X_r} - x_a - (1 - X) \\ &= \sum_1^n F_r \frac{x_a}{X_r} + (1-p)(x_b - x_a) - 1. \end{aligned} \quad (1)$$

Differentiating, we obtain

$$\frac{dE_a}{dx_a} = \frac{1}{n} \sum_1^n F_r (n-r) \frac{x_b}{X_r^2} - (1-p).$$

When $x_a = x_b = c$, this reduces to

$$\frac{1}{nc} \sum_1^n F_r (n-r) - (1-p),$$

which is zero only when

$$c = \frac{n - \sum_1^n F_r r}{n(1-p)}. \quad (2)$$

Now consider the simple and plausible case where the settling on hosts is random. The distribution of r will be binomial and so will be the distribution of the number of a-type associates of the randomly selected a-type female:

$$F_r = \binom{n-1}{r-1} (1-p)^{n-r} p^{r-1}.$$

Then

$$\sum_1^n F_{r,r} = (n-1)p + 1$$

and Eq. 2 becomes

$$c = (n-1)/n. \quad (3)$$

I am satisfied, although I have not strictly proved, that this is indeed the only "unbeatable" sex ratio for the situation: the Y chromosome that produces it has a selective advantage over any other, whatever the current gene frequency.

The above model equilibria do not seem very realistic. Species in which the sex ratio comes to be controlled by Y-linked drive probably become quickly extinct even if they are protected to some extent by grouping of the sort described. Unfortunately no general analysis of the less drastic situation in which there is gametic drive by the X chromosome has been achieved. However, deterministic computer simulation of the population genetics for $n = 2$ shows that the "unbeatable" ratio is between 0.070 and 0.072. This result must also hold if control of the sex ratio depends on the genotype of the male in male haploid species. Such control is certainly unusual, but it seems to occur in the eulophid *Dahlbominus fuscipennis* (17). This is an inbreeding species, and its sex ratio, about 0.09, is of the order expected. But the case is peculiar, and the underlying theory still has a major gap in that it is not known whether the "unbeatable" sex ratio for $n = 3$ is above or below 0.07. In view of the possible relevance to the X-linked sex-ratio effects in *Drosophila*, this point deserves further study.

Although male-haploid inheritance is identical to the sex-linked type, from the point of view of sex ratios a difference enters if the males fail to fertilize all the females. This difference is due to the ability of the females, in cases of male haploidy, to produce all-male broods parthenogenetically. With sex ratios as extreme as those just mentioned, such failure of polygamy would not be surprising. In the case of random mating it is known to introduce a tendency toward unstable alternation of sex ratios which is quickly disastrous if the mated females are being forced to produce only female offspring (18). From this aspect, also, the breeding structure of the model should give a measure of security.

Non-Sex-Linked Control with Local Competition for Mates

Apart from the supposition of sex-linked control, the above model contravenes Fisher's tacit assumption of unrestricted competition for mates. It is interesting, therefore, to consider what this same model situation implies when this is the only assumption broken—that is, when control of sex ratio is of one of the kinds which has been noted to give the relationships of Fisher's principle under the condition of panmixia. The model breeding structure forces sons into competition with one another, so that although there may be, in general, a shortage of males, production of males does not necessarily pay off in terms of grandchildren: whether it does so depends on the sex ratios of offspring produced by other females of the group.

An approximate analysis can follow the lines of the foregoing analysis very closely, provided it is supposed that there are only two types of female, A and B, and that

$$\text{fitness} \propto N \text{ of inseminations by sons} + N \text{ of daughters.} \quad (4)$$

Obviously such a simple scheme cannot give a proper genetical representation of a situation, but, as mentioned below, it has been found to give a fair correspondence to the genetical model for $n = 2$, while, for the panmictic case, it has already been accepted in the literature (19).

Using these assumptions and obvious developments of our notation, we have

$$W_A = \sum_1^n F_r \frac{x_A}{X_r} (1 - X_r) + (1 - x_A)$$

Since we are now concerned with the production of daughters as well as of sons, the mean fitness in the population must be taken as $2(1 - X)$.

Therefore

$$E_A = \sum_1^n F_r \frac{x_A}{X_r} + 2(1 - p)(x_B - x_A) - 1.$$

The foregoing equation is the same as Eq. 1 except for the factor 2 in the second term. Hence, by just the same argument we can arrive at the unbeatable sex ratio

$$(n-1)/2n \quad (5)$$

for the case of random association.

As type-a increases, the situation undergoes a particular kind of approach

to the Fisherian case and, correspondingly, the formula shows the unbeatable ratio tending to approach $1/2$.

At the other extreme, the case $n = 1$ obviously corresponds to a system of completely sibmated lines. That the theoretical equilibrium ratio is then zero merely implies that a female's advantage depends wholly on the number of fertile emigrant females she can produce from her host. It is not in her interest to produce more males than are necessary to ensure the fertilization of all her daughters.

A Biofacies of Extreme Inbreeding and Arrhenotoky

Among small arthropods, wherever reproduction is quite regularly by brother-sister mating there seems to be extreme economy in the production of males, as predicted. Most of the cases which have been noted are listed in Table 1.

It is probable that all of them reproduce by arrhenotoky—that is, by the process in which males are derived always, and only, from unfertilized eggs. This process has been found to be associated with haploidy of the males in all cases that have been investigated cytologically; therefore, male haploidy is a strong supposition for most of the cases in Table 1. However, with a few species not only is there no direct evidence that males are usually impaternate but also there is none that female-to-female parthenogenesis (thelytoky) does not occur. But in view of the general conformity of such cases (for example, the fig insect and the moth ear mite) with the others, and of what is known of related species, it will be surprising if they turn out to be not normally arrhenotokous.

Taken together, the data suggest the outline of an ideal extreme biofacies which may be described as follows:

1) The primary sex ratio is spanandrous—that is, females greatly preponderate.

2) Reproduction is arrhenotokous.

3) There is at least one male in every batch of offspring.

4) There is gregarious development, as a group of siblings, from egg to adult.

5) Adult males eclose first and can mate many times.

6) Mating takes place immediately after (or even before) eclosure of adult females.

7) Males are disinclined, or unable, to emigrate from the batch.

8) Females can store sperm; one insemination serves to fertilize the whole egg production.

Arrhenotoky is a mode of reproduction that readily permits the production of biased sex ratios, with con-

trol of the sex ratio normally dependent on the phenotype of the mother. Therefore it seems either that male-haploid organisms have found themselves pre-adapted for life in niches of the sort characterized by the model or that the evolution of male haploidy has actually accompanied, in several independent

lines, an evolutionary trend to occupy such niches. The latter alternative seems not unlikely for the ancestors of the male-haploid groups included in Table 1, although undoubtedly many of the cases in the Hymenoptera must be derived secondarily from relatively outbreeding species.

