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# KIN RECOGNITION IN ANIMALS[1]

MARY JANE WEST-EBERHARD
*Smithsonian Tropical Research Institute, Balboa, Panama*[2]

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Kin recognition is the ability to distinguish between individuals of different degrees of genetic relatedness, as evidenced by their differential treatment. In nonhuman animals it is an ability that was considered impossible twenty years ago; was considered remarkable ten years ago (when it was discovered in sweat bees and tadpoles); and now is seen to be virtually ubiquitous. Kin recognition has been found in nearly every social (group-living) species in which it has been investigated. This book documents the existence of kin recognition in hundreds of animal species, from isopods to humans. It recounts fascinating stories of animal ingenuity in sizing up kin, as well as scientific ingenuity in figuring out how they do so.

The information explosion that made it possible to assemble an entire book on this subject is a result of the increased research on social behavior engendered by kin-selection theory (Hamilton, 1964*a,* 1964*b*). The extensive evidence for kin recognition presented here certainly strengthens the case for kin selection, which is already strong in view of the widespread documentation of nepotism in animal societies. However, it is a slight exaggeration to suppose (as some authors do in this book) that kin recognition was specifically "predicted" by kin-selection theory or that the validity of the theory depends on it. As several of the authors point out, nepotism (discriminatory treatment favoring kin) can and does occur due to association of close kin with a particular place, such as a nest or a parental territory. Indeed, in view of the lack of evidence and abundance of skepticism regarding kin recognition in the 1960's, Hamilton and others considered that the concept of "population viscosity" (including philopatry—the tendency to remain near home) could explain how cooperative groups come to be composed of kin. In some early studies, discriminatory aid within groups was shown to be influenced by other factors (such as dominance relations and response to different levels of need [e.g., among offspring of different ages]). Given the apparent fine-tuning in the assessment of costs and benefits (e.g., during aggressive contests and the weaning of offspring) and the overall correlation between degree of cooperation and average degree of relatedness of group members, fine-tuning of kin recognition did not seem particularly necessary to explain the examples of differential aid that were known.

It was not until 1979, when Les Greenberg discovered the remarkable precision with which sweat bees (*Lassioglossum*) could discriminate kinship, and Bruce Waldman and Kraig Adler published their surprising evidence for kin recognition in tadpoles, that many students of social behavior began to consider the possible social consequences of refined kin recognition (e.g., during colony fissioning in honeybees or in the differential treatment of full vs. half sibs within a brood). Only then did quantitative geneticists begin to invent models of kin recognition (discussed by R. H. Crozier in this book). Thus, in the history of kin-selection theory, empirical scientists perhaps deserve more credit than they usually receive for advancing understanding of the phenomena that kin selection can be expected to produce.

*Kin Recognition in Animals* contains 13 chapters; three on insects (by E. B. Spiess; C. D. Michener and B. H. Smith; and M. D. Breed and B. Bennett), one on other arthropods, especially desert isopods (by K. E. Linsenmair), three on nonhuman vertebrates (two by A. R. Blaustein, M. Bekoff, and T. J. Daniels; one by J. R. Walters), one on humans (by P. A. Wells), and four on general aspects—theory, definitions, concepts and overviews (by E. O. Wilson; D. J. C. Fletcher; R. H. Crozier; W. D. Hamilton; and the editors, D. J. C. Fletcher and C. D. Michener).

The strong point of this book is that it is an unmatched collection of reviews of research on kin recognition in all of the higher taxa that have been studied in this regard (arthropods and vertebrates). As such, it would be a valuable addition to the library of anyone interested in social behavior, its evolution, or its applications (for example, in the management of captive animals). However, birds are rather neglected in the chapter on nonprimate vertebrates: only four avian species are discussed (for references on others see Colgan [1983]).

These reviews reveal some surprising gaps in knowledge. For example, Walters points out that data on mechanisms of kin recognition are "almost totally lacking for non-human primates" (p. 35); and when this book went to press, there were no studies of kin recognition in reptiles (but see Werner et al. [1987]). Humans are also rather poorly studied in this regard, although the few available studies indicate some unsuspected skills (e.g., for mother-offspring [but not father-offspring] mutual recognition using odors).

