Sex Ratio Theory, Ancient and Modern —
An 18th Century Debate about Intelligent Design and the Development of Models in Evolutionary Biology

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The design argument for the existence of God took a probabilistic turn in the 17th and 18th centuries. Earlier versions, such as Thomas Aquinas' 5th way, usually embraced the premise that goal-directed systems (things that "act for an end" or have a function) *must* have been created by an intelligent designer. This idea – which we might express by the slogan "no design without a designer" – survived into the 17th and 18th centuries,[1] and it is with us still in the writings of many creationists. The new version of the argument, inspired by the emerging mathematical theory of probability, removed the premise of necessity. It begins with the thought that goal-directed systems might have arisen by intelligent design *or by chance*; the problem is to discern which hypothesis is more plausible. With the epistemic concept of plausibility characterized in terms of the mathematical concept of probability, the design argument was given a new direction.

The new probabilistic perspective did not extinguish the older idea of "no design without a designer." The two conflicting approaches coexisted, often with less than perfect clarity about their fundamental difference. At the same time, the details of how the probabilistic perspective ought to be articulated were slow in emerging. These characteristics of uneven development are exemplified in a debate that took place in the 18th century among three probabilists – John Arbuthnot, Nicholas Bernoulli, and Abraham DeMoivre – on the proper explanation of human sex ratio. Arbuthnot proposed a probabilistic version of the design argument, claiming that it is intelligent design, not chance, that provides the better explanation of why slightly more boys than girls are born each year. Bernoulli rejected Arbuthnot's argument. DeMoivre defended Arbuthnot against Bernoulli's criticisms.

The problem of explaining sex ratio, both in human populations and in the rest of nature, experienced another transformation after 1859 -- it became a problem for the theory of evolution by natural selection. Darwin (1871) addressed the question in the first edition of *The Descent of Man* but withdrew his suggestion in the second (Darwin 1874). Carl Düsing (1884) provided a mathematical model that moved beyond the explanation Darwin offered. Fisher (1930) added the new idea of *parental expenditure*. Williams (1966) argued that the sex ratios found in nature provide the opportunity to test hypotheses of group selection against hypotheses of individual selection. Hamilton (1967) constructed a model that generalizes Fisher's approach and represents the effects of both group and individual selection. The theory of natural selection gradually developed the ability to predict sex ratios, not just explain them *post hoc*.

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[1] For example, Newton says, in a letter to Bentley, that the fact that the planets all orbit in the same direction and in the same plane "could not spring from any natural cause alone, but were impressed by an intelligent Agent" (David and Edwards 2001, p. 8). He repeats this argument in the 2nd edition of the *Opticks*, as does Bentley in his inaugural Boyle lectures (see also footnote 7).

Sex ratio thus provides an interesting case study of the problem of whether living things should be regarded as artifacts or as the result of mindless natural processes. If they are artifacts, then their features must be explained by describing the goals and abilities of the artificer. If they are the result of mindless natural processes, which processes are relevant and how should they be conceptualized? The history of these ideas isn't just history; these ideas are with us still in the form of the ongoing controversy about creationism. I'll briefly consider the contemporary controversy at the end of this essay.

1. An 18th century debate

1.1. Arbuthnot on "the exact balance that is maintained between the numbers of men and women … that the Species may never fail, nor perish"

John Arbuthnot, physician to Queen Anne, was the highly regarded satirist who invented the character John Bull. He also translated Christian Huygen's *Ratiociniis in aleae ludo* (Arbuthnot's title was *Of the Laws of Chance, or, a Method of Calculation of the Hazards of Game*), to which he added a preface, whose examples, Hacking (1975, p. 166) says, are "characteristic of a bawdy age." Jonathan Swift said of Arbuthnot that if there had been a dozen men like him in England, that he, Swift, could have burned *Gulliver's Travels* (H.Williams, 1963-5, vol. 3, p. 104; Kendall 1972, p. 35).

FIGURE 1

Arbuthnot's "An Argument for Divine Providence, taken from the constant regularity observ'd in the births of both sexes" appeared in the *Philosophical Transactions of the Royal Society* for 1710. Arbuthnot provides a tabulation of 82 years of London christening records (see Figure 1), noting that more boys than girls are listed in each year. Arbuthnot takes this difference at face value; he must have realized that not every birth gets recorded, but he nonetheless assumes that the records reflect a real difference in the frequencies of male and female births. The main part of the paper is given over to the task of calculating the probability that this pattern would obtain if the sex ratio were due to chance. By "chance," Arbuthnot means that each birth has a probability of ½ of being a boy and ½ of being a girl. According to this hypothesis, there being more boys than girls in a given year has the same probability as there being more girls than boy in that year; the chance hypothesis also allows for a third possibility, namely, there being exactly as many girls as boys:

Pr(more boys than girls born in a given year | Chance) =
Pr(more girls than boys born in a given year | Chance) >>
Pr(exactly as many boys as girls born in a given year | Chance) = *e*.

Arbuthnot goes to the trouble of explaining how *e* might be calculated. The details of his calculation don't matter to the argument; the point is just that for each of the years surveyed, *e* is tiny.

Arbuthnot concludes that the probability of there being more boys than girls in a given year, according to the Chance hypothesis, is just under ½ and that the probability of there being more boys than girls in each of 82 years is therefore less than $(½)^{82}$. He further asserts that if we were to tabulate births in other years and other cities, we would find the same male bias. So the probability of all these data -- both the data that Arbuthnot presents and the data that he does not have but speculates about – is "near an infinitely small quantity, at least less than any assignable fraction." The conclusion is obvious – "that it is Art, not Chance, that governs."

Arbuthnot's calculation of the probability of the observations under a concretely specified Chance hypothesis is a notable achievement.[2] Also notable is his claim that males have higher mortality than females, so that the male-bias at birth gradually gives way to an even sex ratio at the age of marriage. "We must observe," he says, "that the external accidents to which males are subject (who must seek their food with danger) do make a great havock of them, and that this loss exceeds far that of the other sex, occasioned by diseases incident to it, as experience convinces us. To repair that loss, provident Nature, by the disposal of its wise creator, brings forth more males than females." At the end of the paper, Arbuthnot adds, as a Scholium, that "polygamy is contrary to the law of nature and justice, and to the propagation of the human race. For where males and females are in equal number, if one man takes twenty wives, nineteen men must live in celibacy, which is repugnant to the design of nature, nor is it probable that twenty women will be so well impregnated by one man as by twenty." Here Arbuthnot shifts from explaining *what is the case* to urging *what should be the case* – a knowledge of God's intentions evidently underwrites both these claims.

What form of argument is Arbuthnot deploying? It has struck most commentators that Arbuthnot is constructing something like a Fisherian significance test, wherein a hypothesis is rejected on the ground that it says that what we observe is very improbable:

	Data
	Pr(Data | Chance) is tiny.
(Prob Modus Tollens)	=====================
	We should reject the Chance hypothesis.

I draw a double line to separate the conclusion from the premises of this argument to mark the fact that the argument is not deductively valid. I call this form of argument "*probabilistic modus tollens*" because it generalizes a perfectly valid principle of deductive logic:

	D is true.
	If C is true then D is false.
(Modus Tollens)	-------------------
	C is false.

Whereas *modus tollens* tells you to reject C if something happens that it says will not, *probabilistic modus tollens* tells you to reject C if something happens that it says *probably* will not.

