Sex-Biased Birth Ratios in Mammals:

Are some mothers more likely to bear daughters, and others sons?

If you dare to reflect back on your high school biology class, chances are at some point you learned about reproduction. Your teacher probably explained that, for mammals, females carry eggs with many nuclear chromosomes (twenty-two in humans) and one sex chromosome, known as the X-chromosome. Males produce sperm with the same number of nuclear chromosomes (once, again, twenty-two in humans) and one sex chromosome, either an X or a Y. If a sperm with an X-chromosome fertilizes the egg, a beautiful baby girl develops: if the sperm carries a Y-chromosome, a dashing baby boy. And since meiosis—the process of making these sex cells (meaning sperm or eggs)— requires a random splitting of chromosome pairs, sperm end up with 50% Y-bearing and 50% X-bearing sperm. This means that, when the millions of sperm race towards the awaiting egg, the chance of the lucky winner resulting in a male or female is at unity, a 1:1 ratio.

At least that was the story I learned in high school, and generally a correct one. The teacher presented the material as simple and intuitive, and the class copied the drawings of colored X's in circles and moved on. But I didn't understand. This model made no logical sense considering evolution. After all, males could have a much higher reproductive rate if more females existed, which would pose no detriment to the female reproductive rate. In humans, for example, a female can only produce a child about every 10-11 months; males can theoretically produce several children an hour. So why not have more females, since females are the limiting factor in reproductive rates? I raised my hand. "But why?" My teacher responded by repeating the process he just explained: males have an X and a Y chromosome, so, when these cells divide, half the sperm cells receive an X, and half a Y. I persisted, "Yes, but why? Why should we have a 1:1 ratio of the sexes? Wouldn't it be more biologically efficient to have more females?" That afternoon, my teacher recommended that I move down from the honors class to the "regular" section, where we watched nature documentaries and played with candy.

Five years later, in my sophomore year of college, I asked my question again. Why does our population have so many more males than is necessary to reproduce at the same rate? Instead of suggesting I drop out, my professor engaged the entire class in a discussion, though none of us could determine the answer. So, she assigned me an extra credit report: to figure out why only 50% of the population is female.

Apparently, I was far from the first person to find this 1:1 sex ratio illogical. Charles Darwin presented the same paradox in Descent of Man (1871), but then withdrew the section in the second edition, conceding that the "whole problem is so intricate that it is safer to leave its solution to the future" (Darwin, 1871; p 252). Twelve years later, Carl Düsing approached the problem with a mathematical model, which, in 1930, R.A. Fisher converted into a biological principle applicable to most mammalian species. Fisher's principle postulates that, if males and females require the same energetic costs to produce (equal parental expenditure) and males have relatively equal chances at reproductive success (equal access to mates), a population will be at unity—because evolution relies on individual benefit, not species benefit. If fewer males existed (as would be more efficient to the growth of the species), then it would be selectively advantageous for the individual mother to produce a son, since that would increase the chances her son would pass on her genes. But as this trait gets selected for, its advantage dwindles as more males enter the population, until males exceed females, and thus producing a male becomes a disadvantage. Producing females would then get selected for, until they become the majority and therefore no longer advantageous, creating a cycle, such that 1:1 is resulting equilibrium. This argument is a classic example of frequency-dependent selection, which evolutionary biologists often use to explain stable ratios.

Fisher's principle of unity sex ratios depends on two main assumptions: first, that male and female offspring cost the same energetically to produce (Birgersson, 1998; Clutton-Brock, 1991; Trivers and Willard, 1974; Hogg, 1992) and, secondly, that all males and females have equal opportunities to mate (Roed et al. 2005). If bearing sons cost more than daughters – such that maybe a mother couldn't produce as many sons in her reproductive lifetime as she could daughters – that might change the cost-benefit analysis of bearing one sex over another. And if sons were more likely to have opportunities to mate than daughters (for example, if female populations died off before reproducing or most were unable to find mates in their habitats), that could also change the cost-benefit analysis.

In 1973, Robert Trivers and Dan Willard proposed that, in populations where sons and daughters had differential costs and mating opportunities, mothers would select for one sex over the other, a theory they outlined in the ingeniously named Trivers-Willard Model (TWM). This model looks at situations in which males do not have relatively equal access to mates, specifically highly polygynous species where one male dominates an entire harem of females. In these polygynous species, males often require more caloric intake and time to develop, since they tend to have more physical attributes than their female counterparts: traits that allow them to better compete for mates (Darwin, 1871). Examples include increased body size; weaponry (horns, antlers, sharp canines, etc.) for male-male competition; and ornaments (bright colorations, enlarged organs (anything from nose to buttocks), and hundreds of other apparent babe magnets, including manes, inflatable pouches, etc.) to better attract a wandering female. Furthermore, highly polygynous species also tend to have low parental investment. Polygyny cannot pervasively occur within species in which the male needs to stick around and help raise his offspring for the offspring to survive. Birds, for example, are rarely polygynous, because newborn chicks require constant care and energy, more than any single individual could provide. Elephant seals, on the other hand, are highly polygynous, which is possible because baby seals are born relatively self-sufficient, and can receive all necessary nutrients from their mother's milk.

