

BOOKS: HUMAN BIOLOGY

Evolution and Our Reproductive Physiology

Hillard S. Kaplan

Walk down the streets of Manhattan's upper West Side and it will not be long before you see a double stroller with two toddlers of about the same age. Perhaps they are being pushed by a woman who, by appearance, could not be their mother. A likely explanation of the sight is that the children are the happy, if unintended, product of modern fertility treatment for a couple that delayed childbearing until their late thirties or early forties and hired a nanny to care for the children while their mother

**On Fertile Ground
A Natural History of
Human Reproduction**
by Peter Ellison

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works. Standing in stark contrast to this Manhattan scene is the very sad story of a twin birth among Efe pygmies in the Ituri Forest with which Peter Ellison begins *On Fertile Ground*. The two Efe infants died in childbirth and their mother almost lost her life. In fact, twins are greatly feared among most peoples who subsist on hunting and gathering, as our ancestors did throughout our evolutionary past. Even when twins survive the birth process, usually one or both are killed on the spot.

Why? This book elegantly synthesizes the mounting evidence that the physiological regulation of ovulation, fertilization, implantation, and the maintenance of a pregnancy among humans is particularly specialized to produce high-quality, large-brained offspring. Two implications of this specialization are rigid control over embryo quality and a series of adaptations on the parts of both mother and offspring that ensure an adequate energy supply to the nutrient-hungry, fast-growing brain. Twins simply exert too high an energetic demand, especially for women living on a constrained energy budget typical of our evolutionary past.

Ellison, an anthropologist and dean at Harvard University, introduces readers to the complex system of chemical communication between mother and the newly fertilized egg. Raising humans requires a massive investment [in foraging societies, children are provisioned by parents for about 18 years (1)], and this system ensures that in-

vestment in offspring of poor genetic quality is quickly terminated. Implantation and nurturance of the human fetus with a haemochorial placenta, which ensures a large and consistent supply of nutrients, differ from those in most mammals. Fetal growth is more rapid in humans than in gorillas and chimpanzees. Human mothers and offspring store exceptional amounts of fat, probably to support an equally exceptional rate of expensive brain growth during the infant's first five years. Parturition is triggered when sugars in the maternal blood are insufficient to support those energetic demands and the fetus signals that it is starving and needs lipid- and protein-rich milk. Birth is a treacherous affair in humans, because the pelvis is barely large enough to allow the baby's enormous head to pass through. Unlike in other primates and mammals, the affair is usually social, which allows others to assist.

On Fertile Ground provides the finest available integration of detailed information on human reproductive physiology with evolutionary explanations; it can serve as a model for other areas of human biology. Ellison discusses the fundamental tradeoffs that influenced natural selection during our past. Why is the head not smaller or the pelvis not larger? Conflicting demands of female locomotion, brain growth, and birth complications have produced a delicate fitness-maximizing balance. The author examines many similar tradeoffs and he evaluates a wide range of hypotheses that have been offered as evolutionary explanations for different aspects of human reproduction. For example, he considers why human females menstruate when menstruation is so rare in other species.

The book offers a substantial improvement over earlier frameworks focusing on proximate determinants of fertility (2, 3). Going beyond the well-known contraceptive effects of nursing, Ellison's treatment shows

how the physiological control of fertility has evolved to produce plastic, adaptive responses to energetic demands. The control is highly sensitive to energy stores in the form of fat, energy balance (calories consumed minus calories expended), and energy flux (rate of energy turnover per unit time). Low body fat, weight loss due to negative energy balance, and extreme energy flux (either very low intake and very low expenditure, or very high intake and very high expenditure) each lower monthly probabilities of conceiving a child that will survive to birth. Seasonal variations in workloads and diet also affect female fecundity and fertility.

Variations across groups in both age of menarche and fecundity are responses to differences in food intake and work load. Even in modern societies, women who are calorie-stressed (e.g., due to anorexia) or who have chronically high work loads (e.g., long-distance runners) are less fecund.

Aside from the relative paucity of illustrations and figures, more of which would have helped the nonspecialist reader, my only substantive criticism is Ellison's tendency to treat physiology and behavior as alternative causal forces rather than as co-evolved or co-adapted traits. This tendency is particularly



At work in the fields. Studies of the Tamang of the Himalayan foothills in Nepal have provided data on energetic condition and ovarian function in a population that subsists on a combination of agriculture and pastoralism. Tamang women have particularly heavy workloads during the monsoon, when they spend long hours transplanting rice.

evident in his discussion of the reproductive life course. The author reviews three alternative explanations for age at first reproduction: learning and brain maturation necessary for parenting and subsistence behavior, critical body fat, and pelvic size. He concludes that the limiting constraint is the time required for the pelvis to grow large enough to allow the baby's head to pass through it. Although the attainment of some critical pelvic size may trigger other physiological events necessary for reproduction, this conclusion does not reveal much about the action of natural selection on the initiation of reproduction.

