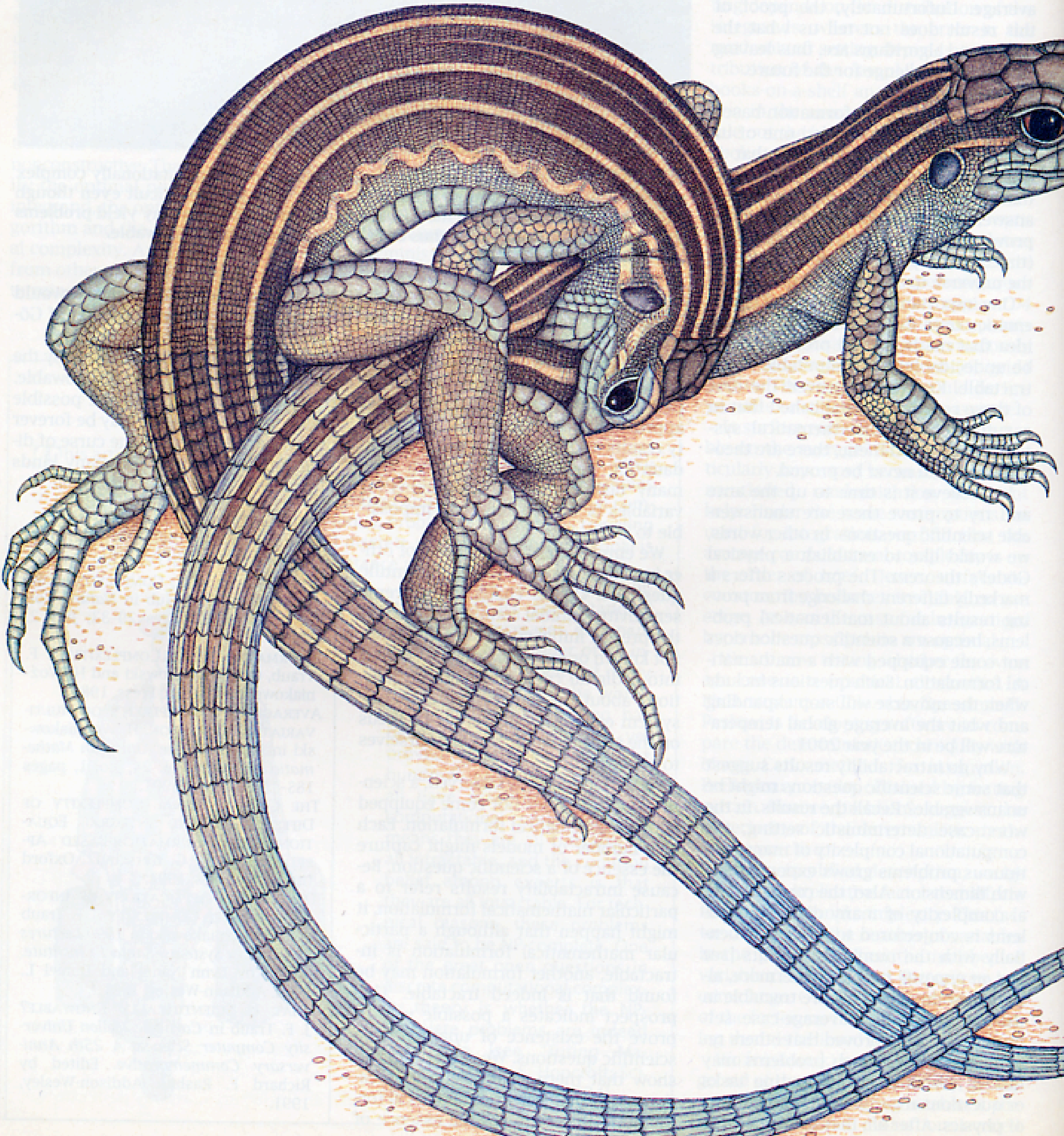
Animal Sexuality

Animals have evolved a range of mechanisms to determine whether an individual takes on masculine or feminine traits. Cross-species comparisons offer some surprising insights into the nature of sexuality

by David Crews



One of the most fundamental characteristics of life is sexuality, the division into male and female. Sexual considerations influence the appearance, form, behavior and chemical makeup of nearly all multicellular organisms. Amazingly enough, scientists cannot conclusively say why sex exists. In recent years, however, animal studies have provided a great deal of information about the multifaceted components of sexuality. These studies reveal that many familiar aspects are less universal than once supposed. The work provides a new framework for understanding the relationship between males and females and a glimpse at how sex evolved.

Among vertebrate animals, sexuality is expressed in a number of ways. Males and females exhibit a wide variety of chemical, anatomic and behavioral disparities. The most obvious of the behavioral divergences lies in an animal's copulatory activity. In general, individuals having testes attempt insemination (male-typical behavior), whereas individuals having ovaries are receptive to being inseminated (female-typical behavior). Males and females often differ in other, less overt ways, such as level of activity, regulation of body weight, level of aggression and learning patterns. Some gender-specific actions are associated with, but not necessarily caused by, systematic dissimilarities in certain parts of the brain.

