Book Reviews

A Physiological Ethology

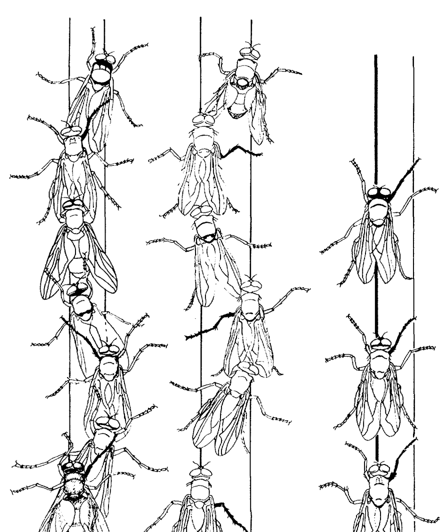
The Hungry Fly. A Physiological Study of the Behavior Associated with Feeding. V. G. DETHIER. Harvard University Press, Cambridge, Mass., 1976. xiv, 490 pp., illus. $30. A Commonwealth Fund Book.

All creatures face the task of sustaining their existence until they can reproduce. Flies, as we all know, are annoyingly successful at this endeavor. For them, feeding has three stages: search, sample, and eat. In the first phase the insect flies about at random until it smells something attractive, and then tracks the odor upwind until it lands nearby. It then walks about until it steps into a potential food source. If all goes well, the fly will lower its proboscis, taste the food, and decide whether to imbibe. If the food is judged edible, pumping begins and continues in bouts until the fly ceases feeding altogether and departs.

According to Konrad Lorenz (*1*), the study of feeding, like that of any other behavior, must be either ethological or behavioristic. Lorenz accuses behaviorists of treating animals as "black boxes," studying "input" and "output" and attempting to relate them through "laws" of behavior. This approach has proved especially tempting in the case of feeding, perhaps because the "input" is so easily weighed and quantified. Behaviorist models of feeding generally invoke several imagined processes to link the stimulus and response. The most suspect of these pieces of conceptual baggage is "motivation," a fudge factor too often used to account for any discrepancy between the expected and the observed.

In his elegant studies of blowfly feeding, Vincent Dethier rejected such traditional exercises in "explanation through naming" as "adding nothing to our understanding" and became the first scientist to choose the ethological approach, defined by Lorenz as requiring that a behavior be observed as a whole and then dissected into parts for analysis. As *The Hungry Fly* makes clear, this approach has worked well for Dethier. Perhaps this is because the feeding system of the blowfly can be (quite literally) dissected into isolated but functionally normal pieces.

The ethological approach usually begins with detailed observation of the animal in its natural habitat. In the case of the ubiquitous blowfly, however, virtually nothing relevant is known (or, in practice, can be known) about the natural history. Dethier had to be content to begin by observing the animal in artificial situations. He therefore had to ignore for the most part the animal's airborne search behavior and concentrate on an accurate description of the walking search, sampling, and eating behaviors. Here he found at least initially useful the classical ethological terminology of releasers, fixed action patterns, action specific energies, and so on. In these studies, persuaded by Tinbergen's "experimentation is necessary" approach (*2*), Dethier developed many elegantly simple behavioral tests, rivaling even those of von Frisch.



"The walking behavior of a fly in the presence of two parallel lines of solution. In the left and middle pairs the concentration of sugar is the same in both tracks. In the right pair the right track is more dilute than the left. The fly walking the middle paired tracks has had the prothoracic legs removed. Note the greater width between the lines. In each case the black leg indicates that the fly has encountered a line different from the one where it is eating at the time." [From *The Hungry Fly*]

By the early 1950's, however, purely behavioral analysis had become unrewarding. With feeding behavior thus broken into separate stages, Dethier began to inquire into the physiological basis of each Lorenzian "part." This insistence on further analysis reflects the rare view that Lorenz's parts are merely smaller black boxes, the naming of which explains nothing. Dethier chose electrophysiology as the primary technique by which to continue the search, and decided to concentrate on what the chemoreceptors tell the blowfly brain and how the fly decides when to begin and when to stop eating.

Then as now, electrophysiology and complicated behavior are rarely compatible subjects for study. Animals with large, identifiable, and easily penetrated nerve cells typically have little in the way of interesting behavior to recommend them [though Gelperin's discovery (*3*) of food avoidance learning in slugs points to a prominent exception], while animals with substantial behavioral repertoires seem invariably to have tiny nerves packaged and positioned in the least convenient ways imaginable. Hence, studies that have sought to combine ethology and electrophysiology have most often been unstable compromises with a pronounced tendency to become purely the one or the other. Dethier not only pioneered the integrated approach, he successfully maintained this unusual and difficult balance by restricting himself primarily to the blowfly's peripheral nervous system—chemoreceptors and proprioceptors for the most part.

Beyond the obvious technical difficulties inherent in neurophysiological studies of insects, Dethier was the first to discover the two major limitations of an electrophysiological ethology: thresholds and road maps. When measuring thresholds, we expect the receptor to be a more sentitive indicator than behavior. Just as often, however, the opposite is true. In the blowfly, for example, the salt receptor can just detect $0.1M$ NaCl. The whole fly, on the other hand, responds to $10^{-4}M$ NaCl. Clearly our electrodes are missing something, and we suppose that the answer must lie in the wiring, in the integration of receptor input. This brought Dethier to the other major limitation: deducing function in simple nervous systems from road maps of the nerves. Brenner's attempt (*4*) to understand how a nematode can do all it does with 260 nerves is a recent example of the optimism with which such studies often begin. Dethier wonders with characteristic wry self-criticism "how it is that the so-called simple nervous system is able to accomplish so much, or, an equally reasonable puzzle, why nervous systems with millions of cells do not accomplish more."

