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The proximate mechanisms underlying mating behavior in naturally occurring species can be fundamentally different from those in more commonly studied laboratory and domesticated forms. In naturally occurring species, reproductive strategies are much more diverse, and mechanisms controlling behavior are correspondingly diverse. A variety of hormonal, environmental, and social cues can be used to activate mating behavior. Which cues are used by particular species depends on differences in environmental and physiological constraints imposed by particular reproductive strategies. Study of this diversity of mechanisms promises to identify specific selective forces that have shaped their evolution. This evolutionary perspective leads to widely applicable generalizations and provides a useful context within which to conceptualize differences between species, populations, and individuals.

THE STUDY OF ANIMAL BEHAVIOR HAS TRADITIONALLY BEEN approached from two directions: one emphasizing proximate physiological mechanisms and the other ultimate evolutionary factors. Because they have asked different questions and concentrated on different kinds of animals, the perspectives have developed independently. This is unfortunate since the advances of one could address the shortcomings of the other. Combining these perspectives should increase understanding of the constraints on, and plasticity of, evolution of fundamental mechanisms controlling behavior.

In this article, we will show that (i) multiple proximate mechanisms triggering sexual behavior have evolved to meet specific environmental challenges, and (ii) this diversity presents natural experiments that can be the basis for further research into the fundamental nature of those mechanisms.

Environmental and Physiological Constraints in the Timing of Reproduction

Evolutionary fitness is best measured by reproductive success, or the survival of an individual's young to the age of first reproduction (*1*). The two major categories of constraints on reproductive success are the environmental and the physiological. Successful reproduction requires that breeding be coordinated with the most favorable time for producing offspring; in many environments this occurs for only part of the year. Food availability, appropriate nesting materials or sites, and predation are ultimate factors shaping the timing of reproductive seasons (*2*). Because of physiological constraints, however, such as the time necessary to grow a mature gamete (*3*) or for young to mature sufficiently before the conditions deteriorate (*4*), species have evolved physiological mechanisms that allow them to anticipate the onset of favorable environmental conditions for reproduction (*5*). Although such constraints do not affect species living in the environments in which favorable conditions are predictable and prolonged, they present serious difficulties for species living in environments with a predictable but abbreviated favorable period and for species living in harsh, unpredictable environments. In both situations, the time available for the female to reproduce and for the young to grow sufficiently that they might survive is brief. This places great selective advantage on phenotypes in which the gametes are available when propitious environmental conditions are present.

From this perspective, the proximate neural mechanisms regulating reproduction can be viewed as adaptational responses to the predictability of favorable environmental conditions. In response to this diversity of environmental conditions, diverse reproductive strategies have evolved (*6*). Recognizing that many known strategies represent points on different continua (*6*), we have chosen to focus on three that reveal some of the fundamental features of the neural mechanisms controlling mating behavior. (i) The associated reproductive pattern is characterized by a close temporal association between gonadal recrudescence and mating (*7*). (ii) The dissociated reproductive pattern is characterized by a complete temporal uncoupling of mating behavior from gonadal maturation and sex steroid hormone secretion; gametes are produced after a breeding season ends and then stored for the subsequent one (*7, 8*). (iii) The constant reproductive pattern is one in which mature gonads are maintained for prolonged periods in a constant state of readiness in preparation for the unpredictable onset of usually brief favorable breeding conditions.

It is not surprising that diverse proximate mechanisms controlling reproductive behavior have evolved. The environmental and physiological constraints on reproductive success also shape the proximate mechanisms controlling sexual behavior. It is useful to regard the evolution of these mechanisms in terms of communication. Behavior, as the link between the internal and external environments, is also the consequence of two dynamic reciprocating systems, one between the organism and its internal physiological state and the other between the organism and its external environment. From this point of view, we can ask how brain mechanisms evolve to exploit internal or external stimuli to ensure that individuals be coordinated with their environment and with one another. A variety of physiological, social, and environmental cues serve as proximate triggers for mating behavior and reproduction; further, the animal's sensitivities to these cues have been evolutionarily modified according to the demands of particular reproductive strategies and environments. This perspective makes it possible to test Ghiselin's proposal that animals "have evolved a nervous system that acts in the interest of [their]gonads, and one attuned to the demands of reproductive competition" (*9*, p. 263).