[2] Beattie (1967, pp. 341-342) shows that Arbuthnot got his data and conclusion from John Graunt's *Natural and Political Observations, Mentioned in a following Index and made upon the Bills of Mortality* (1662), though Beattie concedes that Arbuthnot's method of reasoning was original.

A second possible interpretation is that Arbuthnot is constructing a likelihood inference, in which two hypotheses are compared:

Data
Pr(Data | Chance) is tiny.
Pr(Data | Intelligent Design) is large.
(Likelihood Inference) ----------------------------------
The data favor Intelligent Design over Chance.

Here the conclusion deductively follows from the premises (and so I use a single line to separate them) once we add the following principle, which Hacking (1965) calls the Law of Likelihood:

The data favor hypothesis H_1 over hypothesis H_2 if and only if $Pr(data \mid H_1) > Pr(data \mid H_2)$.

"Favoring" means differential support; the idea is that the evidence points towards the hypothesis that renders that evidence more probable.

Should we understand Arbuthnot as employing *probabilistic modus tollens* or as constructing a likelihood inference? The question may be unanswerable, since the distinction was not one that Arbuthnot had at his fingertips. However, a relevant interpretive consideration may perhaps be found in the fact that *probabilistic modus tollens* requires that one attend only to a single hypothesis, whereas likelihood inference is essentially comparative, involving at least two. The fact that Arbuthnot discusses what an intelligent designer would do inclines me to view him as having likelihood instincts. Arbuthnot believes that a benevolent deity, if such a being existed, would seek to insure an even sex ratio at the age of marriage. Seeing that males die more frequently than females before the age of marriage, he would achieve his goal by ensuring a male-biased sex ratio at birth. If Arbuthnot's argument has as a premise not just the assertion that Pr(Data | Chance) is tiny but also the claim that Pr(Data | Intelligent Design) is large, then we should understand him as advancing a likelihood inference.

Separate from the question of what Arbuthnot intended, we can ask which form of inference makes more sense. Although Hacking (1975, p. 168) follows standard practice in frequentist statistics in regarding *probabilistic modus tollens* as a valid form of inference, I am inclined to agree with Hacking's (1965) earlier point of view, and with that of Edwards (1972) and Royall (1997), that *probabilistic modus tollens* is invalid (Sober 2002, 2004). Perfectly plausible hypotheses sometimes confer extremely low probabilities on the observations, especially when the observations are numerous. Consider, for example, a coin that is tossed a million times. If the coin is fair, the exact sequence of heads and tails that this experiment produces has a probability of $(½)^{1,000,000}$, but that is no reason to reject the hypothesis that the coin is fair.[3] When he introduced the idea of significance testing, Fisher (1956, p. 39) noted that the occurrence of an event that the hypothesis under test says is very improbable licenses the conclusion that a disjunction is true – either the hypothesis is false or something very improbable has occurred. The disjunction is correct; what does not follow is that the hypothesis should be rejected.

[3] Defenders of significance testing will want to say that what should be considered as a description of the experimental outcome is not the exact sequence of heads and tails, but just the proportion of heads. Why this weakened description of the evidence captures everything that is relevant is a mystery from the point of view of that testing philosophy, though attending just to the proportions can be justified from the likelihood point of view (Hacking 1965, pp. 80-81).

A further issue, of which Arbuthnot also seems to have been unaware, became clearer some fifty years later, when Thomas Bayes's paper was published posthumously. Construed as a likelihood inference, Arbuthnot's premises do not allow one to conclude that the observed sex ratio was *probably* brought into being by an intelligent designer. What Arbuthnot discusses are probabilities of the form Pr(data | hypothesis), not probabilities of the form Pr(hypothesis | data). To reach a conclusion about what Arbuthnot calls the "probable cause" of the male bias at birth, Arbuthnot would need additional assumptions about the prior probabilities Pr(Chance) and Pr(Intelligent Design). This is because Bayes's theorem entails that

$$\text{(B)} \qquad \frac{\Pr(\text{Design} \mid \text{Data})}{\Pr(\text{Chance} \mid \text{Data})} = \frac{\Pr(\text{Data} \mid \text{Design})}{\Pr(\text{Data} \mid \text{Chance})} \times \frac{\Pr(\text{Design})}{\Pr(\text{Chance})}.$$

If the left-hand side of this equality is to be greater than unity (i.e., if Pr(Design | Data) > Pr(Chance | Data)), the right-hand side must exceed unity as well. We can add a premise to the materials that Arbuthnot assembles to ensure that this is so. If Pr(Data | Intelligent Design) = i (where i is large) and Pr(Data | Chance) = j (where j is tiny), then one *can* conclude that Intelligent Design has the higher posterior probability, if one is prepared to endorse the further assumption that Pr(Design)/Pr(Chance) > j/i.[4]

Arbuthnot's argument has to be understood in a larger historical context. Like many other writers of his time and place, Arbuthnot sought to debunk Epicureanism (Mayo 1934). The Epicurean Hypothesis holds that particles whirling at random in the void sooner or later form stable combinations, some of which exhibit great order, complexity, and functional appropriateness. In 1735, Arbuthnot published "A Poem -- Know Yourself," in which he expresses his rejection of Epicureanism by posing a series of rhetorical questions (David and Edwards 1991, p. 11):

What am I? how produced? And for what end?
Whence drew I being? To what period tend?
Am I the abandoned orphan of blind chance,
Dropt by wild atoms in disordered dance?
Or from an endless chain of causes wrought?
And of unthinking substance, borne with thought?

It takes probabilistic tools to discover what is wrong with Epicureanism. After all, it *is* possible, as we now would say, for monkeys pounding at random on typewriters to eventually produce the works of Shakespeare.[5] The problem is that this outcome, given some fixed number of monkeys

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[4] Proposition (B) provides an additional reason to regard probabilistic *modus tollens* as invalid. The fact that Pr(Data | H_1) is tiny does not settle whether Pr(Data | H_2) is even smaller, nor does it settle how the prior probabilities of the two hypotheses are related. This means that probabilistic *modus tollens* can lead one to reject H_1 and to not reject H_2, even though H_1 has the higher posterior probability. It also means that this form of inference can lead one to reject each of an exhaustive set of hypotheses, if each says that the observations are very improbable. Frequentists should not dismiss these objections on the grounds that they are "Bayesian." I say this because frequentists ought to grant that prior probabilities have an objective basis in *some* situations (even if not in all), and that is enough to lend weight to these criticisms.

[5] The earliest source I have been able to find for the monkeys-and-typewriters analogy is Borel (1913): "Concevons qu'on ait dressé un million de singes à frapper au hasard sur les touches d'une machine à écrire et que, sous la surveillance de contremaîtres illettrés, ces singes dactylographes travaillent avec ardeur dix heures par jour avec un million de machines à

and typewriters and a limited amount of time, is very improbable. Before typewriters were invented, other metaphors had to be found to convey this point. Arbuthnot's friend Jonathan Swift provides a nice one in Book 3 of *Gulliver's Travels*, where he describes a distinguished professor at the Grand Academy of Lagado (a stand-in for the Royal Society) who sought to "improve speculative knowledge by practical and mechanical operations;" his innovation was to produce random arrangements of words by twiddling the handles of a device that resembles a fooseball game (illustrated in Plate 5 of *Gulliver*, reproduced here in Figure 2). The probability of successfully generating a well-formed sentence of the language -- and one that is a new and useful contribution to speculative knowledge as well -- is not zero; rather, it is exceedingly tiny. It is not impossible that Chance should produce this result, just very improbable that it should do so.[6] When Hume has Philo invoke the Epicurean Hypothesis as a possible alternative to Intelligent Design in the *Dialogues concerning Natural Religion* (1776), he is trotting out an old warhorse that almost everyone took to be risable. The probability of success via Intelligent Design was supposed to be much larger, which is why the evidence was taken to favor Intelligent Design over Chance.

