# FACULTATIVE SEX-RATIO MANIPULATION

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Fisher (1930) persuasively argued that stabilizing selection tends to keep population sex ratios in balance. This occurs because producers of the rare sex leave proportionately more descendants when a population deviates from equilibrium. Fisher hypothesized that the equilibrium secondary sex ratio (the sex ratio at the age when offspring become independent of parental resources) is 0.5 in populations in which the sexes are equally expensive to produce. When one sex is more expensive, fewer individuals of that sex should be produced. Parental investment patterns are influenced by mating system dynamics, which therefore affect the secondary sex ratio (Willson and Pianka 1963). Additional factors that may cause the equilibrium ratio to deviate from 0.5 are inbreeding and/or local mate competition (Hamilton 1967, 1972; Taylor and Bulmer 1980; Werren 1980), kin selection (e.g., Trivers and Hare 1976), and local resource competition (Clark 1978; Bulmer and Taylor 1980$a$).

Fisher's approach has been amplified by many. Some (Bodmer and Edwards 1960; Kolman 1960; Crow and Kimura 1970) have argued that when a population is at equilibrium, producers of all sex ratios are favored equally. However, in several quantitative models, natural selection favors individuals that allocate equal investment to sons and daughters (MacArthur 1965; Verner 1965; Emlen 1968; Leigh 1970; Spieth 1974; Charnov 1975; Taylor and Sauer 1980; see also Williams 1979). An assumption common to these models is that sex ratios are genetically fixed. However, if individuals can change their ratio to capitalize on circumstance (facultative manipulation), it becomes possible to construct models in which equal investment in the sexes is not the optimal tactic (e.g., Werren and Charnov 1978).

Facultative manipulation has been suggested to be adaptive in a number of circumstances; these are categorized and elaborated below. The purpose of this paper is to extend theory and provide an empirical test of sex-ratio manipulation. My theoretical concern focuses on the scope of manipulations potentially available to individuals in the light of possibly conflicting selection pressures. My empirical contribution is a 15-mo experiment performed on a laboratory strain of the house mouse, *Mus musculus*.

REASONS FOR MANIPULATION

In broad terms, the capacity for facultative adjustment may be adaptive when: (1) populations commonly deviate from the equilibrium ratio; (2) the equilibrium sex ratio changes in ecological time; and/or (3) the ability to produce a given sex varies as a function of several circumstances. These possibilities will be considered in turn.

1. Fisher's reasoning suggests one immediate stimulus to sex-ratio manipulation. In a skewed population, producers of the rarer sex benefit disproportionately to their reproductive effort; in such populations selection favors individuals that can detect bias and produce compensatory offspring. This idea assumes a heritable basis to the production of the sexes, but it does not specify the nature of inheritance. Individuals may have a genetic tendency to produce offspring of a particular sex (predisposed sex-biased producers), or they may have facultative capacities. Geodakian et al. (1967) provided experimental evidence that female guppies (*Lebistes reticulatus*) are capable of facultative compensation for a shortage of one sex.

The utility of facultative compensation depends upon its cost and the frequency of occurrence of significantly biased population ratios. Short-term deviations in the sex ratio may result from environmental influences ranging from disease to which there is sex-related resistance to interpopulation conflict (including warfare in humans, e.g., Chagnon 1974). The magnitude and frequency of environmentally induced deviation should vary inversely with population size; in small populations departures from a balanced ratio may be common.

2. The equilibrium sex ratio may be spatially or temporally variable. Kin-selection theory predicts that hymenopterous females should bias their ratio of investment in male and female relatives depending on the relatedness of females within a reproductive group (Hamilton 1964; Trivers and Hare 1976). Relatedness will vary with number of foundresses and matings obtained by breeding individuals, as well as other factors (West Eberhard 1975; Trivers and Hare 1976; Alexander and Sherman 1977). In many parasitic insects, females deposit groups of eggs in one locale, and the resulting offspring mate before dispersing. This circumstance can result in intense local mate competition, favoring offspring sex ratios strongly biased toward females (Hamilton 1972; Bulmer and Taylor 1980*a*, 1980*b*; Taylor and Bulmer 1980). The equilibrium sex ratio in any one locale may vary, depending on the number of individuals residing there (Charnov et al. 1981) and on other life history characteristics (Maynard Smith 1965; Bulmer and Taylor 1980*b*). The optimal production for any female arriving at a locale depends upon whether or not she is the first foundress and the probability that others will deposit eggs at that locale (Werren 1980).

3. When the sex ratio of a population is in equilibrium, individuals may practice manipulation of offspring sex ratios in response to resources available. Several considerations are relevant here. (*A*) For Trivers and Willard (1973), the major variable stimulating manipulation is quantity of investment available. Where males are affected disproportionately by the amount of parental investment, as might be expected in polygynous species, parents with high capabilities are

selected to produce sons, whereas those with below average capabilities benefit from producing daughters. Fiala (1981*a*, 1981*b*) has extended Trivers and Willard's hypothesis to predict that, given a stable population sex ratio, optimal investment by a female in poor condition favors a sex ratio of 0 and that of a female in good condition favors a sex ratio of 1. In some birds and mammals, female reproductive condition appears to vary seasonally. It follows that, for polygynous species, females reproductively active in the favorable portion of the season should produce a higher proportion of sons than those reproducing in less favorable periods. In addition to evidence cited by Trivers and Willard (1973; but see Myers 1978), Howe (1977) and Fiala (1981*b*) have reported seasonal variation in sex ratio for two polygynous avian species with sexual dimorphism. Riddle (1917) reported such variation for a monogamous species with slight dimorphism. None of these ratios approaches Fiala's predicted extremes.

*B*) In addition to the quantity of investment that can be provided, parents should consider quality or type of investment. Where the sexes have different life histories or social roles, different kinds of parental investment may be optimally suited for each sex. The assumption by Trivers and Willard that the same resources that make an inferior male offspring can make an adequate female offspring or that the resources that produce an above average daughter can be better used to make a superior son is likely only to the extent that the social/sexual development of offspring is independent of the quality of their genetic (autosomal) and nongenetic endowment. If type of investment affects offspring fitness, then some parents may be predisposed toward rearing offspring of a certain sex. For example, in species with extensive maternal care (such as primates), females that make exceptionally good mothers might benefit from producing daughters since their daughters will learn good offspring-rearing techniques. Another example involves hierarchy status. If the social organization of a species revolves primarily around a male-defined hierarchy, then females aligned with dominant males may invest primarily in sons, because daughters' chances of reproducing are probably largely independent of paternal status. However, when social organization revolves more around female status, a female's reproductive success may reflect her mother's rank. The optimal reproductive tactic should depend on the relative extent to which the two sexes are affected by maternal status. Altmann (1980) found that high-ranking baboon mothers tend to have daughters, whereas low-ranking individuals have more sons.

*C*) Individuals may also manipulate their production for genetic reasons. For example, consider a polygynous population in which males are subject to "Fisherian" selection, that is, a population in which females mate only with males bearing the most elaborate secondary sexual characteristics (Fisher 1930). For simplicity, permit two males to be genetically identical in every respect except that male X has an allele making him much more "attractive" to females than most other males, whereas male Y has an unattractive allele. Male X (and any female mated to him) should specialize in son production, whereas male Y should not. Within limits, male X should produce an excess of sons even in a male-biased population, because his sons will have differential access to females. Any tendency of male X to produce sons when his phenotype is rare will increase the rate

at which his phenotype spreads through the population, but selection will favor increasing daughter production as the type becomes common. Evidence that variability in attractiveness (of a nongenetic trait experimentally manipulated) affects sex ratio of offspring has been obtained for one monogamous avian species (Burley 1981); negative evidence has been reported for a polygynous species (Patterson and Emlen 1980).

