BIOLOGY AND RELATIONSHIPS: ADAPTATION IN NATURE

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A useful concept in evolutionary biology is that traits that are common are ancient and fundamental, whereas less common traits are more recently evolved. The fact that (1) behavioral facilitation of reproduction occurs in all kinds of organisms, ranging from blue-green algae to mammals, and (2) the diversity of organisms exhibiting behavioral facilitation is greater than the diversity of organisms exhibiting sexual reproduction (meiosis), suggests that behavioral facilitation is more fundamental, or more ancient, than is sexual reproduction. Since behavioral facilitation is an interactive process, this means that relationships and reactivity to these relationships is absolutely fundamental to biological systems.

Because we are evolved beings and subject to the same processes and principles as other organisms, appreciation of the origin and diversity of relationships in natural systems has importance for better understanding the role reactivity to relationships plays in human health and illness. Indeed, in his natural systems theory Murray Bowen considered biology and behavior as having great impact on relationships in the family and society as well as influencing how the individual can control and modify his or her own functioning. The relationship process is basic to the adaptation of life, and reactivity to relationships is built into the biology and behavior of all species. The human condition, both in its positive and negative aspects, has its biological foundations in the aggressive, sexual, and parental bonds that have evolved in response to environmental challenges.

Evolution is a process predicated on reproductive success. Reproductive success can be defined as the production of young that themselves reproduce. In evolutionary terms it is not sufficient for the individual to produce young—for those young may

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not reproduce themselves, thereby ending the genetic contribution of the original individual to future generations. In other words, if the individual is to have an impact at least two generations must follow.

To most people reproduction is equated with sex, and one of the great questions in evolutionary biology is Why does sex exist? To an evolutionary biologist sex means meiosis or the recombination of genes following fertilization or when the chromosomes pair. Recent work suggests that recombination is a way to get rid of deleterious genes. But to most, sex means males and females. It is widely accepted that biparental reproduction developed very early in the origin of life. That is, offspring were produced from the union of two gametes at some stage of the life cycle.

Initially, biparentalism may have involved the union of equal-sized gametes (isogamy), as is the case in some unicellular organisms today. But by far the more common pattern is the union of gametes of unequal size, with small gametes uniting with larger ones (anisogamy). This represents sperm and eggs or, in essence, males and females. The origin of males and females then generated a new set of phenomena such as sexual dimorphisms, sexual selection, the mating system, competition both between and within the sexes, and sex determination. Superimposed on these processes is the possibility for the loss of biparental reproduction through the evolution of parthenogenesis, which I will return to shortly.

Returning to the question of why does sex exist, it can be reformulated, Why do males exist? We specify males because males cannot reproduce themselves, whereas females have that ability. Why are males important? Males are more than simply producers and conveyers of sperm. It turns out that the behavior of males is vital to stimulating the necessary neuroendocrine changes the female must undergo if she is to ovulate and breed. This behavioral interaction between the male and female is a relationship, and a useful way to consider relationships is in terms of stimulus-response complementarity as defined by Frank Beach (1979). At its most basic level, and this sounds deceptively simple and obvious, stimulus-response complementarity means that for a male to successfully mate, the female must be receptive to his efforts and vice versa. (This does not discount forced matings, but these are rare in the animal kingdom.)

There is a functional consequence of this complementarity in mating behaviors. The male not only provides the sperm necessary for fertilization of the female's ova, but he also provides the behavioral stimuli necessary to ensure normal ovarian activity in the female. This behavioral facilitation of reproductive function is reciprocal; that is, the female is crucial to maximizing the male's fertility just as the male is important to the female's reproductive activity. Thus, sexual behavior has functions other than coordinating the meeting of the gametes. The behavior of each individual affects the physiology and thus the behavior of other individuals, thereby synchronizing the complex physiological events that culminate in fertilization.

Behavioral facilitation of reproduction has been described in all sorts of organisms, even in unicellular organisms which do not have sexes in the same manner as multicellular organisms, but rather have mating types. For example, population growth in bacteria is more rapid in colonies that begin with two individuals as compared with colonies that begin with one individual; the immediate facilitation in the former situation insures a more rapid trajectory in population growth.

The most extensive work, however, has been done with vertebrates. An example from my own work with reptiles illustrates the basic paradigm. In the green anole lizard the behavior of the male is important to normal ovarian function of the female. In order for the follicles to grow and ovulate, the female must be courted by a male. If a male is castrated and hence does not court, the female's ovaries will grow only slowly and she will not ovulate (Crews 1979). On the other hand, if a female observes males fighting among themselves, ovarian activity will be suppressed. Thus, the behavior of the male can either stimulate or inhibit reproductive activity in the female. The complement also occurs in that the testes of males are heavier and androgen levels higher if they are exposed to females.