In their original paper, Trivers and Willard used caribou as their polygyny prototype. Caribou have few dominant males that monitor huge harems of females with whom they mate. Accordingly, caribou have extreme sexual dimorphism and low parental investment. Males have huge antlers and are significantly larger in size, and caribou calves are highly precocious, able to stand within 30 minutes of birth, and run within a matter of days. Like most ungulates (such as deer, bighorn sheep, elk, etc.), caribou defy Fisher's two postulates for unity in a mammalian species: firstly, that the two sexes cost the same for the mother to produce (Birgersson, 1998; Clutton-Brock, 1991; Trivers and Willard, 1974; Hogg, 1992) and, secondly, that all members of have equal opportunity to mate (Roed et al. 2005). A successful male caribou will cost much more energetically than a female caribou to physiologically develop, and—at least according to the TWM—only a few dominant males get to reproduce (Trivers and Willard, 1974).

In other words, raising a male caribou is a high-risk investment with high potential

return, an all-or-nothing gamble. If a male can outcompete all the other males and win a harem, he gains unlimited access to females and huge reproductive benefits. Yet, if can't gain a harem, he likely never obtains the opportunity to pass on his genes, a much worse fate than any female.

Raising a female caribou, on the other hand, is a low-risk, safe investment, with moderate and consistent returns, like a treasury bond. A female will get to mate with a strong male no matter what; if a male finds her, he will mate with her, regardless of her status. Thus, a low-quality daughter can nevertheless continue the genetic lineage of her mother.

Therefore, different mothers should theoretically strive to invest their assets appropriately, based on their genes and resources. A genetically strong mother will want to invest in sons. A genetically weaker mother will want to invest in daughters. This is what animal behaviorists call sex-biased allocation. The Trivers-Willard Model dictates that mothers in poorer conditions—meaning those with less resources or less preferable genotypes for male offspring—will want to invest more in daughters. Concomitantly, high quality mothers—those with ample resources and competitive genotypes for male offspring—will want to invest more in sons.

This model, based solely on theoretical strategy, had such intuitive appeal for its logic that scientists around the world lauded its veracity, and sought empirical evidence in the field. Yet proving the existence of sex biased reproductive strategies creates a logistical nightmare. First, researchers must distinguish high-quality from low-quality mothers: a challenging and overly-subjective task that requires converting manifold quantitative variables into a simplified, categorical dichotomy. Factors to determine "quality" usually include rank (dominance in the harem), the body-fat index or size of the female, the richness of her milk, or the magnitude and abundance of her territory. Every study uses a different combination of variables, weighted and scaled to different justifications, such that the characteristics of a "high-quality" female changes in every article.

Once researchers distinguish high-quality from low-quality mothers, they must confirm that male offspring cost more than female offspring. Measuring the mother's greater weight

loss, reduced fecundity, or lower survivorship during birthing and suckling males usually corroborates this (Birgersson, 1998; Clutton-Brock, 1991; Trivers and Willard, 1974; Hogg, 1992). These “costs” must then be distinguished from “investment,” which also needs to be quantitatively evaluated. Typically researchers accomplish this by calculating the suckling time the mother allots to her offspring according to sex. Finally, once maternal condition, and offspring cost and investment have been assessed (though honestly I still don't understand how cost can be empirically distinguished from investment), the differential investment between males and females must be significantly correlated to the quality of the mother, and that correlation must result in enhanced reproductive success. In short, to confirm the Trivers-Willard hypothesis, the data must verify that a) the quality of the offspring reflects the quality of the mother, b) that these qualities “persist into adulthood” (Trivers and Willard, 1973), c) the quality enhances the reproductive success of the offspring differentially according to sex, and d) that the mother invests more in one sex than the other. I believe the scientific term for such a tortuous hypothesis is “Yikes.”

