BOOK REVIEWS

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A TOUCHSTONE IN THE STUDY OF ADAPTATION[1]

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''The introduction needs to be bolder'' is what W. D. Hamilton said after looking at one of my first sex ratio manuscripts. He had scrawled in the margin: ''Sex ratio has become a touchstone in the study of adaptation.'' This sentence captured the spirit of the subject in 1984.

How did sex ratio develop into such an important topic? The answer to this question places in context Ian Hardy's new volume on sex ratios as the first major synthesis since Charnov's (1982) monograph.

History

The history of sex ratio research provides a short list of well-known heroes. Darwin (1871, 1874) recognized the typically even sex ratio as a puzzle that his theory must explain. He had some ideas, but was not satisfied and left the problem open for later work.

Fisher (1930) explained the frequency dependence of sex ratio evolution. When males are relatively rare compared with females, each male on average fathers the offspring of more than one female and therefore transmits more genes than an average female. By contrast, when males are relatively common compared with females, each male on average fathers the offspring of less than one female and therefore transmits fewer genes than an average female. Rare types have an advantage, favoring the evolution of an equal sex ratio.

Hamilton (1967) made four major contributions. First, he showed that when brothers compete for mates, they become genetically redundant with regard to transmitting their mother's genes. Thus, local mate competition favors mothers to shift their sex ratio toward daughters, causing female-biased sex ratios.

Second, Hamilton formulated his models in terms of game theory. This required development of how game-like competitions evolve under natural selection. Hamilton's solution was what he called an evolutionarily ''unbeatable'' strategy, which provides a slightly different technical approach from the later, improved method of the evolutionarily stable strategy (ESS) (Maynard Smith and Price 1973). Although earlier authors had noted game-like aspects to evolutionary problems, Hamilton was the first to develop a full evolutionary method of analysis and to generate important biological insight.

Third, Hamilton placed the meiotic drive of sex chromosomes into the theoretical context of genomic conflict. He emphasized the different directions of evolutionary change in sex ratio favored by different genomic subsets, including the autosomes and the X and Y chromosomes.

Hamilton's fourth contribution was perhaps his most important and least often noted. His theory of local mate competition makes comparative predictions that are easily tested. As fewer mothers contribute eggs to a region that will be a local mating arena in the next generation, the intensity of local mate competition rises and the predicted sex ratio shifts away from sons and toward daughters. Hamilton compared data from different species to illustrate that sex ratio trends could potentially be explained by the degree of local mate competition. He also developed a model in which individual mothers adjusted their sex ratios in direct response to the number of other mothers in the area, suggesting behavioral response of sex ratios to local conditions.

Hamilton's comparative predictions provided a simple way to test his ideas about the evolutionary forces that shape sex ratio adaptations. Can a few lines of mathematics really predict how different species will invest their resources in sons and daughters? Do individual mothers really adjust their sex ratios in ways finely tuned to increase their fitness? If not, where is the limitation? Is it in our reasoning about the evolutionary processes that shape adaptations? Or, are particular cases limited by physiological or behavioral constraints?

Sex ratios are relatively easy to measure, and it is sometimes possible to perform controlled experiments on sex ratio response. If we can learn to reason about and predict sex ratios, then perhaps we can use that reasoning for other behavioral and life history adaptations. And if we fail for sex ratios, then our prospects are not good for other more complex characters.

Trivers and Willard (1973) followed by showing how sexual selection could influence the relation between parental investment and the fitness of progeny. In species with large, combative males, healthy mothers that invest highly in sons get large returns from the many mates won by successful sons. Weaker mothers that cannot produce competitive sons do better by producing a daughter, because an average son may have little success whereas an average daughter may have average success.

Charnov et al. (1981) extended the Trivers-Willard idea and provided elegant experimental confirmation. Charnov et al. observed that parasitoid wasps lay daughters on large hosts and sons on small hosts. They reasoned that in species in which males do not compete directly by combat, fecundity in females would increase more rapidly with size than would mating success in males increase with size. If so, then mothers would gain by assessing the size distribution of hosts available in any season, and laying daughters on relatively large hosts and sons on relatively small hosts. They manipulated

[1] *Sex Ratios: Concepts and Research Methods.* Ian C. W. Hardy, ed. 2002. Cambridge Univ. Press, Cambridge, U.K., xii + 424 pp. HB $120.00, ISBN 0-521-81896-6; PB $48.00, ISBN 0-521-66578-7.

the size distribution of hosts in the laboratory. If a given host size was large relative to others, then it tended to receive relatively more female eggs. If that same host size was relatively small, then it received a relatively higher proportion of male eggs.