Over the past four decades, biologists have pieced together a master outline of the nature of sexuality, known as the organizational concept. Although it is not totally inclusive, the organizational concept broadly accounts for the structure of sexuality in humans and other mammals. A number of my colleagues and I are currently investigating how to apply the outline more generally to all vertebrate animals.

According to the organizational concept, an animal's sex—specifically, the nature of its gonads—is determined at the time of conception by the chromosomal constitution inherited from its parents. The gonads produce sex steroid hormones that circulate during the early stages of embryonic development; these hormones sculpt the individual's masculine or feminine features. Male sexual traits are instigated primarily by androgens, a class of hormones (including testosterone) produced in the testes. Individuals that lack testes develop ovaries, which generate mostly female hormones called estrogens and progestins. In this scenario, the female is the neutral, or default, sex, whereas the male is the organized sex.

A key element of the organizational concept is the central role of sex steroid hormones. Modern understanding of the influence of such hormones on sexual differentiation began with the work of Frank R. Lillie of the University of Chicago. Early in this century, Lillie observed that when cows gave birth to twins of opposite sexes, the female twin was sterile and had masculine traits. Lillie, who was an embryologist by training, suggested that androgenic hormones secreted by the male twin in the womb imbued the female twin with some male traits. Scientists have since thoroughly corroborated Lillie's conjecture that the gonads in embryos secrete the hormones that cause males to differ from females.

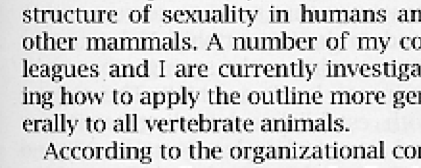
Among mammals, an embryo starts out having a mass of primordial sexual tissue. Genetic signals determine whether that tissue develops into male or female gonads. Subsequent hormonal triggers that act in the embryo control the sex of the genitalia. The testes of genetic males produce significant concentrations of androgens, which induce the formation of the vas deferens, a penis and a scrotum. In the absence of androgens, the embryo acquires female sexual organs: a uterus, a clitoris and vaginal labia.

Accumulating evidence from animal experiments suggests that many components of adult sexuality—not just the structure of the sexual organs—depend on the hormonal environment during fetal development. Some of the most persuasive support of this notion comes from studies of species that produce litters of many young from each pregnancy. During such pregnancies, the fetuses are arranged like peas in a pod inside the uterus. This grouping results in female and male fetuses residing next to one another in random order.

In such an environment, steroid hormones produced by one fetus's gonads could influence the developing neural and secondary and accessory sex structures in an adjacent fetus. Lynwood G. Clemens of Michigan State University discovered that the hormonal surroundings created by neighboring fetuses can profoundly affect adult sexuality in rats. Mertice Clark and Bennett G. Galef of McMaster University have recently observed a similar effect among gerbils.