Table 1. Insects and mites having usual sibmating combined with arrhenotoky and spanandry. Blanks are left where clear data are not available; in some cases equivocal evidence is mentioned in the notes.

Family, genus, and species	Host	Number in typical batch of progeny		Tendency toward inclusion of one male per batch	Usual site of mating	Functional wings present		Males pugnacious	Thelytoky known in species (s), genus (g), family (f)	References and notes
		♂	♀			♂	♀			
Agaontidae <i>Blasophaga psenes</i>	Wild fig	22	235		In fig	—	+		—	(45)
Torymidae <i>Monodontomerus</i> spp.	Bee larva	1	12	+	In host cell	+	+			(46)
Pteromalidae <i>Nasonia vitripennis</i>	Fly pupa	2	19		Just outside host	—	+		s	(36, 47)
Encyrtidae <i>Dusmetia sangwani</i>	Scale insect	1	5	+	In host	+	—		f	(48)
Thysanidae <i>Thysanus elongatus</i>	Parasitoid larvae	1	5			+	+		g	(49)
Eulophidae <i>Melittobia acasta</i>	Pupa of fly or aculeate	1	46	+	In host cocoon	—	+	+	f	(36, 50)
<i>Melittobia chalybii</i>	Aculeate pupa	2	50	+	In host cocoon	—	+	+	f	(51)
<i>Pleurotropis parvulus</i>	Leaf-mining beetle larva	4	13	+	Just outside leaf-mine				f	(52)
Trichogrammatidae <i>Trichogramma semblidis</i>	Alder fly egg mass	10	60		On host		+		g	(53)
<i>Prestwichia aquatica</i>	Aquatic insect egg	1	8	+	In host	—			s?	(54)
Elasmidae <i>Elasmus hispidarum</i>	Leaf-mining beetle larva	4	8	+	Just outside leaf-mine			+		(52, 55)
Mymaridae <i>Caraphractus cinctus</i>	Water beetle egg	{5*	25*	+	Underwater near host	+	+		f	(42)
<i>Anaphoidea calendrae</i>	Weevil egg	1†	6	+		+	+		f	(56)
<i>Anaphoidea nitens</i>	Weevil ootheca	1	3	+	Just outside host		+		f	(57)
Scelionidae <i>Telenomus fariai</i>	Bug egg	1	6	+	In host				g	(58)
<i>Asolcus</i> spp.	Bug egg mass	8	40	+	On host	+	+	+	f	(37, 59)
Bethylidae <i>Cephalonomia quadridentata</i>	Beetle larva or pupa	1	3	+	In group of cocoons		—		f?	(60)
<i>Sclerodermus immigrans</i>	Beetle larva	4	20		On mass of cocoons	+	—		s?	(61)
<i>Perisierola emigrata</i>	Moth larva	2	8		In group of cocoons				f?	(62)
Scolytidae <i>Xyleborus compactus</i>	Twig tissues	1	9		In parent gallery	—	+		—	(29)
Thripidae <i>Limothrips denticornis</i>	Grass plant	3	20	+	Grass, leaf sheath	—	+		f	(63)
Laelaptidae <i>Myrmonyssus phalaenodectes</i>	Moth				Moth ear	—	—		—	(64)
Pyemotidae <i>Pyemotes ventricosus</i>	Mother	4	86	+	On mother	—	—		—	(52)
<i>Siteroptes graminum</i>	Mother	7	140	+	In mother	—	—		—	(65)
<i>Acarophenax tribolii</i>	Mother	1	14	+	In mother	—	—		—	(35)
Tarsonemidae <i>Tarsonemoides</i> spp.	Mother	5	65		In scolytid's egg niche	—	—		—	(66)

* In *Dytiscus* egg. † In *Agabus* egg.

No clear example of the biofacies has been found in the literature on arrhenotokous aleurodids and coccids. For the coccids, an independent and detailed theory of the evolution of male haploidy has already been proposed, by S. W. Brown (20). This is based on an "island" breeding structure, with random mating within the almost-isolated subpopulations, and the fact that all female coccids are wingless while males are often winged certainly suggests random mating. The very complex chromosome cycles known in various fungus gnats of the genus *Sciara* all have a common resemblance to the typical situation of male haploidy in that (i) virtually no chromosomes of paternal origin are passed on by a male, and (ii) the sex of an embryo depends on some influence transmitted by its mother (21).

Although all four combinations of the winged and wingless condition according to sex are known in the Sciaridae, cases in which the female alone is wingless are more numerous than the converse cases (22); in this respect the group tends slightly toward the condition of the coccids. Furthermore, almost entirely unisexual broods are characteristic of some species, and it is clear that, in these, outbreeding must result. It fits well with Fisher's principle that the two types of female, arrhenogenous and thelygenous, which exist in these cases, are thought to be themselves produced according to a simple backcross mechanism which ensures their numerical equality and, consequently fixes the sex ratio at $\frac{1}{2}$ (23).

Thus, the Sciaridae, like the Coccidae, tend to support the view that the evolution of male haploidy can take place under relatively panmictic conditions. Nevertheless, with the Sciaridae, the decaying plant bodies and fungi on which the larvae feed are hosts of the kind specified in our model, and there is one report (24), concerning *Sciara semialata*, of a combination of characters very suggestive of the biofacies, although not in its extreme form. These characters were a sex ratio of about $\frac{1}{4}$, winglessness of males only, and the *Sciara* habit of migrating in a compact column prior to pupation. Furthermore, facts which similarly suggest the biofacies, although somewhat less strongly, are available for gall midges of the related family Cecidomyiidae (25), and this family has unusual chromosome cycles resembling those of the Sciaridae.

Although it is clear from Table 1 that winglessness in the male sex alone

is rather characteristic of the biofacies, the opposite combination is not so rare as might have been expected. Three species are listed in Table 1 which fit quite well in most respects but have winged males and wingless females. I see no simple explanation of this anomaly, but in any case it hardly affects the general correspondence, since, from the accounts on which these listings are based, it is clear that sibmating usually does occur.

Sex Ratios with Polygyny

It is frequently suggested that biased sex ratios are adaptations of the populations that manifest them. In particular, the evolutionary ability to economize in the production of males to the point that gives maximum capacity for increase (an ability which, according to the model, is restricted to sibmating lines) is sometimes imputed to any population, whatever its breeding structure. In one sense the idea of adaptation for the benefit of the population is even less secure than that of adaptation for the benefit of the species. It is true that a population consisting of numerous subgroups has many potential sites for "mutation," and that "mutation" by genetic drift (for example, the complete transience of an altruistic gene) is distinctly possible if the subgroups are small (26). Species, on the other hand, can at least reproduce in isolation from their competitors. The extent to which populations can do so without losing identity through hybridization is not at all clear. As regards sex ratio, even occasional outbreeding should cause the breakdown of any population adaptation. Vagrant males arriving in the predominantly female groups can so effectively propagate the genes which caused their own production that male-producing tendencies must spread. This is the essence of Fisher's principle. Accordingly it is not surprising to find that highly polygynous species with outbreeding habits do not have female-biased primary sex ratios. In polygynous mammals and birds a nonbreeding surplus of males is commonly observed during the breeding season, and, in mammals at least, the sex ratio at birth may be actually male-biased.

