Implications of the Trivers-Willard Sex Ratio Hypothesis for Avian Species and Poultry Production, And a Summary of the Historic Context of this Research

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Abstract

At a theoretical level, the Trivers-Willard Sex Ratio Hypothesis applies to both avian species and mammals. This article, however, conjectures that at the statistical level, sex ratio effects are likely to produce sharper numerical variations among birds than among mammals. We explain this greater statistical variation should likely have beneficial implications for increasing the efficiency of world-wide poultry egg (and perhaps also meat) production.

Keywords and Phrases: Fisher’s Sex Ratio Theory, the Trivers-Willard Hypothesis, Sex Determination Controls among Avian Species, Enhancing Poultry Egg Production.

Mathematics Subject Classification: 92D15; 92D25; 92D40; 92D50

Comment: A 30-minute invited talk summarizing the contents of this article was presented on June 18, 2017 at the NEEPS-2017 Conference at Binghamton University. The Version-1 June 27 (2017) draft of this paper was similar to the 30-minute talk I gave at Binghamton University, and it was disseminated nine days after this talk. This second draft is more detailed and polished because it contains Section 4’s additional evidence.
1 Introduction

The Trivers-Willard Hypothesis is an extension of Fisher’s Sex Equilibrium paradigm \cite{15, 61}. Fisher had noted that essentially all vertebrate species will invest a roughly equal amount of energy raising male and female offspring because such a paradigm corresponds to the favored stabilizing equilibrium state that Darwinian Evolution gravitates towards over an extended period of time. The Trivers-Willard Hypothesis (TW) was based on the observation that some mating couples provide a setting (or have genes) more useful to male reproductive success, while others will be more supportive to a female’s reproductive success. TW predicted that it would be useful, accordingly, for Darwinian Evolution to attempt to guess which settings are more useful to which sex’s reproductive success, and then to adjust the sex ratio to reflect the strategy that maximizes long-term reproductive success. This prediction will be called the Generalized Version of the Trivers-Willard Hypothesis.

I conceived of this version of the TW during a 25-minute bicycle ride, after taking in the Spring of 1968, a philosophy course at SUNY Stony Brook. Its reading material included the Desmond Morris book entitled *The Naked Ape* \cite{35}. During that fateful bicycle ride, I also reconstructed Fisher’s general sex ratio paradigm (without knowing that Fisher conceived of this idea almost forty years earlier). I also noticed that the preceding “Generalized” theory would imply that a mating couple should be more likely to produce male offspring when they are in better health condition (or have an above average nutritional diet). This latter observation was a consequence of the well known anthropological observation that competitive success benefits the reproduction rate of a male more than a female because a male is capable of inseminating simultaneously several females.

At the conclusion of this 1968 bicycle ride, I was left with a quandary as to what to do next? This is because I was uncertain what part of the “Generalized” theory was new, if any part of it was actually new? There were several occasions in the past when I developed theories that I learned, later, others had discovered substantially earlier \footnote{For example during a bicycle ride in 1964, I reconstructed many of the famous integration formulas, taught in a Freshman Calculus course, without knowing about the famous mathematical research done 200 years earlier. The resulting series of brain-storming thoughts actually resulted in my discovering of Euler’s irrational number of “e”, without knowing what Euler had done. Humorously, I naively called this number “w” (for “Willard’s constant) before learning, to my naive teen-age chagrin, that Euler discovered approximately two centuries earlier a comparable irrational number he called “e”.
}. In the end, I decided to make no effort to publish the Generalized Theory in 1968 because I thought it likely that either
someone had thought of a similar idea earlier, or it would be difficult to persuade the academic community that these principles were sound. (My reluctance to publish this “Generalized” theory was further amplified by two family tragedies, where my father experienced a heart attack and my mother was diagnosed with cancer during that same year of 1968. My mother was diagnosed with cancer, actually, only a few weeks after my bicycle ride. I doubt I would have had the temperament to discover the General Theory, had the chronology of these two events been physically reversed.)

The remainder of the history behind the TW discovery has been told by Robert Trivers. In 1970, I attended Harvard University as a graduate student and audited a course taught by Irven Devore, where Robert Trivers was a teaching assistant. In one lecture during that course, Trivers reviewed Fisher’s Sex Ratio Principle, and he mentioned in a subsequent second lecture that it was known that upper class income families were statistically more likely to have male offspring. I was delighted when I heard the first of Trivers’s two lectures because I had inadvertently reconstructed Fisher’s 50/50 sex ratio principle during my earlier 1968 bicycle ride. I explained to Trivers, subsequently after his second lecture, my explanation for the statistical paradigms he mentioned. Trivers warmly encouraged me to publish this result.