Except in the final chapter by Hamilton, the book lacks discussion of kin recognition in a broad evolutionary context. In this respect, it is now partially complemented by Buss's (1987) *The Evolution of Individuality.* Although several authors referred to the theory of "optimal outbreeding" as offering a possible functional context for the evolution of kin recognition, the one chapter on mate choice ("Discrimination Among Prospective Mates in *Drosophila*" by E. B. Spiess) ex-

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[2] Mailing address: Escuela de Biologia, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica.

tensively treats mate-selection cues but has no information on kin recognition.

There is also relatively little discussion of exactly what role kin recognition has played in the social evolution of the groups considered. Is it a by-product of life in family groups, evolved after the establishment of social life under selection to prevent parasitic incursions of unrelated conspecifics? Or is it sometimes a "prerequisite" for specialized group life, a preadaptation evolved in some other context and without which life in family groups would not have persisted? How often is a capacity for recognition present in the solitary relatives of social species? Michener and Smith treat this latter question briefly and speculate that it may have originated among male bees as a device to prevent inbreeding, being subsequently employed by group-living females to exclude unrelated individuals from their nests. It would also be of interest to investigate the nonsocial functions, if any, of the cues used in kin recognition or at least to ascertain whether they are produced by species in related taxa and used in other ways. It is not justifiable to assume (as did one author) that the cues used originated in the context of selection for kin recognition itself. I have often wondered whether there could sometimes be a connection between the cues used to signal aggressiveness (threat pheromones) and those used in kin recognition. There is some evidence for this: Breed and Bennett (p. 252) state that the source of honeybee recognition odors appears to be the mandibular glands, which are known to produce substances responsible for releasing worker aggressiveness against queens. Indeed, dominance status and "recognition" effects may be confounded in some experiments. For example, in one discussed by Fletcher (p. 47), the longer a queen is absent from her resident colony, the more strongly she is attacked when returned, a result that could be attributed to a breakdown of either recognition abilities or dominance relations.

I began this book in keen anticipation of being told, at last, why it is that tadpoles recognize and preferentially associate with their sibs. Kin associations are expected in cooperating social insects, birds, and mammals, but why in tadpoles? It is an important question, because it raises the possibility that kin recognition could occur for no particular functional reason or perhaps be a side effect of some other process. If so, this would throw into doubt the evolutionary origins being assumed by adaptationists interested in kin selection and "optimal outbreeding." However, I was disappointed to find no insightful discussion of this point. There is a brief mention (p. 311) of the possibility that "being able to recognize kin may enable individuals to settle more efficiently in suitable areas," but no reason is given as to why kin should be "more efficient" than other individuals in this regard. Nor is it clear how "maintenance of cohesive family groups" in Cascade frog tadpoles (p. 339) would be an advantage per se or how kin recognition in tadpoles would allow adult frogs to "balance inbreeding and outbreeding" (p. 306), for there is apparently no evidence of kin recognition among adults. I found no mention of a more plausible earlier suggestion (Waldman, 1981) that toad (*Bufo americanus*) tadpoles are distasteful to some predators and that kin may thus sometimes benefit by associating in schools (those happening to be eaten would not have died in vain if nearby relatives are avoided). Readers interested in this question should supplement the Blaustein et al. chapters by reading Waldman (1981, 1982, 1986, 1988).

Surprisingly, the most thoroughly understood sophisticated system of kin recognition is not found in a vertebrate or a social insect, but in an isopod. Desert isopods (*Hemilepsis reaumuri*) live in groups of up to 80 kin. They occupy fiercely defended burrows, located in dense aggregations of frequently interacting but closed family groups, and they use a composite identification odor ("badge") composed of the memorized individual odors of all family members combined. In thousands of field observations, there was not a single case of mistaken identity—and all of this with a brain consisting of only 10,000 neurons, not more than 6,000 of which are concerned with central processing of chemical stimuli. (Compare this to the 20 billion neurons of the human cerebral cortex [Calvin, 1983].) Linsenmair's account (much of it previously unpublished) of this painstaking and ingenious pioneer research was for me the highpoint of this book.