FIGURE 2

1.2. Bernoulli's Objection

In the second edition of his *Essai d'analyze sur les jeux de hazard*, Montmort (1713, pp. 371-375, pp. 388-394) reprints some correspondence between himself and Nicolas Bernoulli. In one letter, Bernoulli says that he feels "obliged to refute" Arbuthnot's argument (Todhunter 1865, pp. 130-131). His central idea is that Arbuthnot had not cast his net widely enough. There are other chance hypotheses besides the one that assigns to each male birth a probability of ½ . Bernoulli considers the possibility that the probability is 18/35 and argues that Arbuthnot's argument falls to pieces, once this new chance hypothesis is explored. To understand Bernouilli's criticism, it is necessary to attend to the *two* claims that Arbuthnot made about the data he cited. First, as already explained, he argued that the persistent sex ratio bias is evidence against Chance (i.e., against the hypothesis that the probability of a male birth is ½). But, in addition, he contended that the variation in sex ratio from year to year is too modest, if the Chance= ½ hypothesis is correct. Although Arbuthnot did a calculation to help support the first of these claims, he did nothing to demonstrate the second. Bernouilli's crisp reply is that if the probability of a male birth is 18/35, and 14,000 babies are born in a given year, then the probability is 300/301 that the resulting sex ratio will fall between the upper and lower figures in Arbuthnot's table of data. Bernoulli

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écrire de types variés. Les contremaîtres illettrés rassembleraient les feuilles noircies et les relieraient en volumes. Et au bout d'un an, ces volumes se trouveraient renfermer la copie exacte des livres de toute nature et de toutes langues conservés dans les plus riches bibliothèques du monde. Telle est la probabilité pour qu'il se produise pendant un instant très court, dans un espace de quelque étendue, un écart notable de ce que la mécanique statistique considère comme la phénomène le plus probable..." Eddington (1928, p. 72) had the same thought when he said that "if an army of monkeys were strumming on typewriters they *might* write all the books in the British Museum." The analogy is sometimes attributed to Huxley, in his 1860 debate with Wilberforce, but there is no transcript of that debate to consult.

[6] Richard Bentley also constructed an argument from "linguistic combinatorics" to deride the atheistic Epicurean hypothesis. In his inaugural Boyle lectures of 1692, he asks what the probability would be that a male and a female of the same species should each arise by chance. He answers by proposing an analogy, derived from Cicero's *Natura Deorum*, between the gigantic number of sequences that can be constructed from the Latin alphabet of 24 letters and the still greater number of arrangements there can be of the 1000 or more parts that comprise the human body (Shoesmith 1987, p. 136).

concludes that Arbuthnot's data provide no argument at all for Divine Providence; the data are perfectly in accord with the chance hypothesis that the probability of a male birth is 18/35.

Bernoulli seems to have understood Arbuthnot as arguing via probabilistic *modus tollens*; Bernoulli's point was to show that the Chance hypothesis cannot be rejected on the basis of the data that Arbuthnot considers, at least not when the Chance hypothesis is formulated in the right way. However, just as Arbuthnot's argument can be stated in terms of the law of likelihood, the same holds for Bernoulli's. The method of *maximum likelihood estimation* instructs us to choose the estimate that maximizes the probability of the observations. To estimate the probability of a male birth at 18/35 strains our credulity less than an estimate of 1/2, because the former renders the data more probable. As it happens, 18/35 is not the best estimate either, but it is better than the one that Arbuthnot discusses (Shoesmith 1985). Understood in this way, Bernoulli's criticism does not contradict Arbuthnot's initial point -- that we should be very surprised at the 82 years of consistent male bias, if the probability of a male birth were ½. However, instead of following Arbuthnot in preferring Intelligent Design to Chance=½, the likelihood recasting of Bernoulli's argument instructs us to conclude only that Chance=18/35 is preferable to Chance=1/2. We see here a familiar property of the Law of Likelihood. The fact that the data favor H_1 over H_2 does not settle how each of these hypotheses compares to a third hypothesis, H_3.[7]

Arbuthnot thought that the year-to-year variation in the data is too narrow if the Chance=½ hypothesis is correct. Bernouilli replied that the range of variation is perfectly in accord with the Chance=18/35 hypothesis. According to Anscombe (1981, p. 301) both were wrong; there is too much variation, regardless of what value is assigned to the probability of a birth's being a boy. Anscombe suggests that the christening records were a biased reflection of the real sex ratios; Hald (1990, p. 284) bolsters this conjecture by noting that there are trends in Arbuthnot's data that point to a political explanation. Before 1642, the number of christenings is around 10,000. During the 1650's it declines to about 6,000 and then increases to about 15,000 in 1700. The years with the most extreme sex ratios were 1659-61; as Hald remarks, "the turning point is about the Restoration." Apparently, the data do reflect the influence of intelligent design, though the designers were of human form.

1.3. DeMoivre's Defense of Arbuthnot – "if we blind not ourselves with metaphysical dust"

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In *The Doctrine of Chances*, DeMoivre (1756, pp. 252-254) comes to Arbuthnot's defense. He begins with a general affirmation of the soundness of the Design Argument:

> … as it is thus demonstrable that there are, in the constitution of things, certain Laws according to which Events happen, it is no less evident from Observation, that those Laws serve to wise, useful and beneficent purposes; to preserve the steadfast Order of the Universe, to propagate the several Species of Beings, and furnish to the sentient Kinds such degrees of happiness as are suited to their State.

[7] Although he does not fault Arbuthnot for using probabilistic *modus tollens*, Hacking (1975, p. 167) does think that Arbuthnot reasons invalidly when he infers that the hypothesis of intelligent design is true. Note that Arbuthnot is rescued from this criticism if he is interpreted as making a likelihood argument in which Intelligent Design and Chance=½ are compared; his mistake would then be that he failed to consider a third hypothesis, not that he reasoned invalidly from his premises.

> But such Laws, as well as the original Design and Purpose of their Establishment, must all be *from without*; the Inertia of matter, and the nature of all created Beings, rendering it impossible that any thing should modify its own essence, or give to itself, or to any thing else, an original determination or propensity. And hence, if we blind not ourselves with metaphysical dust, we shall be led, by a short and obvious way, to the acknowledgement of the great Maker and Governor of all; Himself all-wise, all-powerful and good (p. 252).