Even worse, this data must be collected from sexually dimorphic wild populations (or if captive, fairly uncontrolled). Given their physical size and the duration of their life histories, most studies of ungulate species (deer, elk caribou, etc.) take years to complete, and researchers usually lack the time and resources necessary to systematically monitor all the variables that could affect birth sex ratios, such as diet, stress level, dominance, density, hormone-levels, genetics, territory, mating partners, and more. Tagging and tracking multiple elk-sized animals in their natural habitats takes enough time and energy (not to mention the endless hours of following the individuals to determine the maternal and offspring conditions). Most studies do not also include invasive procedures like blood withdrawal, or if they do, the

researchers usually only endeavor one such invasion. What results is a stewpot mélange of confounding variables, each putting one foot on the proverbial gas and the other on the equally-proverbial break, with little capacity for controls.

Despite these hurdles, scientists have still gone out into the field and compiled data. Most studies do manage to show that the physical quality of the mother typically gets passed onto the offspring; mothers in good condition and high rank make bigger, higher-quality calves, and these traits continue into adulthood (Birgersson and Ekvall, 1997; Clutton-Brock, 1986; Green and Rothstein, 1991; Schultz and Johnson, 1995; Reimers and Lenvik, 1997). This makes sense regardless of the Trivers-Willard Model—a mother with greater access to food that is healthy should have healthy, strong offspring. The postulate that these traits augment the reproductive success for males more than females is typically assumed as a contingency of polygyny; success males have higher fitness than successful females by definition of the mating system. The more dubious step to prove is the last, and the one that would substantiate the existence of the Trivers-Willard Model—that high-quality mothers will therefore produce more sons as a result.

Some articles have found significant data confirming this last exigency in support of a skewed birth sex ratio according to the condition or quality of the mother. In roe deer, Wauters et al. (1995) found that older adult does had 55% male embryos, while younger mothers undergoing their first pregnancy had only 32% males. These results were correlated with the age ($p=0.033$) and body mass ($p=0.0016$) of the female, but not deer density ($p=0.68$) or the crop size ($p=0.77$) of the territory. In another study, Kruuk et al. (1999) reported dominant red deer tend to have more male offspring that subordinates. Saharan arrui (a goat-antelope species) mothers in the upper 40% in regards to rank devote more suckling time to males, and

keep males in closer proximity during the first week of birth than mothers who rank in the lower 60% (Cassinello, 1996). The higher-ranking mothers also birthed higher proportions of male calves. Clutton-Brock, considered the most famous and venerated authority on the Trivers-Willard Model, demonstrated that dominant red deer also have greater proportions of males, and that higher-ranking red deer does allocate more suckling time to males than lower-ranking does (Clutton-Brock et al., 1986; $p<0.05$). Miekle et al. (1996) found that dominant and older swine also produce more males. In roe deer, red deer, reindeer, mule deer, arrui, bison, and pronghorn sheep populations, mothers with higher fat indexes (typically measured by looking at the kidneys post-mortem) produce higher proportions of male offspring (Hewison and Gaillard, 1999; Kucera, 1991; Wauters et al., 1995).

Yet the aforementioned conclusions are anomalous exceptions to the majority of the scientific literature, and moreover their results have not been reproduced in other studies. Furthermore, their results conflate a panoply of factors that can contribute to biased birth sex ratio. For the Wauters et al. (1995) roe deer study concerning the mother's age, and the Miekle et al. (1996) swine study, the skew of the sex ratio negatively correlates with litter size. Most first-time mothers have only one child per pregnancy, while older, fatter adults typically have 2–4 offspring per litter. Thus age may actually be an indirect factor, while litter size is the actual determinant of birth sex ratios, with larger litters containing more males.

Another problem with the roe deer study is the limited sample size taken from a highly disturbed population. The progeny samples were counted from the fetuses found in pregnant mothers during culling season. Hunting is a sex-selective pressure on the population in itself, which confounds the qualities that enhance individuals' lifetime reproductive success. Hunting laws allow more males than females to be hunted, and hunters prefer dominant males with

phenotypes like large body size and antlers. While the Trivers-Willard Model depends on the prediction that the dominant males will have the highest lifetime reproductive success, hunting may in fact select against these dominant traits that would otherwise increase male lifetime reproductive success. None of these possibilities were considered in the paper. Wauters et al. (1995) instead conclude with confidence that their results reflect "control by the female" to determine sex ratios, "and not by differential mortality" (Wauters et al., 1995: p 192).