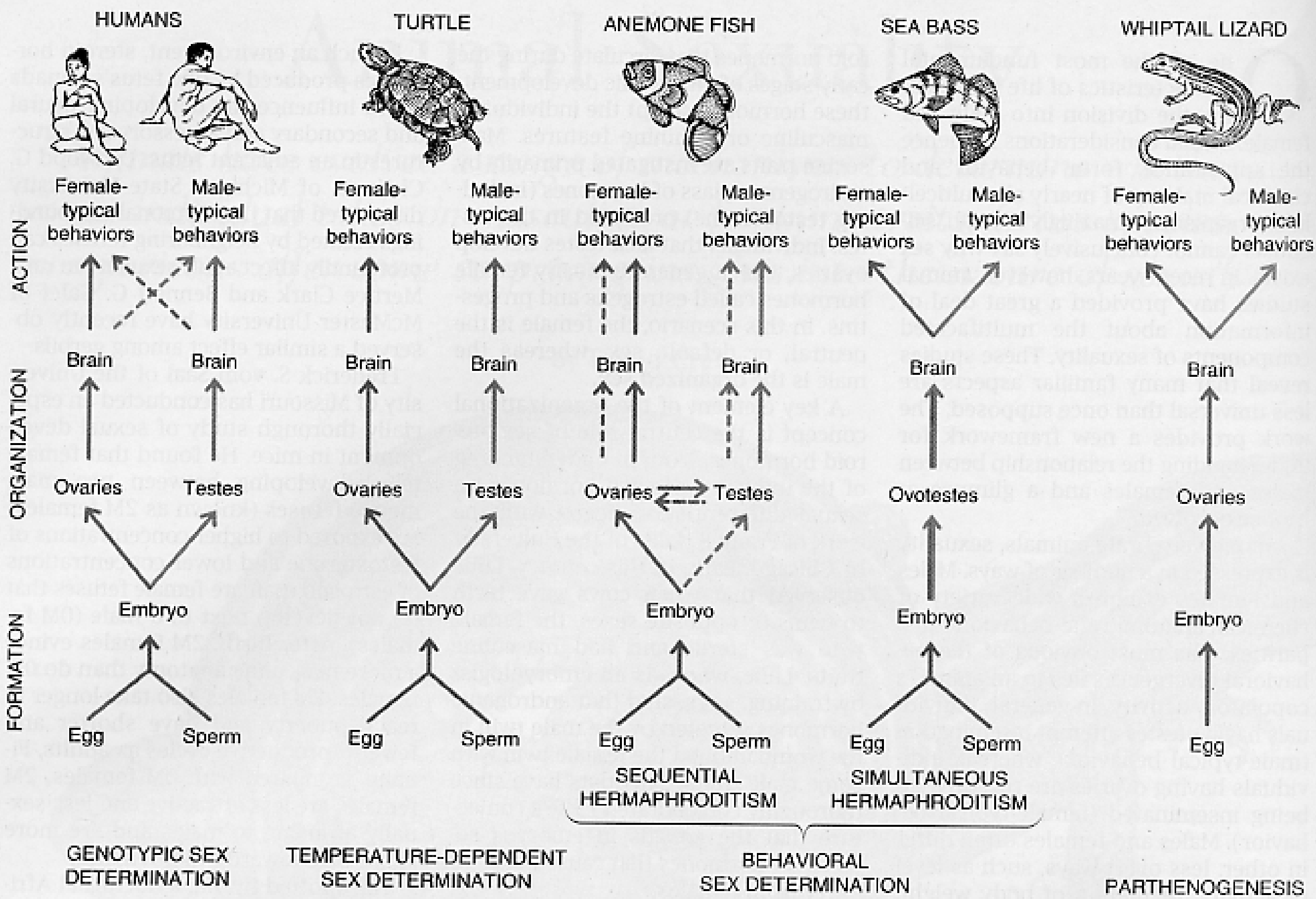
Frederick S. vom Saal of the University of Missouri has conducted an especially thorough study of sexual development in mice. He found that female mice developing between two male mouse fetuses (known as 2M females) are exposed to higher concentrations of testosterone and lower concentrations of estrogen than are female fetuses that do not develop next to a male (0M females). After birth, 2M females evince a more masculine anatomy than do 0M females. 2M females also take longer to reach puberty and have shorter and fewer reproductive cycles as adults. Finally, compared with 0M females, 2M females are less attractive and less sexually arousing to males and are more aggressive toward other females.

The spotted hyena, a nocturnal African carnivore, offers another prime example of how fetal hormones can direct adult sexuality. Female hyenas exhibit many characteristics usually associated with male mammals. Adult female hyenas within a clan, or social group, are larger and heavier than the males; females dominate nearly all of the adult males in aggressive disputes and in access to food. Female spotted hyenas have normal-looking ovaries and internal genitalia, but their external geni-



WHIPTAIL LIZARDS engage in elaborate mating rituals even though some whiptail species consist of self-reproducing females only. Sexual behavior seems to be a deeply ingrained trait that serves biological functions other than just fertilization; for example, mounting induces asexual whiptails to lay more eggs.

DAVID CREWS has spent years exploring the evolutionary roots of sexuality and the role of hormones in controlling sexual differentiation and behavior. He received a Ph.D. in biology from Rutgers University in 1973. In 1982 he moved to the University of Texas at Austin, where he is currently a professor of zoology. Crews's research has focused on sexuality among garter snakes, whiptail lizards and, most recently, red-eared slider turtles and leopard geckos. Crews founded Reproductive Sciences, a biotechnology firm that is using a patented process of hormone-induced sex determination to assist in the breeding of ostriches, emus and other rare birds. In 1992 he also formed Reptile Conservation International, a nonprofit corporation that is using estrogen treatment selectively to build up female populations of endangered turtles in Brazil and Mexico.



SEXUAL DIFFERENTIATION occurs in all vertebrate species but through several quite different mechanisms. In mammals, chromosomes inherited at the time of fertilization dictate whether an individual develops male or female sexual organs. In many reptiles, incubation temperature of the embryo controls an individual's sex. Hermaphroditic animals switch from male to female reproductive behavior, usually triggered by the individual's social environment. Simultaneous hermaphrodites can alternate gender repeatedly. Sequential hermaphrodites change once from male to female, or vice versa. Even parthenogenic species display male- and female-typical sexual behavior.

talia have a strongly masculine morphology. They lack external vaginas, and their labia are fused, forming a scrotal sac complete with two bulging pads of fat that simulate testes. The large, erectile clitoris of a female spotted hyena closely resembles a male's penis. Much like many male animals, female spotted hyenas use their clitorises in greeting displays and in dominance interactions.

Stephen E. Glickman and Laurence G. Frank of the University of California at Berkeley recently deduced that this masculinization occurs in the womb as a consequence of the high levels of the chemical androstenedione in the mother's bloodstream. Androstenedione is an inactive compound that can be converted into either estrogen or testosterone. In the placenta of a pregnant hyena, little of the androstenedione turns into estrogen, which leads to high levels of testosterone in the fetus. The abundant testosterone presumably causes the masculine traits of the female hyenas.