Individuals inherently superior at producing one sex could be selected to preferentially produce that sex. Such individuals can be termed predisposed sex-ratio manipulators. Trivers and Willard appear to discount the notion that predisposed manipulators can be selected for: ''Since females in good condition are assumed to outreproduce females in poor condition, it is not possible for genes producing one sex ratio to accumulate among females in poor condition and genes for the complementary sex ratio to accumulate among females in good condition'' (Trivers and Willard 1973, p. 91). This reasoning is sound as far as it goes. It makes no sense, for example, to conceive of females of low genetic quality producing females, and those of high genetic quality producing males (but see Thornhill 1979). However, if variables other than quantity of parental investment affect offspring reproductive success, then it becomes plausible for individuals to specialize in rearing one sex. This might evolve by a sex-ratio locus becoming linked to loci bearing sex-related implications for fitness. However, given the range of environmental variables determining optimal production at any point in time, it seems reasonable to expect that facultative mechanisms would exist to modulate a genetic tendency to produce a particular sex.

*D*) Another variable that may affect the sex of offspring is the sex of sib(s). For example, where successive clutches overlap (Burley 1980), the sex of elder sibs may affect the ideal sex of younger ones. There may also be an optimal composition within litters. Howard (1942) suggested that sexually biased litter production (monogeny) functions to avoid inbreeding. Where the sexes require different types of investment, parents may raise unisexual clutches more efficiently than bisexual ones. Among laboratory rats (*Rattus norvegicus*), litter composition appears to affect maternal behavior as well as the subsequent reproductive behavior of litter mates. Lactating females discriminate between male and female pups, engaging in more anogenital licking of males (Moore and Morelli 1979; Moore 1981). Rat pups raised in unisexual groups are heavier at weaning and have higher activity levels than pups reared in same-size heterosexual litters having a 0.5 sex ratio (Brain and Griffin 1970). These last findings might suggest an advantage to producing unisexual litters, but evidence bearing on the reproductive behavior of adults that were reared in experimentally produced unisexual litters indicates otherwise. Hård and Larsson (1968) reported that the mating competence of males reared in bisexual litters was superior to that of those reared in unisexual litters. Females from experimentally produced unisexual litters may have a lower tendency to become pregnant (Sharpe 1975) and may produce smaller litters (Sharpe et al. 1973) than females reared in bisexual litters. Females reared in bisexual litters also build more elaborate nests (Sharpe 1975).

Hatching order within clutches could be important if, for example, competitive ability of the sexes differs. Aggregate data for clutches of pigeons and doves (Cole and Kirkpatrick 1915; Whitman 1919), as well as a number of data sets for litters of

wild mammalian species (James 1975; Williams 1979), indicate that within clutches, sex distribution approaches binomial expectations. However, Riddle (1916) and Whitman (1919) reported that for several dove genera (in which clutch size is two), the elder of two squabs of bisexual clutches tended to be male. Apparently, domesticated pigeons (*Columba livia*) do not show this pattern (Cuénot 1900; Cole and Kirkpatrick 1915; Levi 1974). In at least two species with strong sexual dimorphism of dependent young, an alternative adaptation is present: The smaller sex is more precocious (females in red-winged blackbirds, Fiala 1981*b*; males in sparrowhawks, Newton and Marquiss 1979). Optimal between- and within-litter compositions appear sensitive to considerations of social organization, life history, and ecological circumstance, making generalizations difficult.

*E*) An alternative to Trivers and Willard's (1973) ''condition'' hypothesis that might explain the same data can be termed the ''environmental suitability'' hypothesis. The sexes may require different environmental conditions (apart from parental contributions) for optimal development and/or reproduction, and these may be patchily distributed in space or time. If so, individuals will be favored that produce sons in patches most suitable for males and daughters in those most suitable for females (Werren and Charnov 1978; Bull 1981). Myers' (1978) hypothesis that parents may rear the sex more likely to survive when certain resources are in short supply applies here also. The occurrence of environmental sex determination in some invertebrates and reptiles (Charnov and Bull 1977; Bull 1980, 1981) supports the notion that environmental conditions can differentially affect the fitness of the sexes. There is also strong evidence that elevation differentially affects the growth rates of the sexes in dioecious quaking aspen (*Populus tremuloides*, Grant and Mitton 1979). Temporal variations in sex ratios of various species with genetic mechanisms of sex determination have been ascribed to this hypothesis (Howe 1977; Werren and Charnov 1978).

In summary, a range of circumstances would appear to favor some form of sex-ratio manipulation. Individuals of any species routinely living in very small populations might benefit from practicing compensation for deviations from the local, equilibrium sex ratio. Variations in the equilibrium ratio itself appear to be important stimuli to manipulation in certain invertebrate species. Variations in parental resources would seem to be of considerable importance to vertebrates displaying extensive parental care.

Williams (1979) has argued that evidence for facultative manipulation, as well as sex-ratio homeostasis, is lacking for vertebrates with sex chromosomes. However, relatively little experimental work or analytic attention has been paid to the complexities that could result when substantial parental care is involved. In particular, if circumstances generate conflicting pressures, then individuals are likely to display more conservatism than predicted on the basis of a single consideration. This conservatism should be enhanced if, as discussed below, manipulation involves a cost to the parent.

COSTS OF SEX-RATIO CONTROL

Possible control mechanisms can be broadly classified as prezygotic and postzygotic (destruction of zygotes, embryos, and offspring; Trivers and Willard

1973). In Hymenoptera, prezygotic manipulation is, conceptually at least, an easy task, since males normally develop from unfertilized eggs. In species with environmentally determined sex, individuals could presumably search differentially for patches most likely to produce a particular sex. For species with sex genes or sex chromosomes, such manipulation requires the differential destruction or facilitation of gametes: ova in species in which maternal gametes determine sex (e.g., Lepidoptera, birds); sperm where paternal contribution does so (e.g., *Drosophila*, mammals). The potential numbers of prezygotic mechanisms is limited by the number of physical and chemical differences between male and female gametes. In humans, two sex-related properties appear to be motility (male sperm are lighter and faster; Rohde et al. 1973) and sensitivity to the acidity of the surrounding environment (Shettles 1970; but see Diasio and Glass 1971). Mechanisms of manipulation and their possible costs may vary greatly and are not well understood.

   Reasoning from the principle of allocation, sex-ratio manipulation probably entails a cost, lowering a parent's residual reproductive value more than lack of assertion of control. Not all postulated mechanisms are equally expensive, nor would any one mechanism necessarily entail the same reproductive expense to all individuals. If some individuals absorb the costs of manipulation differently or are differentially able to profit from manipulation, then a particular environmental stimulus will not elicit the same response from all members of a population. In species in which the sex ratio varies routinely with female age, natural selection will cause adjustments to become ever more efficient and less costly. Facultative manipulation should involve a cost beyond that associated with obligatory production. Possible costs of facultative manipulation include: the expense of assessing environmental parameters favoring sex-specific production; the lowered efficiency of producing a sex ratio different from one's biological optimum; and the physiological costs of the facultative mechanism itself.

