

BOOK REVIEWS

Ants on the Run

Army Ants. The Biology of Social Predation. WILLIAM H. GOTWALD, JR. Comstock (Cornell University Press), Ithaca, NY, 1995. xviii, 302 pp., illus., + plates. \$39.95 or £31.50. Cornell Series in Arthropod Biology.

Army ants have long enjoyed an exaggerated reputation for ferocity, perhaps no better exemplified than in Carl Stephenson's classic story, "Leiningen versus the Ants," in which a Brazilian plantation owner—later played by Charlton Heston in the movie adaptation, *The Naked Jungle*—attempts to fend off a ravenous horde: "Ten miles long, two miles wide—ants, nothing but ants! And every single one of them a fiend from hell." In his engaging but more objective account, William Gotwald demonstrates that hyperbole is hardly necessary—mythology aside, army ants provide one of the more intriguing spectacles of social life in the insect world.

A key trait of the "true army ants" (members of the subfamilies Aenictinae, Dorylinae, and Ecitoninae) is their mobilization of large numbers of workers during the search for prey, as distinct from the initiation of mass recruitment after food has been located, a much more common occurrence in ants. In consequence they are able to prey upon large arthropods, social insect colonies, and even the occasional small vertebrate. So efficient is this group predation that local resource depletion occurs, and army ants are notable for their high frequency of colony movement. In the more derived species such emigration is cyclic and closely synchronized with the stages of brood development. Army ants have also

achieved enormous colony sizes, exceeding a million workers in some species, all issuing from a single, wingless and grotesquely modified queen. Colony division involves a complicated form of fission or budding, which leads to intranidal conflict over the survival and reproduction of queens and to peculiar selection pressures on dispersing males, who must breach a barrier of alien workers in order to gain access to a mate. Finally, there is a remarkable retinue of symbionts—including mites, millipedes, beetles, flies, and antbirds—that have evolved to exploit various resources associated with army ant colonies, and many of these symbionts have become obligate camp-followers.

Such striking biological phenomena provoke fundamental questions about the functional organization of army ant colonies, the ecological effects of their depredations, and the evolutionary origins of army ants and their associated fauna. Gotwald does an excellent job of summarizing the existing state of knowledge, and he presents useful introductions to some of the general issues that arise from a consideration of group predation by social insects. His coverage of foraging behavior, colony emigration, and the natural history of army ant guests and predators is particularly detailed. Topics with an evolutionary flavor, such as the phylogenetic relationships between army ants and their allies and the operation of kin selection during colony fission, are given less satisfactory treatment. Speciation and coevolution, processes of potential interest in organisms with an army ant life-style, receive almost no mention.

As Gotwald emphasizes, most informa-



"A stinkbug attempts to escape a driver ant attack by climbing vegetation [top]. Although the stinkbug releases a defensive secretion, the ants are not deterred [center] and soon overwhelm it [bottom]." [From *Army Ants*]

tion on army ants comes from studies on a handful of large and conspicuous species that forage above ground. The vast majority of the 300-odd known species are small, elusive, subterranean ants, and we remain profoundly ignorant about most aspects of their biology. There are also significant gaps in our systematic knowledge of these ants. For the Old World taxa, on which Gotwald's work has focused, we lack even a serviceable species-level taxonomy, and for both the Old and the New World army ants there is no robust phylogenetic framework for the comparative analysis of biological traits. Even such a fundamental question as whether the three subfamilies of army ants constitute a monophyletic group remains unresolved. Gotwald suggests that they are polyphyletic, but it is a vague assertion unaccompanied by a specific hypothesis of relationships. Some recent cladistic studies, which Gotwald cites briefly, tend to support the opposite conclusion.

Noting the convergent development of group predation and nomadism in several other ant taxa besides the true army ants, Gotwald argues that the army ant adaptive syndrome is "enormously successful." To make a proper historical assessment of this claim, however, we need to know how many times the constellation of army ant



"Although driver ant foraging columns may be relatively small [as at left], it is not unusual for raiding columns to achieve a density of 13 individuals per square centimeter [right]." [From *Army Ants*]

traits has arisen and to compare the success of these lineages with that of their sister groups. The relevant phylogenetic tests have not been carried out, but it seems quite possible that the army ant groups are no more successful, with respect to net diversification (that is, contemporary species richness), than their generalist sister groups. If success is measured in terms of ecological dominance, then the true army ants are demonstrably important in many tropical and subtropical habitats, but the other groups—the army ant “wannabes”—are more limited in distribution, diversity, and abundance, and their ecological significance remains unclear.

The book concludes with an appeal for increased efforts toward conservation of tropical ecosystems where most army ant species—and biological diversity in general—reside. Despite their large colony sizes and seeming invincibility, army ants and their obligate symbionts are especially vulnerable to habitat fragmentation. This is because population (as opposed to colony) sizes are rather low and because the queens, as wingless individuals reproducing by colony fission, are very poor colonizers of isolated pieces of landscape. In reality, our rampages endanger army ants much more than their activities pose a threat to human life or limb.

