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# ECOLOGICAL SEGREGATION[1]

**By Professor A. S. PEARSE**

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ANIMALS known to science all live in a thin layer which is close to the surface of the earth. The complex group of conditions which surround any animal is called an environment. An area where more or less uniform conditions obtain is a habitat. Animals are in a general way adapted to live in particular habitats in one of the three great ecological realms—sea, fresh water or land. This statement raises the first question: What is adaptation and how does it come about?

## ADAPTATION

To most zoologists adaptation means merely that an animal fits its particular environment. A fish out of water does not fit; an eagle is out of place in the depths of the ocean. Somewhere on the earth there is a place where an animal fits in a more or less precise way. It is impossible to conceive an animal without its environment. If an animal does not fit, it ceases to exist. If an animal continues to exist it must perhaps change its habitat and its bodily constitution somewhat as earth environments change. "Evolution is no more than adaptation of organisms to environment."[2] The past history of the earth indicates that unusual environmental conditions precede new types of adaptation in animals.[3] Animals must in a changing environment remain continually adapted or become extinct.

If one studies in detail the adaptations of animals

[1] Address before Section F—Zoological Sciences, American Association for the Advancement of Science, Boston, December 28, 1933.

[2] S. L. Hora, "Ecology, Binomics and Evolution of the Torrential Fauna, with Special Reference to the Organs of Attachment," *Philosoph. T. Roy. Soc.*, London (B), 218: 171–282, 1930.

[3] H. F. Osborn, "The Origin and Evolution of Life," xxi + 332 pp., New York, 1917.

to environment, he is often surprised at the degree of accuracy with which many of them fit particular habitats. Along the shores of the coral islands at Dry Tortugas there are four species of hermit crabs and each is adapted to life in a particular stratum.[4] A gigantic species which lives at depths of from one to sixty fathoms has 26 gills; another rather small species that lives in a zone about one meter thick just below the tide mark also has 26 gills; a minute species that lives at high-tide mark, exposed to winds and tropical sun, has 18 gills, and the common land hermit crab has but 14 gills. The littoral crabs at Tortugas and along the coast of Carolina[5] are also assorted into rather definite zones and are correspondingly adapted. They form a graded series in regard to the size of their gills. In those that live always below low-tide mark and never leave the ocean the volume of the body is about twenty times that of the gills, but, as habitats and crabs progress upward through the tidal zone, gills dwindle. Above high-tide mark, where certain species of crabs have become terrestrial, the body may have 60 times the volume of the gills. On the coast of Japan[6] and at Tortugas the salinity of the blood of crabs decreases from the ocean through various zones toward land. Species which are adjusted to life on land have less salt in their blood than those which have remained in the ocean, and vary less with changes in the surrounding medium.

At the mouth of the Menam in Siam there are three species of gobioid fishes which live together on the muddy beaches.[7] They do not occupy horizontal zones but skip about together when the tide is out, hunting for food. On examination the largest goby was found to subsist chiefly on fishes and crabs, and the length of its intestine averaged about two thirds that of its body; the goby of medium size had an intestine nearly three times as long as its body and ate little but algae; the small goby fed mostly on insects and had an intestine shorter than its body. The parasites of the gobies were also quite distinct and characteristic. Though the three species of gobies were occupying the same area, each was adjusted quite differently to the environment.

Animals tend to become specialists in their relations with environment. There are bees which find food in only one species of flower, during a limited season of the year, and only during certain hours of the day; there are ants which starve unless they can feed on one species of fungus; there are parasites which can exist in only one species of host. A particular species of animal to obtain food may be adapted structurally, physiologically, psychologically, biographically or numerically,[8] but all tend to become adapted to particular conditions as they exist on the earth.