With insects, evidence on this point might be expected to come from the scolytid bark beetles. Chararas (27) gives a classification that is useful by biological criteria. First, he divides the

group according to whether mating takes place prior to dispersion from the larval host or after arrival at the new host; second, he subdivides the latter group according to whether the males are usually polygynous or monogynous in the new borings.

All three systems occur in the scolytid subfamily Ipinae. The widest survey of representatives of the first system is given by Browne (28), who calls it the system of "extreme polygamy." Polygamy is extreme, but, since this follows from the fact that males are produced in much smaller numbers than females, *spanandry* seems a better term, and is used here. In all species of the tribes Xyleborini, Eecopterini, and Webbini for which Browne gives data, the males are not only relatively few from birth but are also flightless, short-lived, and often blind. Obviously this system closely corresponds to the "extreme biofacies" discussed above; some of the facts for *Xyleborus compactus*, the only species of these tribes for which arrhenotoky has been established (29), are given in Table 1.

With the other two groups considerable outbreeding is expected. Therefore, according to Fisher's principle, a sex ratio of $\frac{1}{2}$ should occur, irrespective of polygamy. This seems to be generally the case. According to Browne, in the Crypturgini, while *Poecilips gedeanus* clearly has the spanandrous system (only 21 males were observed among 196 beetles reared in 18 broods), *Carpinus perakensis* has typical "monogamy" (28): "The young adult bores directly out from its pupal cell"; the male is not degenerate and probably mates with the female in her incipient new gallery, where he subsequently takes part in caring for the nest; and "among 58 young adults examined, 26 were male." It is implied (28) that the sex ratio of $\frac{1}{2}$ holds generally with monogamous species, and other authors confirm this (27).

With the Ipinae of the third group the male flies first to the new host, where he cuts a nuptial chamber. In response to the male's attractant scent, several females (but not more than eight) colonize the nuptial chamber of a successful male, are mated by him, and construct radiating egg galleries. Sex counts show a primary sex ratio of $\frac{1}{2}$ (27, 30); I know of only one possible exception (31). What happens to the surplus males is in no case entirely settled. Probably their numbers are somewhat reduced by the greater hazards involved in their pioneer role,

but, at the same time, there is evidence that many males fail to attract any mate and die as bachelors (27, 30).

With bark beetles of the hylesine genus *Dendroctonus* the situation is rather less clear. *Dendroctonus frontalis*, which is monogamous, has a primary sex ratio of $\frac{1}{2}$ (32). So does *D. pseudotsugae*, which is slightly polygamous (33). For *D. monticolae* a sex ratio of about $\frac{1}{3}$, both before eclosure and after attack, has been given, on the basis of numerous counts (34). The system of *D. monticolae* suggested that

some mating might take place before dispersal, since the "polygamy" amounted to the observation of some monogamous pairs and some lone but inseminated females. But Reid found that, in fact, less than 1 percent of the females had mated before dispersal. Such a proportion of inbreeding certainly could not explain the bias in the sex ratio, but perhaps it was not typical. Another species, *D. micans*, is quite clearly on the road to inbreeding and spanandry. In this case the social biology seems closely similar to that of *Xyle-*

borus, except that the sex ratio is less extreme and males are not degenerate. At least very occasionally the males of *D. micans* fly to join the female in the new gallery (27). Evidently, as a whole the Scolytidae support the view that polygamy is not associated with primary sex ratio bias unless there is also inbreeding.

Thelytoky

Browne remarked that "the evolutionary trend in the extremely polygamous Scolytidae appears to be towards the elimination of the male." He considered, however, that the occurrence of thelytoky in the group was by no means proved. There is no doubt that in the Hymenoptera similar trends have ended in thelytoky in many different evolutionary lines. From an evolutionary point of view, when sibmating is invariable, the sexual breeding system, arrhenotokous or otherwise, gives none of the usually cited advantages over asexual reproduction; it is in effect already a tree whose branches all are, or tend quickly to become after each mutation, completely homozygous. Therefore, in a case of the extreme biofacies, nothing of immediate importance is lost by a changeover to thelytoky, while convenience and perfect economy can be gained. Table 1 shows roughly the extent to which thelytoky occurs in taxa related to the species listed.

As noted above, the argument leading to $(n-1)/2n$ as the "unbeatable" sex ratio when genetic control is by females cannot be expected to apply ex-

