Identifying Relatives

Kin Recognition. PETER G. HEPPER, Ed. Cambridge University Press, New York, 1991. xii, 457 pp., illus. $89.50.

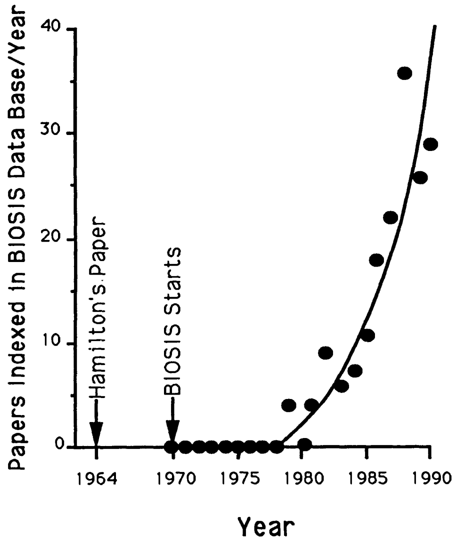
Kin recognition is the ability to identify relatives. Few topics in animal behavior have stirred greater interest and debate in the past decade. Although mechanisms of parent-offspring recognition have been studied for at least 50 years, the recent surge of interest in kin recognition stems from two conceptual advances, inclusive fitness theory (mainly) and optimal outbreeding theory, both of which predict that organisms should recognize collateral relatives as well as descendants. Investigators around the world have looked for—and found—the anticipated recognition abilities in multiple vertebrate and invertebrate taxa, and across the spectra of social and cognitive complexity, from honey bees and humans to tunicates and toads.

This book comprises 14 review chapters that examine the mechanisms, ontogenies, and ecology of kin recognition. The focus is clearly on vertebrates (11 chapters), especially mammals. Parent-offspring and sibling-sibling recognition receive about equal treatment, in the contexts both of dispensing nepotism and of avoiding close inbreeding.

The opening chapters discuss nepotism in primates (I. S. Bernstein) and mutualism in birds and mammals (J. D. Ligon). Subsequent chapters deal more specifically with evidence for kin recognition and its possible adaptive significance in four model systems: ants and social wasps (P. Jaisson), amphibians (B. Waldman), honey bees (W. M. Getz), and humans (R. H. Porter). These are supplemented by three conceptually oriented chapters on classifying ontogenies of kin recognition (P. G. Hepper), processes producing kin-biases in mate choice (C. J. Barnard and P. Aldhous), and limitations of parent-offspring recognition (M. D. Beecher). Unique to this book are analyses of how mammalian kin recognition is affected by learning *in utero* (S. R. Robinson and W. P. Smotherman), filial imprinting (M. H. Johnson), and parental motivational states (R. W. Elwood). Rounding out the volume are discussions of genetic (E. A. Boyse *et al.*) and chemical (Z. T. Halpin) cues used in vertebrate kin recognition.

Several hotly debated issues in kin recognition, including why such behavior occurs, are addressed by the contributors. Kin-biased behavior is often assumed to indicate both that an animal can recognize relatives and that selection favoring discrimination of different degrees of kinship produced such behavior. However, as Barnard and Aldhous point out, in agreement with A. Grafen (*Anim. Behav.* **39**, 42 [1990]), kin-biased behavior does not necessarily imply that selection has favored discriminating kinship *per se*. Instead such behavior may be an incidental effect of habitat, species, or group-member identification. For example, some anuran tadpoles associate with any conspecifics, including kin, that smell like the natal site; remaining near home, rather than associating with kin, is apparently the selective basis for this discrimination. Clearly, whether or not an organism treats kin differently from nonkin is a separate issue from the evolutionary reasons it does so.

Waldman effectively disentangles these two issues. He reviews evidence that amphibians discriminate relatives and examines data supporting three possible selective benefits of such behavior. First, certain species are poisonous, and tadpoles may gain from schooling with similar-looking and equally foul-tasting siblings. Second, abilities to recognize kin can promote outbreeding. Finally, preferential association with related tadpoles enhances growth rate, resulting in a larger fraction of the clutch reaching metamorphosis. Waldman's chapter is also useful because it indicates how little we know about the functions of amphibian kin recognition in nature, emphasizing the importance of obtaining such information.