Upon deeper examination, the lauded logic of the Trivers-Willard Model falls apart, and sounds more like animal eugenics than observation-based science. It would behoove strong mothers to have females as well as males. Some of the maternal traits that make dominant and viable mothers may be more applicable female-related roles and phenotypic expressions than male-related ones. Sons will not inherit the qualities that make a great mother, such as good parenting skills, or high investment in offspring—but daughters will. Therefore a daughter can transmit a greater reproductive value than a son, because her offspring will be of equally high quality. Also, in most ungulate and primate species females inherit the territories of their mothers, which means a strong mother in a rich territory should leave a female heir who can reap the benefits of more resources. Clutton-Brock and Iason chart parental quality in terms of sex ratio advantage as a binomial, an upside-down U-shaped graph that indicates the most advantage distribution of offspring according to increasing rank. According to their model based on field data, low quality mothers would be best off producing a daughter, and higher quality mothers a son. But after one son, the best option for a high-quality female is two daughters, then one of each, then two sons. Yet the highest quality mothers—those with the best resources and physical vigor—should bear three daughters (Clutton-Brock and Iason,

1986). Sons consume so much more energy and milk that mothers can extend their reproductive lifetime by bearing more females and conserving their resources; they can have more offspring overall if they have females. Or they can have a shorter reproductive lifetime and sons who may sire more offspring. In respect to lifetime reproductive success, the reduced cost of daughters can offset the reproductive pay-off of males. Therefore, in the long run, a mother producing better and better mothers with each generation could be just as advantageous, if not more so, than producing macho sons. And when the competition is low and resources abundant, one of her daughters or granddaughters can birth a son.

Frequency-dependent selection may also offset the male advantage for strong mothers. A male advantage depends on competition, not vegetation: how many other dominant males are around determine whether bearing a male could lead to a big fitness gain. If resources are plentiful, then more mothers have the capacity to allocate more milk and energy towards sons, such that all sons will be abundant and the competition for territories more intense. A vigorous male raised in good conditions may still strike out if other males in the vicinity have the same resources, so the proportions of males should keep itself in check (which is the definition of frequency-dependent selection).

These counter-arguments explain why higher-ranked mothers benefit from females, but what incentive could lower-ranking mothers have to produce males? After all, even if dominant does profit from both sexes equally, subordinates with weaker territories or phenotypes may still want to allocate their resources exclusively to females if only the strongest males gain access to matings. The problem with this logic is that since 1973 DNA tests have become a feasible method in animal behavior, and it turns out that the skew is not as skewed as previously thought. Studies in the past two decades, in which the paternity of

offspring could be genetically derived, prove that smaller, weaker males sire fawns as well, especially with females in the out-skirting ranges of a harem territory (Roed et al., 2005, for reindeer; Carling et al. 2003, for pronghorns; DeYoung et al., 2002, for white-tailed deer). So a "weak" mother's effeminate male that may not want to fight with antlers, but he still gains copulations. These subordinate males still have less progeny than the alpha, but they are certainly not evolutionary dead ends, as previously assumed. Furthermore, most studies presume that dominant mothers make stronger, dominant males, this postulate has not been confirmed with significant data. Evolution tends to benefit diversity; when parents have contrasting traits, the offspring often end up stronger as a result of having mixed traits (heterozygous alleles), which make them less vulnerable to disease. A strong mother may be a great parent, but a weaker mother that mates with the biggest pair of antlers she can find could make a competitive alpha by maximizing her offspring's heterozygosity.

Speaking of antlers, the Trivers-Willard Model neglects the fact that the fathers contribute half of the genetic material. The original paper negates the possibility that the male could optimize his chances of siring the advantageous sex, or that his alleles may create beneficial genotypes with subordinate females (increasing heterozygosity). Diversity tends to make more resilient, stronger offspring, so a weak parent with a dominant parent could lead to a more successful child than two subordinates mating or even two alphas. The model also fails to address the possibility that mothers and fathers could conflict in regards to optimizing their respective reproductive lifetimes (Gomendio et al., 2006). If a dominant male may only control his harem for a few years, or if he has access to more females than he could possibly fertilize during rut (which would often be the case in deer populations, in which does are fertile as young as one year old), then the male may want to sire a son, even if the female would have

a longer reproductive lifespan if she had a daughter. So even if the mother devised mechanisms to optimize her reproductive success, the male may want to counter these skewing mechanisms for his own benefit.

In fact, one study examined birth sex ratio in relation to the condition of the father instead of the mother, and showed that the male red deer may actually influence sex birth ratios, not the females. Gomendio et al. (2006) evaluated the fertility of 14 stags by the speed and volume of sperm produced during rut. The researchers then artificially inseminated hundreds of females in good physical condition with unlimited access to food, each at the same ovulation time. Strangely enough, though the females were in similar conditions and never saw their sperm source, the more fertile males sired more sons ($p=0.013$). Gomendio et al. propose that their results could indicate my Y-bearing sperm entering the ejaculate of more fertile males as a reproductive strategy. Since most genes relating to male fertility exist solely in the Y-chromosome, fathers with high fertility could increase their fitness by siring fertile sons. Another possibility is that Y-bearing sperm are faster, stronger competitors in more fertile males—high fertility is highly correlated with having more morphologically normal spermatozoa. Much more research is necessary to conclude if male red deer truly can manipulate the sex ratio of their offspring, but the impressive results of Gomendio et al.—deduced from data with a large sample size and impressive controls—suggest that the male influence in birth sex cannot be neglected.

