tion of the adaptive immune system, of which there is definitive evidence, both at the functional and at the molecular level, in the cartilaginous fish (sharks, skates, and rays). The lamprey and the hagfish are the only two living representatives of the earliest vertebrate class to arise in evolution, and they have failed to yield any indication of an adaptive system built around T and B lymphocytes. Taking into consideration all of the data from the vertebrate and protovertebrate taxa, Smith and Davidson argue that it is unlikely that the adaptive immune system arose *in toto* early in the vertebrate line; they suggest that, like most other physiological systems, the immune system was built bit by bit, with innovations being maintained and subjected to selection as vertebrates became more complex. Whether this supposition is correct or not, it provides a framework for comparative immunologists to position new findings. I personally believe that most of the fundamental signatures of the adaptive immune system emerged in concert, since shark antigen receptor genes undergo rearrangement and somatic mutation and polymorphic major histocompatibility antigens are expressed in a fashion similar to that of mammals.

Those sections of the book that combine the theoretical with the experimental are the most engaging. Chapters on the evolution of the thiol-ester bond, phagocytosis and opsonization, and invertebrate cytokines are particularly informative, especially when comparisons with similar mechanisms in vertebrates are made. One gets the impression that most of the background players that interact with the adaptive immune system arose early in evolution, that is, the Pips, representing an assortment of nonadaptive immune mechanisms, antedated Gladys Knight, symbolizing lymphocytes expressing immunoglobulins and T-cell receptors; the collaboration that ensued is arguably as successful for the immune system as "Midnight Train to Georgia" was for G. K. and the Pips.

What are the origins of the adaptive cellular immune system? Until recently the best model in invertebrates has been a polymorphic histocompatibility system in tunicates that regulates the rejection of genetically disparate colonies. However, vertebrate histocompatibility molecules apparently did not evolve their high level of polymorphism for direct recognition by receptors on lymphocytes but rather for the intracellular acquisition of peptides with diverse sequences; that is, rejection of allogeneic grafts in vertebrates is non-physiological and apparently covergent with the tunicate rejection process. However, a nonadaptive cell-mediated response in vertebrates is performed by natural killer (NK) cells that seemingly scan the body for the *absence* of self-histocompatibility markers. Such a mechanism is suggested in this volume for the colonial tunicates and sponges. Further, the molecules on vertebrate NK cells mediating the recognition process may be C-type lectins, a phylogenetically old and diverse family that is reviewed in detail here. Identification of the receptor-ligand pairs involved in the histocompatibility reactions of invertebrates is needed to judge whether they indeed are forerunners of those used by the vertebrate recognition system.

The book is subtitled "Foundations for the Vertebrate Immune System." Those mechanisms that have been preserved and modified in vertebrates are well portrayed. However, when and how the adaptive immune system arose with its hallmarks of gene rearrangement, epigenetic tolerance induction, and memory sustained by somatic mutation of antigen receptor genes remains obscure. This book does not (and cannot) provide the answers to this last question, but it certainly presents a wealth of information useful for anyone who is curious about the evolution of immunity.

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## Vignettes: Electronic Transformations

The mysteries of religious dogma have throughout history been managed by various tightly knit priesthoods of custodians, regardless of time, culture, or place. What [the availability of the] computer-aided analysis [of the Dead Sea Scrolls] has done . . . is to strike a blow for accessibility and freedom of access to religious information. The silent electronic servant may be as potent a religious force as the Protestant reformer Martin Luther, who posted his 95 Theses "for the purpose of eliciting truth" on the door of All Saints Church in Wittenberg on October 31, 1517.

—*Anne Wells Branscomb*, in *Who Owns Information? From Privacy to Public Access* (BasicBooks)

Similar to the way previous media dissolved social boundaries related to time and space, the latest computer-mediated communications media seem to dissolve boundaries of *identity* as well. One of the things that we "McLuhan's children" around the world who grew up with television and direct-dialing seem to be doing with our time, via Minitel in Paris and commercial computer chat services in Japan, England, and the United States, as well as intercontinental Internet zones like [Multi-User Dungeons], is *pretending to be somebody else*, or even pretending to be several different people at the same time.