DeMoivre then says that Bernoulli, though "a very learned and good man … was led to discard and even to vilify this argument from final causes" when Bernoulli rejects Arbuthnot's argument. DeMoivre then describes Bernoulli's calculations concerning 18/35, after which he abruptly says what he thinks is wrong with Bernouilli's reasoning:

> To which the short answer is this: Dr. Arbuthnot never said "that supposing the facility of the production of a Male to that of the production of a female already fixed to nearly the Ratio of equality, or to that of 18 to 17; he was amazed that the Ratio of the numbers of Males and Females born should, for many years, keep within such narrow bounds:" the only Proposition against which Mr. Bernoulli's reasoning has any force.
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> But he might have said, and we do still insist, that "as, from the observations, we can, with Mr. Bernoulli, infer the facilities of production of the two Sexes to be nearly in a Ratio of equality, so from this Ratio once discovered, and *manifestly serving to a wise purpose*, we conclude the Ratio itself, or if you will, the Form of the Die, to be an effect of Intelligence and Design."
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> As if we were shewn a number of Dice, each with 18 white and 17 black faces, which is Mr. Bernoulli's supposition, we should not doubt but that those Dice had been made by some Artist; and that their form was not owing to Chance, but was adapted to the particular purpose he had in View.

Just as Paley (1802) later pressed the analogy between a watch and the human eye, so Demoivre urged the similarity of a 35-sided die (with 18 white faces and 17 black) and the human reproductive machinery. All exist only because an intelligent designer made them.

Has DeMoivre rescued Arbuthnot's line of reasoning? To answer this question, we should separate DeMoivre's argument from Bernoulli's by using the distinction that evolutionary biologists now draw between "proximate explanation" and "ultimate explanation" (Mayr 1961). The word "ultimate" is perhaps misleading, since the real point is to separate a relatively proximate from a more distal cause of some effect, as depicted in Figure 3. If we begin with the sex ratio data that Arbuthnot cites, we can draw an inference about the proximate mechanism in the human reproductive system that produces the consistent pattern of male bias. This argument, based on the Law of Likelihood, is the one we associated with Bernoulli's reasoning; it is better to view the chance mechanism that decides a baby's sex as having a probability of 18/35 of making the baby a boy than to view that probability as having a value of ½. Having settled the matter of proximate mechanism, we can move to a second problem. It might be suggested that the 18/35 chance set-up is plausibly explained by the hypothesis of intelligent design. This is the ultimate explanation that DeMoivre proposes, but what is the nature of the argument he offers in its defense? No likelihood argument is given – DeMoivre does not compute the probability of the reproductive mechanism's having this 18/35 setting (or any other) if it arose by Chance. Instead, DeMoivre invokes the older idea of "no design without a designer."

FIGURE 3

The problem with Arbuthnot's argument is that he does not keep the tasks of proximate and ultimate explanation separate. When he compares Chance and Intelligent Design, the Chance hypothesis that he considers purports to describe the proximate mechanism at work while his hypothesis of Intelligent Design provides a possible ultimate explanation.[8] This is an apples and oranges comparison. When the arguments are reconfigured to avoid this confusion, we have a likelihood argument concerning the proximate mechanism, which does not mention intelligent design, and DeMoivre's nonprobabilistic argument concerning the ultimate mechanism, which does. However, it is not difficult to supplement the probabilistic argument concerning proximate mechanism with a similar argument concerning ultimate explanation. What is the probability that the human reproductive system would confer on each birth a probability of 18/35 of being male, if that system were the result of chance? Very low. What is the probability that this 18/35 arrangement would arise if it were produced by an Intelligent Designer? Very high. Likelihoods now play a role twice over.

DeMoivre was too generous to Arbuthnot. Arbuthnot *did* make claims that Bernoulli was able to confute. And the argument that DeMoivre claims is sound is not a restatement of Arbuthnot's argument, but a new argument altogether (albeit in an old style). Yet DeMoivre came to accept a compromise that Bernoulli and 'sGravesande (the person from whom Bernoulli first learned of Arburthnot's argument) worked out together – that Bernoulli's Chance=18/35 hypothesis explains the christening data, and intelligent design explains why that chance hypothesis is true (Shoesmith 1987, p. 144).

2. Evolutionary Sex Ratio Theory

These 18th century discussions of sex ratio are interesting in part because of what happened to the problem after 1859. Symmetrically, the new evolutionary perspective is interesting in part because of the light it throws on the 18th century debate. In what follows I will not attempt to give anything like a full account of the history of evolutionary thinking about sex ratio. Rather, I will discuss some of the important episodes.

2.1. Darwin's Argument from Monogamy, and his Retraction

In the first edition of *The Descent of Man*, Darwin (1871, pp. 263 ff.) begins his discussion of the *Numerical Proportion of the Two Sexes* by recording what has actually been observed. Although "the materials are scanty," he provides a "brief abstract" of what is known, giving more details later in a "supplementary discussion." Darwin (p. 264) says that his interest is to ascertain the "proportion of the sexes, not at birth, but at maturity." His overall conclusion is that "… as far as a judgment can be formed, we may conclude from the facts given in the supplement, that the males of some few mammals,

[8] Arbuthnot's favored hypothesis is not that an intelligent designer intervenes directly in each birth; rather, he says that "there seems no more probable cause to be assigned in physicks for this equality of births, than that in our first Parents seed there were at first formed an equal number of both sexes." Arbuthnot's preformationism is interesting here; his reference to "equality" seems to be a slip.

of many birds, of some fish and insects, considerably exceed in number the females." He might have added that his supplement also describes eight groups of insects in which females outnumber males (pp. 314-315). The supplement also provides data on human populations (pp. 300-302). They are consistently male-biased at birth, although the degree of bias varies across populations. At the other end of the life span, "… the females in all old-settled countries, where statistical records have been kept, are found to preponderate considerably over the males." He also notes that male mortality exceeds female mortality in utero and for the first four or five years of life. If male bias at birth gives way to female bias later in life, there must be a cross-over point at which the human sex ratio is even; perhaps this occurs "at maturity," though Darwin does not say this.

So much for the tangle of observations – imperfect as they are and failing to exemplify any single, simple, pattern. How should these observations be explained? Darwin begins his discussion of this question in *On the Power of Natural Selection to regulate the proportional Numbers of the Sexes, and General Fertility* by noting that an uneven sex ratio might be "a great advantage to a species," and "might have been acquired through natural selection, but from their rarity they need not here be further considered." "In all ordinary cases," he adds, "an inequality would be no advantage or disadvantage to certain individuals more than to others; and therefore it could hardly have resulted from natural selection (pp. 315-316)." It is difficult to know how seriously to take Darwin's contrast between advantage to a species and lack of advantage to any individual. A modern biologist might be tempted to conclude that Darwin is saying that group selection can produce an uneven sex ratio but that purely individual selection cannot, and that Darwin is announcing his skepticism about group selection and advocating a purely individualistic approach. Is this interpretation Whiggish? As we will see, Darwin's explanation of even sex ratios invokes what is now usually classified as individual, not group, selection. But even so, it is well to remember that, in other contexts, Darwin slides easily between talking about benefit to the species and benefit to individuals, eliding a distinction that post-1960's biology has found to be exceedingly important. So perhaps we should not make too much of the present passage. What we can say is that Darwin chooses to focus on how natural selection might produce an even sex ratio even though he grants that selection in some circumstances might yield an uneven sex ratio, and even though his data include many species in which the sex ratio is uneven (Orzack 2001, pp. 169-170). One is reminded of the old saw about the drunk who looks for his keys under a lamppost. When asked why he is searching there, he answers that that is where the light is.

