BOOKS: EVOLUTION

Behavioral Just-So Stories, Recast

Patricia Adair Gowaty

Animal Traditions Behavioural Inheritance in Evolution
by Eytan Avital and Eva Jablonka
Cambridge University Press, New York, 2000. 446 pp. $80, £50. ISBN 0-521-66273-7.

Written in opposition to a narrow understanding of the evolutionary process as between-generation changes in gene frequencies, *Animal Traditions* argues that learning and culture are important agents in evolution. The book is stuffed with compelling examples of the behavioral "system of information transmission" (that is, behavioral inheritance). Eytan Avital and Eva Jablonka present these to support their view that the transfer of such socially acquired and transmitted information across generations blurs the classical distinctions between development and evolution. Their picture of selection operating on phenotypes is much like Darwin's, although they explicitly note that it interprets the evolution of behavioral adaptations as involving the inheritance of acquired characteristics.

The authors' basic message is that selection in birds and mammals is affected by behavioral variation arising from learning as well as genes, something most animal behaviorists have appreciated for a long time. Accepting arguments made by geneticist Richard Lewontin and his students, they maintain that habits and traditions are not simply products of evolution but are also agents for constructing the environment in which the habits and traditions are selectively favored or disfavored. Avital and Jablonka emphasize two differences between animal traditions and genetic inheritance: Though both are products of historical evolutionary process, traditions can only be formed during development of behavior, and transmission of much behavioral information depends on its use and display. These are extremely important points, particularly in a gene-centric atmosphere illustrated by conservationists who naïvely but seriously assume that saving a species from extinction may only require electricity and containers for long-term cryogenic storage of gametes and the genes they contain.

Avital and Jablonka offer a balanced discussion of the nature of transmission of acquired behavioral characters. They report many sensible claims, such as anthropologist William Durham's example of lactose absorption as evidence that genes and culture interact and co-evolve in their effects on phenotypes. They also reiterate the question of questions for quantitative geneticists: how many phenotypes can be expressed with a given genotype? Norm of reaction experiments (which examine genotype–environment interactions) remain rare in studies of avian and mammalian behavior, so we still really know very little about the sources of inherited variation in much of animal behavior.

In their introductory chapter, the authors remark on the accumulation of theoretical and empirical studies on learning and culture. They cite works by the geneticists Luigi Luca Cavalli-Sforza and Marcus Feldman, the anthropologist Robert Boyd and the ecologist Peter Richerson, and Richard Dawkins, as well as classic reviews by John Tyler Bonner and Paul Mundinger. Avital and Jablonka note that the focus of their book is on social learning, and *Animal Traditions* contains an informative review of how such learning takes place and what it is good for. The early chapters kindled my anticipation of having these and similar points expanded, because the authors make some radical claims about what the process of writing the book accomplished.

Nongenetic transmission. Alloparenting, which is practiced by these European bee-eaters (*Merops apiaster*), can transfer learned information between generations.

Despite this strong start, I was disappointed in the later chapters. These are antisociobiological, which is unfortunate and ironic because the authors have committed the sociobiologists' original sin: The book is full of just-so stories told with the twist that instead of their genes, their traditions and cultures made them do it. The chapters each begin with simple descriptions of some actual animals doing some real life things, which the authors then interpret from the perspective of how learning and tradition operated to make things so. The problem is that the claims of the adaptive significance of the behaviors, although seemingly logical (just as many sociobiological stories based on genes are logical), are seldom buttressed by observations that would provide confidence in the interpretations or by predictions that would clearly implicate cultural rather than genetic mechanisms of information transfer.

For those of us who find the most significant question to be "How does fitness vary given different behavioral phenotypes?" just-so stories are just not enough. One must do more than spin tales of how learning and tradition serve fitness. It is especially frustrating that Avital and Jablonka, like some sociobiologists before them, offer untestable explanations. Predictive just-so stories are scientific hypotheses, and therefore just-so stories need not be bad. But, like conclusions about more conventional hypotheses, they are bad when their acceptance is based on weak evidence or none at all.

By my reading, the core of the book is actually the authors' objection to the predominance of conflict hypotheses in current studies of social behavior. Avital and Jablonka narrowly construe the arguments over conflicts to be about genetic conflict. But the conflict hypotheses that have motivated and organized so much modern research in behavioral evolution are concerned with conflicts in fitness interests. As the authors argue, genes and fitness are not the same. Unfortunately, Avital and Jablonka err in believing that many of the rest of us think they are. As John Maynard Smith insisted in 1994, "No one's a genetic determinist anymore." In fact, most of us interested in fitness conflicts (even those who believe fitness is exclusively about genetic conflict) measure fitness variation by counting the survival and reproductive success of individuals, that is, phenotypes. Therefore, even genetic determinists often do very credible studies of fitness variation.

As an example of these shortcomings, consider one aspect of the authors' discussion of parent-offspring conflict. Objecting to the hypothesis that weaning conflict arises from divergent evolutionary interests of mother and child, Avital and Jablonka offer an alternative motivational explanation that stresses congruent interests: A

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child's begging is good for the child because mother's withdrawal is a teaching mechanism that prepares the child for an uncertain world where all will not be at his or her fingertips. It appears that the authors mistake a proximate cause (behavior mediated by teaching and learning) for an ultimate one. If the authors are claiming that mother and offspring have congruent fitness interests, then—as an alternative to sociobiologically derived predictions—they might suggest that no matter who typically won these behavioral contests, the fitness of the mother and child relative to other mothers and children would remain unchanged. I would have relished a discussion of how to sort out these alternative hypotheses. Unfortunately, the authors do not take up the potentially fascinating but difficult question of how we might measure the predicted fitness differences among mothers and among offspring.