   Quantification of the costs of manipulation may prove most difficult. Needed information includes the differential mortality of the sexes from conception, and the relative energy devoted to morphological and behavioral dimorphism. Of these, estimation of energy placed into morphological dimorphism may be easiest to obtain. It may be reflected in the weights of offspring at the end of parental care (but see Newton 1978; Newton and Marquiss 1979). Scant or no attention is usually paid to costs associated with possible behavioral dimorphisms, such as differential knowledge or other resources needed to make the sexes functioning adults. Parenting may also involve different risks; for example, juvenile male mammals are often thought to be more mobile than their female sibs and may require extra attention (including protection and retrieval). For organisms exhibiting complex parental behaviors, these costs are very difficult to measure. Offspring of one sex may enjoy a longer period of association with parent(s) (as in several primates in which females remain with their mothers much longer than males; e.g., Wilson 1975; Blaffer Hrdy 1977; Clark 1978; Altmann 1980), perhaps receiving additional benefits such as protection, access to resources, and knowledge acquisition. Lacking information on the cost of production of the sexes, it is difficult to assess the added cost of manipulation. The model developed below predicts patterns of sex-ratio adjustment as a function of two factors: (1) the way

individuals absorb the costs of facultative manipulation; and (2) whether or not there exist individual differences in ability to produce superior sons or daughters that are somewhat independent of quantitative investment abilities.

In iteroparous organisms with clutch or litter size greater than one, costs of facultative manipulation could be borne in several, not mutually exclusive, ways. Manipulators could produce fewer young per litter; they could allocate less energy or resources to each young; they could produce fewer litters. The second alternative appears to be self-defeating because it lowers the quality of the manipulated young and hence counteracts the purpose of manipulation. A fourth variable, alteration of the spacing between successive litters (Burley 1980), is also possible. Since in my model adult mortality rates are high, we might expect females to put as much energy as possible into each litter and to space them closely. Therefore, I will assume that the evolutionary limit to litter packing has been reached: Individuals may increase the interval between successive litters but are unable to decrease it. Natural selection should favor investing as many resources as possible into every litter when adult mortality rates are high, but within any population some variability in allocation is likely. "Superior allocators" efficiently utilize resources, putting the maximum into reproduction. They will tend to produce large litters while "inferior" ones will produce small ones. Alternatively, or additionally, they might produce offspring of superior quality (for example, of greater weight). These strategies may coexist if mortality rates are variable, and especially if superior allocators have higher mortality rates resulting from their reproductive commitment. Inferior allocators could compensate for small litter size by producing more litters.

Several additional assumptions facilitate model development. (1) For simplicity, I assume that only females manipulate the sex ratio. This assumption effectively restricts consideration to questions of female interest; it is not meant to imply that males cannot affect the sex ratio. Where sexual partners "agree" on the manipulation to be performed, the effectiveness of the manipulation should be enhanced. Where the sexes disagree, greater knowledge of the particular circumstances would be needed to predict an outcome, although the parent with greater parental investment should have some advantage (Alexander 1974).

2. Production of a superior son requires more energy or resources than production of a superior daughter. As stated above, this assumption should not be invoked universally. Where superior daughters are more expensive to produce than superior sons, the model would predict a simple reversal of the patterns discussed below. More specific limiting factors could be substituted for energy without altering other aspects of the model.

3. Variation occurs within each "reproductive class" regarding efficiency of resource utilization and hence litter size. *Reproductive class* is defined here as the number of litters produced by a female in her lifetime.

4. Given a maximum lifespan, superior allocators tend to produce fewer, larger litters per lifetime than inferior ones. Superior allocators therefore fall into lower reproductive classes.

5. The basal sex ratio of offspring production is constant (fig. 1a) or declines (fig. 1b) with increased lifetime litter number. That is, in the absence of an environment favoring compensation, either all reproductive classes will allocate
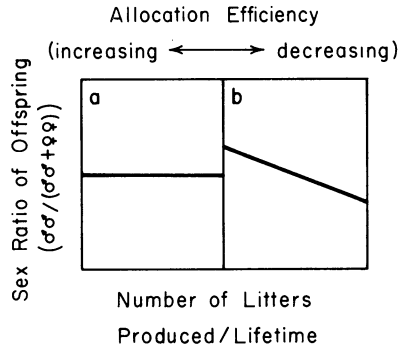
FIG. 1.—The basal sex ratio in absence of an environment favoring manipulation. Alloca-tion efficiency refers to the ability of individuals to rapidly utilize resources for reproduction. Sex-specific production may be independent of allocation efficiency (a), or superior allocators may be superior son producers (b). Superior allocators will tend to partition their lifetime production into fewer reproductive events.

the same relative effort to son production, or superior allocators will have more resources for son production than other individuals.

6. There are three possible means by which the sex of a given offspring may be determined: through chance (i.e., random fusion of gametes not followed by postzygotic mechanisms of offspring selection), through predisposed production (see p. 84), and through facultative manipulation. The first two categories are termed here "nonfacultative" production.

Facultative production involves an expense in addition to that associated with either predisposed production or random (i.e., chance) production. The relative cost of facultative female production, as compard to male production, is un-known. Two possibilities will be considered: (a) a female is always less expensive to produce than a male or (b) nonfacultative males are less costly than facultative females, which are in turn less expensive than facultative males. Other alterna-tives, such as facultative females costing the same as some type of male, are not developed here because they are deemed less likely.

When population sex ratios become skewed, and compensatory reproduction begins, several alternatives are possible. Costs of facultative manipulation may be reflected in lowered number of offspring per litter, or in reduced number of litters produced, or both. The ability of those in different reproductive classes to pro-duce sons or daughters facultatively may vary. Since superior allocators are assumed to be better at nonfacultative male production (because it is more expensive than nonfacultative female production), it is likely that they are also superior facultative producers of sons (which are more expensive still). Three alternatives exist with regard to facultative female production: (1) Superior al-locators are better at facultative female production (because it involves some expense); (2) no group specializes on facultative female production, because it is less expensive than male production (all groups do equally well); (3) if the sexes require different types of investment, inferior allocators may have evolved to

emphasize female production. In the third case, inferior allocators may be superior at facultative production of daughters.

The postulates described above can be graphically illustrated. In the absence of facultative compensation, the shape of the sex-ratio curve conforms to assumption 5 above (fig. 1). Subsequent graphs (figs. 2, 3) illustrate the effect of an environment favoring compensation on the sex ratios produced by various reproductive classes. These graphs allow for the possibility that some individuals may compensate by producing only one sex. Since individuals cannot predict what sex ratio others will produce simultaneously, it is more realistic to expect some conservatism by the compensators.

## Manipulation of Number per Litter

If individuals respond to the costs of compensation by lowering the number of offspring per litter and varying the sex ratio of progeny to favor the rare sex, then curves such as those in figure 2 result. When males are rare in a population the sex ratio produced is more male biased (fig. 2a, 2b). The specific shape of the curve will depend on how many female classes alter their ratios. For example, if all classes compensate equally, the slope of the curve will remain the same (1 in fig. 2). The compensatory sex ratio curve will be steeper than the basal curve whenever superior allocators are better male producers (2 and 3 in fig. 2).

Next, consider facultative female production. If all classes are equally efficient at producing compensatory females, then the sex-ratio curve will fall below but parallel the basal curve (4 and 5 in fig. 2). Alternatively, inferior allocators may be facultative female specialists (6 in fig. 2) or superior ones may be (7 in fig. 2).