Having identified an even sex ratio at maturity as his proper *explanandum*, Darwin then states his argument for why "natural selection will always tend, though sometimes inefficiently, to equalise the relative numbers of the two sexes (p. 318):"

> Let us now take the case of a species producing … an excess of one sex – we will say of males – these being superfluous and useless, or nearly useless. Could the sexes be equalized through natural selection? We may feel sure, from all characters being variable, that certain pairs would produce a somewhat less excess of males over females than other pairs. The former supposing the actual number of the offspring to remain constant, would necessarily produce more females, and would therefore be more productive. On the doctrine of chances a greater number of the offspring of the more productive pairs would survive; and these would inherit a tendency to procreate fewer males and more females. Thus a tendency towards the equalization of the sexes would be brought about… (p. 316).

What does Darwin mean by an "excess" of one sex, where this excess can be due to there being more males than females, or more females than males? He seems to be assuming that reproduction is purely monogamous. When individuals form up into mating pairs, each individual has exactly one partner if the sex ratio is even. However, if the sex ratio is uneven, the formation of mating pairs will prevent some members of the majority sex from finding a partner. These unpaired individuals are what Darwin means by "excess." It is the assumption of monogamy that entails that some individuals must fail to reproduce if the sex ratio is uneven (Edwards 1998).[9,10] Darwin briefly remarks that his argument applies to polygamous species, "if we assume the excess of females to be inordinately great (p. 317)." His point seems to be that selection will reduce a very extreme degree of female bias to one that is more modest, if a polygamous mating scheme is already in place. For example, if each male has three mates, then there will be "excess females" when there are more than 75% females at reproductive age, and so selection will reduce that greater figure to 75%, whereupon there is no longer an "excess." This interpretation of what Darwin meant by the argument's applying to polygamy clashes with his commitment to address only the evolution of an even sex ratio, but I cannot see any other way to interpret it.

Does Darwin's explanation invoke individual or group selection? As noted above, this is a distinction that is more vivid now than it sometimes was in Darwin's own writings, though it certainly is very clear in some of what he wrote. The assumption of monogamy entails that a group with an even sex ratio will be more productive than a group of the same size that has an uneven sex ratio; given monogamy, an even sex ratio thus provides an advantage to the group. Though this is true, it is not Darwin's argument. Darwin is thinking about a single group and asks us to consider the different mating pairs within it. He seeks to identify the best reproductive strategy that a parental pair can use in determining its mix of sons and daughters. If the next generation contains an excess of males, the best strategy for a mating pair is to have more daughters, and if the next generation contains an excess of females, the best strategy is to have more sons. If the mix of sons and daughters produced by a parental pair were regulated just by the mother, or just by the father, it would be perfectly clear that this is an argument about individual advantage. The selection takes place among the individuals in a single population, not among populations, so no group selection is involved. But what if both parents influence their mix of daughters and sons? Is selection among the mating pairs in a population an instance of group selection, the groups each containing two members? Contemporary biologists who dislike the idea of group selection will be loath to see mating pairs as "groups" in the sense of group selection, but those more comfortable with the idea (e.g., Sober and Wilson 1998) will see nothing amiss in classifying Darwin's model in this way. This fine point aside, it is clear that Darwin's argument does not invoke "the good of the species" in any substantive sense.

In the 2nd edition of *The Descent of Man*, Darwin (1874, pp. 267-268) retracts his analysis and substitutes a disclaimer – "I formerly thought that when a tendency to produce the two sexes in equal numbers was advantageous to the species, it would follow from natural selection, but I now see that the whole problem is so intricate that it is safer to leave its solution to the future." He admits that although

[9] When Darwin considers the evolution of an even sex ratio when there is an excess of females, he says that excess females "from not uniting with males would be superfluous and useless (p. 317);" this clearly indicates that he is assuming monogamy.

[10] Recall Arbuthnot's Scholium on polygamy, in which the existence of an even sex ratio at the age of marriage is used to argue for the normative appropriateness of monogamy. Darwin reasons somewhat in reverse -- from the assumed fact of monogamy to the existence of an even sex ratio – except that his argument involves no ethical judgment.

there are circumstances in which one sex ratio or another would be advantageous to the species, "in no case, as far as we can see, would an inherited tendency to produce both sexes in equal numbers or to produce one sex in excess, be a direct advantage or disadvantage to certain individuals more than to others; … and therefore a tendency of this kind could not be gained through natural selection." Here again one needs to consider whether Darwin meant to contrast what is good for the species with what is good for the individual, or rather was using these phrases interchangeably. But even if Darwin *is* demanding that the evolution of sex ratio be explained without invoking the good of the species (an interpretation that Seger and Stubblefield 2002, p. 6, describe), it isn't clear why this led him to doubt his earlier argument.

Darwin does not state his reasons for retracting, but Chapter XX of *The Descent of Man* provides a good reason for him to do so. Darwin (1871, Part 2, pp. 361-362) notes that although Orangs are monogamous, Gorillas, Chimps, and Baboons are not. And the same holds of human beings, both present and past:

> Judging from the social habits of man as he now exists, and from most savages being polygamists, the most probable view is that primeval man aboriginally lived in small communities, each with as many wives as he could support and obtain, whom he would have jealously guarded against all other men. Or he may have lived with several wives by himself, like the Gorilla …

This supplements his earlier remark that "many mammals and some few birds are polygamous (1871, Part 1, p. 266)." A fundamental feature of Darwin's approach in the first edition is that mating scheme explains sex ratio. Monogamy leads an even sex ratio to evolve, and polygamy leads an uneven sex ratio to evolve. If there are polygamous species with even sex ratios, this is a problem for his account.[11] Darwin didn't have to look far from home to find such problem cases.

2.2. The Düsing Model – Monogamy Drops Out

Biologists nowadays often think of R.A. Fisher (1930) as having been the first biologist to grapple substantively with the problem of explaining sex ratio in terms of natural selection, but this is an impression that needs to be corrected. We have already seen that Darwin had a substantive and interesting take on the problem. Unfortunately, Fisher (1930) mentions Darwin's later bewilderment, but not his earlier clarity. And Fisher does not mention the work of Carl Düsing (1884) at all; Düsing produced an algebraic argument for why selection will lead to the evolution of an even sex ratio at reproductive age. Seger and Stubblefield (2002, p. 8) say that Düsing's account is "perhaps the first mathematical model in evolutionary biology." How is Düsing's argument related to Darwin's formulation? Edwards (1998, 2000) and Seger and Stubblefield (2002) see Düsing as putting into mathematical language the ideas that Darwin (1871) had thought through only qualitatively. I see a difference in substance, not just the introduction of algebraic symbols. As I have emphasized, Darwin's (1871) explanation of an even sex ratio rests on the assumption of monogamy. Düsing does without that assumption.

[11] The nature of this problem will be clarified in the last section of this paper.

Düsing's starting idea makes explicit what was only implicit in Darwin – that we need to consider three generations: (1) the parental generation, (2) the generation of offspring, and (3) the generation of grandoffspring. A simplified version Düsing's argument can be put as follows. If there are *m* males and *f* females in generation 2, and if they together produce the *N* individuals who exist in generation 3, then the average male in generation 2 has *N/m* offspring in generation 3 and the average female in generation 2 has *N/f* offspring in generation 3. This means that the minority sex in generation 2 will be more reproductively successful. A parent in generation 1 who wishes to maximize the number of grandoffspring she has in generation 3 should therefore produce offspring in generation 2 who are exclusively of the minority sex. An equilibration process is thus set in motion – if the population is male-biased, selection will favor the overproduction of females, and if it is female-biased, selection will favor the overproduction of males. The population reaches equilibrium when the sex ratio at reproductive age is even, at which time a parent who has one mix of daughters and sons does no better or worse than a parent who has any other. Only when the sex ratio is uneven will there be fitness differences among the different possible "sex ratio strategies" (a modern term) that a parent might follow.

