

Social Facilitation

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Social Facilitation

Hormones and Animal Social Behavior. Elizabeth Adkins-Regan. Princeton University Press, Princeton, NJ, 2005. 411 pp., illus. \$45.00 (ISBN 0691092478 paper).

hirty years ago, while an undergraduate at Berkeley, I worked as a research assistant for Frank A. Beach, a founder of behavioral endocrinology. On a typical afternoon, I purchased an oxtail bone, cut it to a specified dimension, and drove to a field station to conduct behavioral tests on group-housed beagles. Within each five-dog pack, a social pecking order was established. I knew this because, after gaining the dogs' attention, I tossed the bone into the center of the pack and recorded which dog acquired it. This was designated the "alpha dog." I then removed the alpha dog, retrieved the bone, and repeated the procedure to determine the beta dog, and so on. There was little or no fighting—an occasional growl or perhaps a tug-ofwar among the lower-ranking dogs, but no overt aggressive behavior. This was true whether the packs comprised all males or all females. When two packs of dogs were tested together, a new hierarchy was sorted out very quickly, again with little overt conflict. The dogs seemed to understand one another's behavioral and sensory cues.

Particularly interesting was the behavior of female dogs that had been treated earlier in their lives with testosterone, the primary circulating sex steroid hormone in males. Some had been exposed to testosterone *in utero* when their



mothers were injected with it, some were injected soon after birth, and some had been exposed through both routes. Such hormonal treatments had little effect on the males, as the treatments roughly duplicated male puppies' normal endocrine milieu. However, they had drastic effects on females. Indeed, the female puppies that received testosterone both pre- and postnatally looked very much like males, although their behavior was neither stereotypically male nor female. When tested a year or two later, however, those females not only were more aggressive, they didn't seem to understand the social rules. They would walk up to an alpha dog chewing on its newly attained oxtail bone and try to yank it away. They would contest the higher-ranked animals at every turn. Growls and outright fighting occurred with much higher frequency when these masculinized females were in the pen. What remains to be determined is whether this outcome reflects adjustments in the hormonally treated females' behavior or in the altered social cues emitted, or changes in their decisionmaking, perceptual abilities, or risktaking behavior. This study cemented my interest in the effects of hormones on social behavior.

That hormones can have long-lasting effects on social interactions is well known. The mechanisms by which these interactions take place, and the ecological and evolutionary pressures that shape them, are the subject of numerous fascinating studies. However, this literature is spread throughout behavioral, physiological, ecological, and developmental journals, and a concise synthesis has been lacking. Hormones and Animal Social Behavior, written by Elizabeth Adkins-Regan, a professor of psychology and neurobiology at Cornell University, fills this void nicely. I assigned this book for a graduate seminar on hormones, brain, and behavior last term, and the students and I thoroughly enjoyed it.

The book is well written in an informal, entertaining style, and the new data, the novel synthesis, and the effortless

glide across multiple levels of analysis make it remarkable for its depth and breadth. It is nearly a perfect behavioral biology book, suitable for graduate and advanced undergraduate students. When reading it, I kept hearing the ghost of Frank Beach's "The Snark Was a Boojum" paper as Adkins-Regan gently, but persistently, reminded me that knowing how things work in one species does not mean we understand how things work in other species. She conveys the complexity of comparative biology without overwhelming the reader.

The first chapter reviews basic endocrinology, with the presentation limited to those hormones and their receptors that are best documented as influential in social behavior. The chapter discusses why social behavior requires hormonal regulation, and describes the synthesis and metabolism of major steroid hormones. A description of the actions of neuropeptides and prolactin, and the mechanisms of their action, follows. There are concise and highly integrative sections on plasticity and development, as well as on environmental regulation of hormones.

Chapter 2, the longest, covers the behavioral topics most commonly associated with behavioral endocrinology: mating, fighting, parenting, and signaling. Adkins-Regan does a good job of summarizing decades of research, though she also presents a new synthesis of how hormones alter behavior via interactions with neural circuits, networks, and processes. I enjoyed the presentation of daily and seasonal influences of hormones, but I would have appreciated here an explicit statement about the reason underlying daily or seasonal reductions in testosterone: Males cannot continuously manage the costs of high testosterone (a point the author makes later in the book). In contrast, she does a magnificent job on the role of testosterone signaling, and breaks down the costs of testosterone on far-ranging physiological and behavioral parameters into digestible and testable hypotheses.