## Manipulation of Number of Litters

The situation is more complex when individuals respond to the costs of compensatory reproduction by altering the number of litters produced per lifetime. Because of variability within reproductive classes, some individuals move into a new reproductive class by altering their lifetime litter production to pay the costs. Individuals most likely to change class by this method are those most able to compensate. If there is a significant correlation between the ability to facultatively manipulate sex ratio and efficiency of allocation, then, when individuals change class (as a result of the costs of compensation), the sex ratio of the class that the individual had been a member of should be changed. For example, suppose that efficient allocators are superior facultative son producers. When males are rare, the more efficient members of inferior classes should bias their ratios to favor males but in the process move to lower reproductive classes. This occurs because they meet the costs of compensation by reducing their lifetime litter number. Females that remain in higher classes will be the most inferior allocators. The sex ratios displayed by these classes will be more strongly female biased, not because they are facultatively producing more females, but because the more male-biased producers of their class changed class status (fig. 3a). The compensatory sex-ratio curve will cross the basal curve at a point determined by the amount of movement
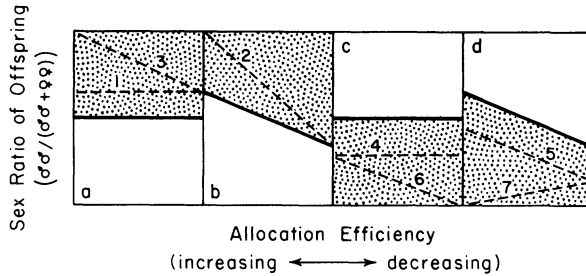
Fɪɢ. 2.—Reproductive compensation involving reduction of litter size. Solid black line represents the basal ratio (see fig. 1). Broken lines represent possible compensatory ratios, which fall into shaded areas. $a$, $b$: Compensation for a shortage of males. 1: All reproductive classes compensate equally. 2, 3: Superior allocators make better facultative compensators. $c$, $d$: Compensation for a shortage of females. 4, 5: All reproductive classes are equally able to compensate. 6: Inferior allocators make better compensators. 7: Superior allocators are better compensators.

between classes; the curve should shift the overall sex ratio upward (since the purpose is to increase male production), in which case the compensatory curve will probably cross the basal curve to the right of the diagonal.

When there is no relationship between manipulation ability and efficiency of allocation, compensation involving change of class will not affect the sex ratio of the class left behind. As a result, compensatory curves will fall above or below the basal curve (fig. 2), not crossing the basal curve (as in fig. 3). Thus, if compensatory curves cross the basal curve, it is possible to infer a link between compensation ability and allocation efficiency.

When populations are male biased, compensatory patterns must include the relative costs of nonfacultative male production versus facultative female produc-
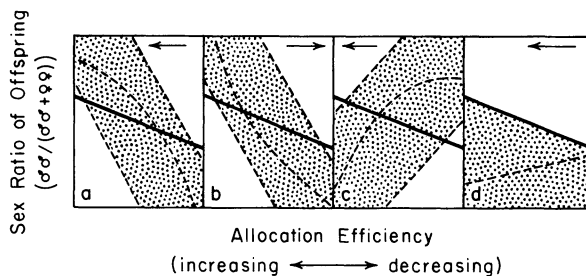


Fɪɢ. 3.—Reproductive compensation involving changes in litter number. Arrow denotes direction of mobility depending on the relative costs of facultative and nonfacultative production. Broken lines represent possible compensatory ratios, which will fall into shaded areas. $a$, Compensation for a shortage of males when superior allocators are the best compensators. $b$, Compensation for a shortage of females when facultative females are less expensive than nonfacultative males and inferior allocators specialize on female production. $c$, Compensation for a shortage of females when facultative females are more expensive than nonfacultative males and inferior allocators specialize on female production. $d$, Compensation for a shortage of females when facultative females are more expensive than nonfacultative males and superior allocators specialize on female production.

tion (see assumption 6, above). In addition to the relative costs of males and females, we must consider presence or absence of specialization on female production. As mentioned earlier, three possibilities exist: (1) superior allocators specialize on female production; (2) inferior allocators do so; or (3) no group specializes on females.

Differential production of daughters would, by definition, increase energy available to mothers and increase the number of litters or the quality of offspring raised by females when daughters are always less expensive to produce than sons. Thus, it makes no sense for superior allocators to specialize on female production. If no specialization occurs the compensatory curve falls under the basal curve (figs. 2c, 2d), and average number of litters produced increases in response to the extra resources available. If inferior allocators specialize on female production, the compensatory curve has a negative slope crossing the basal curve (fig. 3b), since female-biased producers move into higher litter classes, leaving those tending to produce males in lower classes.

Some patterns change if facultative female production is more expensive than nonfacultative female production. First, compensators move in the opposite direction; that is, the extra resources needed to produce facultative females will cause compensators to produce fewer litters. If no specialization occurs, the compensatory curve keeps the same general shape (4 and 5 in fig. 2c, 2d), but the average number of litters produced decreases rather than increases. Specialization by inferior allocators leads to curves crossing the baseline in a positive direction (fig. 3c): The better female producers will migrate into lower classes, leaving behind more male-producing conspecifics. Specialization by superior allocators leads to curves falling under the basal one but not parallel to it (fig. 3d).

In sum, energetic constraints associated with sex compensation and differential specialization for sex production could affect the shape of compensatory sex-ratio curves. Even though some constraints may not be subject to direct verification, evidence of their presence may be obtained by experimental examination.

SEX-RATIO MANIPULATION IN MICE

The social organization and life history of the house mouse provides considerable potential for sex-ratio manipulation. Demographic evidence for relatively dense, commensal populations suggests that this polygynous species is normally found in small effective populations (Petras 1967; Anderson 1970; Selander 1970; Christian 1971; Bronson 1979; but see Baker 1981) characterized by high apparent mortality (Petrusewicz and Andrzejewski 1962; Brown 1963) and low immigration rates (Petrusewicz and Andrzejewski 1962; Petras 1967; Anderson 1970). Because of high mortality, average lifespans are probably well below the species' capacity of a year or more. Less is known about populations existing independently of humans; they tend to be much less dense and to have even higher mortality rates (Bronson 1979 and references therein). It appears that adult males are highly aggressive to one another regardless of ecological circumstance (Bronson 1979).

Fluctuations in population size are common, even species-typical. Some studies (Evans 1949; Petrusewicz and Andrzejewski 1962) have indicated that sex ratios

decline when populations are declining or at low levels. However, other studies (Laurie 1946; Brown 1963) suggest that ratios do not vary with changes in population size. In some populations, males are less common in the spring (Southwick 1958; Berry 1963), perhaps because of a greater tendency to emigrate (Berry and Jakobson 1971). For one feral population, Berry and Jakobson (1971) found that the first litters of a season produced sex ratios of about 0.70, whereas later ones did not show this bias. Since populations are often small, temporal fluctuations in the sex ratio may be common. The occurrence of polygyny and sexual size dimorphism (males are larger) suggests that males may be more expensive to produce and females may be selected to produce males when they are in good physiological condition. Status-related sex biasing of young could also occur.

The laboratory strain selected for study (Swiss Random Bred ICR) was chosen for overall hardiness, relatively large litter size, and ease of sexing young shortly after birth. Females reach reproductive maturity in about 10 wk and produce up to 15 young per litter. The gestation interval is 19 days; offspring are weaned at 21 days.

The purpose of the experiment was to determine whether females respond to experimentally induced, skewed sex ratios in their progeny (and in their cage mates' progeny) by altering the composition of subsequent litters. The primary experimental technique was to force females to raise repeated litters of one sex. If facultative sex-ratio adjustments do occur, this manipulation could result in subsequent alteration of the sex ratio to favor the rare sex. Data were examined for evidence of the differential responses discussed above. Secondarily, I looked for systematic changes in the sex ratio with maternal age and reproductive experience.

## Methods

Swiss Random Bred ICR mice, 5–6 wk old, were purchased from Bio Breeding Laboratories of Canada, Ltd. (Ottawa, Ontario), and housed at McGill University in a homeostatic murine vivarium containing several laboratory strains. Mice were kept in plastic rodent cages, approximately $32 \times 16 \times 13$ cm, adult females housed two per cage, adult males housed individually. Commercial mouse chow and water were continuously available; bedding was changed weekly, or twice weekly when large litters of offspring over 14 days of age were present.