Iason and Clutton-Brock (1996)—the same Clutton-Brock as from the study of red deer mentioned above—looked at 108 articles regarding the Trivers-Willard Model, from which only four met their criteria of demonstrating a sex bias contingent on different quality mothers using objective, reliable methods. Of the four articles that support the Trivers-Willard Model

using reliable methods, three studied macaques, a primate species with much less sexual dimorphism than most ungulate groups. Another review of all peer-reviewed, published articles regarding the Trivers-Willard Model in ungulates found 392 articles whose results refute that "high ranking and/or good condition ungulate mothers produce more sons" (Hewison and Gaillard, 1999); many of which even found a significant negative relationship between maternal rank or condition and male offspring. In comparison, 83 articles either showed significant data supporting the Trivers-Willard Model or did not provide enough data to invalidate it. Out of the sixteen ungulate species of interest in the review, only arrui and pronghorns had more articles supporting rather than rejecting the model (Hewison and Gaillard, 1999).

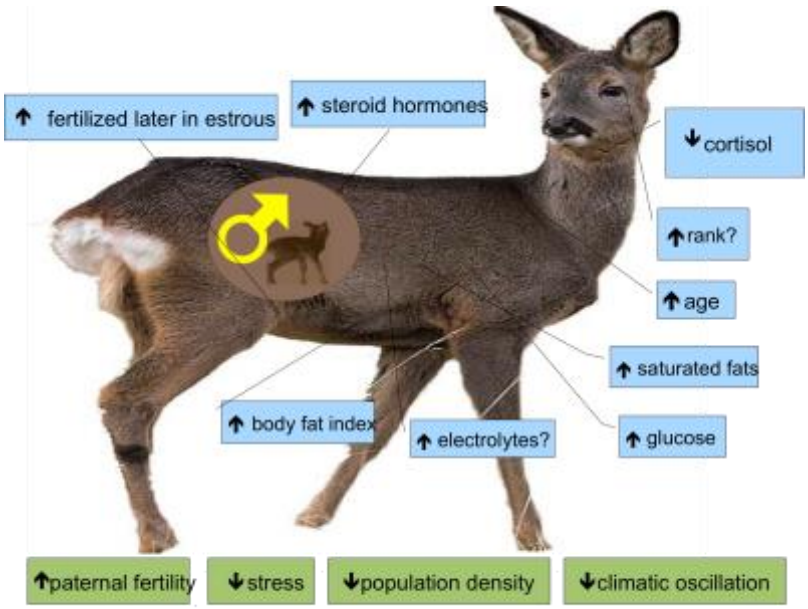
Unfortunately, scientists have major incentives to publish papers supporting the Trivers-Willard Model. The hypothesis is shocking, sexy and carries intuitive appeal, and articles that make waves (and careers) are those that show significant results, not those that affirm the null hypothesis. Researchers therefore design experiments that will maximize the likelihood of significant results. As Trivers himself once bragged to a reporter, "if I'm wrong, it will take them years to find out" (Hrdy, 1987). Yet despite its mendacity, the Trivers-Willard Model irrevocably changed the study of animal behavior, expanding the imaginations of researchers and instigating hypotheses that would never be previously considered. Before Trivers and Willard, no one considered birth sex ratios could be skewed at all. Yet since their theory, researchers have become more receptive to the possibility of skewed sex ratios, and have discovered phenomenon previously thought only for science fiction. The Trivers-Willard Model also opened the door for the Extrinsic Modification Hypothesis (EM). This revised model postulates a birth sex bias from environmental variables. In the strict sense,

the Extrinsic Modification Hypothesis focuses on the environmental condition of the mother—her health—as the determinant of sex biased allocation; that the less costly sex will be produced if the mother lacks resources or is in poor condition (Post et al., 1999). As with the Trivers-Willard Model, weaker mammal mothers are predicted to bear more female offspring, since they don't demand as much energy expenditure while maintaining higher survivorship, but the Extrinsic Modification Hypothesis does not consider this a tactic, but rather an uncontrollable consequence of environmental conditions. Thus if the male-bias is correlated with litter size, as with red deer and swine, the bias may be a consequence of health and not an adaptive strategy. With the Extrinsic Modification Hypothesis, any mother should bear more females if she lacks resources during pregnancy, even if it would enhance her fitness to make a son.