Distracted by the illness of both my parents, as well as the burden of preparing for Harvard’s notoriously hard Ph D Qualifying exam in Mathematics, I did not pursue the TW project further. As a consequence, Bob Trivers helpfully wrote up the manuscript of what would ultimately become our announced result. This joint paper [48] did later become a classic article, according to the MacArthur award-winning philosopher Rebecca Goldstein [21], within sociobiology’s broader and ever-expanding literature.

A period of 49 years has now transpired between the current date and the occasion when I took that fateful 25-minute bicycle ride in 1968. It is accurate to state that no single 25-minute investment of my time (conjoined with Robert Trivers excellent and meticulously diligent write-up of our joint paper [48] ) did produce a greater impact on the academic community from my on-going research. Thus on 23 June 2017, Google Scholar recorded that there were 3,338 citations to [48]’s research, except for one hilarious error, that deserves to be in a Woody Allen movie. It will make the academic community laugh at the silly incompetence of the careless computer engineers, who embedded an amusing, almost schizophrenic bug into what was supposed to be their sagacious Google-Scholar software.

\[\text{2 The amusing error is that neither Dan Willard nor Robert Trivers were listed by Google-Scholar as the authors of the article [48], as recently as 23 June 2017. Instead, “James A. McKanna” is listed as the author}\]
In any case, this little “Google Bug” is of small importance because the significance of the TW article is well known. For instance, there have been four recent mentions of this article in the popular news media [10, 37, 38, 40]. The latter has included one year-2017 article in the Sunday Week in Review section of the New York Times [38].

Our purpose in the current short note will be to achieve three goals. The first will be to suggest that avian species are likely to follow the predictions of the TW hypothesis with greater statistical accuracy than do mammals. A second objective will be to suggest that this prediction is likely to have beneficial implications in enhancing the efficiency of poultry farms. A third goal, confined to §5, will be to provide the reader with a brief summary of my research into symbolic logic and into Gödel’s Incompleteness theorem. This research has, traditionally, been treated as a subfield of mathematics and philosophy. But as we shall explain, it also has nontrivial implications for anthropology and psychology, as well.

2 A New Amendment to the Trivers-Willard Hypothesis for Avian Species

Our interest in applying the TW hypothesis to avian species was initially stimulated by an article by Nancy Burley [5]. It studied the behavior of Australian Zebra Finches, and found that their propensity to produce male offspring would be enhanced if colored bands were attached to their legs that made the males look more attractive and the females less attractive. The reverse sex ratio would be produced if the bands had polar opposite types of sexual attraction features.

I had not predicted such an effect. However with retrospection, I do have an interesting explanation as to why avian species seem to follow the predictions of the Generalized TW Hypothesis with more statistical accuracy than mammals.

of an article with the same title and page numbers as [48]. This error occurred because Science Magazine listed, in 1973, the authors of its articles on the specified article’s last page (rather than on its first page). Moreover, McKanna’s 1973 paper ended on the first column of the same page 90, whose second and third columns were occupied by the TW article. Thus, the supposedly sagacious Google-Scholar software had gone amusingly schizophrenic, when it tried to guess who was the actual author of this particular article with an unusual quantity of 3,338 citations? (This error persisted during all the Winter and Spring months of the year 2017. In fairness to Google, their error was corrected on June 26, 2017, shortly after I gave my June 18 talk at NEEPS-2017. We are not sure exactly why, but Google Scholar’s software has made this persistent error and then corrected it repeatedly, on several occasions, during the last few years.)
It is because sperm type determines the sex of mammal offspring, while it is unfertilized egg type that is the control agent among birds. In particular, it is well known that it is the type, X or Y, of sperm which determines the sex among mammals (e.g. an XX offspring is a daughter and an XY offspring is a son). In contrast among birds, a “ZZ” genetic mix produces a male offspring, and a “ZW” mixture corresponds to a female. The latter implies that it is the unfertilized egg (rather than donated sperm) that functionally determines the sex type for a bird.

Among both mammals and birds, the TW Hypothesis predicts that Darwinian Evolution has an incentive to guess which sex of offspring is likely to produce more grandchildren for a mating couple. The engine, however, to determine which type of sperm will first reach the egg is complicated, when a male mammal donates several million competing sperms, at once. The comparable engine for sex ratio determination among birds is, presumably, much simpler because only a small number of “Z” or “W” unfertilized eggs are deposited by the mother for the purposes of being fertilized by a male.