Dethier's work has not only isolated the difficulties of the electrophysiological approach to ethology, it has also provided the most encouraging signs of ultimate success. Although the chemoreceptor code remains largely unbroken, the details of the ingenious circuits by which the fly controls feeding have been worked out. The most significant of these, discovered by Dethier's student Alan Gelperin, turns feeding on and off according to the output of stretch receptors spanning the crop and foregut (*5*). This *lac* operon of behavior remains the outstanding example of the physiological basis of a behavior.

In looking to the future, Dethier predicts that the most rewarding problems will be those of "specific hunger" and learning. By specific hunger, Dethier means the ability of the blowfly to alter its preference for carbohydrate over protein as egg laying approaches. He expects that another elaborate operon will be found, this time involving the added dimension of hormonal feedback. With regard to learning, he is less enthusiastic. Dethier points out that learning in blowflies is weak (indeed, why do they need to learn at all?) and suggests that they may be deliberately dumb, having "lost the ability to learn . . . in the interests of parsimony." In any case, the success of Quinn *et al.* (*6*) in conditioning *Drosophila* to odor and color, in demonstrating both long-term and short-term memory, and in obtaining mutants blocked in both phases makes a shift away from the blowfly inevitable.

Although Dethier says *The Hungry Fly* is "a book to be enjoyed," it is not a revised edition of his earlier and very entertaining *To Know a Fly* (*7*). Though wittily written, it depends too much on physiological details and methodology to make for light reading. Nor is *The Hungry Fly* merely a summary of the current state of the field, or a source book on feeding and blowfly physiology, though it fills each of these needs. Rather, it is Dethier's personal history of how we came to know what we now think to be true. It is an exciting and fascinating story in its own right, told intelligently and humorously by the pioneer of the physiological approach, and as such is of enduring value.

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Memoirs

Adventures of a Mathematician. S. M. ULAM. Scribner, New York, 1976. xii, 318 pp. + plates. $14.95.

It was inevitable that S. M. Ulam would tell his story. A native of Lwów, Poland, he was a member of its distinguished school of mathematics; later studies and global events led to a series of residences spanning two continents, and his scientific interests spread into physics and then into mathematical biology. Such activity implied, of course, a host of new colleagues. A conversationalist of first magnitude with ample scientific curiosity, Ulam would have much to write. Apart from the time it would take away from scientific meditation, the only real obstacle to the realization of the *Adventures* would be his general impatience. The storyteller, fortunately, has prevailed.

The present volume belongs to a relatively new genre that attempts to get behind the scenes to describe some of the idiosyncrasies, the weaknesses, and the strengths of segments of the scientific community. Laura Fermi's delightful book *Atoms in the Family* is exemplary; she has provided one perspective on researchers' lives outside the laboratory, thereby partially satisfying the public curiosity rendered acute by the relatively recent glitter of science. A companion volume to this is Emilio Segrè's *Enrico Fermi, Physicist*, which is along more traditional lines but has the sparkle derived from the writer's "being there" as a collaborator over an extended period, starting from earliest times. A somewhat different, in parts more specialized, approach is taken in James Watson's famous dramatization of the events leading to one of the great discoveries in biology, *The Double Helix*. Ulam reaches for all three objectives: to describe some of the nontechnical background in several scientific fields; to sketch a few biographies; and to summarize some developments in mathematics and thermonuclear physics. The reader is made privy to the ambitions, frustrations, successes, and bits of professional gossip associated with an interesting collection of superior minds.

The *Adventures* form a natural sequence of four parts: the early years as a student, then the postdoctoral phase and academia in America, followed by the extended Los Alamos period, and, finally, back to the university in 1967.

Most scientists are aware of the brilliance emanating from Budapest in the 1920's and early 1930's created by Szilard, Teller, von Neumann, and Wigner. But except among their confreres, the Polish school of mathematics, developed at Lwów and Warsaw, has until now remained relatively obscure. Ulam is changing all that, and such names as Banach, Kuratowski, Mazur, Sierpinski, and Steinhaus, along with Tarski and Kac, who immigrated here, will begin to have a more familiar ring. It was probably Stefan Banach who, in that formative period, played the central role for the budding mathematician Ulam, whose *modus vivendi*, but for imminent events that were to upset the great globe itself, might well have been *otium cum dignitate*.

The American scene for Ulam is identified with John von Neumann. It was von Neumann who arranged an invitation for Ulam to Princeton's Institute for Advanced Study, thus continuing a series of meetings, started in Europe, that was to lead to a deep friendship. Eight years later, it was von Neumann who suggested to Ulam the possibility of participation in the Los Alamos venture. The wartime period was, strangely enough, a relatively quiet time for the mathematician slowly turning physicist without abandoning his love for abstract mathematics. The war over, Ulam had a brief interlude at the University of Southern California (and an episode of near tragedy) before returning to Los Alamos to renew acquaintance with Enrico Fermi and, of more interest, Edward Teller. Some commentary is given on the Teller-Ulam collaboration in thermonuclear studies. Because the work is classified the reporting is necessarily of a peripheral nature and does not provide much illumination concerning the contributions of each. Later historians may obtain a clearer picture.

Ulam has a feeling for words, and they reveal an intense compassion on exceptional occasions. Perhaps the most moving descriptions are the accounts of last visits with Fermi and with von Neumann, which remain vivid more than two decades later. The last chapter, "Random reflections," will be of particular in-