Though animals generally tend to become specialists, there are those at each period of earth development which remain generalized to some extent. An animal as an individual begins life with a certain group of adaptations which fit it for a particular habitat. It may inherit characters which are of no apparent value in its adaptation to environment—Sumner[9] says that useless characters are common, and that such are often used by taxonomists to distinguish species. Elton[10] maintains that closely related species do not differ in adaptive characters. Probably no one believes that all characters are adaptive at all times. Races of particular species which appear to be well adapted to peculiar environments will in some cases maintain their characteristics when transferred to new and different environments.[11] Their adaptations have in some way become bred into the race. Ecologists well know that in nature versatile species are generally more abundant than narrowly specialized species. Specialists are not dominant in any particular habitat, but those having intermediate degrees of specialization and wider ranges of toleration to varying environmental factors often are.[8] Recent discoveries in the field of genetics, though they extend knowledge of how hereditary characters are transmitted, do not explain adaptation.[12] It has long been known that a maladapted species may continue to live in an environment which is not overpopulated, but, when such a species competes with others, which are particularly adapted to that environment it is the first to be exterminated.[13] Lull[14] states that adaptation results largely from competition.

[4] A. S. Pearse, "Observations on Certain Littoral and Terrestrial Animals at Tortugas, Florida, with Special Reference to Migrations from Marine to Terrestrial Habitats," Pap. Tortugas Sta., Carnegie Inst. Washington, 391: 205–223, 1929.

[5] A. S. Pearse, "The Ecology of Certain Estuarine Crabs at Beaufort, N. C.," *J. Elisha Mitch. Soc.*, 44: 230–237, 1929a.

[6] A. S. Pearse, "Freezing Points of Bloods of Certain Littoral and Estuarine Animals," Carnegie Inst. Washington Publ., 435: 93–102, 1932.

[7] A. S. Pearse, "The Gobies at Paknam," *Jour. Siamese Nat. Hist. Soc.*, 1933 (in press).

[8] A. G. Vestal, "Internal Relations of Terrestrial Associations," *Amer. Nat.*, 48: 413–445, 1914.

[9] F. B. Sumner, "Is Evolution a Continuous or a Discontinuous Process?" *Sci. Mo.*, 29: 72–78, 1929.

[10] C. Elton, "Periodic Fluctuations in the Numbers of Animals: Their Causes and Effects," *Brit. Jour. Exper. Biol.*, 2: 119–163, 1924.

[11] F. B. Sumner, "The Analysis of a Concrete Case of Intergradation between Two Subspecies," *P. Nat. Acad. Sci.*, 15: 110–120, 481–493, 1929a.

[12] M. Caullery, "Present Theories of Evolution and the Problem of Adaptation," 1–19, Philadelphia, 1933.

[13] E. Warming, "Oecology of Plants," xi + 422 pp., Oxford, 1909.

[14] R. S. Lull, "Organic Evolution," xix + 743 pp., New York, 1929.

### COMPETITION

As species animals in their relations with each other may be more or less social, indifferent or antagonistic. Men conserve and increase cattle; squirrels and rabbits occupy the same areas without interfering with each other; brown rats have been known to fight and exterminate black rats under certain conditions. Darwin[15] looked upon competition as a natural phenomenon which checked the unlimited increase of animals—each species struggles to increase and is kept down by competition with others. Lull[14] says that competition is inseparable from life and leads to adaptations and complex interrelationships. Osborn[3] states that competition and selection test all actions, reactions and interactions in nature. Warming[13] asserts that competition produces new species.

Robertson[16] believes that competing species are often not closely related. Borradaile[17] maintains that the individuals of a single species do not compete, but that communities may do so. There is perhaps some doubt about this, but Borradaile makes another point that appears to be a very good one: *i.e.*, that competition may be suspended for a time when a species invades new territory and food is then temporarily plentiful and enemies few. Vestal[8] has listed five types of characters which may be adapted so as to remove animals from competition: (1) structural, which may give animals special advantages in particular habitats (legs of mole); (2) physiological, such as ability to digest and assimilate unusual foods (clothes moth eats keratin) or to exist in peculiar environments (anaerobic animals); (3) psychological, such as preferences for special foods or habitats; (4) biographical, which permit adaptation of life cycles to favorable seasons, feeding to particular times of day, etc., and (5) numerical, by which the numbers of a species produced by reproduction are adjusted to food supply or other limiting environmental factors. Noble[18] has pointed out that species of plethodontid salamanders are most sharply segregated at the time of breeding. They avoid competition by selecting different humidities, types of streams, and other particular qualities in their environments.