Evidently, some mechanism enables the hormonal environment of an embryo to influence that animal's adult sexual behavior. In 1959 Charles H. Phoenix, Robert W. Goy, Arnold A. Gerall and William C. Young, while working at the University of Kansas, proposed that steroid hormones secreted in mammalian embryos help to organize the sexuality of the brain. Subsequent research has shown that in vertebrates steroid hormones act directly on specific neurons that are linked together in circuits. These neural circuits seem to provide the impetus for behavioral differences between males and females.

Several recent discoveries greatly clarify the link between hormones, brain structure and sexual behavior. For instance, Pauline I. Yahr and her colleagues at the University of California at Irvine identified a nucleus in the gerbil brain that is present only in males. This nucleus lies embedded in an area that helps to control copulatory behavior in male gerbils. Female gerbils injected with androgen early in life develop this "male" nucleus and take on some male behavioral characteristics.

Certain species of small songbirds also manifest hormone-influenced brain structures that seem to correspond to gender roles in courtship. Male canaries begin to sing in the spring, when their androgen levels are high. The singing both establishes breeding territories and attracts females. Females respond to the song but do not sing themselves. Fernando Nottebohm of the Rockefeller University and others have determined that the contrasting behavior of male and female canaries and other songbirds is matched by differences in the structures of their brains.

The workers find that singing is mediated by an interconnected series of brain nuclei that control the vocal organs. The song-control regions in the brains of female songbirds normally are much smaller than those in the brains of the males. Steroid hormones in songbird embryos determine which neurons survive and which die. The result is that the size and number of neurons, as well as the quantity of synapses, in the song-control nuclei are much greater in males than in females.

Nottebohm has shown that the song-controlling brain nuclei vary in size seasonally, waxing and waning in conjunction with the flow of the reproductive cycle. By castrating male songbirds (to lower their androgen levels) or injecting them with androgen (to raise those levels), he and his colleagues have artificially re-created such seasonal changes in singing. In related work, female canaries given appropriate injections of androgen have been induced to sing [see "From Bird Song to Neurogenesis," by Fernando Nottebohm; SCIENTIFIC AMERICAN, February 1989].

A particularly exciting and controversial discovery of a link between sexual behavior and brain structure concerns homosexuality in humans. Simon LeVay, then at the Salk Institute for Biological Studies in San Diego, has reported that the size of a nucleus in the anterior hypothalamus of homosexual men more closely resembles the comparable structure in women than that in heterosexual men. Dean H. Hamer and his colleagues at the National Institutes of Health claim to have found a region on the X chromosome that may contain a gene or genes for homosexuality. If so, the associated brain structure may be under direct genetic control. It is also possible, however, that the hormonal environment surrounding the fetus may partially or totally control the development of the brain nucleus.

These discoveries illustrate the inadequacy of stereotypical divisions of male or female. As the organizational concept makes clear, sexuality depends on subtle hormonal controls, not just on either-or genetic labeling. This finding applies to all the tissues associated with reproduction, including the circuits in the brain that underlie sexual behavior.

In most vertebrate species, adults usually exhibit mating behaviors characteristic of their own gonadal sex, known as homotypical sexual behaviors. Not infrequently, however, individuals also perform behavior patterns normally associated with the opposite sex, known as heterotypical behaviors. For example, females sometimes engage in mounting, and males sometimes solicit being mounted.

Such heterotypical sexual behaviors are a frequent and important part of the social biology of many species, especially among mammals. Female cows commonly mount other females, a practice that seems to help synchronize the reproductive cycles of the herd. In rhesus monkeys, mounting functions as an indicator of dominance and so maintains an orderly social hierarchy. Even though embryonic hormones direct neuronal development, it seems that the brain never completely loses the dual circuitry that permits both homotypical and heterotypical sexual behavior.