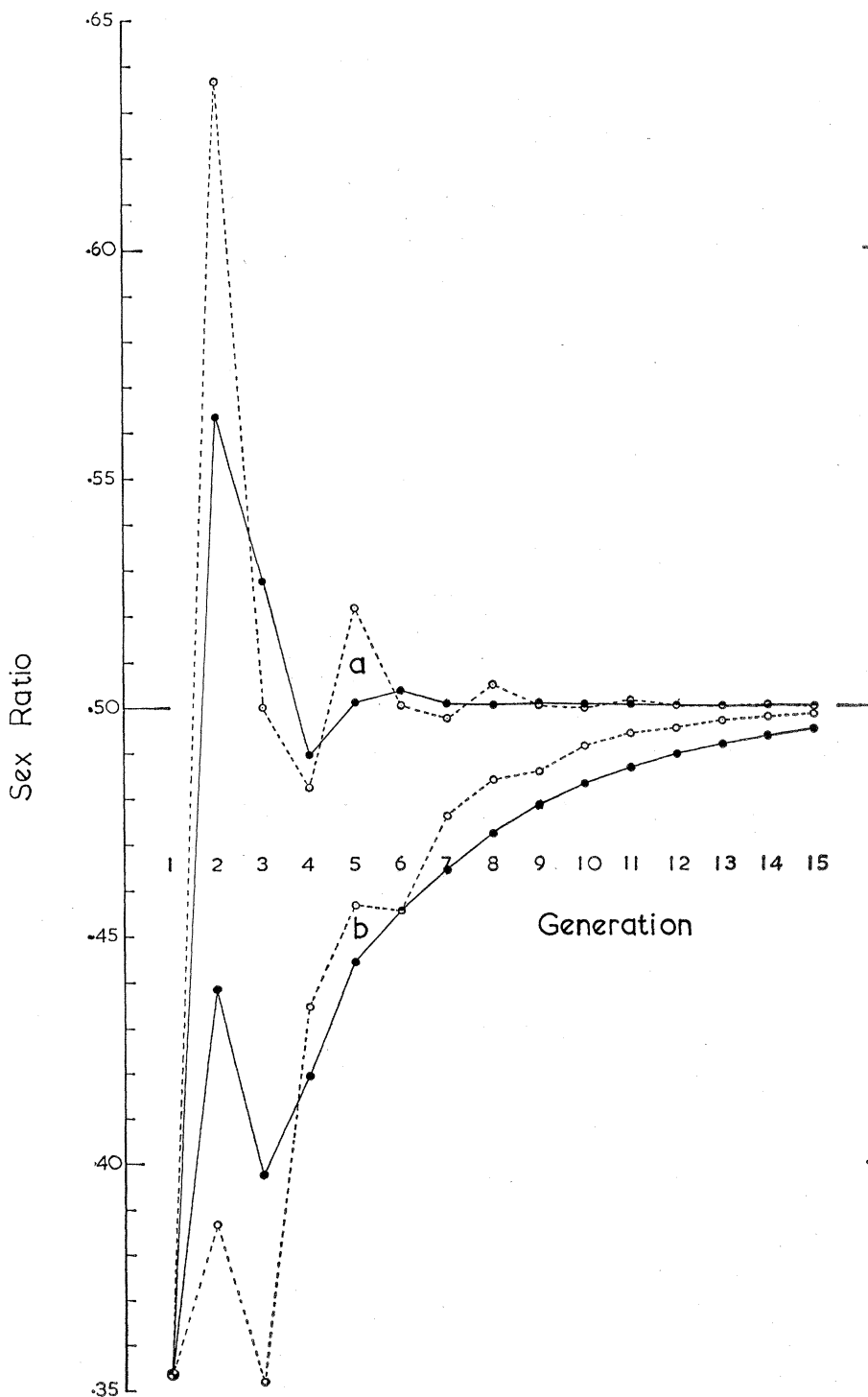


Fig. 3. Equilibration of population sex ratio at $\frac{1}{2}$, under conditions of random mating. In all cases, control of the sex ratio is by the female, and it is assumed that the three genotypes GG, Gg, and gg give sex ratios 1, $\frac{1}{2}$, and 0, respectively. Dashed lines represent male haploids. Equilibrium frequencies of the genotypes GG, Gg, and gg are known, by analysis, to be as follows: in females, $\frac{1}{2}[(2)^2-1]$, $2-(2)^{\frac{1}{2}}$, and $\frac{1}{2}[(2)^{\frac{1}{2}}-1]$; in diploid males, $\frac{1}{2}$, $(2)^{\frac{1}{2}}-1$, and $1\frac{1}{2}-(2)^{\frac{1}{2}}$. For females, the equilibrium under male haploidy is the same; for males, it is G, $1/(2)^{\frac{1}{2}}$, and g, $1-1/(2)^{\frac{1}{2}}$. Runs were started by disturbing equilibrium populations as follows: males were left undisturbed; for (a), all female heterozygotes were removed; for (b), all GG and most Gg females were removed, leaving 1 Gg for every 999 gg. Under male haploidy the approaches to equilibrium are faster and less even; but in case (a) the final approach to the equilibrium sex ratio is from above—it is not oscillatory (67).

actly even to the simplest genetical system of inheritance. Therefore, to gain some idea of how reliable the formula may be expected to be, the case $n = 2$ has been investigated by simulation on a computer. The model is deterministic, the sexual system is male-haploid, and only two alleles are present. The behavior of the model was found to be complex, and here only the results with obvious bearing on the unbeatable ratio are mentioned. When sex ratios 0.23, 0.22, and 0.21 were ascribed to the three female genotypes GG, Gg, and gg, respectively, from any starting frequency the population went slowly homozygous for g. When the ascribed ratios were 0.22, 0.21, and 0.20, it went slowly homozygous for G. When the ratios were 0.225, 0.215, and 0.205, it was apparent that the sex ratio would equilibrate between the two latter values. Thus, the unbeatable sex ratio seems to lie between 0.215 and 0.205. Numerous other runs of the model, with a wide variety of trios of sex ratios, gave no results contradictory to this view.

It is not understood why the unbeatable ratio differs from $\frac{1}{4}$ in this direction. There seems no reason, however, to think that the discrepancies in cases $n > 2$ are any worse than those in the case $n = 2$, for it is known that when n is infinite, corresponding to panmixia, the formula correctly gives the ratio as $\frac{1}{2}$.

It would be interesting to see how some other characteristics of the model, besides the unbeatable ratio, alter as n is increased. In the case of panmixia, if a population sex ratio of $\frac{1}{2}$ cannot be attained homozygously, it is yet established as an equilibrium, provided of course that the range of genotypic sex ratios covers this value. This is shown in the runs of the appropriate deterministic model which are graphed in Fig. 3. The outcome is different with the model for random settling in pairs. Thus, in a run in which the female genotypes were assigned sex ratios 0.4, 0.25, and 0.1, the equilibrium sex ratio was 0.175 [$p(G) = 0.25$]. With ratios 0.3, 0.2, and 0.1, there was a stable equilibrium sex ratio at 0.267 [$p(G) = 0.835$]; but it was evident that for some $p(G)$ between 0.888 and 0.999 there was also an unstable equilibrium.

Although the theoretical position is even less clear for $n > 2$, the ratio now lies, at least in some respects, within known bounds. Since the great majority of recorded sex ratios of

Hymenoptera are in the range $\frac{1}{4}$ to $\frac{1}{2}$, it is thought likely that the model does at least exemplify the forces that are operating.

Occasional Outbreeding; Sex Ratio Games

Among the species listed in Table 1, *Acarophenax tribolii* (35) is the one most likely to conform, in respect of sibmating, to the ideal biofacies. The males of this species usually complete their life cycle, and die, before they are born. In general the lives outlined in Table 1 are not so secluded that outbreeding could not occur. For instance, not all mating of *Siteroptes graminum* takes place before the rupture of the maternal hysterostoma; galleries of *Xyleborus* sometimes coalesce; and so on. Pugnacity of males is a clear independent indication that outbreeding occurs, either through migration of males or through multiple settling as in the model situation. The males could hardly have evolved fighting instincts if their rivals were always of identical genotype, as brothers would be in a long sibmated line. The extreme pugnacity of *Melittobia acasta* males (36) must indicate that it is quite common for two females to attack the same host. With *Asolcus* both sexes are pugnacious. The possessive fighting of the females when parasitizing new hosts (37) would tend to prevent multiple settling—although not very effectively, to judge from the behavior described. But the pugnacity of the males must, on the contrary, tend to cause outbreeding, since all but one of the males released from a batch of host eggs are driven away and must attempt to acquire sexual ownership of other batches. It is doubtless quite possible for them to do so if they find batches where emergence has not yet begun. Thus the pugnacious behavior must both reflect and aggravate the biological need for it.