Populations which result from competition in particular habitats are subject to D'Ancona's laws:[19] (1) periodic cycle, (2) conservation of averages, and (3) disturbance of averages. "The fluctuations of two species are periodic; and the period depends solely upon the coefficients of increase and decrease, and initial conditions. . . . The averages of the number of individuals of two species are constant whatever may be the initial values of the numbers of individuals of two species, just so long as the coefficient of increase and decrease of the two species and that of protection and offence remain constant. . . . If an attempt is made to destroy the individuals of two species uniformly and in proportion to their numbers the average of the number of species that is eaten increases and that of the individuals feeding upon the other diminishes." Chapman has used two useful descriptive terms: "biotic potential" which refers to the ability of a species as a result of all its activities to produce offspring, and "environmental resistance," the obstacles to be overcome in populating a particular habitat. The dominance of an area by a particular species means more than mere survival. "Dominance in a species, then, would seem to include the dependence of other animals upon it, plus the ability to thrive in spite of the drain upon its numbers. . . . Dominant animals appear to be those of moderately specialized habits, rather than those of highly specialized, or relatively unspecialized habits. . . . Species which are relatively free from competition or which have comparatively few enemies may be successful, but are not dominant, and are usually not numerous."[8] Most students of competition seem to have had their minds fixed upon the struggle for existence among animals and little thought has been given to the fact that adaptation so often results in permitting animals to avoid competition.

### HABITATS

The environment must furnish all that animals need to maintain their systems of activities: food, shelter, freedom from competition, opportunity for reproduction. In an area where there is a variety of habitats there will be varied and numerous species; where environment is monotonous and limited there will be few species. Animals commonly seek out habitats which are as near their optimum conditions as a particular environment offers. Where there are transitions from one type of habitat to another species are often arranged in more or less definite zones, as along a seashore or the margin of a forest. Many animals establish homes at particular spots which are apparently no better than hundreds of others, but once selected, are retained with great tenacity. Pond turtles are rather sedentary animals and seldom move a hundred yards during a year; many sea birds return year after year to particular rookeries, even when conditions have become unfavorable; the hom-

[15] C. Darwin, "On the Origin of Species by Means of Natural Selection," xxi + 458 pp., 6th ed., New York, 1875.

[16] C. Robertson, "Ecological Adaptation and Ecological Selection," SCIENCE, 23: 307–310, 1906.

[17] L. A. Borradaile, "The Animal and Its Environment," vii + 399 pp., London, 1923.

[18] G. K. Noble, "The Plethodontid Salamanders; Some Aspects of Their Evolution," *Am. Mus. Nov.*, 249: 1–26, 1927.

[19] R. N. Chapman, "Animal Ecology with Especial Reference to Insects," x + 464 pp., New York, 1931.

ing behavior of pigeons, terns, crabs and snails is well known. A bird may select a particular roosting place in a tree and return to it again and again, not because the particular spot is the best that can be found, but perhaps because it has proved to be satisfactory and its use saves the labor of seeking each day for a suitable situation. There is a very widespread tendency among animals to choose suitable and often particular situations in the environment.

"The common belief that allied species occur in separate habitats is by no means true."[20] Many closely related varieties of mammals occupy separate areas; races of mollusks and insects often live on areas that overlap and related varieties frequently occur together.