The birth and early growth of a field. The number of published papers or abstracts with "kin recognition" or "recognition of kin" in the title (dots) has approximately doubled every three years (curve) since the first papers on this topic were published, in 1979. W. D. Hamilton's paper (*J. Theor. Biol.* 7, 1 [1964]) initiated inclusive fitness theory. The graph is based on a computer search of the BIOSIS Previews data base.

Even failures of kin recognition can illuminate its adaptive significance. For example, although extra-pair matings and parasitism in birds frequently result in broods of mixed relatedness, parents have not been shown to distinguish their own from alien young in the nest. To understand why, Beecher partitions kin recognition into four component processes: *production* of a signal by a sender, *perception* of that signal by a receiver, *decision* by the receiver as to the appropriate response, and *implementation* of that response. Echoing a theme of H. K. Reeve's (*Am. Nat.* **133**, 407 [1989]), Beecher suggests that absence of discrimination might not indicate perceptual failures so much as conservative decision-making: a parent might be pretty sure that an offspring is not its own, but not certain enough to reject it. The youngster, in turn, should not "honestly" signal its identity to a nonparent. Parents can tolerate such a lack of cooperation and the resulting errors "so long as the benefit of a feeding times the probability of a correct feeding exceeds its cost" (p. 121).

Additional chapters provide evidence bearing on the debate over whether individuals learn the mental image or "template" on which kin recognition is based from their environment, close associates such as family members, or themselves. Apparently all three occur; for example, social wasps learn to recognize as nestmates conspecifics who smell like the plant fibers from their natal nest; inbred mice learn the major histocompatibility complex genotypes of family members and base mate choices on those cues; and honey bees learn recognition cues from both their nestmates and themselves.

In fact, Getz's detailed chapter on the complex and fascinating kin recognition mechanisms of honey bees is a highlight of the book. Worker bees are predicted to make two types of discriminations: among hives, to repel honey robbers from foreign colonies, and within hives, since individuals could be either full or half sisters to future queens they help rear owing to multiple mating by the mother queen. Self-referent phenotype matching would allow discrimination among nestmates. Indeed, worker honey bees "retain a sense of self, despite the fact that they also learn and use the signatures of their nestmates for kin discrimination purposes" (p. 392). It will be interesting to see if a self-inspection mechanism also characterizes other social species in which females mate multiply, as well as interspecific parasites. Cowbirds and cuckoos, for example, could recognize conspecifics on the basis of resemblance to themselves, but not to nestmates.

This book updates an exciting and fast-moving field. It should appeal to a broad range of biologists and psychologists. The volume's strengths are its conceptual orientation and multiple investigative approaches. Its primary weakness, apart from some unevenness of quality, is its failure to integrate the widely disparate subject matter and to synthesize this information into a unified framework—a synthesis the field needs at this point. Overall the book should stimulate work on key questions surrounding kin recognition, not the least of which is why such phenomena occur at all.

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Field Chemistry

Principles and Applications of Inorganic Geochemistry. A Comprehensive Textbook for Geology Students. GUNTER FAURE. Macmillan, New York, 1991. xiv, 626 pp., illus. $60.

Academic chemistry has succeeded, over the course of this century, in cutting itself off from the observational sciences, and in particular geochemistry. Gone are the days when Bunsen would make the arduous journey to Iceland to study the eruption of Hecla or when apprenticeship in a School of Mines could lead to the pinnacle of the field and the discovery of new elements. It is difficult to imagine a modern-day chemist of the stature of van't Hoff experimenting on the sequence of precipitation of salts in the evaporation of seawater. Although a few outstanding individuals have in recent years been attracted to the problems of smog formation, ozone destruction, and planetary atmospheres in general, Harold Urey was probably the last great chemist to confront the problems of the natural world in this way.