The somewhat anomalous cases, already mentioned, wherein the male is winged and the female is wingless may be interpreted rather similarly. With *Dusmetia sangwani* and *Cephalonomia quadridentata*, occasional outbreeding is encouraged not only by the males' ability to fly but also by the not uncommon occurrence of all-female groups. In *C. quadridentata*, Van Emden (38) recorded, among 108 groups of progeny from females known to have mated, 30 which were wholly female and, as

if to balance this, nine which were wholly male. In the same record there were 59 groups which had just one male in an otherwise female group; statistically, this pattern, the ideal extreme spanandry, is still very distinctive. But from this and other cases in Table 1 it is evident that the typical occurrence of such extreme ratios does not necessarily imply perfect conformity with the biofacies in other respects.

The model analysis is not applicable to the sex-ratio problems arising from the intrusion of occasional migrant males. In essential features it is applicable to the problem of occasional double parasitism by females, and some recently described actual cases perhaps provide the best evidence yet obtained that, in an evolutionary sense, parasitoid species do really play the sort of sex-ratio game that is suggested by the model.

In a number of parasitoids it has been noted that more males are produced in laboratory culture than in the wild (39). The theory shows that, if crowded conditions of mass culture lead to an increase in outbreeding and if the parent sample contained sufficient genetical variation in sex-ratio tendencies, there could be rapid selection of the more-male-producing genes and shift of the general sex ratio toward $\frac{1}{2}$. However this may be, several comparative studies have shown a more distinct phenomenon—that the sex ratio rises immediately when females are kept in crowded cultures. In some such cases (see, for example, 40) experiments indicate that this rise is due, at least in part, to the greater survival of male larvae under conditions of superparasitism. But recently cases have been reported in which a female, on being crowded or on detecting previous parasitism, seems to alter her oviposition behavior so as to produce a higher proportion of unfertilized eggs. Wylie (41) has shown that this happens in the case of *Nasonia vitripennis*. The normal sex ratio is variously given as 0.10 to 0.30, and this is one of the cases where, under conditions of superparasitism, more male larvae survive. In spite of this usually obscurative factor, by manipulating eggs so as to prevent overparasitization, Wylie showed that females laid more male eggs in response both to the detection of previous parasitism and to the simultaneous presence of other individuals walking over the host, especially if these others were females. When both factors operated together, a sex ratio of 0.59

was obtained, as against 0.20 in the controls. More tentatively, Jackson (42) reached similar conclusions with *Caraphractus cinctus*. The factor of differential mortality could not be controlled in this case, and it must be admitted that, on the basis of the results published, the effect in this case does not seem to have been established absolutely. The response appeared to be connected with crowding of the adults and not with perception of previous attack, even though an experienced female certainly could detect such attack, as Jackson showed.

In these species, double parasitism, at least, must certainly occur occasionally in the wild. From the analysis given above it should be evident that double parasitism confronts the female parasitoid with a difficult sex-ratio problem. In the way in which the success of a chosen sex ratio depends on choices made by the co-parasitizing females, this problem resembles certain problems discussed in the "theory of games." In the foregoing analysis a gamelike element, of a kind, was present and made necessary the use of the word *unbeatable* to describe the ratio finally established. This word was applied in just the same sense in which it could be applied to the "minimax" strategy of a zero-sum two-person game. Such a strategy should not, without qualification, be called optimum because it is not optimum against—although unbeaten by—any strategy differing from itself. This exactly is the case with the "unbeatable" sex ratios referred to. But whereas in the foregoing cases the "game" could be construed only rather artificially, as occurring between successive mutations acting rigidly in the statistical structure of the population as a whole, we are now concerned with a refined version which is very realistically gamelike. Ability to adjust the sex ratio according to clues given by the immediate situation is undoubtedly potentially advantageous, and it leads to individual females behaving as players in a literal sense. As an illustration, let us consider a hypothetical situation which is simpler than the situations which parasitoids like *Nasonia* and *Caraphractus* actually face.

Suppose parasitism can be double but no higher than double; that double parasitism brings no extra mortality; and that the parasitoid must lay all its eggs in the one host. All egg batches should then be of the same size, and the actual size, if it is not too small,

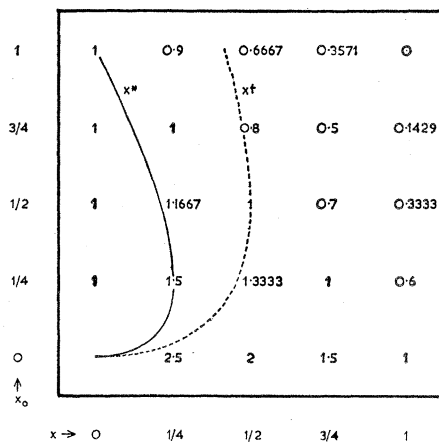


Fig. 4. Sex-ratio-dependent fitness in a pair. Numbers in the box are values of expression 6, showing the fitness of a female using sex ratio x when her partner uses x_0 . The fitness value at 0,0 is indeterminate; if sex ratio zero means strictly "no males produced," the value actually must be between 0 and 1; but if it means merely "extremely few males produced," the value depends on the ratio $x:x_0$ and on the male's ability to fertilize a large number of females—the theoretical upper limit of the fitness value is 3. The solid and dashed lines correspond to Eqs. 7 and 8, respectively; their significance is explained in the text.

can be left out of the argument. Suppose the parasitoid is ideally gifted and can detect not only previous parasitism but also the sex ratio (x_0) of the eggs previously laid. If it lays its own eggs to give a sex ratio x , we find, from relation 4, that its fitness is proportional to

$$\frac{x}{x + x_0} [(1 - x) + (1 - x_0)] + (1 - x) \quad \text{or}$$

$$1 - 2x + \frac{2x}{x + x_0} \quad (6)$$

By differentiating, the value of x which gives the highest possible value for expression 6 is found to be given by

$$x^* = (x_0)^{\frac{1}{2}} - x_0. \quad (7)$$

Thus, the highest value x^* itself can take is $\frac{1}{4}$, corresponding to $x_0 = \frac{1}{4}$. For $x_0 > \frac{1}{4}$, $x^* < \frac{1}{4}$; for $x_0 < \frac{1}{4}$, $x_0 < x^* < \frac{1}{4}$. Hence it is evident that, through trial and error, two naive players would quickly learn that constant playing of $\frac{1}{4}$ was the optimum-yielding strategy.