One hundred and one females were received in two lots; set 1 was received 87 days before set 2. Females were divided into four groups: controls (group C), those permitted to rear only daughters (F), those permitted to rear only sons (M), and "exchange" (X) females, whose offspring were used to supply experimental females with young. Both females housed in one cage belonged to the same group.

The procedure for assigning females to groups varied between the two lots. In the first lot, females were not assigned to groups until after copulation had occurred. This was done to match F and M females so that sufficient young would be produced for offspring exchange (see below). An unintended effect of the procedure, noted before the second lot was received, was that F and M females became pregnant sooner than C females. This bias was countered by assigning a

larger fraction of the second lot to the C category. The second lot was divided into groups upon receipt, using a table of random numbers.

The sex of offspring was determined between birth and 36 h of age by visual inspection. The live male offspring of F females were then exchanged for same-age daughters of M and X females. The live female offspring of M females were exchanged for same-age sons of F and X females. When uncertainty over the sex of an F or M offspring occurred, it was placed with an X foster mother, whose own litter was removed simultaneously, and its sex was determined at weaning. The actual (F or M) mother reared a substitute young of appropriate sex. When insufficient offspring were available for switching (approximately 5% of all litters), litter size was reduced by one (in 0.5% by two) offspring. In other cases, mothers received the same number of offspring that were alive when the litter was first noticed, but they reared offspring of only one sex.

After sexing the offspring of C females, all young of one sex in each litter were switched with same-sex, same-age offspring of X females or C females residing in a different cage. C females raised litters whose sex composition was identical to that living when the litters were first noticed, but mothers were actually related, on average, to only about half the litter. When uncertainty existed over the sex of a C female's offspring, it was left with the mother and its sex determined by sexing the entire litter at weaning. Young were removed from their mother's cage at 21 to 23 days of age.

For all groups, only offspring that were alive at the time of sexing were counted. This procedure was employed because mothers routinely consume dead offspring, making determination of number of offspring actually delivered difficult. The sex of every offspring of C, F, and M females was double-checked within two days of weaning. Less than 1% of the offspring of F, M, and C mothers were incorrectly sexed at birth.

Females remained in the groups to which they were originally assigned until their death or until the end of the study. Periodically, all groups were placed synchronously in mating cages for up to 6 days to permit copulation. Mating cages contained one male and one to three females. Females were removed from mating cages when vaginal plugs were observed. After 6 days all remaining females were removed from mating cages regardless of evidence of sexual activity. When females failed to conceive during this interval, they remained without offspring until the next cycle. This procedure was employed because it is impossible to switch young of nonsynchronized females. The procedure was repeated 1 wk after weaning of the last litter of the previous cycle.

At the beginning of a cycle, each female was placed in the cage of a male. In most instances two females from the same cage were placed with different males. Females were later returned from mating cages to clean breeding cages. The decision of which females to place together in a breeding cage was based primarily on date of copulation (when such date was determined). I attempted to space birth of litters in the same cage two days apart so that correct litter composition could be assigned to each mother both at birth and at weaning. Where vaginal plugs were not observed, females were paired randomly. No attempt was made to pair females on the basis of prior experience together.

To minimize possible age-related effects on the sex of spermatozoa produced, males were replaced intermittently throughout the study. Age of males used in copulatory cycles varied between 10 and 22 wk; each group of males fathered one or two cycles. Males that apparently failed to copulate with any of three females during the first cycle were not used a second time. Males that killed or seriously injured females were destroyed, and surviving females were distributed to other breeding cages.

The synchronization procedure outlined above is satisfactory as long as a majority of females become pregnant during each cycle. When pregnancy rates are low, females produce few litters by this method, since each female remains nonpregnant for a considerable period of time. During the last cycle in which this procedure was employed, only about 20% of the females delivered litters. From this point on (May through August 1979) females were allowed continuous access to males until pregnancy resulted.

With the exception of the last 45 days of the study, the number of litters refers to those reared to weaning (one or more young surviving), rather than to those born. (During the last 45 days, offspring and mother were destroyed after a litter was sexed.) The discrepancy between the number of litters born and weaned results from the disappearance of entire litters within 72 h after birth (about 5% of all litters). Most of these cases seemed to be the result of killing and consumption of the litter by the mother.

RESULTS AND DISCUSSION

*Number of litters and duration of breeding.*—Between July 15, 1978 and August 31, 1979, C, F, and M females produced between 0 and 5 litters (table 1). Attention is focused on females that successfully reared three or more litters. The majority of females that failed to produce at least three litters died before the termination of the study. Three females were killed in breeding cages, presumably by males. One female was killed by another female. I killed two healthy females, one after she killed her cage mate, the other after she killed her cage mate's newborn litter. (Females that killed their own litters were not destroyed.) Two mice died in advanced pregnancy. Two females died in apparent good health, but eight others died or were killed following the growth of tumors, or after experiencing consider-able weight loss or chronic bleeding. One female disappeared from her cage.

Principal functions of the C group were to provide a standard for comparison of the sex ratios produced by F and M females and to provide baseline information on production of young over time. Early in the experiment it appeared that set 1 C females did not form an adequate group for comparison. They tended not to give birth in the first cycle and, overall, had fewer litters than F and M females (table 1). A Fisher exact test of their relative tendency to produce fewer than three litters was significant ($P = .01$). For this reason, C data from set 1 were eliminated from further analysis; the proportion of C's in set 2 had been increased in anticipation of this finding. The relative number of litters produced by set 2 C females does not differ from those produced by F and M females of either or both sets (Fisher exact tests, $P$'s NS).

TABLE 1

NUMBER OF LITTERS PRODUCED BY EXPERIMENTAL AND CONTROL FEMALES OF THE
FIRST (subscript 1) AND SECOND (subscript 2) SETS

| No. of Litters Produced per Lifetime | $F_1 \& M_1$ | $C_1$ | $F_2 \& M_2$ | $C_2$ |
|---|---|---|---|---|
| 5 | 4 | 1 | 2 | 0 |
| 4 | 10 | 0 | 2 | 6 |
| 3 | 10 | 4 | 6 | 11 |
| 2 | 3 | 4 | 6 | 1 |
| 1 | 2 | 2 | 0 | 1 |
| 0 | 3 | 5 | 0 | 1 |
| Total | 32 | 16 | 16 | 20 |

NOTE.—C = control mothers; F = mothers rearing only female offspring; M = mothers rearing males.

Sets 1 and 2 differed in that the first had a longer time to reproduce. Counting the day the first litter of set 1 was born as day 1, the mean date of delivery of first litters for set 1 was day 51, whereas the mean date for set 2 was day 126. Thus, on average, set 1 females had 75 more days available for reproduction than set 2 females. In theory, they could have reared one, or possibly two, additional litters. In actuality, only one female of set 1 and seven of set 2 gave birth during the final 75 days. No female was visibly pregnant at the end of the experiment. Thus the effect of the longer interval available to the first set is minor. Because of the very low rates of copulation and reproduction during the final 75 days, I am reasonably confident I measured the lifetime reproductive success of most individuals.

*Reproduction of C females.*—Results are reported by number of litters produced. Females that produced three (3C) and four (4C) litters during their lifetimes began reproducing at about the same time (primarily November 21–24, 1978). This is not surprising since they were purposefully synchronized by denying them access to males until they were fully mature, at which time they were placed simultaneously in breeding cages. Lifetime reproductive spans were closely proportional to the number of litters produced, i.e., it took 3C females approximately ¾ the time taken by 4C females to produce all their offspring (table 2). Production of a fourth litter increased individuals' lifetime reproductive success by about 24% (table 3). No C female produced a fifth litter.