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Diversity of Mechanisms Controlling Mating Behavior

Studies of species representing nearly every vertebrate class (*10*) have provided evidence that the dependence of mating behavior on hormones is central to vertebrate behavioral endocrinology (*11*); castration of males and females of many species results in a decline in mating behavior that can be restored by replacing the appropriate gonadal steroid hormone. These sex hormones act on specific regions of the hypothalamus—often by modulating the production and release of hypothalamic hormones and neurotransmitters—to alter the probability that an individual will behave in a particular manner.

Because of their essential role in gamete maturation, changing concentrations of sex steroid hormones are particularly well suited as internal signals for triggering mating behavior, especially in those species exhibiting an associated reproductive pattern. In these species, maturation of the gonads and increasing or maximum concentrations of sex steroid hormone secretion immediately precede or coincide with mating.

The variety of organisms whose reproductive behavior depends on steroid hormones has been taken as evidence for an intrinsic functional association among gamete production, sex hormone secretion, and mating behavior, reflecting an evolutionary conservation of hormone-brain-behavior regulating mechanisms (*12*). However, all the data supporting the popular belief of a deterministic relationship between secretion of sex steroid hormones and sexual behavior in vertebrates have come from species exhibiting similar associated reproductive patterns (*7*). Recent studies of species with different reproductive strategies indicate that the similarities in steroid hormone control of mating behavior are as likely due to repeated convergent evolution (homoplasy and analogy) as to descent from a common ancestor (homology).

The male red-sided garter snake (*Thamnophis sirtalis parietalis*) exhibits a dissociated reproductive tactic, in which mating behavior does not coincide with testicular recrudescence or with elevated gonadal hormones (*13*). Most matings occur in the spring on emergence from winter dormancy, when males have small testes and minimal circulating androgen; spermatogenesis and the accompanying high concentrations of androgens occur in late summer. The sperm produced are stored in the epididymis and vas deferens until the following spring (*14*). In early fall the testes regress and the snakes enter hibernacula to spend the winter.

Mating behavior in the red-sided garter snake is activated in direct response to increased ambient temperature following dormancy (*13*). Adult males display courtship and copulatory behavior only if returned to warm temperatures after a period of cold. The display of sexual behavior will be neither inhibited nor prolonged by castration, hypophysectomy, or androgen replacement (*13, 15*); further, administration of a variety of hypothalamic hormones and neurotransmitters (*15*) and even implantation of testosterone directly into the anterior hypothalamus–preoptic area (AH-POA) (*16*) will not activate courtship behavior in adult males maintained under summer-like conditions.

Mating behavior in male red-sided garter snakes can be abolished by placing lesions in the AH-POA either when they emerge from (*17*) or before they enter hibernation (*18*). This region contains temperature-sensitive neurons as well as neurons that concentrate sex steroid hormones (*19*). In view of the uniform lack of effects of sex steroid hormones on mating behavior, it is possible that the decline or absence of sexual behavior in males with lesions in the AH-POA is due to the destruction of these temperature-sensitive neurons. Male red-sided garter snakes with lesions in the AH-POA do not behaviorally thermoregulate (*18*). Thus, the red-sided garter snake seems to have evolved a behavioral response to a specific environmental cue—a shift in temperature—rather than to surges in gonadal steroid hormones.

The research with the red-sided garter snake shows that the mechanisms underlying reproductive behavior in animals with a dissociated reproductive pattern can be fundamentally different from those found in animals with an associated reproductive pattern. In species having a mixed reproductive pattern (in which the sexes exhibit different reproductive patterns), the mechanisms regulating reproduction and mating behavior can differ between the sexes (*7*). For example, in male Asian musk shrews (*Suncus murinus*), mating behavior coincides with testicular growth and depends on testicular androgen; in the female, however, sexual receptivity precedes ovarian recrudescence and is independent of gonadal hormone control (*20*).