—*Howard Rheingold*, in *The Virtual Community: Homesteading on the Electronic Frontier* (Addison-Wesley)

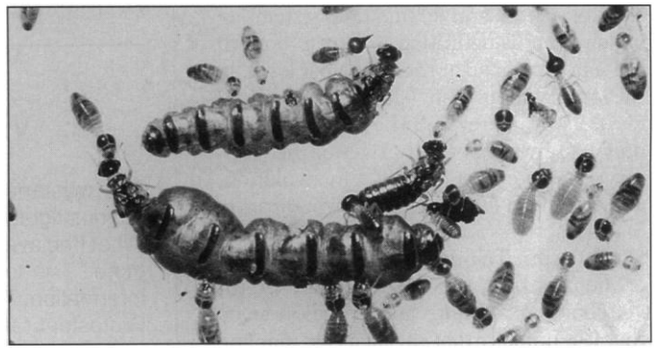
## The Second Sociality

**Queen Number and Sociality in Insects.** LAURENT KELLER, Ed. Oxford University Press, New York, 1993. xii, 439 pp., illus. $75 or £50.

It probably appears an annoying distraction to many that many social insects have many queens per colony and that these may all be fertile. The textbook picture of single-queen colonies enables one to understand the evolution of eusociality, namely that form of sociality characterized by reproductive self-sacrifice, castes, and relatively greater longevity of the reproducing females. But we should be ready to take on new complexities now that we understand that kin selection is indeed the engine that, without exception, drives all models for the evolution of eusociality and that male haploidy (the genetic system in which males arise from unfertilized eggs and are haploid), through its effects on sex allocation, indeed promotes the evolution of eusociality.

The occurrence of many queens per nest has been called (originally by Rosengren and Pamilo) the "second sociality" and poses its own problems. After all, given that kin selection drove the evolution of eusociality in the first place, how can selection of any kind favor the addition of further queens to a colony, which dilutes the relat-

edness ties that bind the group together? This is the story of the book under review, a notable collection of theoretical and empirical studies providing an authoritative and readable entry to a field at the cutting edge of evolutionary biology.



"Two queens and one king from a small nest of *Nasutitermesnovarum hebridarum*. Of 44 nests of this species dissected, this was the only one containing more than one queen. The queens' weights were, respectively, 0.20 and 0.10 g. Since weight ratios between coexisting queens are usually close to unity in termites . . ., the high weight ratio recorded here could indicate that the smaller queen was on the way to elimination to the benefit of the larger one." [From Y. Roisin's paper in *Queen Number and Sociality in Insects*]

But what are queens? As discussed by Keller and Vargo, a functional definition, the queen as mated egg-layer, would enable all students of eusocial species to talk of their species' having queens, because in primitively eusocial species queens and workers are morphologically the same. However, a morphological definition copes better with the complex diversity of ant life patterns. Clearly not everyone will be happy with the same definition, and the consistent use of inconsistent concepts will persist.

The nature of queens can be considered in another setting. The royal connotation of the term invokes a picture of control, yet this could only be true for small colonies where a queen's dominance activities directly influence other individuals (Heinze). For large colonies the wisdom of Proverbs 6 holds, that the worker lacks "chief, officer or ruler": the queens' signals are just that, with the workers responding adaptively to them. This view gives a fresh slant, for example, on the use by honeybee queens of a pheromone to label their eggs, which enables workers to recognize and destroy the eggs of other workers (although they are not perfect at it, as Page and Erikson have documented). This case exemplifies the social insect colony as rife with both competition and cooperation but raises the additional question of why selection doesn't favor workers' using the same pheromone. The answer might be an increased cost of intra-colony conflict, as has been suggested by Cole (1986), Ratnieks (1988), and Pamilo (1991), if worker egg-laying is uninhibited.

Polygyny cannot be understood without recourse to ecological conditions, determining the cost-benefit parameter of Hamilton's rule. In this context, group-level selection is a theme throughout the book. In many ant species several queens associate to found a colony. When the first workers emerge, all queens save one are eliminated. Solitary queens are much less successful than groups at colony foundation, so that even though most cofoundresses do not survive colony-founding it still pays to join. For established colonies, the same principle holds for at least some species; nests of the ant *Leptothorax longispinosus* that have two or three queens have higher survival over winter than nests with one or none (Herbers).

