Genetic Intrigues

Evolution of Social Insect Colonies. Sex Allocation and Kin Selection. ROSS H. CROZIER and PEKKA PAMILO. Oxford University Press, New York, 1996. viii, 306 pp., illus. $70 or £39.50, ISBN 0-19-854943-1; paper, $35 or £19.95, ISBN 0-19-854942-3. Oxford Series in Ecology and Evolution.

Vignette: Natural Languages

Every people thinks its own speech near to nature, since the merest child learns it with ease. Flawless vocabulary and grammar made French the vehicle of Cartesian clarity, its syntax the very mirror of innate infant thought. . . .

Linguistic chauvinism peaked in the 17th century, but similar views remain current. To this day, the writer Franz Stark acclaims German as a "highly precise yet graphic and emotional language of clear and direct expression" and creative force, *the* tongue of science and intellect. Dutch and Portugese speakers boast a range of speech sounds that lets them master any language. English, the current lingua franca, inspires Voltairean accolades. "Our infinitely adaptable mother tongue," intones Simon Jenkins, is globally dominant due not to imperial diffusion but inherent merit—"no clicks, tones or implosives," a phonetic alphabet, creative flexibility: "the sooner the world speaks English, the happier and more prosperous it will be." Thus language seems an inherited blessing unique to us, yet at the same time a nonpareil that others should adopt or emulate.

—*David Lowenthal*, in *Possessed by the Past: The Heritage Crusade and the Spoils of History* (Free Press)

Few things figure big in animal behavior. To meet personal needs, there are food, health, shelter, and sex. Then there is the well-being of other individuals, some of them unrelated, others closely related. That distinction is crucial. Animals generally act more altruistically toward relatives, and are more competitive *vis-à-vis* unrelated individuals. In birds that have helpers at the nest, helpers generally choose to aid close relatives. Ground squirrels are more likely to emit alarm calls to warn relatives. Workers of naked mole-rats and paper wasps work harder when assisting a closely related queen.

As for nepotism, of course, humans are no exception. A brief survey of history—and anyone's daily life—will reveal ample evidence. Nepotism is moreover institutionalized in many laws. In the absence of a written will, for example, the law dictates that property is passed on to the closest relatives. Tax laws reflect relatedness in some countries. In Germany, wealth passed on to close relatives is taxed substantially less than wealth passed on to distant ones.

Why would relatedness matter? And why would naked mole-rats and paper wasps care about closely versus distantly related queens? In *Evolution of Social Insect Colonies*, Crozier and Pamilo provide evolutionary answers to these questions based on the tenets of kin-selection theory. Kin-selection theory proposes that, in a world governed by natural selection, heritable traits are perpetuated not only through the production of offspring but also through the enhancement of the well-being of kin that also carry these traits. Like begets like, therefore, not only directly, by producing descendant copies, but also indirectly, by fostering collaterals. So goes the theory.

Empirically, kin-selection theory has been confirmed in the most diverse organisms, but no group has figured more centrally and more controversially in its development than the social Hymenoptera (ants, bees, and wasps). Because of the genetic quirks of a "haplodiploid" system of sex-determination (males are haploid, females are diploid), workers are more closely related to their sisters than to their brothers, and under some circumstances are more closely related to their sisters than to their own offspring. These unusual relations provide a litmus test for kin-selection theory, because workers should favor their closely related sisters over their own offspring and both of these over their distantly related brothers. This, then, according to the theory, is a genetic *raison d'être* for sociality: Worker behavior evolves because workers are selected to rear their closest relatives, which sometimes happen to be sisters rather than offspring. Also, worker favoritism of sisters over brothers alters the sex ratio, and this, again according to the theory, conflicts with the more balanced sex ratio preferred by the queen. Female-biased sex ratios therefore create a fundamental conflict between queens and workers, yet at the same time facilitate social evolution.

Hence the subtitle "Sex Allocation and Kin Selection" of Crozier and Pamilo's superb book, a much-needed summary of the vast body of literature generated since W. D. Hamilton's seminal work on kin selection 30 years ago. In summarizing the literature, the book is exceptionally complete (close to 700 references are cited). The ground covered is astounding, including detailed treatments of both theoretical and empirical studies on social insects. Crozier and Pamilo themselves have contributed substantially to the field, and it is fair to say that no better team could have tackled the enormous task of writing this book.

Evolution of Social Insect Colonies focuses entirely on the so-called "genetic" factors in social evolution, particularly the interplay between sex ratio and relatedness in modulating social evolution, as well as the various modulators of relatedness such as mating frequency and queen number. In contrast, the book (as the authors admit) gives short shrift to ecological factors that also shape processes of social evolution. Thus it does not resolve the long-standing debate of the relative importance of genetic versus ecological factors in hymenopteran social evolution. But it lays out a convincing case regarding genetic factors. Any future debate now will have to incorporate both genetics and ecology.

Crozier and Pamilo's discussion of theory is at times fairly mathematical, but this should not deter the mathematically illiterate (like me) from reading the book. Though the mathematical arguments require a working knowledge of population genetics, models are carefully embedded in qualitative discussion of biological implications, easily accessible to non-theoreticians. In addition, detailed summaries at the end of each chapter highlight basic issues and broader implications in non-mathematical terms.