Little is known about the proximate mechanisms regulating mating behavior in species exhibiting a constant reproductive pattern. These animals often live in unpredictable environments and are opportunistic breeders (*21*). They frequently initiate gonadal growth in the absence of favorable breeding conditions and maintain mature or nearly mature gonads for long periods. Mating takes place as soon as breeding conditions become favorable. Thus, these species are similar to those with a dissociated pattern in that mating occurs well after the gametes have matured; however, they differ in that mating occurs when the gonads are large and functionally active. As in dissociated species, the surge in gonadal sex steroids that accompanies gonadal maturation would be inappropriate as a cue to activate mating behavior in species with a constant reproductive pattern. However, because successful mating in these species requires the presence of a previously matured gonad, it seems reasonable to expect that gonadal hormones will have only a permissive role. In other words, mating behavior in species exhibiting a constant reproductive pattern is likely activated not by a hormonal cue but rather by an environmental cue associated with the unpredictable onset of favorable breeding conditions. Because these conditions occur unpredictably, some members of the population may still be sexually immature when they are favorable. A permissive requirement for elevated gonadal sex steroid hormones will prevent these sexually immature individuals from exhibiting sexual behavior.

The only well-studied opportunistic breeder is the desert-dwelling zebra finch (*Taeniopygia guttata castanotis*). Male zebra finches maintain spermatogenically active testes, and females have ovaries containing follicles in an advanced resting state until appropriate conditions are encountered (*22, 23*). Rainfall initiates reproductive behavior; zebra finches have been observed to copulate within 10 minutes, to build nests within 4 hours, and to lay eggs within a week after it begins to rain. Although the androgen-dependence of sexual behavior in adult male zebra finches is well established (*24*), elevated androgen concentrations may play only a permissive role; the activational role of water is as yet untested (*23*) since in all studies on mating behavior conducted to date, water has been freely available.

Diversity of mechanisms controlling mating behavior is not restricted to those species exhibiting dissociated or constant reproductive patterns. Other constraints have caused some species with associated patterns to evolve different proximate mechanisms.

The white-crowned sparrow (*Zonotrichia leucophrys*) exhibits a classic associated reproductive pattern. Mating in both sexes coincides with gonadal maturation and occurs in the spring shortly after the birds arrive on the breeding grounds. Only in the female, however, does mating behavior depend on sex steroid hormones (*25*). Male mounting behavior is activated in direct response to a social cue; males in any reproductive or hormonal state will respond to solicitation displays by females by mounting and copulating (*25*).

If they have been exposed to one period of long days at some time in their lives, even long-term castrated, sexually inexperienced males will repeatedly mount sexually receptive females (*25*).

In many vertebrates, the expression of sexual and aggressive behavior coincides with mating, and both are hormonally controlled. In male white-crowned sparrows, however, sexual and aggressive behavior are exhibited by males at different stages of the reproductive cycle, making it unlikely that both behaviors are activated by the same hormonal cue. In this instance, aggressive behavior is activated by hormonal cues whereas sexual behavior is triggered by a social cue (*26*). In white-crowned sparrows there is apparently no selective advantage of linking male mating behavior to hormonal control; even though males are sexually responsive the year round, courtship and mating behaviors occur only for a brief period during which females solicit copulations. Linking the expression of male mating behavior to hormonal control would have no effect on the temporal precision of its expression. Territorial aggression, in contrast, is initiated by the male. Because of this, linking the behavior to hormonal control may have selective advantages; the behavior is expressed only in the breeding season (*27*). Thus, conflicting demands on the hormonal signal may have important evolutionary consequences for whether a behavior is a direct response to a social or environmental cue or is endogenously triggered.

Evolution of Hormone-Brain-Behavior Relationships

The evolution of hormone-brain-behavior relationships can be examined by comparing closely related species. For example, one-third of the 45 species of whiptail lizard (***Cnemidophorus***) consist only of females, reproducing by true parthenogenesis (*28*). The continued existence of the gonochoristic (two sexes) ancestral species of these parthenoforms (*29*) offers a rare opportunity to probe behavior controlling mechanisms.

During the reproductive cycle, parthenogenetic whiptail lizards alternately display female-like and male-like pseudosexual behaviors that resemble those exhibited by the ancestral species (*30–32*). In many gonochoristic vertebrates, the courtship and copulatory behavior of the conspecific male is crucial to normal ovarian growth in the female (*33*). Such stimulation is important even in species that do not reproduce sexually (*34*). In ***Cnemidophorus uniparens***, the presence and behavior of conspecifics facilitate reproduction, maximizing fecundity (*31, 35*). Thus, the pseudosexual behavior is not a useless vestige of the sexual ancestry of this species but serves a biological function, thereby constituting a positive selection pressure favoring maintenance of male-typical behaviors.