In an era when maternal effects are the rage even among quantitative geneticists, *Animal Traditions* is poised to be influential. It is full of natural history that is fun and interesting to read. However, I wish the authors had not recapitulated sociobiology's principal failing and instead had used this opportunity to move our discipline's discussion further away from the unproductive nature-nurture debates.

BOOKS: CELL BIOLOGY

Manifesto for a Cytoplasmic Revolution

Thomas P. Stossel

The goals of this extremely readable and cleverly illustrated book are not modest. Gerald Pollack, professor of bioengineering at the University of Washington, begins by demeaning textbook renditions of cell biology as analogous to Ptolemaic epicycles. These renditions, he claims, are pedantic minutiae to be overthrown by a Copernican revolution that will leave us with a "new, unifying approach to cell function," one unencumbered by the mass of molecular details usually trolled by biologists in search of mechanisms.

Cells, Gels and the Engines of Life is an eloquent and accessible statement of a heresy that has smoldered at the fringe of orthodox biology for about 30 years. Having often watched eyes glaze over as I try to preach that cytoskeletal polymer phase transitions are important for cell motility, I was ready to embrace a work that unabashedly and eloquently celebrates cells as polymer gels, without resorting to a single mathematical equation. Too little imagination, I have thought, has been applied to thinking through possible ways that biological gels (such as fibrin, collagen, elastin, and actin) influence human physiology and disease.

After challenging the notion that pumps and channels manage solute gradients across a continuous membrane envelope at the cell surface, Pollack reviews the physical chemistry of water and solutes and the effects of immobile polymers on this chemistry. He claims that these interactions are sufficient to explain solute partitioning between cells and the outside world. The principles of structured water and the power of cytoskeletal liquid-gel phase transitions then provide specific explanations for a wide range of cellular phenomena: the neural and muscular action potential, the exportation of packaged secretions, cell locomotion, movements produced by molecular motors, mitosis, and muscle contraction. Energy in the form of complex phosphates, rather than running scores of little machines on a highly individualized basis, works primarily to order of layered water.

Cells, Gels and the Engines of Life
A New, Unifying Approach to Cell Function
by Gerald H. Pollack
Ebner, Seattle, 2001. 319 pp. Paper, $27.95. ISBN 0-9626895-2-1.

Though Pollack's interpretations challenge conventional wisdom, such challenges should always be welcome. Sometimes a reformation must await the right instigator at the right time. Has the time come? Will cell physiologists now throw away their patch clamps and impale themselves on their micropipettes? Probably not. Most cell biologists hardly think of cells as bags of diffusing solutes. Others, studying signal transduction reactions or mining genetic databases for new drug targets, wouldn't necessarily be less productive in their pursuits if they did. Pollack believes that the elegant and powerful equilibrium phase transitions discovered by the late Toyoichi Tanaka, which can do amazing work in applications ranging from disposable diapers to artificial muscles, have similar effects in living cells. A tiny variation in pH, for example, can generate huge changes in volume of a charged polymer gel. The application of these reactions to biology, however, steps into the pitfall of reasoning by analogy. Although physics reigns over biology, biological processes operate far from physical and chemical equilibria. Temperature shifts can expand or contract metal springs, and liquid running down a hill can look like a migrating ameboid cell, but muscle contraction and cell locomotion simply don't work the same way as these similar-looking phenomena.

Biologists' imposition of molecular rigor, of chemistry, on the underlying polymer physics of cells has predictably multiplied the ingredients in the system. But I believe that these details, rather than being annoying distractions, are the essence of biological meaning. Whereas molecular interactions and molecular machines clearly operate within a context of bulk polymers that strongly influence the aqueous and ionic environment, the subtle differences in molecular interactions and molecular machines are what make yeasts different from humans and humans different from one another. Perhaps someday we may define these interactions in terms of water and ions, but at the moment the fun and profit are in the molecular specifics.

Defenders of pumps, channels, and molecular details will notice that most of the references Pollack cites to support his claims are elderly. I suspect that many of the specific arguments are susceptible to the accusation that the author cherry-picks evidence (a technique not restricted to the heterodox). Mainstream biologists can cite findings from modern molecular genetics that illustrate how genetic point mutations that subtly affect macromolecular functions powerfully influence a cell's behavior without grossly disrupting the structure of its polymers. One example among many is the wobbly weaver mouse, which lacks cerebellar neurons because of a mutation in the pore region of a potassium channel. Another is the ability of the blood's complement system to poke holes in and destroy red blood cells: a tribute to the existence of coherent cell membranes and the basis of an entire industry devoted to assuring that blood transfusions are immunologically compatible.

Although I enjoyed reading *Cells, Gels and the Engines of Life*, and I believe that it is valuable for directing one's thinking toward cellular machinery in a broad and interesting way, it didn't deliver what I was seeking. I hope that having gotten this book out of his system, Pollack will now write an equally readable but more balanced fundamental cell biology (or physical chemistry) text for students of the health professions. A well-illustrated, lively description of cell biology (without equations) that conveys the big picture about the contributions of physical principles to cellular function might help practitioners better appreciate the beauty and practical relevance of biological science and feel less intimidated by its complexity. These practitioners might then be willing to use their credibility as healers with the public to promote the value of research to our political leaders.

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