One significant difference between the two classes is that the 3Cs were somewhat heavier at age of first reproduction (means 30.00 vs. 27.82 g, $t$-test, $t_s = 2.662$, df = 15, $P < .02$; table 2). They also tended to produce somewhat larger first litters (means of 10.4 vs. 8.0 young, Wilcoxon rank sum $P = .05$; table 3; the distribution of litter sizes did not correspond to those assumed by parametric tests). Differential production of litters was not due primarily to mortality, since eight of 11 3C females were alive when the study ended. Five of six 4C females were alive at that time.

| Female Class | n | Mean Wt. (g) | Mean Reproductive Span (days) |
|---|---|---|---|
| 4C$_2$ ..................... | 6 | 27.82* | 207 |
| 3C$_2$ ..................... | 11 | 30.00* | 158 |
| 4F′ ..................... | 9 | 31.54 | 223 |
| 3F ..................... | 8 | 31.61 | 170 |
| 4M′ ..................... | 9 | 31.63 | 226 |
| 3M ..................... | 8 | 31.20 | 143 |

NOTE.—Weight at first reproduction is approximated as the weight of a female just prior to being placed in a breeding cage during the cycle in which she first conceived. Reproductive span is calculated as the days between delivery of the first and third litters for 3C, 3M, and 3F females, or as the interval between the first and fourth litters for 4F, 5F, 4M, and 5M females. 4F′ = 4F and 5F; 4M′ = 4M and 5M.

* $P < .02$ (t-test).

C females displayed no consistent age-related variation in sex ratio of litters. Nor were any "seasonal" trends apparent over the 8-mo interval in which C litters were produced. 3C females had a slightly higher sex ratio (0.53) than 4C females (0.49), but the difference is not statistically significant (table 3). Additional evidence suggests a relationship between litter number and sex ratio. Of the 11 3C females, 9 produced lifetime sex ratios greater than 0.5. Only 2 of 6 4C females produced male-biased sex ratios. This difference is not significant (Fisher exact test, two-tailed $P \approx .12$), but is suggestive, particularly since the two 3C females producing female-biased ratios died before their fourth litters could have been produced.

Since the average lifetime reproductive success of 4C females is considerably greater than 3Cs (38.7 vs. 31.3 offspring, table 3), it is tempting to conclude that 4C females are reproductively superior. However, they achieve this advantage only if permitted to live out their natural life span. If predation or other causes of mortality are high, few individuals will live so long. Where survivorship is less than maximal, 3C females may have an advantage. Considering the first three litters, 3Cs produced somewhat more offspring, and a slightly more male-biased ratio, than 4Cs (table 3). In terms of ability to mobilize resources, 3Cs appear superior. The relatively small differences between the groups may have resulted to some extent from the enforced synchrony of onset of reproduction and from conditions optimal for reproduction afforded by the laboratory environment.

*Reproduction of F and M females.*—While no C female produced 5 litters, two F females and four M females did so. Since I am not certain that some C females (all of which came from set 2) would not have produced a fifth litter had the experiment been continued, I report results for F and M females in two ways: by number of litters produced (3, 4, or 5) and by truncated production through the fourth litter. In the second case, data for the last litter of 5-litter producers have been eliminated, and 4- and 5-litter producers are grouped together (4F′ and 4M′). Comparisons relevant only to the experimental classes (F vs. M) utilize all data;

TABLE 3

OFFSPRING PRODUCTION AND LITTER SIZES OF CONTROL AND EXPERIMENTAL FEMALES

| GROUP | NUMBER $n$ | LITTER SEQUENCE ($\delta\delta:\female\female$) | | | | | $\Sigma\bar{x}$ | SEX RATIO $[\delta\delta/(\delta\delta + \female\female)]$ |
|---|---|---|---|---|---|---|---|---|
| | | 1st | 2d | 3d | 4th | 5th | | |
| 4C ........ | 6 | 24:24 | 25:36 | 35:32 | 30:26 | ... | 38.7 | .491 |
| | | 8.0 | 10.2 | 11.2 | 9.3 | ... | | |
| 3C ........ | 11 | 61:53 | 59:52 | 61:58 | ... | ... | 31.3 | .526 |
| | | 10.4 | 10.1 | 10.8 | ... | ... | | |
| 5F ........ | 2 | 5:12 | 9:15 | 12:13 | 9:10 | 2:5 | 46.0 | .402 |
| | | 8.5 | 12.0 | 12.5 | 9.5 | 3.5 | | |
| 4F ........ | 7 | 30:24 | 48:44 | 37:33 | 29:32 | ... | 39.5 | .520 |
| | | 7.7 | 13.1 | 10.0 | 8.7 | ... | | |
| 3F ........ | 8 | 41:36 | 58:34 | 38:26 | ... | ... | 29.1 | .588 |
| | | 9.6 | 11.5 | 8.0 | ... | ... | | |
| 4F' ........ | 9 | 35:36 | 57:59 | 49:46 | 38:42 | ... | 41.3 | .494 |
| | | 7.9 | 12.9 | 10.2 | 8.9 | ... | | |
| 5M ........ | 4 | 14:27 | 26:23 | 19:19 | 19:16 | 10:7 | 45.0 | .488 |
| | | 10.2 | 12.2 | 9.5 | 8.8 | 4.2 | | |
| 4M ........ | 5 | 29:17 | 29:19 | 15:28 | 21:21 | ... | 35.8 | .525 |
| | | 9.2 | 9.6 | 8.6 | 8.4 | ... | | |
| 3M ........ | 8 | 35:33 | 33:34 | 36:39 | ... | ... | 26.3 | .495 |
| | | 8.5 | 8.4 | 9.4 | ... | ... | | |
| 4M' ........ | 9 | 43:44 | 55:42 | 33:48 | 40:37 | ... | 38.1 | .500 |
| | | 9.7 | 10.8 | 9.0 | 8.6 | ... | | |

NOTE.—$\bar{x}$ = mean live litter size at time of sexing. 4F' = 4F and 5F through the fourth litter; 4M' = 4M and 5M through the fourth litter.

comparisons involving C females use the more conservative, truncated measure (table 3).

For both F and M females, differences in size of first litter were not significant for 3- versus 4-litter producers, or F versus M females (Wilcoxon rank sum tests, table 3). Weights at first reproduction were very similar for M and F females (table 2). For F females, production of a fourth litter increased lifetime reproductive success by about 25% (table 3), and lifetime reproductive spans were closely proportional to the number of litters produced (table 2). 3F females produced a considerably higher sex ratio than 4F′ (0.59 vs. 0.49, table 3). Seven of eight 3F and seven of nine 4F females were alive at or near the end of the study.

*Sex-ratio manipulation*.—The effect of the primary experimental manipulation can be assessed by comparing the sex ratio of offspring of F and M females. If females compensate for the rare sex as predicted, F females should display a more male-biased sex ratio than M females. Overall, there is little difference between the ratios of progeny produced by F and M females (F females, 318 sons : 284 daughters; M females, 286 sons : 283 daughters). However, this estimate of compensation does not reflect the possibility of differential compensation (that low litter producers will behave differently than high litter producers) or that, because of the expense involved, manipulators may produce fewer offspring than non-manipulators. Finally, of course, no compensation could be expected in the first litter (though some might have occurred because not all females were synchronized), and it seems unreasonable to expect maximum compensation in the second. For these reasons, very large samples may be needed to detect shifts at an aggregate scale.