Notice that there is no need to impose the requirement of monogamy to see what happens to the average male and the average female in generation 2. Even with polygamy, it remains true that the male average is N/m and the female average is N/f. True, some males have more than N/m offspring while other have none at all, and it also may be true that the female variance is less than the male variance. But Düsing saw that this does not matter – "whilst the female sex shows a much greater constancy in the strength of reproduction, the widest variation may occur in the case of the male individuals. But in our calculation it is not a matter of how far any extremes deviate, but what the average number of offspring is, and this number is of the same magnitude for male and female individuals at normal [i.e., even] sex ratios (translated in Edwards 2000)." Here Düsing underscores his earlier remark that "it is true that in each individual case [the number of offspring produced] is subject to considerable variation, but if one wants to illustrate and calculate the total effect in an example one must naturally use the average number." Whereas Darwin considers what happens to *each* male and *each* female in the second generation, Düsing considers just the *average* male and the *average* female.

When there is monogamy, Darwin and Düsing both think of natural selection as "aiming" at an even sex ratio at reproductive age. If males die more frequently than females before reproductive age, Darwin and Düsing both can make sense of the fact that there is a male-biased sex ratio at birth. But Darwin and Düsing part ways over polygamous species that have even sex ratios at reproductive age; these are a problem for Darwin, but not for Düsing. On the other hand, an uneven sex ratio at reproductive age is a problem for Düsing, whereas Darwin's argument makes room for uneven sex ratios when there is polygamy.

2.3. Fisher and Parental Expenditure

Fisher gives a characteristically compressed treatment of the evolution of sex ratio in his landmark book *The Genetical Theory of Natural Selection* (Fisher 1930, pp. 158-160). Like Darwin's account, Fisher's is purely verbal, with no mathematical symbols in sight. How is Fisher's theory related to the theories of Darwin and Düsing? Edwards (2000) says that Düsing gave a mathematical account "based on the same argument that Darwin had advanced," and that Fisher "gave a verbal account of the argument in *The Genetical Theory of Natural Selection*…" I have already tried to separate Düsing's account from Darwin's; I now want to separate Fisher's from Düsing's.

The simple point is that Fisher's and Düsing's models predict different equilibrium values – different endpoints towards which the process of natural selection will tend to "push" a population. Whereas Düsing argues that natural selection will lead to an even sex ratio at "the time of reproduction" (Edwards 2000, p. 256), Fisher's fundamental idea is that natural selection leads to equal "parental expenditure," and equal expenditure need not manifest itself as equal numbers of the two sexes at reproductive age. As already noted, Düsing had room in his account for male-biased sex ratios at birth. What Düsing rules out, but Fisher does not, is a biased sex ratio at reproductive age.

Fisher's concept of parental expenditure encompasses both the creation of sons and daughters and the rearing of those offspring to independence. If each mother in a population has a package of resources to spend on creating and sustaining her sons and daughters, what percentage of that package should she devote to sons and which to daughters? That is, what division will natural selection favor? The standard way to think about this question is to suppose that all the parents in a population use one division of resources, and then to ask when a novel parent using a different division will do better, in the sense of having higher fitness, which in this context means having more grandoffspring.

Suppose that each mother in the population has a total package of resources T and that she devotes pT to build and maintain her sons and $(1-p)T$ to build and maintain her daughters. She does this during a time that begins with conception and ends when her children begin to live independently; perhaps a bit more time passes before her offspring reproduce. Suppose that each mother in the population spends c_m on the average son and c_f on the average daughter, and that the average son brings her b_m units of benefit (in terms of providing her with grandoffspring) and the average daughter brings her b_f. Then a mother's total fitness, taking account of both her costs and her benefits, is

$$b_m[pT/c_m] + b_f[(1-p)T/c_f] .$$

The symbols inside the square brackets represent the number of sons and daughters she has, and the whole expression sums the benefit she receives from her sons and the benefit she receives from her daughters.

The evolutionary question can be posed as follows: When will a mutant mom have higher fitness than these resident females by producing some other mix (p* and (1-p*)) of sons and daughters? The mutant mom's total fitness is

$$b_m[p^*T/c_m] + b_f[(1-p^*)T/c_f],$$

so our question is when it will be true that

$$b_m[p^*T/c_m] + b_f[(1-p^*)T/c_f] > b_m[pT/c_m] + b_f[(1-p)T/c_f] .$$

This simplifies to

$(b_m/c_m - b_f/c_f)(p^* - p) > 0.$

For the product on the left-hand side to be positive, both product terms must be positive or both must be negative. This means that the mutant mom has higher fitness than a resident mom precisely when either

$[b_m/c_m > b_f/c_f$ and $p^* > p]$ or $[b_m/c_m < b_f/c_f$ and $p^* < p]$.

In other words, if sons have a higher benefit to cost ratio than daughters, then for the mutant mom to be fitter than the others, she should produce a higher proportion of sons than the resident moms do; on the other hand, if sons have a lower ratio than daughters, then the mutant should produce a lower proportion of sons than the residents produce. But notice something simpler: the mutant can't do better than a resident if $b_m/c_m = b_f/c_f$. When this equality holds, the selective evolution of sex ratio stops. But what mix of males and females does this equality represent?

To answer this question, we have to further clarify the meaning of the benefit terms b_m and b_f. Suppose that the offspring generation produced by the original generation of parents has *m* males and *f* females at the end of the period of parental care. Not all of these individuals need live to reproductive age, but the fact remains that if there are *N* offspring in the third generation, the average second generation male at the end of the period of parental care has *N/m* offspring and the average female has *N/f*. These are the benefits that sons and daughters provide. So the mutant mom will have the same fitness as the residents precisely when

$N/mc_m = N/fc_f.$

Fisher's principle of equal expenditure is simply the idea that $mc_m = fc_f$; at equilibrium, the parental population's total investment in sons equals its total investment in daughters. Notice that this expression also can be written as

$m/f = c_f / c_m.$

An even sex ratio (m = f) at the end of the period of parental care is an equilibrium if $c_f = c_m$., but if $c_f > c_m$, the equilibrium will require there to be more males than females. The investment made in the average male will be less than the investment made in the average female if males have a higher mortality rate during the period of parental care. So greater male mortality during the period of dependence predicts a male-biased sex ratio at the end of that time.

It may seem that Düsing's model is a special case of Fisher's, with Düsing's derived from Fisher's by letting $c_f = c_m$. This is not correct. Düsing calculates the sex ratio "at the time of reproduction" (Edwards 2000, p. 256), whereas Fisher's model predicts the sex ratio at the time of independence, which may come earlier. Stipulating that $c_f = c_m$ in Fisher's model entails an even sex ratio at the end of the period of parental care, which is not what Düsing claims.[12] As Fisher notes,

[12] Of course, Düsing's claim that selection leads to the evolution of an even sex ratio at reproductive age will be a consequence of Fisher's model if we assume that the costs of sons and daughters while they are being reared is the same and that there is zero time between independence and reproductive age. However, the time between independence and maturity is not a variable in Fisher's model.

> the sex ratio at the end of the period of expenditure thus depends upon differential mortality during that period …it will not be influenced by differential mortality during a self-supporting period; the relative numbers of the sexes attaining maturity may thus be influenced without compensation by differential mortality during the period intervening between the period of dependence and the attainment of maturity (pp. 159-160).