The final chapter, by W. D. Hamilton on "Discriminating Nepotism: Expectable, Common, Overlooked," is as informal, candid, fascinating, and vulnerable as a letter to a friend. It falls into that special genre of faintly presumptuous and occasionally brilliant essays by great figures—a genre that enjoys something like diplomatic immunity to criticism. I found most of the brilliance in the first half and most of the vulnerability in the last, which takes up the delicate subject of man (and woman). This essay contains some statements that are of interest to students of kin-selection theory, because they represent, if not a change in thinking, at least a change in emphasis. Hamilton considers kin selection to involve ". . . evolution mediated by genes of small effect not obligately expressed in their bearers. Each adds to a set already there and this set—to which, in effect, the new gene is applying for admission—is a part of the 'environment' over which gene effects must be averaged in determining whether selective effects will allow it to rise in frequency" (p. 418). That is, kin selection is important primarily in the modification (not the origin) of facultatively expressed helping behavior (in a footnote Hamilton mentions that "conditionality, although mentioned, was insufficiently emphasized" in his previous work).

Perhaps the most important general contribution of kin-recognition research for the student of organic evolution and adaptation is its demonstration of the widespread capacity of nonhuman animals for assessment of parameters (such as relatedness) enabling them to make complex evaluations of potentially adaptive options. Not only can individuals discern relatedness, but they actually use this information (along with other indicators of costs and benefits) to decide whether to give or withhold aid, whether to abandon or to join, whether to parasitize or to ignore, and whether to mate or to wait. The life of an anthropocentric skeptic has to change with the realization that an isopod can remember 12 special odors at once, or that a bee can instantly tell the difference between a half and a full sister and can act accordingly. Similar discoveries are being made regarding the integrated assessment of costs, benefits, and risks by students of animal foraging behavior. If these things are known, what remarkable capacities for assessment and judgement remain to be discovered? We have probably severely underestimated the abilities of nonhuman animals for adaptive plasticity and overestimated the gap between animal and human minds.

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# THE BUTTERFLIES OF COSTA RICA[1]

GEORGE T. AUSTIN
*Nevada State Museum and Historical Society, 700 Twin Lakes Drive, Las Vegas, NV 89107*

AND

PAUL A. OPLER
*U.S. Fish and Wildlife Service, 1025 Pennock Place, Fort Collins, CO 80524*

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Philip DeVries is to be congratulated for producing the first comprehensive handbook on a portion of the diverse butterfly fauna of the Neotropics. Overall, the book is excellent and concise. As its title suggests, this is more than a field guide because it summarizes what is known of the life histories, host plants, behavior, ecology, and distributions of the nearly 550 species of Papilionidae, Pieridae, and Nymphalidae known from Costa Rica. This compares with about 300 species in these same families in all of North America north of Mexico. We are aware of a few species that were omitted, but DeVries' coverage is at least 95% complete.

The introductory sections very briefly review butterfly biology, structure, systematics, and collection techniques (one wishes for more on baits and trapping). A short section covers mimicry, and several interesting pages describe predation and parasites, a topic usually ignored in regional works. Following this is a chapter briefly outlining the faunal regions of Costa Rica, their seasonality, and their diversity.

Each family, subfamily (occasionally tribe), and genus is introduced with explanations of distinguishing characters and generalizations on host plants, early stages, and general biology. Each species account includes the scientific name, the forewing length, a brief account of the general distribution (and that of the Costa Rican subspecies, where applicable), the host plants (when known), brief descriptions of the early stages (when known), a brief description of the adult and its distinguishing characters, comments on similar species, habits, behavior (including activity times, adult resources, etc.), and distribution (geographical, ecological, and often seasonal).

Numerous figures throughout the text illustrate typical larvae, pupae, and occasionally important structural details of adults (e.g., venation of the various ithomiine genera). Fifty excellent color plates are bound together at the center of the book and illustrate all but a handful of species which are very rare or hypothetical in Costa Rica, usually including males and females (when very different), upper and lower surfaces, and sometimes seasonal forms and polymorphisms. Another color plate (in the introduction) illustrates members of various mimicry complexes. In a few instances, the colors are slightly off that of the butterfly. The yellows on plate 8 are too rich, and the reds on plate 25 seem washed out. The latter, at least, may be due to the use of old, faded specimens, because the colors of some taxa on the same plate are true. The book concludes with appendixes (collecting localities, summary of host

[1] *The Butterflies of Costa Rica and Their Natural History: Papilionidae, Pieridae, Nymphalidae.* Philip J. DeVries. 1987. xxii + 327 pp. Princeton Univ. Press, Princeton, NJ. $60.00 cloth, $22.50 paper.