A comparison of the production of various litter classes suggests that manipulation does occur. The difference between the relative numbers of each sex produced by 3M and 3F females is significant ($\chi^2 = 3.83$, 1 df, $P \approx .05$). The interpretation that this difference is caused by a nonrandom process is strengthened by the fact that the ratio produced by the 3C class (0.53) lies between those produced by 3F (0.59) and 3M (0.50) females. The sex ratios produced by class 5 females differ significantly (0.40 vs. 0.49, $P > .10$). Production by class 4F and 4M females was almost identical (0.52). If females did compensate in response to the experimental manipulation, the production of individual F females should have become increasingly male-biased over successive litters, whereas that of M females should have become increasingly female biased. To test for trend, Goodman and Kruskal's gamma (Ghent 1976) was calculated for each female. Twelve F females displayed increasing male production, with five showing increasing female production; six M females showed increasing male production, while 11 M females displayed increasing female production (Fisher exact test, one-tailed $P = 0.042$). By contrast, nine C females displayed increasing male production, seven showed increasing female production, and one showed no change.

The implications of these results are best understood through graphical analysis (fig. 4). Interpretation is hindered by the lack of fifth litter production by C females, but it appears that the curve for F females would cross an extension of the basal or C female curve. The model indicates this will occur when females adjust for the cost of compensatory male production by reducing the number of litters produced per lifetime (fig. 3a). Moreover, a low sex ratio in the highest litter
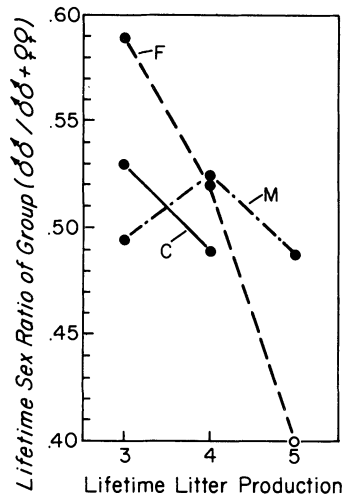
FIG. 4.—Lifetime reproduction of female mice producing three, four, or five litters. C = control mothers; F = mothers that reared only females; M = mothers that reared only males.

classes suggests that more male-biased females are engaged in manipulation and that as they move to lower reproductive classes they leave behind highly female-biased producers.

The M curve intersects the C curve in a positive direction and appears to lie above the basal curve to the right of the point of intersection. Of all the possible curves generated for female compensation, the M curve fits within the bounds prescribed by only one case (fig. 3c). The conditions of this case are that: females allocate costs by altering number of litters produced; facultative females are more expensive to produce than nonfacultative males; and inferior allocators specialize on facultative female production. The shape of the M line may be caused by differential migration (i.e., 4Ms may migrate to 3M more often than 5Ms move to 4M. This is to be expected since class 5 was much smaller than class 4).

In summary, it appears that for both sexes compensation may entail reduction of litter number. If so, low litter producers tend to specialize on males whereas high litter producers specialize on females. If this interpretation is correct, the tendency of individuals to show increasing compensation over successive litters should be greatest among low litter producers. Going from 5- to 3-litter producers, the direction of change was as predicted for both M and F females: Among M females, there was an increasing tendency for increasing female production over litters (Goodman and Kruskal's gamma $= +0.63$; one-tailed $P = 0.029$); for F females, there was an increasing tendency for increasing male production over litters (gamma $= -0.37$; $P$ NS). Control females showed an intermediate tendency for increasing female production (gamma $= +0.33$; $P$ NS).

## Offspring Weights and Mortality

Data are consistent with the hypothesis that individual females most able to mobilize energy are most likely to produce sons. Under this circumstance, it might

TABLE 4

WEIGHTS OF OFFSPRING PRODUCED BY CONTROL CLASSES

|  | No. of Litters | WEIGHTS | | |
| --- | --- | --- | --- | --- |
|  |  | $\bar{x}$ wt/$\male$ (g) | $\bar{x}$ wt/$\female$ (g) | $\male$/$\female$ (g) |
| 4C, when no 4 × 3 synchrony ........... | 13 | 9.2 | 9.1 | (1.01) |
| 3C, no 3 × 4 synchrony ................ | 17 | 11.1 | 9.2 | (1.20)** |

NOTE.—All offspring weighed at 21–23 days of age. Synchrony refers to delivery of two litters in one cage within 48 h.
** $P < .01$ for Wilcoxon rank sum test.

further be predicted that weights of offspring of superior allocators are greater than those of inferior allocators. However, a tendency for smaller litters to have greater offspring weights would counter this possibility if inferior allocators produce smaller litters as predicted.

To assess these possibilities, I examined data on litter weights of 3C and 4C mothers. Data are not included for cases in which a 3C and 4C female housed in the same cage delivered litters within a 2-day span, because in such cases it was not possible to discriminate litters at weaning age. Offspring were weighed in unisexual groups; as a result mean weights can be determined, but variance of weight is not known. Mean weight of female offspring is the same for both classes, but weight of male offspring of 3C females is considerably greater (table 4; Wilcoxon rank sum $P < .01$). The disparity in the ratio of investment by female class (1.20 for 3Cs vs. 1.01 for 4Cs, table 4) strongly suggests that 3C females do indeed allocate relatively more effort to male offspring.

An index of relative reproductive allocation that reflects both sex ratio and sex-specific weights of progeny is the product of the mean number of offspring per reproductive class and their relative weaning weights. I have computed this index for the cases in which 3 × 4 within-cage synchrony of delivery was absent. This calculation reveals an increase in the difference of sex-specific investment between 3C and 4C females (table 5a). Assuming that the greater investment per male offspring made by 3C females increases their fitness, the index also reflects a decrease in the discrepancy between the lifetime production of the female classes (compare tables 5 and 3).

The above calculation ignores mortality of offspring between sexing age and weaning. Ten of 344 (2.9%) offspring of 3C females died, while 21 of 232 (9.1%) offspring of 4Cs died between the time a litter was first discovered and sexed and the time of weaning. This threefold difference between classes is significant ($\chi^2 = 10.3$, 1 df, $P < .005$). If offspring mortality rates are included in estimates of relative lifetime effort (table 5a), performance of 3C females improves again (table 5b).

With these final estimates, relative lifetime reproductive expectations can be calculated for females that die before completing their potential lifespan. Since there are no apparent age-related sex biases in production, and since reproductive

TABLE 5

LIFETIME REPRODUCTIVE ALLOCATION OF C FEMALES

|  | ♂♂ | ♀♀ | Total |
|---|---|---|---|
| (a) 4C, no 4 × 3 synchrony ................ | 19.2 | 19.7 | 38.9 |
| 3C, no 4 × 3 synchrony ................ | 20.7 | 15.0 | 35.7 |
| (b) 4C, no 4 × 3 synchrony ................ | 17.9 | 17.5 | 35.4 |
| 3C, no 4 × 3 synchrony ................ | 20.6 | 14.2 | 34.8 |

NOTE.—(a) Estimates based on the number of offspring alive at sexing and relative weights of offspring of each sex at weaning. (b) Values from (a) recalculated to include differential mortality of offspring between sexing and weaning.

success is roughly proportional to the number of litters produced (table 3), this figure can be obtained by dividing lifetime reproductive allocation by number of litters produced. Assuming identical mortality rates for both groups, the resulting estimates (table 6) clearly show that 3C females outreproduce 4C females if lifespans are curtailed. However, this assumption may be erroneous; possibly, for example, 3C females incur risks associated with their greater energy expenditure that lower their survivorship. This could result in a balancing of the reproductive success of the two groups.

It could be argued that male or female production is not a tactic per se, but that females which happen to produce many males cease reproduction earlier because of the greater strain involved. This position asserts a reversal of the cause and effect relationship between litter number and sex ratio. At a proximate level it is probably true that class 3 individuals stop reproducing because of physiological exhaustion; if not, they should continue to reproduce. But this interpretation does not explain other findings. In particular it does not explain why the reproductive classes apparently apportion energy to sons and daughters differently (table 4), nor why the experimental manipulation resulted in the observed changes in sex ratios among classes (table 3, fig. 4). Thus, litter number appears to indicate differences in evolved tactics, rather than chance happenings, at least when individuals are given maximal opportunity to reproduce.