Such a situation is peculiar among the sciences. The rooting of biology and biochemistry in the natural world goes without saying. Both physics and applied mathematics are also vigorously involved in the study of natural processes through their alliances with meteorology, oceanography, solid-earth geophysics, solar and planetary sciences, and cosmology. By contrast chemists appear to have been diverted from the messier processes that occur outside the laboratory by the elegance of laboratory experimentation and the virtuosity with which matter can be manipulated.

The consequences of this diversion are becoming increasingly serious. Formal recruitment of chemistry students into the field of geochemistry is impossible. A student of chemistry has somehow to discover the field, convince herself that it is respectable, and then be stiff-necked enough to withstand the scorn of many of her peers and undergraduate professors. The random and determined personalities that manage this have given geochemistry unique liveliness as a discipline. Now, as society confronts the shambles it has made of the environment, the number of chemists coming into the field must be greatly expanded.

In the present situation geochemistry has as much intellectual association with chemical engineering as it does with pure chemistry. Our vision of the geochemical cycle of the elements is borrowed wholesale from engineering process theory. The maintenance of an oxygenated atmosphere is not a test-tube affair, and environmental geochemistry is, by default, becoming the province of chemical (and civil) engineers and of geologists. Thus recruitment efforts are strongly dependent on these fields rather than chemistry. Which brings us to the present textbook.

The author is a well-known isotope geochemist who has written what is now the standard textbook on that subject. Though his present book must be reviewed on its face, as a textbook, it is useful also to look at it as a document reflecting the state of play in environmental geochemistry as viewed from the trenches. The title is misleading. The book deals largely with low-temperature processes rather than with mineral-melt relations at high T-P, the core concern of classical geochemistry as pioneered by Bowen. It is explicitly directed at seniors in geology, which is what makes it interesting as a document.

The book begins in a low-key way as if the author is wary of his audience. There is a chapter on the origins of geochemistry that is notable for its lack of hilarity—some corporate image-building here. There are then a couple of schematic chapters on the origins of the universe and the solar system, followed by very basic discussions of atomic structure and weights, bonding, and crystal chemistry and a short chapter on radioactive decay and its applications in geochronology. This section ends with a review of chemical fractionation processes in the solar system as a whole and in the earth, the only reference to high-temperature reactions.

The style of presentation then changes abruptly, an indication, perhaps, that the Drop Date will have been passed. The core of the text contains a comprehensive treatment of the low-temperature reaction chemistry of the important geologic minerals with aqueous solutions. This is the basic mechanics of the field. The author covers this well-trodden ground in an attractive manner, with lots of clear figures, comprehensive tables, and worked examples of the complex reactions of the aluminosilicates. The treatment is unique in that it involves isotopic chemistry as an integral component. For reasons that are mysterious, the authors of previous textbooks in this field have afforded no more than a passing glance at the stable and radioactive isotopes, despite the fact that much of what we really understand about geochemical processes is based on their behavior. The present work does have the common failing of relying too heavily on equilibrium rather than kinetic controls on chemical transformations. A lot of quite spectacular things would happen if the world suddenly adhered strictly to the first and second laws of thermodynamics. Biospheric interactions are referred to only in passing.

The final part of the book discusses applications to soil formation, fluvial chemistry, the weathering of ore bodies, and the disposal of radioactive waste. There is also a short discussion of the overall geochemical cycle of the elements.

The problems presented at the end of each chapter call for a substantial extension of the material in the text. Clearly the author expects some hard work from his students.

Who should read this book? Certainly the geology seniors at whom it is directed. Civil engineers will also find it useful. Chemists and chemical engineers contemplating a career in the environmental sciences and hungry for information on this unadvertised subject will rush through the first two sections, even if they are put off by the mineralogical jargon, the inconsistency of units (chemistry comes in moles), and the unfamiliar-looking reactions. They will be surprised that many of the pioneers of their own disciplines are similarly claimed by geochemistry. They will be equally surprised that there is little discussion of atmospheric photochemistry, the one area with which they are familiar, and no real attempt to present the earth as a chemical system—this opportunity was lost among the arrows and boxes of the chapter on geochemical cycles. They will probably feel uncomfortable with