In the "game" under discussion, however, the play of $\frac{1}{4}$, although ultimately optimum-yielding, should be described as "unexploitable" rather than "unbeatable." This distinction arises because the game is not "zero-sum." Biologically each parasitoid succeeds

in so far as it contributes to the gene pool at large. Evolved instincts will cause it to seek the highest payoff in the sense of expression 4; except, perhaps, when the population is very small, it could have no interest simply in outscoring its co-parasitoid. But if, on the contrary, the players of such a game are opponents motivated to outscore, they would find that $\frac{1}{4}$ is beaten by a higher ratio; x^\dagger , the value of x which gives its player the greatest possible advantage over the player playing x_0 , is found to be given by the relationship

$$x^\dagger = (2x_0)^{\frac{1}{2}} - x_0, \quad (8)$$

and this shows $\frac{1}{2}$ to be the unbeatable play.

Relations 7 and 8 are shown graphically on Fig. 4. This figure also shows fitnesses (derived from expression 6) as a superimposed table, and it can be seen that the curve of x^* traces the maxima with respect to x on the implied fitness surface. If the diagram is rotated clockwise through one right angle the tabulation takes the conventional form of a payoff matrix, say \mathbf{W} , showing "payoffs" to the "player" who has choice of row. The transpose, say \mathbf{W}_0 , of such a matrix would show payoffs to the player having choice of column, and in Fig. 4 the curve of x^\dagger traces maxima with respect to x on the surface corresponding to the matrix of differences $\mathbf{W} - \mathbf{W}_0$.

Apart from the considerations just given, our earlier analysis (for $n = 2$) showed that, unless extra refinements of behavior are added, inclinations to use sex ratios aggressively as directed by Eq. 8 have no prospects under natural selection. Nevertheless, an arithmetical illustration of the earlier result seems useful and leads on to an interesting point. Suppose sex ratios are fixed by genotype and suppose that only types giving $\frac{1}{2}$ and $\frac{1}{4}$ are present in the population. Then the average fitness of type $\frac{1}{4}$ will be some weighted average between $1\frac{1}{2}$ and $1\frac{1}{6}$. Similarly the average fitness of type $\frac{1}{2}$ will be some weighted average between $1\frac{1}{3}$ and 1. The weights in the two cases depend on the frequencies of the different types of pair. Thus, if pairing is random, the weights are the same for both averages, being simply the frequencies of the types, and it is clear that, for all frequencies, type $\frac{1}{4}$ will have the higher average (43).

If pairing is nonrandom, however, unequal weightings result. Among nonrandom cases an interesting one is that in which $\frac{1}{2}$ contrives to pair off as

often as possible with $\frac{1}{4}:\frac{1}{2}$ then spreads when $\frac{1}{2}$ and $\frac{1}{4}$ are equally common, although it is still unable to do so when it is very rare or very common. But if a genetic type could dissort in this way it should easily evolve the further ability to adjust its sex ratio according to whether it was paired with its own type or with the other type, and then if it played 0 in the former case and $\frac{1}{2}$ [or, even better, $(2x_0)^{\frac{1}{2}} - x_0$] in the latter, it would spread easily at all frequencies of occurrence against any nondiscriminating type.

No such refined discrimination can be expected in parasitoids. Ability to detect whether a host is already parasitized is well known, but no clear case where a female is able to assess even the quantity of previous parasitism has yet been reported (44); therefore, ability to assess sex ratio is extremely improbable. However, although this limits the precision with which a parasitoid can take advantage of a predecessor (in theory, by use of Eq. 7), it does not lessen the gamelike character of the situation, or even change the unbeatable ratio for the case of groups always of a fixed size.

With the case of occasional double parasitism likewise it may be seen that game-theory considerations apply and prescribe definite policies. Evolved tendencies will be such that first-comers to the host will use a sex ratio less female-biased than the workable extreme in order to allow for the chance that double parasitism will occur. The first-comers' best sex ratio will depend both on this chance (p , say), and on the sex ratio that second-comers can be expected to use. The second-comers' best sex ratio, assuming they can detect previous parasitism, will be based only on the expected sex ratio of the first-comers. Hence it can be shown either by game-theory reasoning (each individual supposedly considering the intelligent policy of the other) or, more realistically, by supposed behavior gradually "learned" by the species through natural selection, that, in the idealized conditions we are considering, the following responses will finally become established: first-comers will use sex-ratio $p^2/(1+p)^2$ and second-comers will use $p/(1+p)^2$. Thus, a first-comer, because of the handicap of its uncertainty, has lower fitness than a second-comer.

It might be hoped that these two formulas would give a basis for checking the theory against experimental re-

sults. But, in its failure to take into account extra mortality due to superparasitism, the fact that females lay varying numbers of eggs and may move on from one host to another, and so on, the basis is certainly much too simple. Obviously the formulas do not check with Wylie's results, since they cannot account for sex ratios above $\frac{1}{4}$. In fact the ratio of 0.59 Wylie obtained in one experiment is too high even to be the best ratio for the outscoring game. But the variability of Wylie's ratios from ratios for controls and the fact that his experimental stock was not fresh from the wild (where triple parasitism should be very uncommon) also discourage hope of any detailed check. It can only be said that, in its direction, the effect that Wylie and Jackson have independently reported accords with the theory.