Selection for pseudosexual behavior in *C.* ***uniparens*** seems to have resulted in the evolution of a novel hormone-brain-behavior relationship. Both female-like and male-like pseudosexual behaviors of the parthenogenetic whiptail lizard *C.* ***uniparens*** are hormonally mediated; intact, reproductively inactive females and ovariectomized females do not engage in this activity (*31, 32, 36*). Female-like behavior is displayed only by individuals having yolking follicles (*30, 32*). This coincides with maximum circulating concentrations of estradiol (*36*); female-like behavior can be induced in ovariectomized individuals treated with exogenous estrogen (*31, 37*). Thus, female-like behavior is expressed in *C.* ***uniparens*** in the same temporal relationship to the ovarian cycle as in many other vertebrates exhibiting an associated reproductive pattern, and it seems to be controlled by a similar estrogen-dependent mechanism.

Male-typical mounting behavior is common among females of sexually reproducing species, serving to establish dominance or advertise estrus (*38*). In *C.* ***uniparens***, however, the display of masculine coital patterns has a different temporal relationship to the reproductive cycle than is observed in females of many gonochoristic species, occurring most frequently during the postovulatory phases of the cycle (*30–32*). Although male-like behavior can be induced in *C.* ***uniparens*** by exogenous androgens (*31, 35, 37*), neither testosterone nor dihydrotestosterone are present in biologically significant amounts at any time during the ovarian cycle (*36, 39*). In male *C.* ***inornatus***, a direct sexual ancestor of *C.* ***uniparens***, courtship and copulatory behavior depend on testicular androgens (*40*). Therefore, male-like behavior in *C.* ***uniparens*** does not seem to be activated by the same hormonal mechanism that controls courtship and copulatory behavior in a gonochoristic ancestor of *C.* ***uniparens***.

Currently two lines of evidence suggest that the periovulatory surge in circulating progesterone triggers male-like pseudosexual behavior in *C.* ***uniparens***: (i) changes in the concentration of circulating progesterone are closely related to changes in the expression of male-like behavior (*31*), and (ii) administration of exogenous progesterone to ovariectomized females induces male-like pseudosexual behavior (*41*). Progesterone could be acting in *C.* ***uniparens*** directly by binding to androgen receptors (*42*) or by being converted to androgen in the brain (*43*). In mammals and birds, exogenous progesterone has the opposite effect of suppressing androgen-dependent sexual behaviors in males (*44*).

Together, these results indicate that in *C.* ***uniparens*** (i) the neural mechanisms subserving sex-typical behaviors must have been retained from the species' gonochoristic ancestors, (ii) the hormonal sensitivity of the neural substrates of courtship and copulatory behavior has been preserved, and (iii) a hormonal cue other than androgen has been exploited to trigger male-like courtship and copulatory behavior.

Comparative Studies as Natural Experiments

Animal diversity presents natural experiments that enable us to examine the evolution of proximate mechanisms controlling mating behavior as well as to tease apart their component parts. The examples above illustrate that environmental, social, or hormonal cues can be used to trigger mating behavior depending on the specific demands of particular environments and reproductive strategies. In the face of this diversity, are generalizations possible or are we left with the unsatisfying conclusion that there are no underlying patterns?

Certain components of the mechanisms controlling mating behavior have been conserved during evolution. For example, the cellular mechanisms of the action of gonadal hormones on the brain seem uniform across all species studied so far (*45*). However, as the examples described above show, depending on the circumstances, the brain may exploit any convenient and appropriate signal to trigger mating behavior. Can we generalize about the situations that favor exploiting one cue over the other?

For most vertebrates with associated reproductive patterns, mating coincides with gonadal maturation. Thus, the ancient relation between steroid hormones and gametogenesis (*12*) makes the surge in gonadal hormones during gonadal recrudescence an appropriate trigger for mating behavior; no external or social cue could so precisely indicate the timing of gamete maturation. Thus, that mating behavior in many gonochoristic vertebrates depends on gonadal steroid hormones is not because of an evolutionary conservation of mechanism, but because the presence of a hormonal surge is frequently the most appropriate signal for timing reproductive behavior.