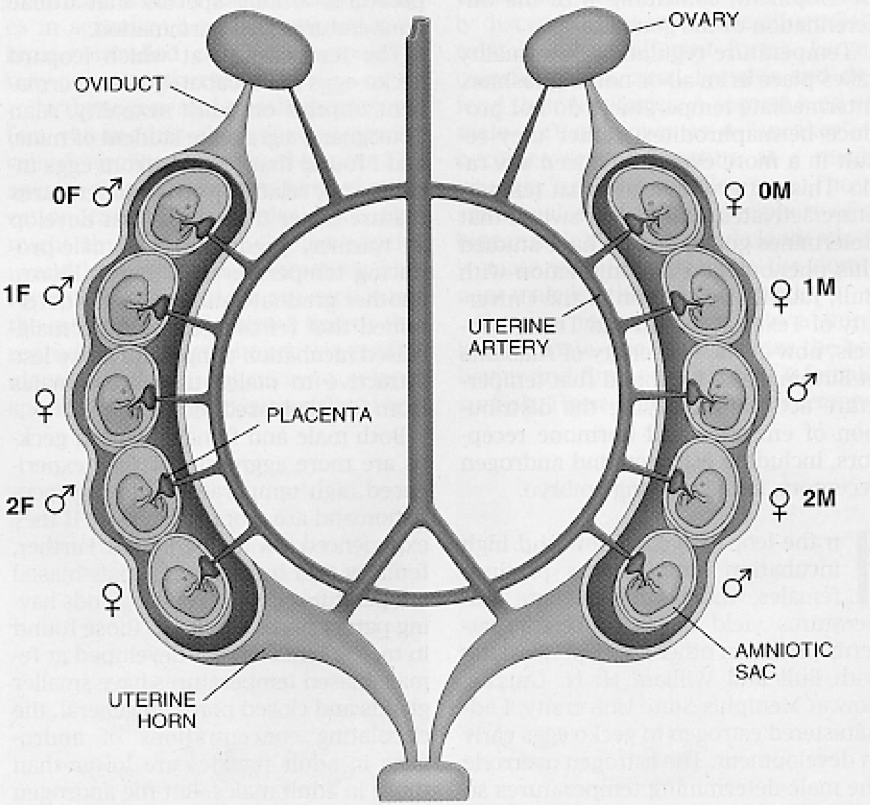
So far the organizational concept seems to offer a complete framework by which to understand animal sexuality. There is, however, a danger in making sweeping statements about its nature on the basis of observations of a very small number of species, all of them warm-blooded vertebrates, such as birds and mammals. To evaluate the resulting conclusions about sexuality, one must look at a far more comprehensive range of vertebrate species. Much of my own research has concentrated on determining how well the organizational concept applies to cold-blooded reptiles and fish.

Such investigations are crucial for elaborating a more complete picture of animal sexuality. The kinds of sexual maturation and behavior found in any particular mammal or bird may reflect the unique adaptations of that species. Sexual traits that are shared by many different kinds of vertebrates, in contrast, presumably date from a more ancient evolutionary stage. Likewise, sexual behaviors (such as mounting) that appear in both males and females may predate more familiar, sex-specific mating activities. Only by knowing the evolutionary roots of sexuality will scientists be able to learn the rules that govern this omnipresent life process.

When viewed through a broadened perspective that embraces the full diversity of vertebrate animals, the organizational concept clearly fails. I see only one truly essential component of animal sexuality: the organizing effects of sex steroid hormones on the tissues that mediate reproduction. The mechanism that directs those effects varies considerably, however.

In the organizational concept, the sex chromosomes exert ultimate control over whether an animal develops into a male or a female. Yet many fish and reptiles lack sex chromosomes. These species depend on nongenetic triggers to guide sexual differentiation.

Among such species, an individual's gender usually depends on the environment it experiences. In some cases, the determining factor is the temperature at which the embryo develops (tem-



HORMONAL ENVIRONMENT in the uterus affects adult sexuality in mice, gerbils and rats. Female embryos surrounded by males on both sides (2M females) are exposed to higher levels of testosterone than those that do not develop next to a male (0M females). Mature 2M females have a masculinized anatomy; they are also more aggressive and less attractive to males than are 0M females. The opposite, feminizing effect is seen in males surrounded by females (2F males).

perature-dependent sex determination). In other instances, the adult's social surroundings control its sex (behavior-dependent sex determination). Certain animal species even dispense with sexual differentiation and reproduce asexually, a process known as parthenogenesis. These nongenetic methods of sexual differentiation may be evolutionary precursors of the chromosomal control used in mammals.

Temperature-dependent sex determination was identified more than 25 years ago, when Madeline Charnier of the University of Dakar in Senegal reported that the temperature at which rainbow lizard eggs are incubated governs that animal's sex ratio. In the late 1970s James J. Bull and Richard Vogt, then at the University of Wisconsin, conclusively demonstrated that temperature activates some as yet unknown sex-determining mechanism.

Scientists now know that temperature controls gender in many kinds of reptiles, including all crocodilians, many turtles and some lizards. Although all temperature-dependent reptiles lack sex chromosomes, their gender, once set, remains permanent throughout their life. In these species, sex determination occurs in the middle of embryological development, coinciding with the differentiation of the gonads.

Temperature regulation of sexuality takes place in an all-or-nothing fashion. Intermediate temperatures do not produce hermaphrodites; rather they result in a more evenly balanced sex ratio. This pattern indicates that temperature activates a biological switch that determines gonadal sex. I have studied this phenomenon in conjunction with Bull, Judith M. Bergeron of the University of Texas at Austin and Thane Wibbels, now at the University of Alabama at Birmingham. We found that temperature acts by modifying the distribution of enzymes and hormone receptors, including estrogen and androgen receptors, in the growing embryo.