In any habitat there is some degree of environmental resistance to population. At Tortugas certain species of sponges serve as living hotels for hundreds of commensals and parasites; other species which are of about the same size and structure contain few or none. Some species of sponges are apparently more favorable habitats for animals than others. There are many cases of an extreme degree of adaptation in the host specificity of parasites. Many bird lice are restricted to a single host species. Other nearly related hosts are not favorable environments. Biotic potential in any habitat must overcome environmental resistance. Elton[21] has pointed out some very good illustrations of the control of animal populations by variations in climate, food and other factors. He cites certain owls, gulls and other animals which rear larger broods or breed only in "lemming years," when an abundance of food is available.

A habitat is the salvation or the destruction of an animal. Variations continually take place in both environment and organism. If either varies beyond the limits of toleration of the other, the organism must migrate to a more favorable environment, adjust its system of activities to new ranges of toleration, or die.

## SEGREGATION

Segregation is a familiar phenomenon in biology. Crystals, colloids, genes, sexes, races, species, communities and other systems of activities segregate. They thus attain more or less individuality and independence from other systems and in some cases are thus perhaps better adapted to existing environments. In considering why segregations take place one is confronted with several possibilities. No animal, except among lowly asexual types, can live wholly alone, and many animals are adapted to more or less complex communal relations. Some substances, like oil and water, will not mix and when forcibly brought together separate again. Some qualities of living organisms, such perhaps as those which are concerned with sterility and lethal factors, are perhaps incompatible in somewhat the same way. Quite another aspect of segregation is shown by such tendencies as those which gradually lead to the formation of subspecies and species. It is possible that orthogenetic variation may produce new races and species without the influence of environment, except that variants must always fit well enough to survive. Assortative mating may segregate groups within a species and thus lead to the formation of new races or species.

There have been many adherents of the view that geographic isolation is essential for the formation of ecologically different groups. Jordan[22] pointed out that two subspecies seldom occupy the same area. During a careful survey of the distribution of the marine animals at Woods Hole, Massachusetts, Sumner, Cole, and Osburn[23] supported this view. They found that the ranges of subspecies and even species in the same genus often overlapped but were never identical. Such observations suggest that the requirements or ranges of toleration may be different in two such groups of animals. Yet Goldschmidt[24] says, "there is in my opinion no reliable fact known which would force us to assume that geographic variation or formation of subspecies has anything to do with speciation; the results of genetical analysis and of sober evaluation of other facts are positively in contradiction to such an assumption." Sumner[25] takes the position that the boundaries between subspecies of mice of the genus *Peromyscus* are geographical rather than morphological. The local distribution of any animal community, especially on land, depends on the extent of the physical environment to which it is adapted and more or less directly on the local distribution of plants which furnish food and shelter. In Florida Sumner[25] found a rather sharp boundary between two subspecies of mice. One lived on the light-colored sands near the coast and was pale; the other was found inland and was dark in color. Over a narrow strip two or three miles wide there were some intergradations between the two subspecies.

It has been suggested often that segregation, not

[20] O. W. Richards and G. C. Robson, "The Species Problem and Evolution," *Nature*, 117; 345–347, 382–384, 1926.

[21] C. Elton, "Animal Ecology," xx + 207 pp., N. Y., 1927.

[22] D. S. Jordan, "The Origin of Species through Isolation," SCIENCE, 22: 545–562, 1905.

[23] R. C. Osburn and L. J. Cole, "A Biological Survey of the Waters of Woods Hole and Vicinity, I, Physical and Zoological," *Bull. U. S. Bur. Fisheries*, 31: 1–442, 1913.

[24] R. Goldschmidt, "Some Aspects of Evolution," SCIENCE, 78: 539–547, 1933.