As these examples indicate, however, the constraints responsible for a complex reproductive strategy may stimulate the evolution of alternative mechanisms. Conflicting demands on the hormonal signal have resulted in the social activation of mating behavior in male white-crowned sparrows. The absence of males and the low and unchanging concentrations of circulating androgens make the surge in progesterone after ovulation an appropriate cue for triggering the expression of male-like behavior in unisexual whiptail lizards. In species with dissociated reproductive patterns, gonadal maturation follows the optimum time for mating; mature gametes are stored, and mating may occur at any time thereafter. In this instance the surge of sex steroid hormones that accompanies gametogenesis would not be an appropriate cue to activate mating behavior. Species that store gametes, such as the red-sided garter snakes, must use some environmental or social cue to trigger mating.

Gonadal hormones, of course, do more than signal the timing of gamete maturation. Most mating behaviors are sex-specific, and gonadal hormones can act during development to organize neural areas that later regulate these sex-specific mating patterns and physiology in the adult (*46*). This action may be expressed structurally in the growth and death of central nervous system neurons (*47*), or functionally by sensitizing neural substrates to hormone secreted during adulthood (*46*). Gonadal hormones also alter perception, allowing the organism to respond adaptively to appropriate internal and external cues (*48*).

During sexual differentiation, gonadal steroid hormones can be thought of as imprinting the sensory and motor systems to specific stimuli so that the adult animal mates when experiencing a certain constellation of stimulus conditions. The exact neural substrates can be predicted from knowledge of the biologically important stimuli that must be detected for the adult to exhibit mating behavior. These systems should contain steroid hormone receptors and should project directly to the preoptic area and the hypothalamus, the final common pathway in the neural control of mating behavior. These developmental actions of gonadal hormones also account for observed similarities and differences in the distribution of steroid hormone receptors in extrahypothalamic regions of the brain.

In those species in which mating behavior in the adult is independent of direct control by sex steroid hormones, gonadal hormones should play an important role only early in life. This hypothesis is supported by studies on newborn red-sided garter snakes. Although sex steroid hormones are not necessary for the display of courtship behavior in the adult male, the ability to express reproductive behavior in adulthood is affected by treating neonates with testosterone (*49*). Thus, androgens produced during the initial period of gonadal development in this species program the brain so that warm temperatures the following spring initiate mating behavior.

The two factors of paramount importance in determining whether mating behavior is controlled by internal or external signals are whether the behavior (i) is sexually dimorphic and (ii) varies seasonally or developmentally during an organism's life. Because most mating behaviors are at least somewhat sexually dimorphic and because gonadal steroid hormones are the most sexually dimorphic of all hormones in the pattern of their secretion, mating behaviors of most species will probably be organized neonatally by sex steroid hormones. This fact, along with the other known actions of sex steroid hormones on the brain (such as negative feedback regulation of pituitary hormones), accounts for the apparent evolutionary conservation of the cellular mechanism of steroid hormone action on the brain. However, whether a hormonal signal is the most appropriate to activate mating behavior in the adult depends also on the coincidence of the signal with the appropriate time for expression of mating behavior. In males of many species with associated reproductive patterns, a surge of testosterone coincides with the optimum time for activation of male mating behavior. On the other hand, an external cue should be used if it is a more accurate predictor of the appropriate time for mating; in the red-sided garter snake the cue is a change in temperature, and in the white-crowned sparrow it is female solicitation displays. Finally, because relatively few hormonal signals regulate the often complex behavioral transitions, hormonal cues cannot be used when there are conflicting demands on the signal they provide. When such conflicts arise, the availability of alternative cues, both internal and external, becomes important.