In the leopard gecko, low and high incubation temperatures produce females, whereas intermediate temperatures yield males (different patterns prevail in other species). Working with Bull and William H. N. Gutzke, now at Memphis State University, I administered estrogen to gecko eggs early in development. The estrogen overrode the male-determining temperatures so that all of the young had ovaries.

At temperatures close to those that produce females, lower dosages of estrogen suffice to induce the formation of ovaries. Bergeron, Wibbels and I recently recognized that chemicals that inhibit the production of estrogens and androgens can prevent an embryo from developing the usual, temperature-controlled male or female gonads. It seems that sex hormones function as the physiological equivalent of incubation temperatures among species that utilize temperature sex determination.

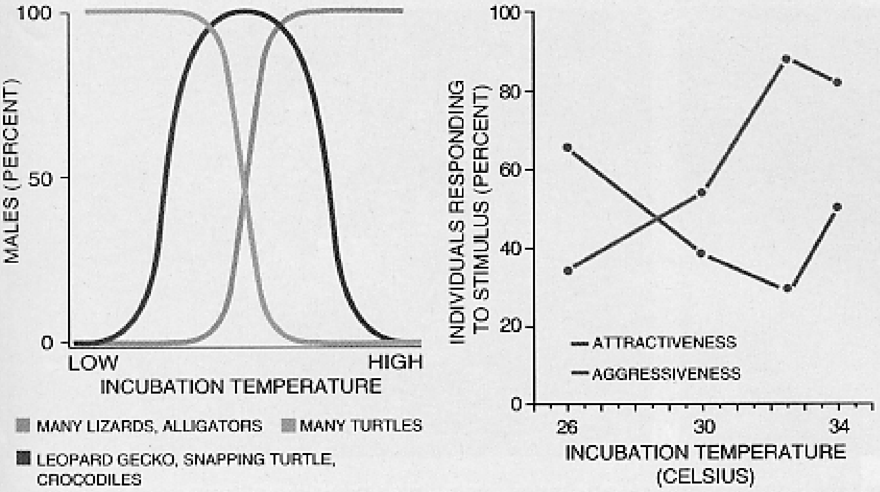
The temperature at which leopard gecko eggs are incubated has a permanent imprint on adult sexuality. Alan Tousignant, a graduate student of mine, and I found that females from eggs incubated at relatively cool temperatures mature faster than those that develop at warmer, predominantly male-producing temperatures. Deborah Flores, another graduate student, and I determined that female geckos from male-biased incubation temperatures are less attractive to males than are females from female-biased temperatures.

Both male and female leopard geckos are more aggressive if they experienced high temperatures during incubation and are more submissive if they experienced low temperatures. Further, females that incubated at male-biased temperatures develop pubic glands having patent pores similar to those found in males; females that developed at female-biased temperatures have smaller glands and closed pores. In general, the circulating concentrations of androgens in adult females are lower than those in adult males. But the androgen levels in females from male-biased temperatures are higher, and estrogen levels lower, than in those that developed at female-biased temperatures. It seems that adult behavior and sexual chemistry reflect an individual's early, temperature-modulated hormonal environment.

Temperature-dependent sex determination may be an evolutionary precursor to the genetic control of gender found in mammals. If so, relics of temperature-sensitive behavior might survive in some higher vertebrates. Several workers, including Evelyn Satinoff of the University of Illinois and Christiana L. Williams of Hunter College, report that modifying the temperature drastically influences the behavior of rat pups. This finding hints that even in mammals temperature changes may modulate the organizing effects of steroid hormones. Perhaps the fairly constant body temperatures of warm-blooded animals mask a surviving mechanism whereby temperature can affect the sexual differentiation of the fetus.

Among temperature-dependent species, sex remains fixed once it is set. But species that experience behavior-dependent sex determination, the other main form of nongenetic control of gender, stray even further from the organizational concept and from genetically determined sex. In most cases, these animals are hermaphrodites—that is, individuals that possess both male and female gonads. The social environment controls whether an individual takes on a male or female reproductive role; in other words, sensory stimuli rather than chromosomes direct sexual differentiation. Even so, hermaphroditic species share many chemical and behavioral characteristics with warm-blooded vertebrates.

Some behavior-dependent species of fish are sequential hermaphrodites.



INCUBATION TEMPERATURE of embryos determines the sex ratio in many kinds of reptiles. Depending on the species, the embryos develop into males predominantly at low, intermediate or high temperatures (*above, left*). Among female leopard geckos, warmer incubation temperatures (up to 32.5 degrees Celsius) engender heightened aggressiveness and reduced attractiveness to males (*above, right*). The photograph (*far left*) shows normal courtship among leopard geckos.

These creatures change from one sex to another during their lifetime but express only one gonadal sex at any given time. Orange and white anemone fish are born male and later develop into females. Certain coral reef fish in the Pacific Ocean and in the Caribbean Sea follow the opposite course, starting out female and becoming male. The timing of the sex change depends on a social trigger, such as the disappearance of a dominant male or female.