What about organisms that reproduce parthenogenetically or by asexual means? In organisms that reproduce by cloning, or parthenogenesis, the egg undergoes complete development with the result that each individual is a genetic copy of the mother and this continues through multiple generations. Several kinds of parthenogenetic species exist in nature. There is the scourge of the garden, the aphid. In certain environmental conditions the aphid reproduces parthenogenetically, with all the young produced being female and genetically identical to the mother. Other species are called facultative parthenogens. These species also consist entirely of females but individuals need to mate with males of another species. An example of this condition is the Amazon Molly. Although the male's sperm activates the egg, his genetic material is not incorporated into the embryo's genome. Finally, there are species of whiptail lizard which consist solely of females but do not require mating with males of other sexual species to reproduce.

Do parthenogenetic animals exhibit a behavioral facilitation and synchronization of reproduction? This idea evidently did not occur to anyone until twenty years ago (Crews 1982). But an examination of cloning species for this trait reveals surprisingly clear evidence for behavioral facilitation of reproduction. Indeed, if we look we find examples of this principle of behavioral facilitation of reproduction in all life forms. In the parthenogenetic whiptail lizards, individuals mount one another and in so doing stimulate reproduction. In this instance then, even though there no longer is a need for sperm, there continues to be a need for male-typical behaviors for reproduction.

Behavioral facilitation of reproduction occurs even in plants. This may not seem possible because plants tend to be sedentary, have a poorly developed sensory system, and do not behave in the same way as do animals. So how could plants exhibit behavioral facilitation of reproduction? Consider the wild garlic which reproduces by cloning. Dr. Linda Ronsheim recently demonstrated that wild garlic surrounded by genetically identical neighbors outperforms other wild garlic surrounded by unrelated neighbors (Ronsheim 1996). She provides other examples of this positive interaction in other asexual plant species, suggesting that this behavioral facilitation of reproduction may be common in plants. So, even though plants may not behave in the classical sense, they do interact and through this interaction exhibit a phenomenon equivalent to a facilitation of reproduction as occurs in animals.

It appears that life itself originated with the asexual form of reproduction, but the advantages of two sexes quickly dominated. Indeed, all but one of the parthenogenetic species that exist today had sexual ancestors. That is, they have lost their sexuality and the parthenogenesis is secondarily evolved.

The oldest known organism is believed to be the green algae or cyanobacteria. The cyanobacteria are asexual and are believed to have always been so since their inception. Cyanobacteria reproduce *en masse*, known as blooms, as do other algae. These aggregations are facilitated by a chemical cue, or a pheromone, that facilitates the reproductive process.

With this information, we can ask another question: What came first, sex or sexual behavior? Because we define sexual behavior in terms of sex, most would argue that it had to have evolved *after* the evolution of sex. But if we think instead of sexual behavior in terms of its functional consequence of facilitating reproduction, another answer emerges. Traits or characteristics shared by many different kinds of organisms are evolutionarily more ancient, and hence more fundamental, than those traits less widely shared and hence more advanced. This is known as the biogenetic law. This principle has been spectacularly confirmed by studies in molecular biology where many of the genes found in humans are present in insects and even yeast. A principal tenet has emerged that genes are not lost but are modified either in structure or more commonly in their regulation.

That (1) behavioral facilitation of reproduction occurs in all kinds of organisms, ranging from blue-green algae to mammals, and (2) the diversity of organisms exhibiting behavioral facilitation is greater than the diversity of organisms exhibiting sexual reproduction (meiosis) suggests that behavioral facilitation is more fundamental, or more ancient, than is sexual reproduction. Since behavioral facilitation is an interactive process, this means that relationships and reactivity to these relationships is absolutely fundamental to biological systems.

If reproductive success is the vehicle of evolution, then variation is the fabric of evolution. It is the material with which evolution weaves its many expressions. This brings us to a basic problem. Most of our knowledge is based on studies of very few species. Rats and mice are the favorite animals in biomedical research today. We only know what we study and, unfortunately, we tend to study only what we know. We have assumed that the mechanisms observed in conventional animal model systems are similar to those of humans, but too often this leap of faith has proven false. When we study other species we often find that our concepts must be modified.