Trivers and Hare (1976) developed the idea of conflict over the sex ratio between queen and workers of social Hymenoptera. Queens are equally related to sons and daughters and favor an equal sex ratio. By contrast, the haplodiploid workers are three times more closely related to sisters than to brothers when the queen only mates once. Thus, workers often favor strongly female-biased sex ratios. Once again, the sex ratio is a relatively easily measured character that provides a window onto complex aspects of social evolution.

Charnov (1982) provided a synthesis of theory and data. Charnov also developed diverse kinds of problems, including simultaneous hermaphroditism and aspects of reproductive allocation in plants. His monograph showed the power of simple theories to illuminate so many different problems in resource allocation and life history. Perhaps for the first time, a rich and predictive theory of adaptation appeared readily testable.

So many issues seemed to funnel through sex ratio: sexual selection affects relative returns on investment in males and females; conflict between hymenopteran nestmates influences differential investment in the sexes; the growth patterns and life history of sequentially hermaphroditic fish can only be understood in the context of sex ratio competition; and genomic conflict is often expressed by genomic subsets that distort the sex ratio and subsets that repress the distorters. To understand the forces and limitations of sex ratio adaptation seemed very nearly a proxy for understanding behavioral and life-history adaptation. In addition, genomic conflict and other forces that shape sex determination provide a window into many aspects of genomic evolution (Bull 1983).

I spent much of the 1980s working on empirical and theoretical studies of sex ratios. I revisited the topic in 1998 with a reformulation and synthesis of formal sex ratio theory (Frank 1998), but otherwise I have not kept up with new empirical work after 1990. So I was eager to read Hardy's volume and learn how the subject had developed.

Overview

I believe that an earlier version of the book was titled *The Sex Ratio Handbook*, and the contents reflect the goal of a working guide for active researchers. The book does not try to provide a synthesis of sex ratio and the big questions of adaptation. Nonetheless, most of the pieces that would lead to the big questions are here, along with much helpful information on methods of research and on progress in various taxonomic groups.

Part 1 begins with two chapters on sex ratio theory. Part 2 follows with four chapters on statistical analyses of sex ratio data, including how to handle binomial data and how to put sex ratios into a comparative, evolutionary framework. Part 3 turns to the genetics of sex ratio and sex determination, with chapters looking separately at vertebrates, invertebrates, and sex ratio distorters.

Parts 4 and 5 cover different taxonomic groups in eight chapters. Each chapter summarizes the interesting conceptual issues associated with each group, as well as a review of empirical work. Part 6 finishes with three chapters on applications of sex ratios. Here we have some reflection on the value and limitations of sex ratios for studying adaptation.

Commentary

The book works well with the advantages and limitations of the edited volume format. The authors of each chapter generally do a good job of using their expertise on particular methods and the details of empirical work in particular taxonomic groups. The big picture of sex ratio as a touchstone is largely implicit in the progress and limitations nicely described by specialized topic or taxonomic group.

Anyone working on sex ratios will want a copy of this book. However, this is not a new synthesis. After 20 years, there is still a great opportunity for a new version of Charnov's monograph that smoothly blends theories, tests, and a broad vision of the importance of the subject. I understand that someone is working on such a monograph—a worthy challenge for the most ambitious.

Now comes my own challenge as a reviewer of an edited volume. I made notes on all chapters, but had to cut my list to a small subset for publication.

In chapter 1, J. Seger and W. Stubblefield lead off with an overview of sex ratio theory. They start with a fine scholarly treatment of the first theoretical analyses, beginning with Darwin's (1871, 1874) insightful yet confusing arguments that come close to getting some of the pieces, but then back off because the pieces do not all fit. Seger and Stubblefield follow with precursors to Fisher's (1930) famous passages, in particular Düsing's (1884) work, then on through Fisher and the first modern mathematical arguments by Shaw and Mohler (1953). The math for these particular models is built up as a tutorial, followed by a listing of key results for many of the topics I mentioned in my history. I have found it diffcult to judge what sort of mathematical tutorial works for newcomers—this would probably be a good first dose.