This distinction suggests it will likely be substantially easier for avian species to gain full dexterous control over the sex of their offspring than the analogous paradigm, occurring among mammal species.

Our suggested amendment to the TW Hypothesis will probably be very difficult to empirically check for its correctness. It would require a meticulous study that compares various species of mammals to sundry species of birds. It would, however, be theoretically interesting if Avian species were found to obey the predictions of the TW Hypothesis with greater statistical levels of accuracy than among mammals. Moreover, the next section will suggest that our predictions, if correct, could increase the world-wide efficiency of poultry egg production.

3 Poultry Farms

It is well known that the efficiency of Poultry Farms shall increase if more female chickens are born. In that case, egg production will quickly increase, and also poultry meat production should also likely increase, somewhat.

It is apparent that if chickens do function similarly to Australian Zebra Finches, then a mating couple will produce more female offspring, if they are artificially endowed with female color features.
Moreover, a large variety of other techniques are likely to be also available for influencing the sex of offspring. For instance, if an excess of male rooster-like sounds were pumped into a chicken farm then it is probable that more females will be born (because the illusion of an excess supply of males would have been temporarily created).

One drawback of such strategies is that the inbred supply of farm animals will naturally evolve in a direction that is exactly the opposite to a farmer’s intentions. This is because the classic local farm animal population will degrade, spontaneously, in a direction towards a 50/50 sex ratio, according to Fisher’s Sex Equilibrium argument [15].

A useful remedy is for a concerned farmer to keep a log of which chickens come from a genetic lineage producing more female offspring — and to encourage those particular chickens to breed.

Unfortunately, such a log would require a labor-intensive effort to maintain, thus undermining its cost effectiveness. Fortunately, there is a solution to this challenge in the modern computer age. A unique computerized bar-code name identifier could be attached to each chicken, and a robot could ascertain that the correct genetic line of chickens are breeding.

In other words, we are suggesting that a computerized algorithm could maintain some type of desired protocol to enhance the ratio of female offspring, and that this protocol will probably be cost effective in the new age of computerized robotics that is now emerging. In any case, it is evident that the efficiency of poultry production should be increased if farmers could gain better control of the sex of raised chickens.

4 Supporting Data

A diversity of articles, by several authors, will probably be necessary to confirm our twin conjectures, suggesting that:

A. Avian species do follow the predictions of the Trivers-Willard hypothesis with greater accuracy than do mammals.

B. This paradigm can increase the efficiency of poultry production.

There is, however, adequate evidence in the already-published literature to make these two conjectures quite credible.
It firstly should be noted that there are some species of laboratory animals, drawn from
the Vertebrate kingdom, where human experimenters have gained essentially 100% control of
the manipulated sex of the studied offspring. For instance, it has been observed that reptiles
and amphibians neither follow the mammal XX/XY or the bird ZZ/ZW chromosomal method
to control the sex of offspring. Instead, both sexes have identical chromosome structures, and
it has been observed that laboratory scientists can gain 100% control of the sex of offspring in
14 different genres of turtles by changing the incubation temperatures for turtle eggs. (Thus,
[3, 4, 14, 49] observed that a 25 Celsius incubation temperature produces an all-male rate of
offspring, while a 31 Celsius incubation temperature leads to an all-female population among 14
different tested genres of turtles.) A similar temperature-control effect has also been observed
to occur in several species of reptiles [2].

Exact analogs of the preceding paradigm will not apply to mating chickens, since poultry
uses a ZZ/ZW model, where a ZZ animal is genetically a male and ZW is female. It has,
however, been observed that lowering the incubation temperature does increase the frequency
of female births, partly because of sex-differential mortality rates and also because some ge-
etically male (e.g. ZZ) chickens possess a female anatomy and own an observed female-like
ability to lay eggs [7, 22, 23, 32], if the incubating temperature is lowered soon after the ZZ-egg
is fertilized.

There is a serious interest in the poultry industry to increase the ratio of female births, as
noted by [34, 39, 43, 44, 62] among other sources. Several published articles have studied the
implications of TW hypothesis for avian species [1, 5, 6, 9, 11, 12, 18, 29, 30, 31, 41, 45, 46,
47, 50, 51], and they have noted it has had a documented measured effect. We suspect there
in not yet enough available unambiguous evidence to determine whether our conjecture (A)
is precisely correct (e.g. that the TW hypothesis has significantly greater implications among
birds, than among mammals). This particular topic should be investigated in much greater
detail in the future.