The study of different organisms has challenged some of our present-day concepts in behavioral biology. In vertebrates there are three basic components to reproduction: gametes, steroid hormones, and behavior. For years it was taken for granted that there was fundamental linkage between the production of gametes, the secretion of gonadal steroid hormones, and the expression of sexual behavior. We now know that of the six relationships possible among these three elements, only one, namely that gametes cannot be produced independent of steroid hormone secretion, can be regarded as fundamental. The other relationships that may be observed in various species are adaptations that have arisen in response to various challenges. This realization has led to new paradigms that recognize the ecological, phylogenetic, developmental, and physiological constraints that may be responsible for the wide variety of neuroendocrine mechanisms that subserve sexual behavior among vertebrate animals.

While sex may seem to be one thing, it actually consists of many different components. In all vertebrates there is genetic, gonadal, physiological, morphological, and behavioral sex (Crews 1987). While we tend to think of all of these elements as essential and functionally linked, there exists in nature species that simply have deleted one or more of these sexes. Take, for example, genetic sex. In a genotypic sex-determining system, the sex ratio is fixed at 1:1 or unity. But sex chromosomes are not the only means by which sex can be determined. Some animals lack sex chromosomes entirely and instead depend upon some aspect of the environment to determine sex. The notable difference is that even though male and female individuals are formed, the sex ratio can be all-male, all-female, or anywhere in between.

While environmental sex determination has been known for some time in plants, single-celled organisms, invertebrates, and even some fish, it was not known to occur in the higher vertebrates until about twenty years ago. Since then, it has been discovered that in many turtles and lizards, it is the temperature experienced during the mid-trimester of embryonic development that determines whether the hatchling is a male or a female (Crews 1996). As might be imagined, the mechanisms of sex determination in species exhibiting environmental sex determination must be different from those found in species with sex chromosomes. This means that the process of sexual differentiation of the phenotype, particularly the brain which gives rise to the complementary behaviors, must be different.

What are some of the consequences of these discoveries on our thinking about sex and sexuality? Let us consider the organizational concept which postulates that the female is the neutral, passive, or the default sex, and the male is the dominant or organized sex. In mammals a genetic trigger present on the short arm of the Y chromosome initiates a cascade of events that causes the embryonic gonads to differentiate as testes, producing hormones that act throughout the body to shape the male phenotype;

the absence of this trigger results in the development of ovaries and the female phenotype. Later in life the sex steroid hormones secreted by the mature gonads act on these organized tissues to stimulate reproductive and behavioral changes.

But clearly the organizational concept cannot apply to vertebrates lacking sex chromosomes. Each and every individual has the ability to become a male or a female. Rather than the sex determining trigger being a genetic switch inherited from the parents, it is provided by the environment. This means that both male and female must be organized states and that in the sex determination process one gonad determining cascade must be turned off, and the other turned on. In other words, being male means also not being female, and being female means not being male.

In both genotypic sex determination and environmental sex determination, it is important to separate effects due to the presence (or absence) of specific chromosomes or environmental factors from the effects of sex hormones. In genotypic sex determination hormones secreted by the embryonic gonad organize the brain, thereby affecting the probability that female-typical behaviors (for example, receptivity) and male-typical behaviors (for example, mounting and intromission) will be displayed by the breeding adult. Although comparable information is not available for the sexual differentiation process in the other modes of reproduction, it stands to reason that the differentiation of the neuroendocrine mechanisms that underlie complementary sexual behaviors must be different in species that have different sex determining mechanisms. That is, the neuroendocrine mechanisms that underlie complementary sexual behaviors must be different in species that have different sex determining mechanisms.

It is important to study the diversity of natural systems not only because it increases our knowledge of how organisms can adapt to their peculiar conditions, but because such studies also tells us about what is common to all animals versus what is unique to particular animals. The phenomenon of pseudosexual behavior in all-female species raises the question of homosexuality in humans. If one defines homosexuality as sexual activity between individuals of the same sex, then it is as common among animals as it is in humans. But this is an anthropocentric view. Homosexuality is the sexual preference for individuals of the same sex and is rare among nonhuman animals. Thus, homosexual behavior is biological reality, but homosexuality is a human societal issue and not an issue of biology. Sexual orientation is still a third element. I take the position that an individual's genetic constitution predisposes an individual's sexual orientation, while events, including hormones, experienced both before and after birth, shape an individual's sexual orientation.

A key to understanding the variation in the natural world lies in understanding the constraints impinging on the organism. Species evolving under different constraints exhibit fundamentally different mechanisms controlling behavior, and recognition of these ecological, phylogenetic, developmental, and physiological constraints has changed many basic paradigms in behavioral biology. This comparative approach also has revealed that the behavioral interactions among individuals are absolutely essential to the sustained reproduction and continuation of species. ❋

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