Many studies purportedly confirming the Trivers-Willard Model actually better fit the Extrinsic Modification Hypothesis. The roe deer, red deer, and swine studies (Wauters et al., 1995; Miekle et al., 1996) could be reflecting the Extrinsic Modification Hypothesis, as corroborated by the strong correlation to litter size, which is a proxy of strong health and access to nutrition. The male-bias amongst dominant mothers in red deer also disappears with increased population density or winter rainfall, both of which cause intense physiological stress on the mothers. Increased population density intensifies resource competition, such that mothers can have less access to high-nutrition foods. Winter rainfall can be highly detrimental to the health and survival of deer because the wet, cold conditions increase thermoregulatory demands, which results in many dying of hypothermia (Kruuk et al., 1999).

By emphasizing environmental conditions rather than evolutionary strategy, the Extrinsic Modification Hypothesis is less equivocal and easier to research than the Trivers-

Willard Model, which requires calibrating post-birth investment and determining the reproductive success of the progeny. Consequently, research to verify the Extrinsic Model tends to be simpler while still leading to fascinating results. Rodents with higher androgen levels or android fat distributions—those with more male sex steroid hormones—had higher percentages of male offspring (Krackow, 1995). Accordingly, females born between males—having adjacent older and younger brothers—tend to birth more males than mothers born with no adjacent male siblings, probably as a result of hormone washing or androgen predisposition of the female as a fetus in utero (James, 1997). In other words, a female with brothers is exposed to more male sex hormones in utero, which for some reason causes her to bear more sons when she reaches adulthood. Mice with high electrolyte diets also had more sons, for which no cogent explanation exists. In one study, the sex ratio of mice litters upon birth (the primary sex ratio) skewed with diet, but not weight. Mothers that fed primarily on saturated fats had 67% males, and those that fed on carbohydrates had only 39% males, even though the quantity of food consumed and body size did not significantly differ (Rosenfeld et al., 2003). In golden hamsters, the youngest and oldest mothers—less than 100 days old or more than 455 days old—birthed less sons than mothers of moderate ages. Also in golden hamsters, the first three litters had more offspring with a higher proportion of males than subsequent litters, from which both size and sex ratio consistently decreased. Stressed female mice, as determined by high cortisol levels, and those in high-density environments, also had more daughters and smaller litters (Huck et al., 1988). Even the dominance rank of the mother's neighbors influenced primary sex ratios. High-ranking female mice housed next to subordinates produced more daughters (and smaller litters) than if alone or beside another high-ranking female (Krackow, 1997).



Variables that increase or decrease the likelihood of bearing a male in most mammalian species.

All these results support the EM, while characterizing its vast complexity. Sure, environmental conditions can influence the primary sex ratio of polygynous species, but evaluating conditions requires calibrating myriad variables. Does a young female, crowded with high-ranking neighbors, who has moderate stress, low androgen levels, and a saturated fat diet, live in "poor" or "good" conditions? Will she still produce a skewed birth ratio, or will contrasting variables somehow counterbalance into unity (1:1)? Before I can answer these questions, studies need to clarify if each variable can be uniformly evaluated in regards to its influence, so that statistical predictions can be formulated. As far as I can gather from the 112 articles I analyzed, such standardized methodologies have yet to be established.

Furthermore, none of the articles confirm what biological mechanism could be inducing a sex-biased birth ratio. Although the details have not been determined, the most common suggestion from researchers in the discussion sections of their articles is a hormonally

controlled protein that aborts zygotes of the less-manageable sex. Hormones can dictate response patterns to stimuli. They trigger animals to migrate, hibernate, and, most importantly, to mate—the word "hormone" actually means to arouse or excite in Greek (Biology Reference: Encyclopedia Britannica, 2011). Scientists first began using the word hormone in 1930, when they noticed chemicals in our body that could change how our nervous system functions (Biology Reference: Encyclopedia Britannica, 2011). They are the reason we can adjust to changing and complex environments with appropriate responses, and they moderate thousands of physiological functions: allowing our hearts to beat, our kidneys to regulate our blood content, our intestines to digest food and more. Sex steroid hormone in particular—progesterone, estrogen, and testosterone—dictate sexual development and reproduction, and likely sexuality (Biology Reference: Encyclopedia Britannica, 2011). Thus if some biological trigger is causing a skewed birth sex ratio, it would make sense that the signal should be hormonal.