Natural selection may of course reduce the rates of mortality that each sex experiences between independence and maturity, but this isn't relevant to how natural selection affects the mix of sons and daughters that parents produce. For Fisher, selection for sex ratio should be understood in terms of a prediction concerning the sex ratio that obtains at the age of independence, not the sex ratio that obtains at reproductive age. Darwin and Düsing had addressed the wrong question.

2.4. Williams and Hamilton – Group versus Individual Selection

The subject of sex ratio evolution took another step forward in 1966, when George C. Williams published *Adaptation and Natural Selection*. Williams's main subject was the difference between the processes of group selection and individual selection. As noted earlier, group selection occurs when there is competition among groups; it promotes the evolution of traits that reduce a group's risk of extinction and increase its productivity. Individual selection occurs when there is competition among the individuals in a group; it promotes the evolution of traits that enhance the viability and fertility of the individuals that have them. The concept of altruism shows that there can be a conflict of interest between what is good for the group and what is good for an individual. Consider a now-standard (and simplified) example: it may help a group of prairie dogs if an individual issues a warning cry when a predator approaches, but the warning cry may endanger the sentinel by attracting the attention of the predator; from that sentinel's selfish point of view, it does better by remaining silent. Group selection may lead to the evolution of sentinel behavior, but individual selection will drive that altruistic behavior to extinction.

Williams recognized that Fisher's treatment of sex ratio uses the idea of individual selection. As already noted, Fisher asked what *an individual parent* should do to maximize the number of grandoffspring she has. Williams then posed a different question – what sex ratio should we observe if the trait evolved by the process of group selection? His answer was that individuals should be able to adjust the mix of sons and daughters they produce. When groups have the opportunity to grow larger, there should be a female-biased sex ratio, since this maximizes group productivity. But when the population is in danger of over-exploiting its environment and crashing to extinction, the population should shift to a male-biased sex ratio, since this will reduce its productivity. Williams' idea was that the hypothesis of group selection could be tested against the hypothesis of individual selection by seeing what sex ratios are present in nature. He reports that "in all well-studied animals of obligate sexuality, such as man, the fruitfly, and farm animals, a sex ratio close to one is apparent at most stages of development in most populations (p. 151)." This statement is incorrect, not just as a claim about nature, but as a claim about what was known about nature in 1966. In any event, Williams concluded that sex ratio data provide strong empirical evidence against group selection. It is curious that Williams saw no difficulty in placing this empirical argument side-by-side with other arguments against group selection that are nearly *a priori* in character.[13] The purpose of *Adaptation and Natural Selection* was to decisively discredit the idea of group selection. For Williams, the hypothesis was not just factually mistaken – it was a product of fuzzy thinking, and a deplorable encouragement for more of the same.[14]

A year later W.D. Hamilton published his landmark paper "Extraordinary Sex Ratios," in which he provided a mathematical model in which evolutionary outcomes very different from the ones treated by Fisher could occur. Unlike Williams (1966), Hamilton (1967) was aware that the sex ratios in many insects are strongly female-biased. His approach to understanding how this arrangement might evolve was to consider a hypothetical species of parasitic wasp in which one or more fertilized females lay eggs in a host; when the eggs hatch, the offspring reproduce with each other and the fertilized females then take flight to find new hosts to parasitize. Hamilton asked the same three-generation question that Darwin, Düsing, and Fisher posed, but he got a different answer. Suppose each host is parasitized by a single fertilized female. What mix of sons and daughters should she produce in order to maximize her number of grandoffspring? Clearly, she should produce the smallest number of sons needed to fertilize all her daughters. Because there is strong inbreeding, a female-biased sex ratio will evolve.

Hamilton's point was not to refute Fisher's model, but to show that it rests on special assumptions. Fisher's model is correct when there is random mating in a large population. In fact, Hamilton's model has Fisher's as a special case. Hamilton's model describes what sex ratio will evolve if groups are founded by one, two, or *n* fertilized females. As the number of foundresses is increased, the predictions of Hamilton's model get closer to Fisher's.

Although Hamilton's model was framed in terms of inbreeding and local mate competition, it also can be framed in terms of within- and between-group selection, as Hamilton (1967) noted in a footnote and Williams (1992) later acknowledged. In Hamilton's model, pure group selection favors a strongly female-biased sex ratio – this is what maximizes group productivity; pure individual selection favors the Fisherian solution of equal investment in the two sexes.[15] In the real world, organisms may simultaneously experience both group and individual selection; if there is both competition among groups and competition within groups, the resulting sex ratio will be a compromise between what happens in the two pure cases. An example in which groups are founded simultaneously by two fertilized females is analyzed in the Appendix.

3. Evolutionary Reflections on the 18th Century Debate

According to the evolutionary ideas just summarized, what is good for the group (a female-biased sex ratio, if the group does best by maximizing its productivity) differs from what is good for the individual (equal investment in sons and daughters). With this thought in mind, we can return to

[13] The incoherence of claiming both that group selection is *a priori* impossible and that it is empirically disconfirmed is discussed in Sober (1984).
[14] For further discussion of sex ratio theory and its relation to the units of selection problem, see Sober and Wilson (1998).
[15] Hamilton (1967) does not explore Williams' suggestion that group selection will favor organisms that facultatively adjust their sex ratios. However, his model does describe the situation in which there is variation in the number of females who found a nest. If females can detect how many other foundresses there are or will be, they should adjust the mix of sons and daughters they produce. The parasitic wasp *Nasonia vitripennis* is a case in point; for empirical details on how closely this organism conforms to the predictions of Hamilton's model, see Orzack *et al.* (1991).

Arbuthnot's argument and ask a new question. An even sex ratio at reproductive age, according to Arbuthnot, is good for the species ("that it may not perish") and good for individuals as well. Arbuthnot, I take it, did not know that there are many insect species in which the sex ratio is female-biased, but we nonetheless can ask what he and his latter day epigones would say about this curious situation. Was God malevolent when he made these insects thus? Intelligent design theorists, both ancient and modern, can be expected to reply in the negative -- God was benevolently disposed to human beings when he gave us an (almost) even sex ratio and benevolently disposed to those insects when he made them female-biased. But what do intelligent design theorists mean by "benevolence" when the term is used so flexibly? To begin with, we can't automatically assume that God would think of what is good for insects or human beings in terms of what maximizes the number of grandoffspring. And even if the concept of goodness is given a purely reproductive reading, it still isn't clear what "good" means. Does it mean good-for-the-individual, or good-for-the-species, or good-for-the-ecosystem? The term "good," as used by intelligent design theorists, apparently means good-for-something-they-know-not-what; the word is irremediably vague. The hypothesis that an omnipotent, omniscient, and benevolent intelligent designer produced the sex ratios of different species in fact makes no predictions at all about the sex ratios we should observe (Sober 2002, 2004). One half of Arbuthnot's likelihood argument – his claim that Pr(Data | Intelligent Design) is large -- involves an undefended, and still indefensible, assumption. Arbuthnot *assumes* that God wants the sex ratio at the age of marriage to be even, but how does Arbuthnot know that? And even if God does want this outcome, why does he achieve it by making the sex ratio at birth uneven, rather than by reducing the male mortality rate, or increasing the female? An answer to this question can doubtless be *invented*; the point is that there is no *independent evidence* that the invented story is *true.*