In chapter 3, which describes social relationships and organization, Adkins-Regan begins to add function to mechanism. She also brings ecological factors to bear in addressing cause-and-effect relationships.

In chapter 4, a description of the development of sex differences and withinsex morphs, Adkins-Regan reviews the organizational (programming) and activational effects of sex steroid hormones. In chapter 5, she reviews the evidence for endocrine contributions to individual differences in social behavior. These wideranging chapters use Tinbergen's four formal questions underlying the study of behavior to present sex and individual differences and the hypothetical reasons for these. Adkins-Regan examines the genetic, molecular, endocrine, and neural mechanisms underlying such differences, as well as their development, phylogeny, and adaptive significance. She encourages more mechanistic studies while emphasizing the desirability of a stronger link between behavioral endocrinology and evolutionary biology.

In chapter 6, life stages and life histories are considered. The author presents the typical species-level and individuallevel trade-offs between somatic functions and reproduction that shape the evolution of life histories (for example, survival mechanisms versus growth). She then brilliantly describes the importance of hormones in life stages such as hatching and birth, metamorphosis, puberty, peripubertal dispersal, and the onset of reproductive senescence. The author focuses on trade-offs between mating and parental efforts; I wish there had been more emphasis on the core life history trade-offs, such as that between reproductive effort and immune function, a proxy for survival mechanism. The influences of sex steroid hormones, as well as glucocorticoids, on immune function have profound effects on survival and reproduction, and the trade-offs can vary as a function of time of year.

In the final chapter, Adkins-Regan examines phylogeny in the context of evolutionary conservation and innovation. She notes that whereas genomes, steroid

mechanisms, and brain structures are generally conserved across phylogeny, social relationships and organization are quite diverse. Why? The author suggests several possibilities. Hormones allow for diverse social behaviors by allowing the action of a variety of conserved and innovative mechanisms (e.g., changes in the distribution of receptors in various brain regions). She also emphasizes that some developmental mechanisms can be repeated across phylogeny to produce specific behaviors (e.g., vocalization linked to both innate and acquired social cues).

Behavioral endocrinology has matured since I watched beagles form social hierarchies nearly 30 years ago. The field has changed from merely measuring and manipulating circulating hormone concentrations to examining gene transcription, hormone receptors, and other molecular and cellular parameters, as well as the neural circuitry and social environment associated with various behaviors. Researchers would benefit by heeding the overarching message in



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Adkins-Regan's book: It is always critical to consider the pressures that shape behavioral mechanisms.

Hormones and Animal Social Behavior masterfully achieves Adkins-Regan's goal of integrating behavioral endocrinology with ecological and evolutionary studies. One could quibble with the relative shortage of figures, the lack of detailed referencing of statements in the text, or possibly a slight overemphasis on birds (I would have liked to have seen more mammalian examples, because behavioral endocrinology will be important in future attempts to conserve species as critical conditions change). Nonetheless, I predict that this outstanding book will soon become a classic in behavioral biology.

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SEEING CLEARLY NOW

From Resource Scarcity to Ecological Security: Exploring New Limits to Growth. Dennis Pirages and Ken Cousins, eds. Cambridge, MA, MIT Press, 2005. 280 pp. \$24.00 (ISBN 0262661896 paper).

ow accurate were the models and projections of *The Global 2000 Report to the President*, commissioned by Jimmy Carter and released in 1980? Dennis Pirages, Harrison Professor of International Environmental Politics at the University of Maryland, and Ken Cousins, a doctoral student at the same university, have collected essays by 19 authors who provide assessments of the projections in 12 areas. It turns out—not too surprisingly, if one thinks about it—that the record is mixed, the scorecard spotty; some projections have turned out to be remarkably accurate, while others

were way off. The big news, however—and it *is* big, if not really news—is that the questions, perhaps more than our answers to them, have changed.

