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**What turned you on to biology in the first place?** I came to biology through a love of natural history. As a young boy, growing up in Canberra, the family home was on the other side of the road from a sheep station. Parrots would fly into drink at our fish pond and I have vivid memories of thornbills feeding a much larger cuckoo chick. I became a fanatical bird watcher until academic biology created different obsessions. Colleagues have come to biology for different reasons. Some want to understand how things work, to cure disease, or to find an outlet for their mathematical talents. These initial motivations often have long-lasting effects on what questions are found interesting. As a general rule, biologists who start as naturalists are more likely to be interested in questions of adaptive function and less motivated by questions of mechanism. As a university student, I gradually moved from a primary focus on traditional ecology to an interest in the natural history of the genome, but my ecological training remains of great value. It is the environment that selects which phenotypes transmit their genes to future generations. In this very real sense, it is ecology, mediated by phenotype, that determines genotype. Understanding biological systems, even at a molecular level, is going to require a combination of bottom-up and top-down approaches.

**Who were your key early influences?** My mother was a biology teacher. I received a broad education in classical biology at Macquarie University without taking a course in molecular biology (that was still possible). My most important mentors were Mark Westoby and Dick Frankham my guides in ecology and genetics. Mark became my doctoral advisor. Naomi Pierce nominated me for a Junior Fellowship that brought me to Harvard.

**If you had to choose a different field of biology, what would it be?** If I had the freedom of a doctoral student to take on a new area for evolutionary analysis it might be endocrinology. The major adaptive tradeoffs in organismal life histories are mediated by hormones that constitute summaries, one might say principal components, of where an organism stands in the adaptive
space of life-history tradeoffs. A better understanding of these tradeoffs should illuminate the organization of the endocrine system and an adaptationist perspective on endocrinology should inform understanding of life-history evolution.

**What paper has most influenced you?** Much of my career has been spent exploring implications of Robert Trivers’ paper on parent–offspring conflict from 1974. Many at the time rejected the concept because it seemed obvious that parents obtain their fitness through offspring and what is best for one should be best for the other. Forty years on, I still hear versions of these arguments. Part of the resistance is a trivial misunderstanding. The theory of parent–offspring conflict defines the conditions under which interests conflict but at the same time defines the conditions under which they coincide. Cooperation and conflict are two sides of one coin. Yet one often hears argument of the form “parents have evolved to care for their offspring, therefore there is no conflict”. The premise is impeccable but the conclusion fallacious, but I suspect resistance to parent–offspring conflict has deeper roots because it challenges some deeply held myths about parents and offspring in particular and the evolutionary process in general.

**What do you mean by myths?** We have a deep desire to see the natural world as fundamentally beneficent and natural selection as promoting individual well-being. Maximizing the probability of survival of an individual child is different from maximizing the number of surviving children. Therefore, adaptations of parents are expected to balance benefits to particular children against costs to fertility. Modern parents are not fitness maximizers but our psychology has been shaped by this evolutionary trade-off. We balance parental responsibilities with other demands on our time but feel uncomfortable with the suggestion that sometimes our needs are ranked above those of our children. We tell ourselves, and our children, we want only what is best for them. But our children recognize such parental protestations can be self-serving.

A close conceptual relation exists between the myth of the invisible hand in economics—everybody will be better-off if everybody follows their own interests—and the myth that natural selection always acts to increase the fit of an organism to its environment. Myths express truths. There are domains in which free markets deliver economic goods and in which natural selection
maximizes individual fitness. But myths express partial truths. The invisible hand is bad at providing and preserving public goods. Similarly, natural selection increases adaptation to the physical environment but can produce inefficient outcomes when the main selective force is social competition for shared resources. The finite capacity for maternal care is overexploited because of competition among offspring. It is a tragedy of the commons.

Fathers do not always pull their weight. Relations between the sexes were once viewed by many evolutionary biologists as fundamentally cooperative with sexual divisions of labor serving mutual interests. Robert Trivers and the women’s movement have contributed to an understanding that what is best for males is not always best for females. Sexual conflict is now widely accepted, but a similar appreciation of the interplay between cooperation and conflict in relations between parents and offspring is still to enter the mainstream. Theoreticians have a vested interest in ignoring conflict because it limits what their models can predict about the world. Biological anthropologists, for example, usually model optimal birth spacing for mothers without considering advantages to offspring of longer interbirth intervals. If a phenotype, such as the interbirth interval, is subject to parent–offspring conflict then a simple model cannot predict what interval should be observed because parents and offspring have different optima and both can influence the phenotype. What sort of compromise is achieved will be determined by messy details of mechanisms and relative power that are specific to each particular case and not easily incorporated into publishable models.