[25] F. B. Sumner, "Genetic, Distributional and Evolutionary Studies of the Subspecies of Deer Mice (*Peromyscus*)," *Bibliogr. Genet.*, 9: 1–106, 1932.

necessarily in the nature of geographic isolation, is necessary to maintain a species or a variety. Many biologists hold the belief that a new species has its inception when a group of animals or plants forms a community with a new or a restricted environment.[26, 2] Regan has stressed what he calls habitudinal segregation as a primary factor in the origin of races and species. Robertson[16] maintains that specific characters are the result rather than the cause of such segregation. He points out that various species of bees of the genus Colletes fly out to search for food at different times of the day and at different seasons of the year. Though their structures for collecting pollen and nectar are quite similar, they do not subsist on the same foods. Again the tendency of organisms to become specialized to particular environmental conditions is apparent. One group of animals may be deterred from association with another by habitat preferences, peculiar odors, the structure of copulatory organs, assortative mating, and countless other qualities, as well as by geographic or genetic isolation.

### Environment and Species

An organism can never reach a condition of complete stability. It undergoes rhythmical and progressive internal changes and makes adjustments to changes outside itself. It must live continually in a changing environment. With a given range of hereditary qualities which make it fit into a particular niche in nature it must struggle to survive and produce offspring. There seems to be no doubt that new species have evolved from previously existing species in the past and that they are doing so at the present time. There are three views generally held in regard to the relation of environment to such changes in the constitution of the living systems of activities known as species: (1) the changes are brought about by causes wholly within the organism itself—they are automatic; (2) the germ cells are changed by external causes, and (3) the soma is changed by environment and in turn influences the germ. Those who think chiefly about adaptation often lean toward the last explanation; those who accumulate evidence by breeding and genetic experiment perhaps most often adhere to the first. At present there appears to be no evidence to decide which of these views is correct. All that can be done is to continue to accumulate evidence until there is enough to prove something. The logical thing to do then is to review the limited group of facts that scientific investigation has accumulated, and go to work. The writer will attempt to discuss some of the known facts which ecologists believe may be related to the origin of species.

[26] C. T. Regan, "Mendelism and Evolution," *Nature*, 113: 569, 1924.

It is probable that mutations and natural selection operate to produce new species. Genes which can be demonstrated by crossing over are concerned with the inheritance of varietal, or racial, significance only.[27] Specific characters which are transmitted as hereditary qualities may be useful for survival, but often they apparently are not.[20] All diversity is not the result of selection based on utility.[11] Secondary sex characters are often used by taxonomists as a basis for separating species. Their evolution is "usually not progressive and continuous but haphazard and often parallel in not closely related stocks."[18] A new species probably never arises as the result of one mutation. Changes which lead to the production of new species apparently may be continuous, gradual and adaptive,[26] discontinuous and non-adaptive, or slow and non-adaptive.[20]

As has been pointed out, there is a wide-spread belief among ecologists that animals that take on new habits and habitats initiate new species.[16, 26, 20, 2] New races often originate on areas which are more or less remote from those occupied by the parent stock.[25] Specific characters are probably the result rather than the cause of segregation.[20] New races of mammals appear to arise where optimum environmental conditions alternate with unfavorable conditions.[10, 25] When environmental conditions are close to the optimum for a species an area becomes thickly (perhaps over) populated and variants which have non-adaptive characters may become established. When an area becomes overpopulated epidemics are more likely to occur and predacious enemies increase. The population is then greatly reduced and a small group of peculiarly adapted survivors may remain. When lemmings are abundant in Northern Europe ptarmigans are not often eaten by foxes and owls and may increase in numbers, but after a great migration and epidemic among lemmings ptarmigans are preyed upon and in turn decrease. Thus successive periods of overpopulation, epidemic and survival may result in the evolution of a new species; a heritable variation is left in a small group of animals after depopulation.[10]

A species is a complex of characteristic but more or less variable structures, functions, instincts, habits and other qualities. Fulton[28] recently separated three races of the cricket, *Nemobius fasciatus*, chiefly because they have different songs. These races "are more distinct physiologically than morphologically," but "they seldom if ever interbreed under natural conditions." When a species is in the making it is

[27] L. Plate, Vererbungslehre, mit besonderer Berucksichtung der Abstammungslehre und des Menschen. I. Mendelismus, x + 554 pp., Jena, 1932.