Other fish species are simultaneously hermaphroditic, meaning they possess a gonad containing both ovarian and testicular tissue. Interestingly, individuals of these species almost never fertilize their own eggs. Instead they continue to mate, perhaps so as to retain the advantages of genetic diversity provided by sexual reproduction. Eric A. Fischer, then at the University of Washington, showed that mating pairs of hermaphroditic butter hamlet alternate between male and female behavioral roles during successive matings. The sex expressed by an individual fish depends on its social surroundings.

How do sequentially hermaphroditic fish accomplish their gender switch? Such species may change from male to female sexual behavior within minutes after witnessing an appropriate change in the number or social structure of the surrounding fish. That rapid transformation must result from signals originating in the brain. Neural connections between the hypothalamus and the gonads exist in all vertebrates. Leo S. Demski of New College of the University of South Florida observed that electrical stimulation in the hypothalamus region of the brain of the hermaphroditic sea bass can induce the release of eggs or sperm. Perhaps in sequential hermaphrodites these nerves alter the hormonal environment within the gonad; the hormones, in turn, carry the ultimate responsibility for executing changes in sexuality. Less obvious kinds of brain-controlled changes in sexuality may occur in other animals.

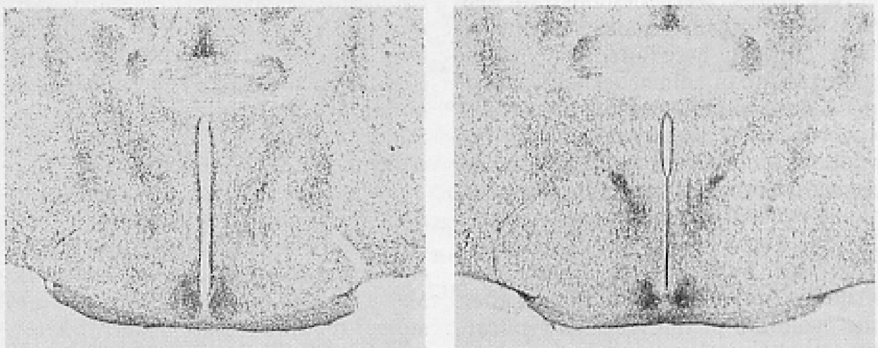
Parthenogenesis, or self-cloning, offers yet another alternative to genetically determined reproductive roles. The species that perform this kind of replication consist of females only. One might think that self-cloning species would have no need of any noticeable form of sexual behavior, yet such is not the case. Species of whiptail lizards that reproduce by parthenogenesis exhibit identical mating behavior to related species that engage in conventional sex, except that each individual alternates between male and female behavior. I have determined that this behavior is controlled by hormones, much as it is in related, sexual species of whiptails.

The persistence of sexual behavior even in an all-female species indicates that such activity is not just a vestigial trait but one that serves an important biological function [see "Courtship in Unisexual Lizards: A Model for Brain Evolution," by David Crews; SCIENTIFIC AMERICAN, December 1987]. Among whiptail lizards, sexual interactions cause the animals to lay many more eggs than they would if they were alone.

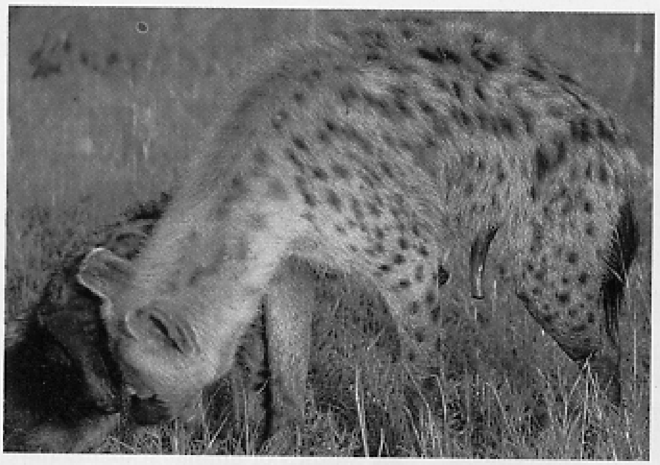
My studies of animal sexuality have convinced me that coordinated, complementary, male and female behaviors are crucial for healthy reproduction, even in single-sex species. It is noteworthy that in certain conventional male-and-female species, members of one sex may turn such coordination to their advantage by imitating members of the opposite sex. Such activity may be thought of as another nongenetic form of sexual differentiation.