A striking difference between humans and other great apes lies in the ontogenetic pattern of growth rates. Growth is very rapid during fetal development, intermediate in infancy and early childhood, exceptionally slow during middle childhood, and very rapid again during the adolescent

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growth spurt. The pattern suggests—especially because parental provisioning could allow very rapid attainment of adult stature if doing so would maximize biological fitness—that rather than being a critical constraint, the growth rate itself is molded by natural selection in relation to other features of the human life history. It does not appear to be coincidental that abstract logical reasoning, adult stature, and body fat storage are all timed to develop during late adolescence so that in most foraging societies reproduction is initiated at age 18 or 19. The learning-intensive foraging strategy practiced by hunter-gatherers and, perhaps, learning-intensive parenting strategies require many years of cumulative knowledge. Maybe it simply does not pay to grow to adult stature until the brain is ready for successful parenting and for the acquisition of energy to support reproduction. Viewing these behavioral, physiological, and anatomical characteristics as co-evolved components of a unique brain-based life history pattern helps explain the specialized features of human gestation and birth so elegantly described in the book; otherwise, the brain itself is an unexplained determinant.

A novel synthesis of a fast-growing field, *On Fertile Ground* will interest specialists and nonspecialists alike and can be used as an undergraduate text as well. It is an excellent read that significantly advances our understanding of human reproduction.

References

1. H. S. Kaplan, J. B. Lancaster, K. R. Hill, A. M. Hurtado, *Evol. Anthropol.* **9**, 156 (2000).
2. J. Bongaarts, R. G. Porter, *Fertility, Biology and Behavior: An Analysis of Proximate Determinants* (Academic Press, New York, 1983).
3. J. W. Wood, *Dynamics of Human Reproduction: Biology, Biometry and Demography* (Aldine de Gruyter, New York, 1994).

BOOKS: GENETICS

Writing About the Unseen

Andrew Berry

Jennifer Ackerman's previous book, *Notes from the Shore*, was about horseshoe crabs, whales, and seagulls. Her new one, *Chance in the House of Fate*, is about transposons, apoptosis, and hox genes. Ackerman has in effect undertaken a grand literary experiment: She has tried to export her nature-writing skills from the visible, tangible world of natural history to the unseen, microscopic world of the cell.

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To do this, she weaves together three narrative strands. Along with the science, we get plenty of history of science (Galen, Cuvier, and Redi are all there) plus a good dose of Ackerman's personal story. Not only do we follow her mother and grandmother as they fall prey to cancer and Alzheimer's, but we also learn that Ackerman keeps seashells on a windowsill in her study and has a dog called Lucy. This is certainly not standard science-writing fare. Even the structure of the book departs from convention. There seems to be no particular theme binding together its 18 chapters or four sections; the book is best viewed as a collection of essays or—because the chapters generally lack the formal argument that characterizes an essay—meditations on molecular biology and genetics.

The book's strengths are its lightness of touch and breadth of coverage. *Chance in the House of Fate* contains a great deal of biology (circadian rhythms, the tumor suppressor protein p53 and cancer, the molecular components of the eye, imprinting, and plenty more). Much of it is deftly presented, and Ackerman can be a thoughtful commentator: "The conservation of genes across species was revealed not as Dar-

Herrings signal in soft chirps. Sea robins squawk, toadfish grunt, and striped bass utter an 'unk.' Molecular biology also provides the author with lists: "The motifs [of proteins] carry such names as kringle (for the Danish pastry it resembles), apple, kunitz, link, zipper, zinc finger, forkhead, sushi domain, and home-odomain." This is, I admit, an unfair comparison—the onomatopoeia of fish utterances is inevitably lyrical while the names devised for newly discovered protein motifs over pizza and cheap beer at lab get-togethers are just as inevitably prosaic—but the comparison nevertheless crystal-

lizes Ackerman's problem. Nature writing is best applied to nature. Writing that is evocative and poetical in one context is merely whimsical and obtuse in another. Lucy the dog is our introduction to a discussion of the molecular basis of smell: "She has caught an aromatic vapor from unseen origins, and she lingers for a moment, savoring, then snuffles forward to seek other faint effluvia."

Although I do not think that Ackerman's nature-writing-meets-molecules approach succeeds, I applaud her for trying. The world within the cell is, after all, every bit as wondrous, and even as beautiful, as the world of a tropical forest; so why not apply the same language to describing them both? I think the answer lies in the extent to which each world is tangible. A description of a stroll through a forest in which each encounter—the call of a bird, the rustle of a fleeing lizard, the flash of a butterfly's wings in a sunspot—is described only fleetingly can successfully convey a concrete sense of that forest. This, I suspect, is because we all have some experience of forests. But we

have no equivalent experience of the sub-cellular world. Fleetingly described encounters with mitochondria ("these prominent little generators"), ribosomes (those "splendid little structures"), and DNA ("a serpentine coil of atoms with an odd stringent beauty, long and skinny, like its name, deoxyribonucleic acid") fail to yield a concrete sense of the inside of a cell. Sadly, my imagination remains firmly aground on the didactic schematics in introductory biology textbooks. I conclude from Ackerman's experiment that it is mighty difficult to write evocatively about worlds that lie beyond our normal sensory universe.

Chance in the House of Fate
A Natural History of Heredity
by Jennifer Ackerman
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win's discoveries were—by seeing what others had seen and thinking what no one had thought—but through a kit of new technological tools." But ultimately her efforts are not satisfying: She fails to elicit any new or deep appreciation of what she refers to as "the gnomonic workings of the living order, nature's inventive jack-in-the-box surprises that shift our view of life like the sudden twist of a kaleidoscope."

Ackerman likes to enshrine diversity in a list. In her earlier book, she describes the noises that fish make. They "thump, cluck, croak, bark, rasp, hiss, growl, swish, spit, scratch, and quack. Eels bubble and thud.