The beginning of Seger and Stubblefield's article focuses on Darwin's various attempts to understand natural selection of the sex ratio. Edwards (1998) argued that Darwin expressed the key theoretical issues correctly in the first edition of the *Descent of Man*, but Darwin deleted the main points in the second edition. Because the second edition was the one in wide circulation, Edwards believes that later readers missed Darwin's insight. Seger and Stubblefield walk through various passages from Darwin's first and second editions. They conclude that it is confusing why Darwin got close to the right argument and then retreated.

I believe that Darwin's passages and ultimate retraction can be understood by recognizing a single assumption that he used. To get started in reasoning about how numbers of males and females affect fertility, he assumed monogamy. He starts along the correct lines in reasoning about frequency dependence: ''Let us now take the case of a species producing . . . an excess of one sex—we will say males—these being superfluous and useless, or nearly useless. Could the sexes be equalized by natural selection?'' (p. 4) That seems a modern way to start the frequency dependence argument, although we would not say that males are ''superfluous and useless'' when they are in excess, unless we were considering the productivity of the species.

The weakness in the argument becomes clear later in that paragraph: ''. . . if we assume that females instead of males are produced in excess . . . such females from not uniting with males would be superfluous and useless.'' (p. 5) Why would females be useless if in excess? The only explanation I can think of is that Darwin assumed monogamous pairings as a simplified way of seeing how numbers of the sexes affected fertility. This explains why members of the sex in excess of the other sex are useless, and why Darwin gave up his own argument. He felt that he depended on maximizing the number of monogamous mated pairs by equalization of the sex ratio, a species selection argument. This explains the otherwise confusing aspects of the quotes here and in Seger and Stubblefield's chapter.

In chapter 2, I. Pen and F. J. Weissing step through a series of more realistic and more complex models. This provides a good sample of the techniques needed to solve real sex ratio problems that arise in current research. Someone looking to construct their own models would find this chapter a very fast way to see what sorts of tools are available and what sorts of questions others are asking.

The book contains four chapters on statistical inference for sex ratio data. These chapters by themselves form a small and valuable textbook devoted to the special tools and problems for analyzing proportion data. Those working with data or planning experiments will find these chapters worth the price of the book.

In K. Wilson and I. C. W. Hardy's overview in chapter 3, I particularly liked the strong emphasis on both type I and type II errors, on the approaches that can be used to determine which method is best for a particular problem, and on the clear recognition that different approaches trade-off different costs and benefits when using data to learn about the natural world.

In chapter 4, J. J. Boomsma and G. Nachman focus on the problem of analyzing sex ratios in social insects. Each sex ratio observation for a colony is both a fraction of investment in males versus females and a clutch size for numbers of males and females from that colony. The special challenge here is working with observations in which clutch size varies greatly, causing the information in each sample to vary. The authors begin with an evolutionary prediction about kin selection and split sex ratios among colonies. They then turn to how one handles data to test the predictions, including a detailed SAS program and output from the SAS analysis (SAS, Cary, NC). This would be a good supplement to a graduate course in biostatistics, showing the range of issues that arise when moving from an interesting prediction to tests with real data.

Sex ratio data often come as short sequences of male and female offspring. For example, solitary bees and wasps sometimes lay eggs as a sequence of individual cells in a long tube with a single opening at one end. If males tend to emerge earlier than females, it may be that the favored sequence is females early and deep in the tube and males late and nearer to the entrance. In birds and mammals, various theories including the Trivers-Willard (1973) hypothesis predict particular sequences of males and females within broods. In chapter 5, S. Krackow, E. Meelis, and I. C. W. Hardy discuss how one can test sequence data for departures from random expectations under a binomial model. Again, this is a nice connection between theoretical predictions and statistical inference.

In chapter 6, P. J. Mayhew and I. Pen finish the statistical set with comparative analyses of sex ratios in a phylogenetic context. They include a worked example on the sex ratios of nonpollinating fig wasps from data collected by West and Herre (1998). This data set includes some species with wingless males and some species with winged males. Wings have the potential to be correlated with phylogeny and with mating structure. These data present an interesting challenge in separating the causes of sex ratio variation.

The core of the book provides a series of reviews for topics such as sex determination or for particular groups such as aphids. Readers who have followed the literature will recognize the subjects and appreciate the updates. Readers new to the area will find a good introduction to the diversity of topics. I limit my comments to three of these chapters.