Modern sex ratio theory, in contrast, makes testable predictions about the sex ratios we should observe. However, those predictions need to be understood probabilistically. It would be a mistake to think that Fisher's model predicts that random mating will *always* be associated with equal investment, or that Hamilton's model predicts that strong inbreeding will *always* be associated with female bias. Nor would it be correct to substitute "usually" for "always." Rather, we should regard the models as saying that different breeding structures are "positive causal factors" for different sex ratios (Sober 1984; Orzack and Sober 2001). Random mating raises the probability of equal expenditure, and inbreeding raises the probability of female bias. Breeding pattern is to sex ratio as smoking is to cancer. The two causal hypotheses may be tested in the same way. The prediction for the smoking hypothesis is that smokers should get cancer more often than nonsmokers who are otherwise similar; the prediction for the sex ratio hypotheses is that this or that sex ratio should occur more frequently in populations with one breeding structure than it does in populations with another that are otherwise similar. Spelling out how this test should be structured would bring in a number of interesting complications, but there isn't space here to provide details; in any event, they aren't relevant for present purposes, since the main point is this: The models that currently comprise evolutionary sex ratio theory can be tested by observing breeding structures and sex ratios (as well as other biological variables) in different populations. It might turn out that a model makes accurate predictions about sex ratios in one group of species, but inaccurate predictions about sex ratios in another. Evolutionary theory involves no *a priori* commitment to the thesis that a trait found in different branches of the tree of life always evolves for the same reason. If contemporary sex ratio theory makes inaccurate predictions about a group of organisms, other evolutionary explanations will have to be found and they will have to be testable if they are to pass scientific muster.

Historians will probably be less interested in criticizing 18th century sex ratio theory than in understanding its conceptual structure. Even so, the evolutionary perspective developed in the 20th century helps us recognize an important property of Arbuthnot's thinking. The idea of the harmony of nature was a fundamental commitment for this 18th century writer, as it was for many of his contemporaries. That commitment had the effect of rendering conflicts of interest invisible. Arbuthnot thought that what is good for each individual is also good for the species, just as Adam Smith thought that if each individual in a market economy pursues his own selfish advantage, a side effect, wrought "as if by an invisible hand," would be an improvement in collective well-being.[16] Although Darwin often fell into the rhetoric of assuming that traits that help an individual survive and reproduce are automatically good for the species, the logic of his theory undermines that automatic assumption (Sober 1994). Selection processes at different levels of organization promote different evolutionary outcomes.[17] Individual selection can cause a population to evolve a configuration that drives it straight to extinction, just as group selection can lead to a configuration in which some individuals drastically reduce their own prospects for surviving and reproducing. When both processes influence the evolution of a given trait, the character of the resulting compromise will depend on contingent details. Those who believe only in individual selection may think of natural selection as "aiming" exclusively at the evolution of traits that promote an individual's survival and reproduction. However, from the point of view of multi-level selection theory (Sober and Wilson 1998), there is no such thing as *the* one and only kind of trait that selection always promotes. The idea of conflicts of interest makes it much harder to think of the living world as due to a designer's benevolence, not because there is so much moral evil in the world (though there is), but because we do not know what benevolence even means in this connection.

Appendix – An example of Hamiltonian sex ratio evolution in groups with two foundresses

Suppose there are two sex ratio strategies a female wasp can follow – Even (producing 5 sons and 5 daughters), and Biased (producing 1 son and 9 daughters). If each group is founded by two fertilized females who simultaneously lay their eggs, there are three types of group – those founded by two Even females, those founded by an Even and a Biased female, and those founded by two Biased females. After the eggs in a nest hatch, there is mating exclusively among nest-mates; the fertilized females then disperse and pairs of fertilized females then establish a new generation of nests, as before. Notice that the three types of group produce different numbers of grandoffspring: 100 (two Evens), 140 (one Even and one Biased), and 180 (two Biased). The Biased trait is advantageous to the group; the more Biased foundresses the better, as far as group productivity is concerned. Group selection therefore favors the evolution of this trait.

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[16] See Hirschman (1977) for discussion of the historical context in which Smith developed his views concerning the relationship of individual self-interest and the wealth of nations.

[17] Fisher (1930, p. 49) notes that his fundamental theorem of natural selection applies to traits that provide an "advantage to the individual," but that "it affords no corresponding explanation for any properties of animals or plants which, without being individually advantageous, are supposed to be of service to the species to which they belong." He then adds that "this distinction was unknown to the earlier speculations to which the perfection of adaptive contrivances naturally gave rise. For the interpretation that these were due to the particular intention of the Creator would be equally appropriate whether the profit of the individual or of the species were the objective in view."

What is the nature of the selection process that occurs at the individual level – at the level of individuals who live in the same group? Homogeneous groups (Even-Even and Biased-Biased) contain no variation, so no individual selection occurs there. However, individual selection does occur in mixed groups. When an Even and a Biased individual together found a group, which will have the larger number of grandoffspring? The Even female has 5 of the 6 sons in the group and 5 of the 14 daughters. The Biased female has 1 of the 6 sons and 9 of the 14 daughters. If the 6 males and 14 females in the second generation mate at random, what will be the expected pedigrees of the individuals in the third generation – that is, to which of the two foundresses can they be expected to trace back? These expected pedigrees are depicted in Figure 4.

FIGURE 4

The grandoffspring in the upper-right and lower-left cells of Figure 4 trace back to both foundresses (to one through their father and to the other through their mother) while the grandoffspring in the upper-left cell come exclusively from the Even foundress and those in the lower-right cell come exclusively from the Biased foundress. It should be clear from this that the Even foundress has been more successful in producing grandoffspring. Selection at the individual level – within mixed groups – therefore favors the Even trait.[18]

It follows that Even is a selfish trait, and Biased is altruistic. The Biased trait enhances the fitness of the group, but is disadvantageous to individuals in mixed groups (Colwell 1981).

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[18] The same conclusion would follow if the Biased trait produced any other unequal mix of sons and daughters. Furthermore, in a competition between two strategies that show different degrees of bias, the one that is closer to producing an even mix of sons and daughters will be favored at the within-group (individual) level.

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Figure 3

Distal cause		Proximate cause		Effect
God	→	Human reproductive mechanism	→	Observed sex ratio

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DeMoivre   Bernoulli

Figure 4

		Pedigree frequencies of females in the 2nd generation: 5/14 Even	9/14 Biased
Pedigree frequencies of males in the 2nd generation	5/6 Even	25/84	45/84
	1/6 Biased	5/84	9/84

Figure Captions

Figure 1: Arbuthnot's 1710 tabulation of male and female births in London in each of 82 years.

Figure 2: Plate 5 of Swift's *Gulliver's Travels* depicts a device for randomly generating sentences, used in the Kingdom of Lagado to "improve speculative knowledge by practical and mechanical operations."

Figure 3: Bernouilli offered a proximate explanation of Arbuthnot's sex ratio data, while DeMoivre offered a more distal explanation.

Figure 4: A group is founded by two fertilized females; the Even female has 5 sons and 5 daughters while the Biased female has 1 son and 9 daughters. If there is random mating within this offspring generation, what pedigrees should we expect the individuals in the grandoffspring generation to have? The four cells in the table indicate the percentage of individuals in the third generation who can be expected to trace back to just one foundress, or just to the other, or to both.