The results of most studies also corroborate a hormone-based device. While a dominant female mouse housed next to subordinates will have more daughters, she will revert back to having more sons if her subordinate neighbor receives progesterone treatment (Krackow, 1997). The fact that the hormonal status of her neighbor impacts the higher-ranking mother's litter suggests her own hormone levels shift as a response to this environmental stimuli, since hormone levels will typically change in accordance to those in proximity—her progesterone levels probably increased when her neighbor's did. The female mice who bore more sons on a diet of saturated fat probably also had more sex steroid hormones than those solely eating carbohydrates: saturated fats can be broken down into cholesterol, which is a precursor to sex steroid hormones (Rosenfeld et al., 2003). Progesterone can become either androgens—male

sex steroid hormones—or cortisol, a stress hormone, depending on which enzymes are present to convert progesterone to its next form. Thus animals with increased cortisol will often have less androgen steroids. This could explain why mothers under various stressors—nutritional starvation, extreme climate, population density—tend to have more daughters.

One study attributed the trend of hamsters dosed with caffeine having more daughters to the attenuation of cAMP phosphodiesterase activity (Weathersbee et al., 1975). Phosphodiesterase breaks the phosphate bonds between 5-carbon sugars, such as those in the second messenger, cyclic adenosine monophosphate (cAMP). As a second messenger, cyclic AMP picks up the signal sent by hormones in the blood when they bind to the outside of a cell, and relays the message to the inside of the cell. This message triggers a chain of enzyme activities that lead to a physiological response. Cyclic AMP specifically interprets the signals of hormones glucagon and adrenaline. When cAMP phosphodiesterase breaks the phosphate off the messenger, it no longer functions and cannot trigger the cascade of enzymatic activity that results in a response to the hormone. So when we get a rush of adrenaline, cAMP is communicating to our cells that we need to initiate our stress-triggered nervous system mode, known as the sympathetic nervous system. Cyclic AMP allows us to increase our heart rate, constrict our blood vessels and other physiological mechanisms for a fight-or-flight situation. Once the threat is gone, thankfully cAMP phosphodiesterase breaks down our messenger and we can calm down. Caffeine, however, inhibits cAMP phosphodiesterase such that the adrenaline ride can keep going longer. As a result hamsters fed high doses of caffeine probably produced more daughters because the caffeine acted as a stressor (Weathersbee et al., 1975).

Many studies also purport that the timing of fertilization influences the sex ratio of the offspring, namely that more sons are born if the female is inseminated later in her estrous

cycle, when she is “in heat” (Hammond, 1934; Huck et al., 1988; Foote, 1977; Napier and Mullany, 1974; Verme and Ozoga, 1981). This time is also the peak of her hormone levels [though Huck et al. (1988) actually propose that the skew is caused by vaginal pH, although no other study suggests this possibility and I have not found any evidence to suggest this could be a valid explanation.]

No study has yet to detect which hormone is the key player in sex-biased birth ratios, or when these hormones would be stimulated (or what proteins they would trigger). Most studies suggest that the mechanism would have to take action after fertilization. An egg cannot select sperm, and sperm always come in a 50-50 ratio [with the exception of perhaps red deer according to Gomendio et al. (2006)]. The millisecond a sperm reaches an egg it immediately fuses and becomes a zygote. Thus the selective mechanism would have to be post-fertilization. Furthermore, that larger litters tend to have more males suggests that the male embryos get aborted post-fertilization when the female does not have the capacity to bear such an energetically costly fetus.

Studies of marsupials support the hypothesis for male-biased abortion, in which the males die off later in development. Delean et al. (2009) examined the birth sex ratios of rock-wallabies, a polygynous species that continuously breeds. In mothers of both poor- and good-condition, the birth sex remained at unity. Yet after birth, the likelihood of sons reaching weaning age in lighter mothers living in poor conditions was 0.28, in comparison to the 0.46 likelihood of females (Delean et al, 2009). Since marsupials deliver their young while still developing, examining the offspring between birth and weaning can be comparable to examining other mammals during gestation (Austad and Sunquist, 1986), and thus Delean et al. suggest the sex-biased birth ratio in mammals can be attributed to the Extrinsic

Modification Hypothesis, and is a result of male fetuses dying more easily than female fetuses.

On the other hand, Cameron (2004) argues that the skew must occur near the time of conception. Cameron examined 422 articles testing for a birth sex ratio skew in mammals, of which 47.8% of the studies showed a trend in support of a skew, (42.5% of which had significant results). She then organized the studies according to whether they measured maternal condition during conception, gestation or birth. Of the studies measuring condition during gestation, 41% supported a significant skew, while 5% supported a skew during birth. During conception, however 92% of the studies supported a skewed birth sex ratio. Cameron therefore proposes that the decision-making point is near conception. She suggests future research examine a protein released by the embryo called interferon-tau. Interferon-tau binds to receptors on the cells of the uterine lumen, subsequently communicates to the mother's body that she is pregnant. The release of interferon-tau happens quite early in gestation, and the levels released differ between males and females, which means it could possibly provide the information that could allow the mother to reject the embryo according to a sex-bias. However, the protein has only been detected in cows and sheep, and scientists still do not understand the specifics regarding its purpose (Bagnell, C., 2005).