[28] B. B. Fulton, "Inheritance of Song in Hybrids of Two Subspecies of *Nemobius fasciatus (Orthoptera)*." *Ann. Entomol. Soc. Amer.*, 26; 368–376, 1933.

not certain whether changes in such qualities as structures or habits, assortative matings or interracial sterilities come first. No one knows whether a group of animals by living in a new habitat gradually acquires new structures or whether animals with peculiar structures are especially fitted from the beginning to live in different habitats than those occupied by the parent stock.

Available knowledge shows that there has been evolution. The mechanisms of heredity are quite well known. The great biological mystery to-day is variation. About all that scientists at the present time are able to do is point out the conditions under which animals vary. So there are well-understood examples of hybridization, the establishment of pure lines, the changing of the phylogenetic record as represented during ontogeny by acceleration and larval adaptation, even the modification of gene characters by experimentally controlled environmental factors; but why animals vary no one knows.

When factors which have played a leading rôle in the formation of species are considered, an ecologist thinks first of environment. Present-day evidence does not indicate that environment has caused animals to vary. It does suggest that new species have arisen by segregation—structural, physiological, reproductive, genetic, habitatic and biographical. Ecological segregation is one factor which has been associated with the production of new species, which are perhaps at times produced by competitive, struggling selection and at times by groups of animals which by becoming adapted to peculiar and previously unoccupied niches in environment are able to escape competition. *Quien sabe?*

# TISSUE REACTIONS IN IMMUNITY: XIV. THE SPECIFIC REACTING CAPACITIES OF DIFFERENT TISSUES OF AN IMMUNIZED ANIMAL[1,2]

By Dr. REUBEN L. KAHN

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THE protective forces of a bacterial-immunized animal, according to modern immunologic knowledge, are centered largely in the fluids and the wandering cells. The great controversy of half a century ago regarding the humoral and cellular theories of immunity is at present of historical interest only; it is now generally accepted that humoral antibodies as well as phagocytes are lined up in defense of the host when attacked by bacteria. Although bacterial attacks generally involve fixed tissues, such as the skin, muscle, etc., yet the rôle of these tissues in immunity is far from established. Indeed, these tissues are regarded as hypersensitive to the very organisms against which the protective forces of the fluids and phagocytes are directed.

Let us consider two basic and readily measurable responses of a rabbit immunized with a protein solution or a bacterial suspension, namely, the reaction between serum and antigen and the reaction between skin and antigen. The former is classed under the familiar antigen-antibody reactions, while the latter is referred to as local anaphylaxis, tissue hypersusceptibility or hypersensitiveness. The basis for the latter terminology is the fact that specific antigen injected into the skin of an immunized rabbit calls forth an inflammatory response not given by a normal rabbit. It is this inflammatory response that is interpreted to be the result of a specific hypersusceptible state of the skin.

In spite of this interpretation of skin hypersusceptibility to the antigen, it is not generally assumed that the skin actually enters into a union with the antigen in producing the inflammatory reaction. The view is prevalent that the inflammation is due to an interaction between circulating antibodies and the introduced antigen, that this interaction results in substances toxic to the tissues, thus causing the inflammatory response. If this view is accepted, it would appear that the tissue in which the specific inflammation occurs is merely a "neutral bystander" in a reaction that takes place between an antigen and antibody.

The experimental data to be herewith considered

[1] This paper contains an account of the work by Dr. Kahn for which the eleventh annual award of the American Association for the Advancement of Science was made at the Boston meeting.

[2] For previous publications in this field, the reader is referred to: R. L. Kahn, "Skin Response as a Measure of Immunization and Sensitization," *Jour. Bacter.*, 25: 81, January, 1933; "Studies on Sensitization," Papers I to VI, *Proceed. Soc. Exp. Biol. and Med.*, 30: 603, March, 1933; "Studies on Tissue Reactions in Immunity," Papers VII to XIII, *Jour. Immunol.*, 25: 295, October, 1933. Papers XV and XVI, in press, give detailed experimental data of the present article.