The relative importance of environmental versus genetic influences in determining number of litters and sex ratio produced is unknown. Falconer (1954) found no divergence in sex ratios of mouse lines artificially selected for extreme

TABLE 6

HYPOTHESIZED EFFECT OF ADULT FEMALE MORTALITY ON LIFETIME REPRODUCTIVE EFFORT OF 3C AND 4C FEMALES

|  | NO. OF LITTERS PRODUCED | | | |
|---|---|---|---|---|
|  | 1 | 2 | 3 | 4 |
| 4C ...................... | 8.84 | 17.68 | 26.52 | 35.36 |
| 3C ...................... | 11.59 | 23.18 | 34.76 | . . . |

NOTE.—Data calculated from tables 3 and 5.

sex production over four generations. However, it should be noted that if off-spring of highly skewed litters tend to facultatively produce the rare sex, genetic tendencies may be obscured. A suggestive experiment performed on domestic rats (*Rattus norvegicus*) indicates a strong influence of the social environment: Fe-males reared in unisexual litters produced a much lower sex ratio (over 3 litters) than did females in same-size litters having a 0.5 sex ratio (Sharpe and Wyatt 1974). The design of this experiment limits interpretation because in two of the three litters, the mates of the unisexually reared females were unisexually reared males, while the mates of the bisexually reared females were bisexually reared males. Nevertheless, an early influence on later reproductive tendency is indi-cated for at least one sex in rats. Interaction of genetic and nongenetic effects seems likely, but examination of this possibility would necessitate a sophisticated experimental design.

## Other Implications

Because of the tremendous difference in reproductive capacity of individuals of the two sexes, a common technique of mouse geneticists is to selectively discard male progeny shortly after birth. Results of this experiment suggest that such a routine procedure may have undesirable consequences. Compensatory produc-tion of males by female mice deprived of sons could affect results whenever sex-linked traits, or traits having differential effects on mortality, were under study. This experiment indicates a possible effect on results when individuals are repeatedly subjected to the same manipulation. Offspring growing up in a sex-biased environment may also be affected reproductively. Although I have focused on female reproductive behavior, it seems quite possible that males could affect the sex ratio as well. Methodological as well as theoretical considerations indicate that further work is warranted.

### FUTURE WORK

This study attempted to determine if female mice have the capacity to faculta-tively change the sex ratio of their offspring. The evidence suggests that they may. The question of the relative significance of sex-ratio compensation among murine reproductive tactics remains unanswered, in part because of the nature of the experimental design.

One indication that sex-ratio compensation may not be an important tactic is that, despite extreme experimental manipulation, the overall sex ratios of the ex-perimental groups did not vary. However, I have given several reasons why this may have occurred (p. 98). An additional (and artifactual) reason that F females' overall sex ratio may not have been more male biased is that noncompensators had energy available for raising additional litters (since they reared only females). In compensatory efforts the advantage to the manipulators declines as more and more individuals compensate. Hence the importance of compensation (to indi-viduals) cannot be measured by the numbers of individuals that compensate.

A limitation of the experimental design is that it enforces uniformity of results

through synchronization of females. Since females cannot become pregnant whenever ready, the design reduces variation among individuals. A modified experimental design would allow females continuous access to males until they become pregnant. This, however, would necessitate a very large population size to obtain sufficient offspring for switching.

A very large population would increase the range of the number of litters produced by females. The model discussed here predicts that females producing the greatest number of litters would have the most female-biased ratios, and that those producing the fewest litters would have the most male-biased ratios. This second prediction seems unreasonable for mice. Females that live for a year but produce only one litter would hardly qualify as superior allocators. A more sophisticated model would directly incorporate rates of reproduction and the concept of an upper limit to litter size. Taking these factors into account, I would predict that, for females living an appreciable length of time and having continuous access to mates, those producing the fewest number of litters would be female-biased producers, those with intermediate litter numbers would be male-biased, and those with the greatest number, female-biased. Females producing the fewest litters should not be effective facultative manipulators.

An artificial aspect of the experiment is the necessity of females to switch the sex composition of their offspring largely in response to their own reared litter composition. An improvement would be to measure the sex production of females that grow up in a strongly sex-biased environment. A related problem involves housing facilities. Mice were kept in a vivarium of variable population size, one that at maximum capacity easily held several thousand individuals. Since mice presumably communicate information about sex ratio chemically (Moore and Morelli 1979; Moore 1981), more dramatic results might be obtained by isolating F, M, and C groups.

Finally, to obtain unbiased estimates of litter weights and ascertain maternity, it would be preferable to house adult females individually. Since this would reduce female knowledge of the litter compositions of other mothers, it may be better to separate females by wire mesh or some other barrier that permits limited contact while keeping offspring with their mother.

SUMMARY

Several conditions favor the evolution of parental control over offspring sex. (1) When deviations from the equilibrium sex ratio are common, individuals may benefit from adjusting their production to favor the rare sex. (2) The equilibrium sex ratio itself may vary spatially or temporally, particularly as a result of variability in the extent of kin interactions and fluctuations in the intensity of local mate competition. (3) Parental resources may vary, making some individuals superior son producers and others superior producers of daughters. These resources include: (a) the quantity of parental investment available; (b) the quality of parental investment available; (c) environmental suitability, that is, the impact of a particular environment on the relative fitness of the two sexes; (d) genetic suitability, that is, variation in individual propensity to produce superior offspring

of one sex for genetic reasons; and (e) the composition of family groups, that is, the sex of siblings produced simultaneously or sequentially. Conservatism (failure to produce extreme ratios) by facultative manipulators may be expected if more than one of the above potentially conflicting factors affects optimal allocation, and if manuipulation involves as additional expense. Conservatism by facultative compensators may also be expected if the sex composition produced by others in the population is somewhat unpredictable, or if others are likely to practice compensation as well.

A graphic model is presented for facultative compensation of the sex ratio by females of iteroparous, polygynous species. The model assumes that sex-ratio adjustment entails some cost, and it predicts compensatory patterns based on how individuals absorb these costs and on the existence of specialized production of the sexes. The model assumes a continuum of types ranging from superior to inferior resource allocators. Superior allocators place relatively large amounts of energy into each reproductive attempt and therefore achieve their lifetime reproductive success in fewer litters than inferior individuals. Superior allocators are assumed to be superior predisposed and facultative producers of sons. Depending on the relative costs of facultative female production, a series of curves is generated corresponding to specialization on females by (1) inferior allocators, (2) superior allocators, or (3) no female class.

An experiment on facultative compensation by female mice (*Mus musculus*) involved the repeated rearing of unisexual litters. One group (F) reared only daughters, a second (M) reared only sons, and a third (C) reared litters of the same composition as born. The overall production by F and M females did not differ significantly, but the distribution of reproduction varied among classes. Results were in accordance with the model for the case in which facultative production of females is more expensive than nonfacultative production of males and in which inferior allocators are female specialists.

Weaning weights of offspring of C females support a hypothesis of sex specialization. Relatively superior allocators wean males at about 120% the weight of females. Inferior allocators wean the sexes at about equal weight.

Several important questions remain unresolved; principal among them are the cause and nature of specialization on females, and the overall importance of compensatory reproduction as a mouse reproductive tactic. For theoretical reasons and because of a tendency among mouse geneticists to differentially discard male offspring at birth, murine sex-ratio manipulation deserves further study.

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