If you are looking for a good taxonomic group for research on sex determination and sex allocation, M. W. Sabelis, C. J. Nagelkerke, and J. A. J. Breeuwer make a strong case for mites in chapter 11. This group is widely abundant and exceptionally diverse in almost all aspects of its biology. Some have typical diploid genetics, some produce haploid males by eliminating the paternal genome, and others have standard haplodiploid genetics with males developing from unfertilized eggs. Sex determination of mites is further complicated by wide distribution of *Wolbachia*. Population structures vary from strong local interactions among kin to panmixia. Most importantly for study, mites often have short generation times and are relatively easy to manipulate in the lab, allowing controlled experiments. There should also be opportunity for experimental evolution, in which one studies mites' evolutionary response to manipulated environmental challenges.

If you are more radical and think the mites sound too old-school, take up malaria. A. F. Read, T. G. Smith, S. Nee, and S. A. West give a fascinating overview of sex ratios in malaria parasites and other protozoa in chapter 15. In the malarial *Plasmodium* genus, mosquitos inject haploid parasites into the host. Asexual proliferation begins in the liver and then spreads as the merozoites infect and multiply in red blood cells. Infected red blood cells eventually burst, releasing more merozoites. Some of the haploid merozoites differentiate into haploid gametocytes, which may be either male or female. Mosquitos pick up gametocytes in a blood meal. In the mosquito, each male gametocyte releases many male gametes, whereas each female gametocyte releases one female gamete. Fertilization followed by meiosis occurs in the mosquito. The haploid meiotic products infect new hosts and continue the cycle.

The sex ratio can be measured as the number of male and female gametocytes circulating in the host. Observed sex ratios vary widely in these single-celled organisms. Population structure is determined by the number of different genotypes mixed in the mating arena within the mosquito vector. Some data suggest that population structures vary widely, with instances of high inbreeding and potential local mate competition and other cases of panmixia. Read et al. argue that local mate competition theory can be used to understand sex ratio variation in protozoa. They also suggest that observed sex ratios may be indicators of underlying population structure—female-biased sex ratios indicating strong local structure and inbreeding, even sex ratios indicating panmixia.

Finally, I turn to human sex ratios. J. Lazarus lays out some issues, predictions, and difficulties in chapter 14. I agree with him that evolutionary reasoning can in principle help to understand some aspects of human sex allocation. The difficulty has always been in the testing of ideas.

The topic reminds me of a passage from *The Thousand and One Nights:*

> There are five things which only Allah knows: the hour of death, the fall of rain, the sex of a child in its mother's womb, what will happen tomorrow, and the place of death (Surah 31, Verse 34).

What would happen if humans could choose the sex of their babies? I heard that question asked and quickly dismissed after a seminar several years ago. Now the question, slightly rephrased, seems to me a very interesting and important one: What will happen when, in a few years, humans can easily choose the sex of their babies?

Various methods are already being used for sex choice. Cost, availability, medical, moral, and legal issues prevent widespread access at present. The power of modern biotechnology coupled with potentially huge profits, however, virtually guarantees the development of a simple and effective method.

When a technique becomes readily available, how widely will it be used? What sex will parents choose? Who will try to prevent choice? For academics who like to place bets from the grandstand, sex choice seems a wonderful opportunity. There has never been a shortage of ideas, but few have sought a dangerous arena in which their predictions could be tested.

I propose a contest. I encourage all to enter who have theories of human behavior, evolutionary or otherwise. The goal is to predict what will happen when sex choice technology advances to the point where it could be widely used. Will people want to use it? What will their choice be? How will choice vary by key explanatory variables, such as culture, religion, economics, the sex ratio, and so on? What sorts of conflicts will arise within families and societies? What about conflicts between nations with regard to fertility, sex-biased migration, and potential for male bias and aggression? What mechanisms will mediate sex choice and conflicts of interest?

When reading theories of human behavior—evolutionary and otherwise—I have sometimes found it difficult to tell whether there is a real scientific idea or just a description of some behaviors and some opinions. If a theory were entered in my contest, the author would be forced to express how the theory works to formulate a prediction. The scientific merits of various ideas could be evaluated with regard to logic, comprehensiveness, and coherence. In a few years we may be able to see if anyone really understands how the complex array of behavioral and social processes together shape human decisions about investment in male and female offspring.

In summary, has sex ratio lived up to its promise as a touchstone for the study of adaptation? We will have to wait for an updated Charnov-type monograph to make a comprehensive case. Meanwhile, for those who wish to contribute to what West and Herre call ''the jewel in the crown of evolutionary ecology'' (1998, p. 399), this new book provides everything one needs to get started.

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