References and Notes

- R. A. Fisher, *The Genetical Theory of Natural Selection* (Dover, New York, ed. 2, 1958), p. 158.
- W. F. Bodmer and A. W. F. Edwards, *Ann. Human Genet.* **24**, 239 (1960); W. A. Kolman, *Am. Naturalist* **94**, 373 (1960).
- J. Verner, *Am. Naturalist* **99**, 419 (1965). Verner claims to show that, given factors causing fluctuations of the population's primary sex ratio, a 1:1 sex-ratio production proves the best overall genotypic strategy.
- W. D. Hamilton, *J. Theoret. Biol.* **7**, 17 (1964).
- E. Novitski, *Genetics* **32**, 526 (1947).
- L. C. Dunn, *Science* **144**, 260 (1964); L. Sandler and Y. Hirazumi, *Can. J. Genet. Cytol.* **3**, 34 (1961).
- W. A. Hickey and G. B. Craig, Jr., *Genetics* **53**, 1177 (1966); *Can. J. Genet. Cytol.* **8**, 260 (1966).
- D. F. Owen, *Heredity* **21**, 443 (1966).
- B. Wallace [in *Evolution* **2**, 189 (1948)] documents an actual case of X-linked sex-ratio drive. J. B. S. Haldane and S. D. Jayaker [in *J. Genet.* **59**, 29 (1964)] give conditions for equilibrium: a driving sex chromosome X' is not arrested unless XX' is more fit than XX' by at least $1/3$.
- H. D. Stalker, *Genetics* **46**, 177 (1961).
- S. W. Brown, *Science* **151**, 417 (1966).
- G. D. Hanks, *Genetics* **50**, 123 (1964).
- J. D. McCloskey, *Am. Naturalist* **100**, 211 (1966).
- A. S. Parkes, in *The Numbers of Man and of Animals*, J. B. Cragg and N. W. Pirie, Eds. (Oliver and Boyd, Edinburgh, 1955); G. Sundell, *J. Emb. Exp. Morphol.* **10**, 58 (1962); The work of J. A. Weir [*Genetics* **45**, 1539 (1960)] emphasizes the importance of the father in determining sex ratios in the mouse.
- E. Schilling, *J. Reprod. Fertility* **11**, 469 (1966).
- D. Lewis, *Biol. Rev. Cambridge Phil. Soc.* **17**, 46 (1942).
- A. Wilkes, *Science* **144**, 305 (1964); *Can. Entomologist* **97**, 647 (1965).
- If each haploid male can mate with k females and if mated females produce sex ratio e , some females fail to be mated if $k < (1-e)/e$. Such cases finally have a regular alternation of sex ratios between e and $1-ke$. Between these values there is an unstable sex ratio equilibrium at $\frac{1}{2} \{2 + kf - [kf(4 + kf)]^{\frac{1}{2}}\}$, where $f = 1 - e$. In 1917 C. B. Williams gave arithmetical models showing alternation [*J. Genet.* **6**, 189 (1917)] and A. F. Shull published observations suggesting that alternations may occur in thrips in the wild [*Genetics* **2**, 480 (1917)].
- W. F. Bodmer and A. W. F. Edwards, *Ann. Human Genet.* **24**, 239 (1960). They imply (I think incorrectly) that there is a possible situation for which their analysis is exact.
- S. W. Brown, *Genetics* **49**, 797 (1964).
- M. J. D. White, *Animal Cytology and Evolution* (Cambridge Univ. Press, London, 1954), pp. 239-246.
- F. W. Edwards, *Entomologist's Monthly Mag.* **70**, 140 (1934).
- C. W. Metz, *Am. Naturalist* **72**, 485 (1938).
- F. W. Edwards, *Entomologist's Monthly Mag.* **49**, 209 (1913).
- H. F. Barnes, *Gall Midges of Economic Importance*, vols. 1-6 (Crosby Lockwood, London, 1946-56).
- S. Wright, *Ecology* **26**, 415 (1945).
- C. Chararas, *Étude biologique des Scolytides des Conifères, Encyclopédie Entomologique* (Lechevalier, Paris, 1962).
- F. G. Browne, *Malayan Forest Rec.* **22**, 1 (1961).
- P. F. Entwistle, *Proc. Roy. Entomol. Soc. London Ser. A* **39**, 83 (1964); 14 percent of broods had no male.
- M. W. Blackman, *N.Y. State Col. Forestry Tech. Pub.* **16**, No. 1, 11 (1915); D. L. Wood, *Pan-Pacific Entomologist* **38**, 141 (1962). Comparable evidence for polygynous birds is cited by J. Verner and M. F. Willson [*Ecology* **47**, 143 (1966)].
- G. R. Hopping [in *Can. Entomologist* **94**, 506 (1962)] reports the existence of a thelygenous strain in *Ips tridens*. Such strains are unlikely to be widespread in the genus (compare the "sex ratio" traits of *Drosophila pseudoobscura* and its allies).
- E. A. Osgood, Jr., and E. W. Clark, *Can. Entomologist* **95**, 1106 (1963).
- J. P. Vité and J. A. Rudinsky, *Forest Sci.* **3**, 156 (1957).
- R. W. Reid, *Can. Entomologist* **90**, 505 (1958).
- R. Newstead and H. M. Duvall, *Roy. Soc. Rep. No. 2 of Grain Pests (War) Committee*, London (1918). A report by E. A. Elbadry and M. F. S. Tawfik [in *Ann. Entomol. Soc. Am.* **59**, 458 (1966)] shows that *Adactylidium* has biology very similar to *Acarophenax*.
- G. S. Graham-Smith, *Parasitol.* **11**, 347 (1919).
- F. Wilson, *Australian J. Zool.* **9**, 737 (1961).
- F. Van Emden, *Z. Morphol. Oekol. Tiere* **23**, 425 (1931). Even in the absence of occasional outbreeding, all female batches are not necessarily doomed. Unmated females of *Cephalonomia quadridentata* produce daughters after mating with their sons. This ability is widespread among arrhenotokous organisms, and is developed into a remarkable adaption in *Melittobia acasta* [see F. B. Browne, *Parasitol.* **14**, 349 (1922)]. *Xyleborus compactus* has the ability, and data suggest that it must be frequently used in nature [see note 29]. In *Podapolipus diander* the female is regularly mated by a precocious son arising from her first egg [M. Volkonsky, *Arch. Inst. Pasteur Algerie* **18**, 321 (1940)].
- C. P. Clausen, *J. N.Y. Entomol. Soc.* **47**, 1 (1939).
- G. Salt, *J. Exp. Biol.* **13**, 363 (1936). This effect accords with Fisher's principle. Superparasitism brings unlike genotypes together and causes at least partial outbreeding; therefore, since males are scarcer, they are under more intense selection for competition ability.
- H. G. Wylie, *Can. Entomologist* **98**, 645 (1966).
- D. J. Jackson, *Trans. Roy. Entomol. Soc. London* **118**, 23 (1966).
- A similar argument shows that the play 0 also loses to the play $\frac{1}{4}$. The combination 0,0 gives the highest possible payoff to the group (namely, 4), so this "solution" should be favored by a "group-selectionist." From what has been said, the "solution" $\frac{1}{2}, \frac{1}{2}$, with group payoff 2, should be favored by the extreme believer in biological *bellum omnium contra omnes*. It is pleasing, therefore, to find that what turns out to be the true solution in this case, $\frac{1}{4}, \frac{1}{4}$, lies exactly midway between the others, both in position and in payoff.
- G. Salt, *Symp. Soc. Exp. Biol.* **15**, 96 (1961).
- G. Grandi, *Boll. Lab. Entomol. Roy. Inst. Super. Agr. Bologna* **2**, 1 (1929).
- P. Rau, *Ann. Entomol. Soc. Amer.* **40**, 221 (1947); J. H. Fabre, *Souvenirs Entomologiques* **3**, 179 (1886).
- A. A. Moursi [Bull. Soc. Fouad Inst. Entomol. **30**, 21 (1946); *ibid.*, p. 39] reported very rare thelytoky.
- M. F. Schuster, *Ann. Entomol. Soc. Amer.* **58**, 272 (1965).
- C. P. Clausen, *Univ. Calif. (Berkeley) Pub. Entomol.* **3**, 253 (1924).
- F. B. Browne, *Parasitol.* **14**, 349 (1922). These are feeble, reluctant fliers.
- E. R. Buckell, *Pan-Pacific Entomologist* **5**, 14