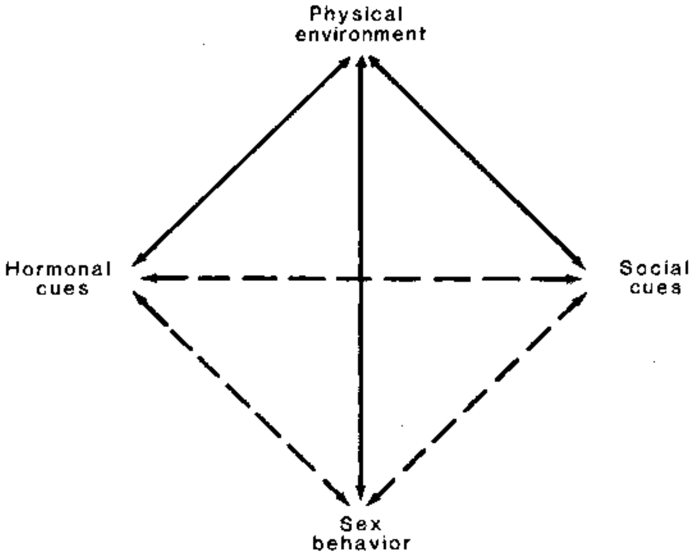

Fig. 1. Because the expression of mating behavior must be synchronized with optimal environmental conditions, differences in the mechanisms controlling mating behavior can be viewed as alternative informational pathways between the physical environment and the central nervous system. Solid lines indicate possible direct effects of the physical environment on the organism; dashed lines indicate possible secondary pathways influencing the expression of sexual behavior. For example, in the most thoroughly studied vertebrates, which have an associated reproductive pattern, the pathway consists of environmental stimulation of gonadal recrudescence, followed in turn by gonadal sex hormone action on the brain; in some of these species social cues may also play a role. In other species, such as the white-crowned sparrow, the pathway is less direct; changes in the environment stimulate ovarian hormone secretion in the female, activating female solicitation displays, a social cue which in turn triggers male mating behavior. In the red-sided garter snake, a species exhibiting a dissociated reproductive pattern, the pathway is more direct, with environmental stimuli (temperature) activating mating behavior.

Study of diverse species also provides information on how the fundamental nature of certain functional associations in reproduction are altered by evolution (*12*). For example, unlike the parthenogenetic whiptail lizards, parthenogenetic female ***Drosophila mercatorum*** have suffered genetic loss of female sexual receptivity (*50,51*). This difference may relate to different origins of the two parthenogenetic forms (*52*). Unisexual lizards arose from hybridization of gonochoristic species (*29*) and have retained the neural mechanisms subserving reproductive behavior, whereas unisexual ***Drosophila*** arose from isolated virgin females (*53*) and have lost these mechanisms.

Although relatively few species have been examined, preliminary generalizations about the relative importance of various factors in the evolution of proximate mechanisms controlling mating behavior are beginning to emerge. These species differences can be usefully conceptualized as differences in informational pathways between the environment and the central nervous system (Fig. 1). Precise conclusions about the relative importance of factors favoring the evolution of one informational pathway over the other require further study of species exhibiting diverse reproductive patterns and subjected to different ecological conditions.

Conclusions

Variation is the fabric of evolution, and the evolutionary perspective can provide the context to interpret observed variation. Reproductive success ultimately depends on a precise synchronization of an organism's activities with its external environment. In response to selection pressures to maximize reproductive success, alternative reproductive strategies and multiple proximate mechanisms underlying mating behavior have evolved, even within the same species. During evolution, any stimulus from the internal or external environments may be co-opted by the brain as a signal and serve as the trigger for mating behavior.

The purpose of this article has not been to provide answers so much as to point to new directions in research, namely the need for (i) investigation of diverse organisms under ecologically relevant conditions and (ii) comparative studies of closely related species or taxa. As evolutionary and physiological perspectives are integrated, another view of the relation between the different levels of organization necessary for reproduction will emerge. Especially needed are further studies of species in which (i) temporal expression of social behaviors does not coincide with gonadal maturation, (ii) social behaviors are not sexually dimorphic or are "reversed" in their dimorphism, and (iii) complex expression of social behaviors places conflicting demands on hormonal signals. These studies should allow us to predict the specific circumstances in which an internal versus an external stimulus will trigger mating behavior. Similar advances will come from the study of species in which individuals exhibit alternative life history strategies (*54*) or differences in reproductive responsiveness to environmental stimuli (*55*). Only through studies of diverse species both in the field and in the laboratory will the evolution, and hence the ultimate plasticity, of proximate mechanisms controlling mating behavior be revealed.

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