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The WAM Report

Dynamics and Modelling of Ocean Waves.

G. J. KOMEN, L. CAVALERI, M. DONELAN, K. HASSELMANN, S. HASSELMANN, AND P. A. E. M. JANSSEN. Cambridge University Press, New York, 1994. xxii, 532 pp., illus. \$59.95 or £40.

That water waves are generated by wind was known to the ancients and proclaimed by such polymaths as Leonardo da Vinci and Benjamin Franklin, but scientific prediction of these phenomena has been attempted only in the past 50 years. The complete problem comprises two, essentially distinct parts: the prediction of the wind field, which is the province of meteorologists, and the prediction of the resulting response of the ocean surface, which is the province of oceanographers. The present monograph, which appears as the final report of the WAM (Wave Modelling) group, provides a state-of-the-art survey of the latter problem. The title page lists six authors,

but 35 scientists from 12 nations are listed as “contributors” and the WAM-group list comprises 71 individuals. This is manifestly an international effort.

The first predictive model, developed by Sverdrup and Munk (1943–1947) in response to the need for sea and swell forecasts for the Allied invasion of North Africa, was based on empirical relations between characteristic parameters of the wave and wind fields and antedated the statistical description of the problem by Pierson, Neumann, and James in 1955. The starting point for subsequent models, including those covered in the volume under review, is the Boltzmann-like transport equation.

$$\frac{\partial F}{\partial t} + \mathbf{v} \cdot \nabla F = S_{in} + S_{nl} + S_{ds},$$

which governs the evolution of the surface-wave field in space ($\mathbf{x}$) and time (t); $F = F(f, \theta; \mathbf{x}, t)$ is the two-dimensional spectral density in frequency f and direction of propagation θ , $\mathbf{v} = \mathbf{v}(f, \theta)$ is the group velocity, S_{in} is the input from the wind, S_{nl} is the nonlinear transfer through wave interactions, and S_{ds} is the dissipation. This approach became practical only in the early 1960s with the theoretical studies of Phillips (1957) and Miles (1957), which provided a basis for the representation of S_{in} , and the discovery of resonant interactions by Hasselmann (1960) and Phillips (1960), which provided the basis for the representation of S_{nl} ; the representation of S_{ds} was, and remains, empirical, with turbulence as an ineluctable antagonist.

Models based on the equation given above have been described as first-, second-, or third-generation, in which nonlinear interactions are, respectively, neglected, described in simplified parametric form, or incorporated within the limits of current knowledge and computing power. First-generation models failed to describe the nonlinear transfer of energy from higher frequencies, where wind generation is more efficient, to lower frequencies, where dissipation is weaker, and yielded rather misleading results. Second-generation models, which incorporated these effects, although not always successfully, were described in *Ocean Wave Modeling* by the SWAMP (SeaWave Modelling Project) Group, which I reviewed in *Science* (229, 377) in 1985 with the conclusion that “Future (‘third generation’) models, already under development, will incorporate more sophisticated parameterizations of S_{nl} and may exploit our theoretical knowledge to its present limits, after which the lack of a rational model of dissipation and the effects of finite, variable depth are likely to present barriers to further progress.”

The present volume fulfills that promise,

and, although the barriers remain, they may now be better described as impediments. Moreover, whereas the SWAMP book was primarily a progress report on second-generation models, Komen *et al.* provide full expositions of the basic fluid dynamics, numerical modeling, and incorporation of global satellite measurements. The development is not seamless, but, considering the number of contributors, the principal authors have done an admirable job of assembling a coherent whole and of providing a firm base for the exploration of the many challenging problems that remain.

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Visual Perception

Image and Brain. The Resolution of the Imagery Debate. STEPHEN M. KOSSLYN. MIT Press, Cambridge, MA, 1994. x, 516 pp., illus. \$45 or £38.50.

Kosslyn's *Image and Brain* is a *tour de force* in the analysis of visual perception and imagery, looked upon from all possible perspectives. It is an examination of work done during the past 15 years on visual imagery by a variety of methods, from chronometric measurements to computer models to functional brain imaging, bringing a systematic approach to bear on this multitude of data to delineate the issues of brain mechanisms underlying visual perception and imagery. The scheme adopted posits a number of systems and subsystems (for example for edge detection and for encoding motion relations) that process specific kinds of information and that together make for an apparently seamless operation of visual perception and imagery. This analytical approach is open-ended, in the sense that more processing stations can be added if need or evidence for them arises; it is flexible, so that rearrangements in processing order are allowed for; and it is powerful, so that it can be applied rigorously to complex data. The net result is a coherent theory of visual perception and imagery in which results obtained by a diversity of methodologies—observations in normal and brain-damaged people, neuroimaging, neurophysiological experiments, and computer modeling—can be accommodated and used to explore and fill in gaps in our account of observed phenomena. This calculus of processes, as it were, that Kosslyn develops can be applied to diverse situations. An excel-