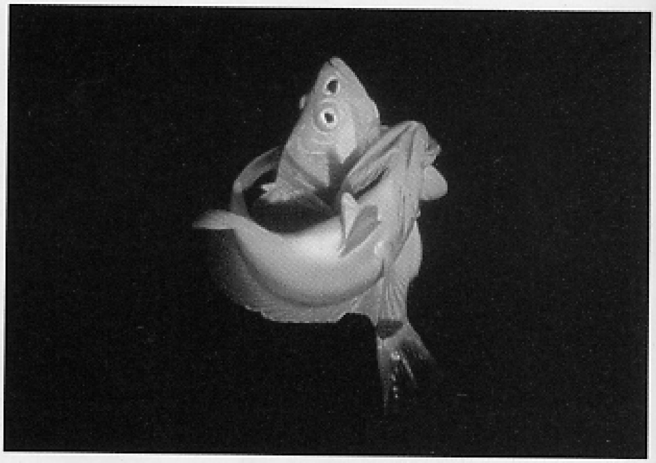
The bluegill sunfish engages in an intriguing form of such gender bending. Wallace Dominey, while at Cornell University, and Mart R. Gross, now at the University of Toronto, independently discerned that male bluegill sunfish exist in three different forms. Large, colorful males court females and defend their territories. A second kind of male—often known as a "sneaker"—becomes sexually mature at a much younger age and smaller size. These small males live on the periphery of a bigger male's territory and clandestinely mate with females while the dominant male is otherwise occupied.

Sneaker males mature into a third kind of male, one that assumes the behavior and drab coloration of a female sunfish. These female mimics intervene



BRAIN STRUCTURE has been linked to sexual behavior in many species. These images show neural differences in the preoptic region of female (*left*) and male (*right*) gerbil brains. That region is involved in the control of masculine copulatory behavior and scent marking, behaviors influenced by androgenic hormones. Females given androgens early in life develop masculine brain structures.





SEXUAL BEHAVIOR does not always cleave neatly into male and female categories. Female spotted hyenas, such as this one with a cub (*left*), have many male behavioral and physical attributes, including a penislike clitoris used in greeting displays. Pairs of hermaphroditic butter hamlet (*right*) repeatedly trade gender roles during mating.

between a territorial male and the female he is courting. The female mimic, rather than the courting male, usually ends up fertilizing the eggs.

Male red-sided garter snakes enact a similar form of sexual mimicry. At times of peak sexual activity, males congregate around females, forming a so-called mating ball. Robert T. Mason, a former graduate student of mine now at Oregon State University, examined many such balls. He found that in 16 percent of the balls, the snake being courted by the males was in fact a disguised male, which we call a she-male. She-males have testes that produce normal sperm, and they court and mate with females. But in addition to exhibiting male-typical behaviors, she-males produce the same attractiveness pheromone as do adult females. In the mating ball, this second source of the pheromone confuses the more prevalent conventional males, giving the she-male a decided mating advantage.

Numerous studies of lower vertebrates clearly demonstrate that the organizational concept we have outlined here offers an incomplete picture of animal sexuality. I propose that a slightly broader view could encompass all vertebrates. I look beyond the kind of genetically determined sexuality encompassed in the organizational concept toward a more comprehensive, evolutionary view of sexuality. That view builds on the notion that males most certainly evolved only after the evolution of the first self-replicating (and hence female) organisms.

In the organizational concept the female is the default sex and the male the organized sex, imposed on the female by the action of hormones. In my alternative scenario, the female is the ancestral sex and the male the derived sex. Consider hermaphroditic fishes. Douglas Y. Shapiro of Eastern Michigan University has found that fish species that are born male and become female nevertheless pass through a modified ovarian stage before developing testes. To me, such observations suggest that males may be more like females than females are like males.

Given that every male must contain evolutionary traces of femaleness, biologists might be well served to focus less on the differences between the sexes and more in terms of the similarities. A logical place to concentrate that search would be the sex hormones that are ubiquitous among vertebrates. Some research directed along these lines is in fact paying off. Endocrinologists have found evidence that estrogen and progesterone, both usually associated only with female sexual behavior, may function actively in the sexuality of both genders. In some species, testosterone is converted to estrogen in the brain; in those species, estrogen activates both copulatory behavior in males and sexual receptivity in females. In songbirds, estrogen originates primarily in the brain, implying that its presence transcends gender boundaries and hinting at the existence of brain-controlled sexuality in some higher vertebrates.

Progesterone is generally thought to inhibit sexual activity in males; it even has been used as a form of chemical castration in felony rape convictions. Most researchers therefore have assumed that progesterone has no place in normal male sexuality. Male rats and humans, however, show a pronounced daily rhythm in progesterone secretion; peak progesterone levels occur at the onset of night, when copulatory behavior most often occurs. Diane Witt of the National Institute of Mental Health, Larry Young, one of my graduate students, and I recently observed that physiological dosages of progesterone can induce castrated male rats to resume mounting. Moreover, injections of RU 486, a hormone that chemically nullifies progesterone, reduces sexual behavior in intact male rats. Like estrogen, progesterone seems to be both a female and a male hormone—an evolutionary relic extending beyond the confines of the organizational concept.

Further investigation of the similarities of males and females may turn up additional instances of "female" aspects of sexuality that might be more correctly viewed as "ancestral." Such work may yield more clues about the mode of action and evolutionary origins of sex steroid hormones. It may also illuminate connections between the mechanisms by which temperature, brain function and genetics determine gender. In this way, researchers will achieve a deeper and richer understanding of the essential nature of sex.

FURTHER READING

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