If our conjecture (B) is correct (that poultry farms can have their productivity increased
by even a few percentage points through a better understanding of the implications of the TW
hypothesis) then the avian version of the TW hypothesis deserves as much study as the 3,338
articles that have already examined its implications for mostly mammals.

There is one particular experiment that I would recommend be undertaken. It is known
that the sex ratios within human societies change in the aftermath of wars [24, 27]. Would the
same be true among poultry species? That is, what would happen if mating chickens repeatedly
heard sounds from an electronic speaker of tape-recordings from a cock-fight?

The preceding experiment is a little awkward and embarrassing to undertake, but the scientific information that it supplied could actually be quite valuable and sobering.

5 Historic Context of this Research

The first chapter of this article had mentioned that Willard’s main contribution to the TW paper [48] consisted of a flash insight that I developed during a short bicycle ride when I was 20 years old. The curiosity of many readers may have been stirred by this fact. Some readers may, perhaps, begin to wonder what other intellectual projects I have worked on, subsequently, in the aftermath of [48]’s publication.

Essentially, my research has had two focal points. Prior to 1992, my focus was on mainly classical topics concerning computer algorithm design. My best known work in this area consisted of a joint study with Fredman to determine the optimal cost for computerized sorting and related searching methodologies. Our joint work showed that the then-commonly-held presumption that computerized sorting could run no faster than in $O(N \log(N))$ time was incorrect (i.e. a theoretical speed-up for sorting and searching was demonstrated in [16, 17]). These two projects produced four papers (if one counts separately their journal and conference publications). It is reported in Google Scholar that 920 academic citations to these four variations of our work had subsequently appeared. Moreover, the 1991 Annual Report of the National Science Foundation [36] cited this particular “Fusion Tree” investigation as the chronologically first among only six projects that were mentioned in its 1991 Mathematics and Computer Science section.

Starting in 1993, I started publishing papers [52]-[60] about Gödel’s historic Incompleteness Theorem. Gödel’s work has traditionally been of interest to researchers in fields as broadly diverse as mathematics, philosophy and computing (as a reader can quickly surmise by looking at any one of Gödel’s biographies [8, 20, 63]). His “First Incompleteness Theorem” indicated there existed no systematic manner to categorize all the technically true statements in even the simplest branch of mathematics. Gödel’s “Second Incompleteness Theorem” indicated conventional logical systems are also unable to confirm their own consistency, in a fully formal sense [13, 33].

There is no question that both these incompleteness results are rigorously correct, but they raise the question about whether Darwinian Evolution might favor the evolving of a more
advanced specie of primate, that finds it adaptive to employ an unconventional mode of thought, in order to maintain some type (?) of specially modified knowledge of its own consistency. The latter topic was the stimulus for our on-going investigations in [52]–[60]. These articles proposed a variety of unconventional revisions of arithmetic’s formal axiomatic structure. They found these delicate revisions could preserve most of the pragmatic content of traditional arithmetic, while simultaneously providing at least some type of philosophically meaningful, albeit partially diluted, formalized appreciation of their own internal self consistency.

The best and indeed preferred paper to examine first, in the preceding 24-year long series of papers, is our final article [60]. The Remark 7.5 of [60] mentions that we suspect some variation of our proposed “IQFS” formalism has applications to anthropology, psychology and philosophy, as well as to linguistics. We do not suggest this paper is of easy reading. A reader can, however, at least partially appreciate [60]’s gist, when its examination is conjoined with also a reading of at least some select parts of the books [8, 13, 20, 33, 63].

We do not want to overstate this point, but the Remark 7.5 of [60] does indicate that our newly proposed “indeterminate function symbol” θ should have implications for each of the fields of anthropology, psychology and philosophy, as well as linguistics. A wide spectrum of readers is, thus, encouraged to, at least, glance briefly at [60]’s discussion.

6 Concluding Remarks

The main purpose of this article was to introduce our proposed avian amendment to the TW Sex Ratio Theory. This article also included §5’s brief summary of our other research, during the last 44 years, because we suspected some readers would find its short review to be informative, as well.

The main reason the observations in this short note will be of interest is because it is possible that the world-wide egg (and plausibly also poultry meat) production could undergo an approximate minimal 2-3 percentage or greater increase, if the number of born female chicklets is significantly enhanced. Such a difference will, certainly, not resolve world-wide famine challenges. It would, however, be a useful development, beneficial to mankind.

ACKNOWLEDGMENT: I thank Glenn Geher for his useful suggestion, conveyed on June 18 to me at the NEEPS-2017 conference [19], that my article should also discuss the
relevance of fascinating aspects of sex ratio effects, that have been documented for a variety of different species of turtles.

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