**What do you think of theories of parent–offspring coadaptation?** Coadaptation is a comforting word with an unclear meaning. *Plasmodium falciparum* and humans have a long history of living together in intimate association, are very important actors in each other’s lives, and have evolved reciprocal adaptations. One could say they are coadapted. But something more is clearly meant by coadaptation in the context of parent–offspring or maternal–fetal relations. If nothing more is meant than that parents and offspring have mutual interests then I have no problem. The theory of parent–offspring conflict recognizes both cooperation and conflict between the generations. But when coadaptation is promoted as an alternative to, or a denial of, conflict then this is simply a defense of the myth of intergenerational harmony. The Madonna and child is a powerful image.
Where would such ideas make a practical difference? An understanding of the basics of parent–offspring conflict should be central to all training in obstetrics. Our bodies normally function well, year after year, but pregnancy is a puzzling exception with substantial risks for both mother and fetus crammed into a few short months. Gestation is central to reproduction so why shouldn’t it function even more smoothly than other physiological processes? The biblical explanation was that pain in childbirth was Eve’s punishment for tasting of the tree of knowledge. A more recent version of the fall from grace is that complications of pregnancy are side-effects of our upright stance and the recent expansion of our brains. But I do not find these explanations compelling. We are not the only species to have difficult pregnancies.

Natural selection typically promotes exquisite coordination of physiological processes because all genes of an individual benefit from the same outcomes. Pregnancy differs because it involves distinct individuals whose fitnesses are maximized by different outcomes. Natural selection now acts at cross-purposes on genes expressed in mothers and fetuses. As a result pregnancy lacks many of the homeostatic controls of other physiological processes and is inherently unstable. Medicine traditionally distinguishes between the physiological, when the body functions as it should, and the pathological, when some part is broken or some process perturbed. But this distinction breaks down when what is physiological for the fetus is pathological for the mother, or the reverse. An understanding of the diseases of pregnancy will require a conceptual separation of the adaptations of mothers from the adaptations of fetuses and how one party adaptively responds to malfunction in the other.

How does this relate to genomic imprinting? The idea that imprinted gene expression evolves because of evolutionary conflict between genes of maternal and paternal origin was directly inspired by thinking about parent–offspring conflict. The group of paternal genes that compete for maternal care is larger than the group of maternal genes that compete for the same care. Thus the tragedy of the commons is exacerbated for paternal genes that are therefore predicted to more strongly favor selfish interests over collective interests. The organism now has aspects of a society of agents with different agendas. Just as there has been resistance to seeing parent–offspring
relations as imbued with conflict there has been resistance to recognizing conflict within the organism. A view of the body as a smoothly functioning machine is a powerful myth and there is resistance to polluting this vision with the messiness of internal politics. Systems biology has much to learn from the social sciences as well as from the physical sciences.

What do you think are the major challenges facing universities? There have been profound changes in the educational and research missions of universities over the past century. A hundred years ago, only a small proportion of the population attended university. The life of the mind was the principal motivation for many of these students. A degree was not a prerequisite for doing well in life. Now young people are told they need secondary education if they are to get a good job. Many professors still see their primary educational role as educating students with similar values to themselves in preparation for academic careers. There is a disconnect between what society sees as the role of the faculty and how the faculty see their role. Pressures for education to serve utilitarian ends are decried as a degradation of academic values. Probably more students than ever before, measured as a proportion of the general population, are studying literature and the arts but, rather than celebrating, faculty in these fields are conscious of losing ground relative to other disciplines within the academy. The nature of research has also changed. A hundred years ago, most scientific research was relatively cheap and supported by private or university funds. Faculty did much of the work themselves. Now expensive research is supported by government funds with benchwork performed by the indentured labor of graduate students and postdocs. The head of laboratory functions as a kind of Chief Executive Officer directing this labor.

With more expected of universities, there are pressures for universities to be more accountable, accompanied by a managerial revolution that seeks objective metrics of productivity in aid of the efficient allocation of resources. The problem with metrics is that they assess what is easy to measure and are rapidly corrupted as individuals modify their behaviors to conform, or to appear to conform, to whatever metric provides material rewards. Activity is easier to measure than thought and counting is quicker than reading. All these requirements eat into the time of the faculty while expanding the size of the managerial class. Universities are seeing the same trends
as the broader society, increasing inequality, less time, and a greater proportion of goods expropriated by managers. Advancement of knowledge and education of the young are public goods and extending the reach of the invisible hand may not be the best way to supply these goods.