- (1928); R. G. Scmieder, *Biol. Bull.* **74**, 256 (1938). The sex ratio is of Scmieder's second form.
52. T. H. C. Taylor, *The Biological Control of an Insect in Fiji. An Account of the Coconut Leaf-mining Beetle and Its Parasite Complex* (Imperial Institute of Entomology, London, 1937).
 53. G. Salt, *Parasitol.* **29**, 539 (1937); *ibid.* **30**, 511 (1938). The males are winged when bred on hosts other than *Sialis*.
 54. F. Enoch, *Entomologist's Monthly Mag.* **34**, 152 (1898). M. Rimsky-Korsakov [*Rusk. Entomol. Obozr.* **16**, 211 (1917)] reports that females are dimorphic; some are apterous. K. L. Henriksen [*Ann. Biol. Lacustre* **11**, 19 (1922)] suggests the existence of a thelytokous race; like R. Heymons [*Deut. Entomol. Z.* **1908**, 137 (1908)], he observed fewer males, and no mating in the host egg.
 55. The sex ratio (from cols. 3 and 4) is typical for 3rd-instar hosts.
 56. A. F. Satterthwait, *J. N.Y. Entomol. Soc.* **39**, 171 (1931).
 57. M. C. Mossop, *Union S. Africa Dept. Agr. Sci. Bull. No. 81* (1929).
 58. A. de Costa Lima, *Inst. Oswaldo Cruz Mem.* **21**, 201 (1928); A. Dreyfus and M. E. Breuer, *Genetics* **29**, 75 (1944). Sex ratio for *Triatoma megista* hosts.
 59. Sex ratio for *Asoleus basalis*. A definite tendency toward the inclusion of at least one male among eggs laid in a host by *A. semistriatus* has been observed by M. Javahery (personal communication).
 60. F. Van Emden, *Z. Morphol. Oekol. Tiere* **23**, 425 (1931). The males are dimorphic; some are apterous.
 61. J. C. Bridwell, *Proc. Hawaii Entomol. Soc.* **4**, 291 (1920). Aptery occurs, but rarely. C. E. Keeler [*Psyche* **36**, 41 (1929); *ibid.*, p. 121] found a thelytokous race.
 62. H. F. Willard, *U.S. Dept. Agr. Tech. Bull.* **19**, 1 (1927); A. Busck, *Insector Inscitiae menstruus* **5**, 3 (1917).
 63. E. Pussard-Radulesco, *Ann. Ephyphyties* **16**, 103 (1930).
 64. A. E. Treat, *Proc. 10th Intern. Congr. Entomology* **2**, 475 (1956).
 65. K. W. Cooper, *Proc. Nat. Acad. Sci. U.S.* **23**, 41 (1937).
 66. E. E. Lindquist and W. D. Bedard, *Can. Entomologist* **93**, 982 (1961).
 67. The results of Bodmer and Edwards [in *Ann. Human Genet.* **24**, 239 (1960)] on rate of approach to equilibrium do not apply in detail to such extreme genetical cases as those of Fig. 3. In general it is true, as these workers concluded, that rate of approach depends positively on the variance [in the cases shown, $\Delta X / (\frac{1}{2} - X)$ is ultimately 2.086V for normal reproduction and 2.88V for male haploidy]. But if, for example, Gg gives all females, as in *Sciara coprophila* and *Chrysomyia rufifacies* [C. W. Metz, *Am. Naturalist* **72**, 485 (1938); F. H. Ullerich, *Chromosoma* **14**, 45 (1963)], equilibrium is reached immediately.
 68. I thank Dr. D. Bevan for information about bark beetles and Dr. T. Lewis for information about thrips.

NEWS AND COMMENT

The National Academy of Sciences: Profile of an Institution (III)

Two principal positions exist on the use that the National Academy of Sciences should make of what are considered to be its greatest assets, prestige and public confidence.

The first position is centered on the belief that the Academy should actively, and, if need be, on its own initiative, use these assets to promote the progress and wise use of science and technology. In a period of limited expansion of federal support for scientific research, some advocates of activism would like to see the Academy devise and recommend priorities for allocating the available funds. Concerning the uses to which science and technology are put, there are persons in this camp who would like to see the Academy initiate studies and issue pronouncements on controversial matters such as missile defense and chemical and biological weapons.

The second point of view is represented by those who contend that, however desirable such a role may be, the Academy can never be an effective vehicle for carrying it out. They argue that prestige and confidence are fragile commodities that are rarely enhanced by frequent involvement in controversy. They emphasize that the Academy is not a representative body; that, with its diffuse membership, it cannot reason-

ably aspire to take up complex issues and arrive at positions that reflect the informed conclusions of the membership. They also point out that the Academy possesses a modest mandate—to advise when advice is requested. No one need request the Academy's advice, nor, having requested it, need one follow it. Furthermore, they note the Academy has very limited resources for addressing itself to matters outside the interest of its clients. Its income from endowment last year came to \$398,000—as compared with \$19.4 million that it received in grants and contracts from its advice seekers. (The Academy pays its way mostly with overhead fees, usually 28 percent, that it charges its customers.) Therefore, the holders of this viewpoint believe, the Academy should not go out hunting for trouble; rather, it should husband its prestige and reputation so that it will command respect when it deals with issues that come its way.

Now, until quite recently the second camp wholly prevailed in Academy affairs. As an institution, the Academy has always been tone-deaf to the concerns that produced offshoots of the scientific community such as the Federation of American Scientists and other organizations concerned with issues that

generally come under the heading of "science and society." And, as an institution, it still tends to be tone-deaf to these concerns. Recently, for example, 127 Academy members joined several thousand scientists in petitioning President Johnson to order a study of chemical and biological weapons (CBW). There is no legal or technical impediment to the Academy's studying at least the nonclassified aspects of this subject on its own initiative. But, in raising the CBW issue the petitioners obviously hoped to encourage the administration to renounce the use of such weapons. Johnson was not inclined to snap at the bait, and the Academy was not inclined to volunteer itself into the middle of a controversy over CBW. When it comes to issues that can offend those capable of counterattack, the Academy still tends to avoid looking for trouble. Furthermore, as an advisory organization it prefers (and so its clients have come to realize) chewable problems—clear-cut issues concerned with *how* something might be done, or what will be the consequences of doing it, not with *whether* something should be done.

Nevertheless, a careful examination leads to the conclusion that here and there things are stirring inside the venerable institution, and at a few points there is even to be found a definite spirit of adventure. While the significance and potential of these developments are difficult to assess, it is clear that the affairs of the Academy are no longer wholly dominated by cautious traditionalists, for in five separate and most important areas there have been changes and activity that in many respects point the way to a significant