The chapters of the book unfold as well-informed authors survey current trends in global population, water availability, food policy, energy, political challenges, climate change policy, forestry, and biodiversity protection, and compare the best available current information with the projections of the 1980 report. It's fun to read the book as a sort of ideological scorecard—Paul Ehrlich and neo-Malthusian cohorts set against Julian Simon and the cornucopians and each chapter brims with facts and with surprising as well as commonplace observations about the current state of the problem areas highlighted by The Global 2000 Report. For example, the report was prescient in identifying rising CO₂ emissions as an impending threat, and its dire predictions of tropical deforestation and degradation, while difficult to measure, are generally considered accurate. On the other hand, the report's projections of world population growth overestimated growth from a 1970 baseline to the year 2000 by about one-third. Likewise, the 1980 report significantly overestimated water demand in 2000, and alarmist predictions that the world would run out of petroleum in the short term turned out to be in error. In the area of world hunger, food supplies have grown more rapidly than projected in

For this reader, however, the important message is not about the differences between the report's projections for 2000 and the actual figures for that year. The message, rather, is in the ways straightforward questions, once boldly queried, must be qualified and redirected. According to this message, environmental problems are more complex today, and the issues involved in environmental and resource policies are less clear than they were on the original Earth Day. For example, most demographers 30 years ago would have considered the more-rapidthan-expected drop in birthrates, especially in South Asia, to be positive news, because it reduced rapid population growth and strongly affected projected growth in the future. But now many countries, especially in South Asia, face aging populations, which may threaten their rapid economic growth when productivity decreases as the workforce share of the population dwindles because of retirements.

One key aspect of this shift is to put more emphasis on questions of equity and access than on shortages and available supply.

The editors' choice of title captures the central theme of the book: The concept of "resource scarcity"—and the exercise of projecting dates of impending exhaustion of a given resource—has proved too simplistic to capture the complexity of today's environmental and resource-use problems. The editors propose adopting a goal of "ecological security" as a more constructive characterization of environmental challenges. One key aspect of this shift is to put more emphasis on questions of equity and access than on shortages and available supply. When measured against the old standard, per capita production of cereal grains increased 28 percent during the last three decades of the 20th century in the developing world, leading to lower prices; but if measured against the goal of universal food security, there are now more food-insecure people in South Asia than before, because rapid population growth outstripped gains on the supply side.

The editors, I think intentionally, use the term "security" in two ways. Speaking narrowly, authors and editors speak of "food security" and "energy security" as implying a concern for both supply and equitable access. More broadly, I think they mean to connect resource issues to safety and security, as many renewable resource systems, especially in developing nations, are ravaged by war, and famine is often the result if the agriculturalists cannot protect their crops. So one aspect of the new approach developed here is to link resource security to military security.

Another aspect of the shift in thinking—and in the questions asked—is a recognition that, in general, there is more a shortage of "sinks" for wastes than there is a shortage of resources. Global warming and degradation of waters, caused by pollution and sedimentation, lead to ecological insecurity that is visited upon individuals, even as supplies of many resources glut world markets.

One resource that is in short supply, given the degradation just mentioned, is fresh water. Humans now use 54 percent of accessible fresh water run-off (p. 63). Since human usage competes with the needs of wildlife, and in-stream flow is needed for other ecological reasons, water will surely become more scarce, and how this scarcity is managed is fraught with dangers. Improving the efficiency of water use seems to demand the development of markets, so that water would flow to the best use based on willingness to pay; but traditional access rights to water may be seriously infringed if international water markets dominate access to water supplies and traditional users are excluded. Again, when looked at through the lens of ecological security, the challenge is daunting: How to improve efficiency and retain equitable access to water supplies for individuals is as much a social as a technical problem.

The exercise of rechecking The Global 2000 Report's projections is a useful one, but its use is much wider than monitoring trends that seemed important 30 years ago. Taking stock also stimulates a reconsideration of the nature of environmental problems, and forces us to confront the simplicity of earlier formulations of the problems of resource scarcity. From Resource Scarcity to Ecological Security contributes to a better understanding of how to address future problems by setting in relief current trends with earlier projections. The recognition that ecological security still eludes many inhabitants of today's world, even as productivity increases and prices for natural resource products remain level or fall, shows that addressing the world's problems will require more attention to equity and to access, and equity and access require a socially secure situation. Only community building and capacity building can meet the daunting social task of protecting the vulnerable from insecurity in the age of globalization. Perhaps this new formulation of some old problems will encourage more integrated thinking about resource use.