Evolution of Social Insect Colonies is the most comprehensive treatment to date of issues of sex allocation and kin selection, starting with Shaw-Mohler's conceptualization of sex-ratio evolution and ending with the most recent developments, such as Boomsma-Grafen's split sex-ratio theory. Thus I recommend the book as an introduction for novices, as well as as a refresher for veterans in the field. It undoubtedly will provide ample inspiration to research on social insects. The numerous tables summarizing parameters from empirical studies will, I predict, stimulate further debate ar-

guing this or that in social insect evolution. In fact, the book is worth buying just for these exhaustive tables.

Overall, then, the book is a tour through the genetic intrigues of social insect life. Readers interested in hard facts will find examples from all the social insects, including not only ants, bees, and wasps but also thrips, termites, and bark beetles. Readers interested in theory will find a guide to relevant models. Readers will come to appreciate how social evolution progresses; which type of insect society can be realized, and which not, by the power of natural selection; whether any such society can be totally free of conflicts or whether the respective interests of workers and queens always remain partially incongruent; and what would happen if social Hymenoptera ever evolved tax laws. For, in the parliament of the hive, workers lobby that drones should be taxed more and females less; while the queen lobbies that drones be taxed like females. The logic behind this may seem as strange as the bickering between Republicans and Democrats (all of them diploids, I think) but undoubtedly is natural to haplodiploid organisms like ants, bees, and wasps.

Ulrich G. Mueller
Smithsonian Tropical Research Institute, Balboa, Republic of Panama, and Department of Zoology, University of Maryland, College Park, MD 20742, USA

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Also Noteworthy

Ship Fever and Other Stories. ANDREA BARRETT. Norton, New York, 1996. 255 pp. $21 or C$27.99; paper, $12.

Books about science are rarely considered for literary awards, but this year the wall has been partially breached with the bestowal of the National Book Award for fiction on this collection of short stories with (in the words of the author) "love of science" as a principal theme. Two of the eight stories in the book have 18th-century settings: "The English Pupil" recounts a visit of the elderly and mentally failing Linnaeus to his country retreat, and in "The Rare Bird" an intellectually lonely and unappreciated Englishwoman finds a kindred spirit with whom she puts to an empirical test (and refutes) an idea about the wintering of swallows dogmatically defended by Linnaeus. The title story, about a typhus epidemic among Irish immigrants to Canada in the 19th century, records some of the uncertainties of the time about the transmission of the disease, another story of that period deals with a would-be naturalist *à la* Alfred Russel Wallace, and an account of Darwin's travels is embedded in a story that the widow of a pharmaceutical executive. These historical recountings are not entirely free of an air of didacticism, and to this reader the most graceful stories in the book are two set in the present day: In "The Behavior of the Hawkweeds" a geneticist's wife recalls her horticulturalist grandfather, who knew Mendel, and "The Littoral Zone" portrays a couple making the best of a costly marriage that had its origins in a marine biology summer course. Present-day science also figures, though not dominantly, in the remaining story in the book, in which the main characters are two sisters who shared a youthful love of biochemistry. These are three of the stories in which the author's other stated concern, "the science of love," is most fully developed.

Katherine Livingston

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Books Received

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Bacterial Adhesion. Molecular and Ecological Diversity. Madilyn Fletcher, Ed. Wiley-Liss, New York, 1996. xii, 361 pp., illus. $95. Wiley Series in Ecological and Applied Microbiology.

Chemical Evolution. Physics of the Origin and Evolution of Life. Julian Chela-Flores and François Raulin, Eds. Kluwer, Norwell, MA, 1996. xiv, 413 pp., illus. $190 or £130 or Dfl. 295. From a conference, Trieste, Italy, Sept. 1995.

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Coulomb Interactions in Nuclear and Atomic Few-Body Collisions. Frank S. Levin and David A. Micha, Eds. Plenum, New York, 1996. xvi, 347 pp., illus. $89.50. Finite Systems and Multiparticle Dynamics.

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Ecosystem Management in the United States. An Assessment of Current Experience. Steven L. Yaffee *et al.* Island Press, Washington, DC, 1996. xx, 352 pp. Paper, $30. A collaborative effort of the University of Michigan and The Wilderness Society.

The Evolution of Modern Human Diversity. A Study of Cranial Variation. Marta Mirazón Lahr. Cambridge University Press, New York, 1996. xvi, 416 pp., illus. $74.95. Cambridge Studies in Biological Anthropology, 18.

Experiments and Observations on the Gastric Juice and the Physiology of Digestion. William Beaumont. Dover, New York, 1996. xl, 280 pp., illus. Paper, $10.95. Reprint, 1833 ed.

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An Introduction to Composite Materials. D. Hull and T. W. Clyne. 2nd ed. Cambridge University Press, New York, 1996. xvi, 326 pp., illus. $90; paper, $34.95. Cambridge Solid State Science.

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Lemaître, Big Bang and the Quantum Universe. With His Original Manuscript. Michael Heller. Pachart, Tucson, AZ, 1996. 108 pp., illus. Paper, $37. Pachart History of Astronomy, vol. 10.

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The Myth of the Framework. In Defence of Science and Rationality. Karl R. Popper. Edited by M. A. Nottur. Routledge, New York, 1996. xiv, 230 pp. Paper, $16.95 or C$23.95. Reprint, 1994 ed.

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Patterns in Evolution. The New Molecular View. Roger Lewin. Scientific American Library (HPHLP), New York, 1996 (distributor, Freeman, New York). x, 246 pp., illus. $32.95. No. 62.

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Prairie Conservation. Preserving North America's Most Endangered Ecosystem. Fred B. Samson and Fritz L. Knopf, Eds. Island Press, Washington, DC, 1996. xii, 340 pp., illus. $50; paper, $28.

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