If dispersal is sufficiently hazardous then selection may favor daughter queens' rejoining their original colony. Selection may favor a queen's joining, but may not favor her being admitted by all groups in the colony. The colony comprises groups differing in genetic interests, and it is risky to think of a unified colony response. Where conditions favor the workers' allowing a queen to join, it becomes increasingly pointless for resident queens to resist a newcomer the more residents there are. Hence the many hundreds of queens in some *Formica* colonies (Rosengren *et al.*), little if at all related, reflect a runaway process of queen admittance. Thus, polygyny involving small numbers of queens (usually related) differs in more than just degree from polygyny involving large numbers.

The colony as a field of competition yields other surprises. Why do fire-ant queens (Keller and Vargo) produce pheromones inhibiting each other's reproduction? The pheromone is not aimed at workers, because these have no ovaries to be suppressed. Does producing this pheromone confer some resistance to it, so that the pheromone is a competitive device between queens? If not, queens would save energy if they did not produce the pheromone. One concludes tentatively that queens have been selected to maximize their numbers while keeping egg production under control.

The book is well produced. All the chapters were reviewed before publication; all have summaries, and there is a glossary to assist neophytes. In the first chapter Seger lightly sketches the ecological theater for the sociobiological play. Reeve and Ratnieks discuss the bribes (in reproduction) necessary to induce subordinate queens to

stay, Boomsma the effects of variation in queen number on colony sex allocation, Nonacs polygyny and life history parameters, and Queller the estimation of relatedness between lineages within colonies. The natural history background is covered for highly eusocial (Hughes *et al.*, Peeters, Herbers, Elmes and Keller, Rosengren *et al.*, Heinze, Carlin *et al.*, and Roisin, the last contributing the only non-Hymenoptera chapter) and primitively eusocial species (Itô, Gadagkar *et al.*, Packer).

Evolutionary biology stresses extrinsic factors molding the characteristics of organisms—that is what selection and adaptation are all about, hence the ecological slant here. And yet molecular biology has important contributions to make here too. Queller notes that new molecular markers enable many more questions to be answered than hitherto, as demanded by insatiable theorists. Polygyny also affects caste-determination, as shown by changes in the relative sizes of queens and workers, so that it would be cogent for polygyny researchers to ask about the evolving thresholds for queenness and about genes active in one caste but not another. What about the impact of selfish genetic elements, which are potentially more important in polygyny than under monogyny? The games-theoretic approach may be incomplete without attention to such factors, and to possible constraints.

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## Books Received

**Ancient DNA**. Recovery and Analysis of Genetic Material from Paleontological, Archaeological, Museum, Medical, and Forensic Specimens. Bernd Herrmann and Susanne Hummel, Eds. Springer-Verlag, New York, 1994. xii, 263 pp., illus. Paper, $34.95.

**The Butterflies of the West Indies and South Florida**. David Spencer Smith, Lee D. Miller, and Jacqueline Y. Miller. Richard Lewington, illustrator. Oxford University Press, New York, 1994. x, 264 pp., illus., + plates. $125.

**Control of Spacecraft and Aircraft**. Arthur E. Bryson, Jr. Princeton University Press, Princeton, NJ, 1994. xxvi, 378 pp., illus. $55 or £35.

**Design Paradigms**. Case Histories of Error and Judgment in Engineering. Henry Petroski. Cambridge University Press, New York, 1994. xii, 209 pp., illus. $42.95; paper, $17.95.

**Empirico-Statistical Analysis of Narrative Material and Its Applications to Historical Dating**. A. T. Fomenko. Kluwer, Norwell, MA, 1993. 2 vols. Vol. 1, The Development of the Statistical Tools. xxii, 204 pp., illus. Vol. 2, The Analysis of Ancient and Medieval Records. xiv, 455 pp., illus. The two, $282 or £186 or Dfl. 465. Translated from the Russian.

**Galileo**. For Copernicanism and for the Church. Annibale Fantoli. Vatican Observatory Publications, Vatican City State, Rome, 1994 (U.S. distributor, University of Notre Dame Press, Notre Dame, IN). xx, 540 pp., illus. Paper, $21.95. Studi Galileiani, vol. 3. Translated from the Italian edition by George V. Coyne.