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EVEN FOR ENTOMOPHOBES

For Love of Insects. Thomas Eisner. Harvard University Press, Belknap. Cambridge, MA, 2005. 448 pp., illus. \$19.95 (ISBN 0674018273 paper).

s Thomas Eisner writes in the pro-Alogue, For Love of Insects is "a retrospective of a lifetime of exploration of a group of animals that truly can be said to have conquered the planet." But this is not just anyone's lifetime of research. Eisner is a world authority on animal behavior, ecology, and evolution, as well as one of the pioneers of chemical ecology, the discipline dealing with the chemical interactions of organisms. His work has spanned more than five decades, and he has published hundreds of peer-reviewed articles. Eisner is the recipient of many, many awards, including the National Medal of Science and the Tyler Prize for Environmental Achievement, and he is a member of the National Academy of Sciences.

Eisner is also an avid conservationist, as well as an artist. He repeatedly speaks out for endangered species and on behalf of the Endangered Species Act, and he played a key role in efforts to preserve wilderness areas in Florida and Texas. A well-known nature photographer, Eisner has helped make awardwinning film documentaries. He is an accomplished pianist—he even installed a piano in his laboratory at Cornell University—and an occasional conductor.

For Love of Insects is part biography, part travelogue, and part scientific journal, with history and humor thrown in for good measure.

Tom Eisner has always been gifted at taking complex concepts and making them not only understandable but also entertaining. So when he publishes a retrospective of his work, it is reasonable to expect a good read; with *For Love of Insects*, he delivers.

When I first picked up For Love of Insects, I assumed it would focus primarily on chemical ecology (Eisner's specialty) and insects. Although the book does include explorations into chemical ecology, it is so much more, drawing deeply on the author's enthusiasm for art and history, as well as other aspects of his scientific work.

Using a series of case studies that provide a personal account of Eisner's findings over the years, *For Love of Insects* is part biography, part travelogue, and part scientific journal, with history and humor thrown in for good measure. Each case study lays out an entire story, from initial concept or discovery to the way in which Eisner and his colleagues provided scientific proof of their findings.

This new paperback edition maintains the well-captioned and stunning photographs that illustrated the text of the hardcover. Not only is the book well written, it is also engaging and fun. In one section Eisner uses modern art and even an illustration from a story about Babar the Elephant, wherein Babar paints eyes on the other elephants' behinds to scare off

their rhino enemies, to illustrate how eyespots on Lepidoptera confound their enemies.

For Love of Insects contains enough depth and description to engage even the most dedicated entomologist, yet because the material is presented in Eisner's engaging style, the reader never gets lost in a maze of scientific jargon. My background is not in chemical ecology, and I wondered if I would have to think back some years to my graduate teaching assistantship in chemistry to grasp the content of the book. But I need not have worried. As Eisner points out, most species on the planet use chemical means to orient, communicate, and defend themselves, and I was fascinated to read about ants that use formic acid to ward off foes and bombardier beetles that eject defensive sprays as hot as boiling water. Eisner also covers some of the ingenious ways in which insects have evolved to camouflage or confuse their predators, from caterpillars disguising themselves as flowers by fastening petals to their bodies to beetles that use coloration to mimic predatory wasps.

For Love of Insects would add significantly to anyone's understanding of chemical ecology and entomology, including entomologists and chemical ecologists. However, the wealth of knowledge within this book makes it valuable beyond these subjects. I believe this book perhaps one of the best all-around natural history books I've ever read—is a must for any student studying the natural sciences. The scientific method that Eisner describes in such detail shows how biology is a process of trial and error, while his accounts of deriving inspiration not from staying in the classroom or the library but from observing events outdoors demonstrate that the best laboratory researchers are curious investigators who find questions in all natural phenomena. For those who are especially interested, Eisner even suggests topics that beg for further research.

Another stated goal of the book is to change the attitude of entomophobes. This book is not so much about insects as it is about a long journey through the natural world, guided by an inquisitive mind and at times imbued with an

almost childlike sense of delight at the astounding things to be discovered. I think it would be hard for any reader to come away from this book without sharing in the author's sense of wonder at the amazing ways in which insects have evolved to defend, mate, and live.

With fewer and fewer people engaged in the study of biology and natural history, this book could serve to explain to nonscientists why insects deserve respect. Now if we could just make it required reading in all business courses....

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NEW TITLES

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