As for humans, analyses of long-term databases have managed to distinguish a few trends, but our own species undoubtedly has the most confounding variables with the least potential for environmental controls. Still, evidence suggests historical polygamy in humans, and statistically men are larger and demand a higher caloric intake than females. So how does the skew apply to us? Birth ratios in Western societies have shown a reduction of male births in the past century (Rosenfeld and Roberts, 2004), which can be ascribed to women procreating

later in life. An analysis of all birth records in Spain from 1945–1997 found a negative correlation between the number of males born and the mother's age ($p<0.01$) (Gutiérrez-Adán et al., 2000). In baboons, this trend has been observed only in subordinate mothers, who have more sons when younger (Clutton-Brock and Iason, 1986). In Modena, Italy, an analyses of the weight of 10,000 women demonstrated that thinner women produce more daughters (Cagnacci et al., 2004). Given the current standards of beauty, weight may also be contributing to the reduced male births in Western societies. A comprehensive study of birth records showed that malnutritioned women bear more daughters than sons as well; in rural Ethiopia, a positive correlation was found between the body mass and muscle indices of mothers and the proportion of sons birthed (Gibson and Mace, 2003).

Researchers have compiled significant evidence in all kinds of mammals that females in better condition—possessing more nutritional and energetic resources—can bear more males. However, no one has yet to confirm the skewing mechanism. High androgens and estrogens in both parents seem to correlate with more male births (James, 1997; Krackow 1995), but no explanation of how the hormones execute the sex bias has been confirmed. Most studies conjecture that the hormones either enhance the fertilization potential of sex-specific sperm, or affect the mortality of the embryo. Nutritional stress also skews the birth sex ratio, and typically reduces hormone levels because the deprived body lacks the necessary fats. Nutritional sex could also pose a bias from a lower survival rate of male embryos in poor-nutrient conditions.

Such differential embryo survival could explain the results of younger, heavier roe deer producing more males, a study which claimed to corroborate the Trivers-Willard Model. Wauters et al. briefly discuss the possibility of higher male mortality—since male embryos

require more resources—but quickly refute this because the skew exists in utero, and "the frequency of male embryos increased with litter size. If differential mortality was responsible for the male bias, no such relationship would be expected" (Wauters et al., 1995; p 192). Yet these adult does are in better condition and larger, which is why they can manage larger litters in the first place. As for the in utero argument, the fetuses were already developed enough to see the genital slit in females, meaning that more male embryos could still fail to survive earlier in development. This later explanation supports that female condition biases sex-specific fitness, but does not confirm the Trivers-Willard Model, since the nutritional stress is not selectively advantageous, but rather a contingency of environment.

When reading scientific articles, I continuously ask myself, "Why?" Why did they make that hypothesis? Why did they choose to distinguish groups by sex, not color or weight or gestation time? Why did they use that statistical test? In high school, this made me a bad scientist. Apparently as a scientist I should solely be concerned with the results collected, not why someone decided to collect them. Science claims to investigate strictly the how and the what; if data is incontrovertible and pure, immutable, the why is impertinent. But these questions have to come together to comprehensively examine a study and determine its legitimacy. Trivers and Willard obsessed over answering the why, but never bothered to propose a mechanism (or a why that could be followed to its logical conclusion). The Extrinsic Modification Hypothesis answers the what (and to some extent the why); subordinate mothers with less resources or hormone levels will default to birthing more females in many species, because males require more energy and more hormonal input. Yet this explanation is still conjecture and lacks validity without a clear how.

Even though these answers do not yet exist, the questions do. Researchers can now ask if and how certain individuals could be predisposed to birthing more males or more females, which twenty years ago would have been a ludicrous inquiry. Scientists can even seek a correlation between birth sex ratios and certain genes, opening a whole new possibility for a genetic predisposition to birth more of one sex over another. New discoveries will also have to lead to new explanations, turning Fisher's frequency-dependent theory on its head. After all, if the parents can biologically bias the chances of raising a male or a female, then the advantage of having the sex that would benefit most from your resources and genes could counter the advantage of having the less common sex. So next time some naïve high school student asks, "But why? Why should we have a 1:1 ratio of the sexes?" watch out. The answers could turn science fiction into reality.

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