THE EVOLUTIONARY ANTECEDENTS TO LOVE

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SUMMARY

Behaviors are adaptations to the physical, biotic, and social environments. Great diversity exists among vertebrates in reproductive behaviors and the neuroendocrine mechanisms underlying these behaviors. Study of this diversity illuminates species, population, and sex differences in hormone–brain–behavior relations. It also can provide insights into how and why certain neuroendocrine mechanisms evolved. Discoveries in evolution and ecology, neuroscience and endocrinology, are complementary and interrelated, and when applied in behavioral neuroscience, the investigator’s perspective is less constrained by existing dogma. Naturally-occurring organisms not typically studied can be especially useful as their unusual adaptations illustrate alternative solutions to particular problems. Indeed, they ‘often force one to abandon standard methods and standard points of view’ with the result that, ‘in trying to comprehend their special and often unusual adaptation, one often serendipitously stumbles on new insights’ (Bartholomew, 1982). Thus, to ignore comparative research would greatly limit our understanding of the evolution of hormone-behavior relations. As Bullock (1984) admonishes, ‘without due consideration of the neural and behavioral correlates of differences between higher taxa and between closely related families, species, sexes, and stages, we cannot expect to understand our nervous systems or ourselves’. © 1998 Elsevier Science Ltd. All rights reserved.

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INTRODUCTION

Love, according to Webster’s Unabridged Dictionary, is a strong, usually passionate, affection for a person. The Oxford English Dictionary defines love as an intense feeling of deep affection or fondness for a person or thing, a sexual passion, or sexual relations. Love then is an emotion often associated with consensual sexual activity, or the willing, even eager, participation of the individuals involved.

It is my opinion that love is a human emotion that has its biological foundations in the sexual and parental bonds described by many of the other papers in this symposium. It also is my opinion that the question of whether ‘love’ exists in animals is anthropocentric. When looking for evolutionary antecedents, it is more parsimonious to focus on the sexual and reproductive behaviors associated with love, not on our individual understandings of the emotion called love. This essay will develop the concept that association or affiliation, an essential component of love, is essential in social organisms because it increases fitness.
The nonhuman equivalent of consensual sexual activity is stimulus–response complementarity as defined by Beach (1976, 1979). At its most basic level, S–R complementarity means that for a male to successfully mate, the female must be receptive to his efforts (Fig. 1) (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. For example, the male not only provides the sperm necessary for fertilization of the female's ova, but he also provides the behavioral stimuli necessary to insure 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 females' normal reproductive activity (Crews, 1974; Stacey and Cardwell, 1996). This behavioral interaction thus is a major component of fitness.

First described 60 years ago by Marshall (1936), the behavioral facilitation of reproduction has been demonstrated in numerous vertebrate and invertebrate species in the 40 years since the first experiments of Lehrman (1956) (Table I). In fact, 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 eukaryotes, but rather have mating types.

Fig. 1. The complementarity of mating behaviors. There is a reciprocal relationship between the internal and external environments in the control of mating behavior in vertebrates. The behavior of the male and the female help to synchronize the maturation and release of the sperm and eggs so that fertilization occurs. Changes in climate, ecology, or behavior of other members of the species initiate and modulate gonadal and hormonal changes during reproduction. Thus, hormones regulate behavior in the individual animal and are themselves affected by other stimuli, including the behavior and, indirectly, the physiology of its mate. In such dynamic systems, each successive phase of reproduction depends upon preceding events and, at the same time, sets the stage for the following phase.
Table I. Some examples of behavioral facilitation of gonadal growth, sex hormone secretion, fecundity, or the abundance and quality of sperm in vertebrates

<table>
<thead>
<tr>
<th>Species</th>
<th>Male → Female</th>
<th>Female → Male</th>
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</thead>
<tbody>
<tr>
<td>Mammals</td>
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<tr>
<td>Rats</td>
<td>+</td>
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<tr>
<td>Musk shrew</td>
<td>+</td>
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<tr>
<td>Vole spp.</td>
<td>+</td>
<td>+</td>
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<tr>
<td>Rabbit</td>
<td>+</td>
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<tr>
<td>Ferret</td>
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<td>Cat</td>
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<td>Birds</td>
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<tr>
<td>Ring dove</td>
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<tr>
<td>Canvasback duck</td>
<td>+</td>
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<tr>
<td>White-crowned sparrow</td>
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<tr>
<td>Reptiles</td>
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<tr>
<td>Green anole lizard</td>
<td>+</td>
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<tr>
<td>Red-sided garter snake</td>
<td>+</td>
<td>+</td>
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<tr>
<td>Leopard gecko</td>
<td>+</td>
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<tr>
<td>Whiptail lizards</td>
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<td>+</td>
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<tr>
<td>Amphibians</td>
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<tr>
<td>Bullfrog</td>
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<tr>
<td>Clawed frog</td>
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<td>Fish</td>
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<td>Goldfish</td>
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Arrow symbol indicates the direction of the effect.

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 population growth trajectory.

What about organisms that reproduce by asexual means? Do they exhibit a behavioral facilitation and synchronization of reproduction? This idea evidently had not occurred to anyone before our initial studies (Crews and Fitzgerald, 1980). But an examination of cloning species for this trait reveals surprisingly clear evidence for behavioral facilitation of reproduction. For example, the entire reproductive cycle of the slime mold is predicated on the behavioral interaction of individual organisms. In parthenogenetic lizards, interacting with clone-mates increases the number of eggs laid.

But what about plants? Plants tend to be sedentary, have a poorly developed sensory system, and do not behave as do animals. Yet there is evidence of behavioral facilitation of reproduction in plants, indicating its fundamental nature in reproduction. Consider the dandelion, which produces both pollen and ovules, yet it reproduces asexually or by cloning. Although the dandelion produces pollen, it is pseudogamous in that the pollen cannot fertilize other dandelions. Does this presence of dioecious primary sexual characters in the dandelion represent an evolutionary vestige from its sexual ancestry, or is there a functional significance waiting to be uncovered? The latter appears to be the case. Consider the wild garlic. Ronsheim (1996) recently has demonstrated that wild garlic surrounded by genetically identical neighbors outperform other wild garlic surrounded by unrelated neighbors. Ronsheim also discusses other examples of this positive interaction in other asexual plants, suggesting that it may be common.
Finally, in the one organism believed to have always been asexual since its inception, the blue-green algae or cyanobacteria, interaction appears to underlie the reproductive ‘blooms’. Starr et al. (1995) recently have isolated and identified a pheromone in green algae (*Chlamydomonas* spp.) that facilitates the reproductive process (Jaenicke, 1991). 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.

These two facts, that: (i) behavioral facilitation of reproduction occurs in all kinds of organisms, ranging from blue-green algae to mammals; and (ii) the diversity of organisms exhibiting behavioral facilitation is greater than the diversity of organisms exhibiting sexual reproduction (meiosis), suggest that behavioral facilitation is more fundamental, or more ancient, than is sexual reproduction.

**DIVERSITY OF REPRODUCTIVE PATTERNS AND THEIR UNDERLYING PROXIMATE MECHANISMS**

Reproductive success, along with variation, are the essential ingredients of evolution. Reproductive success can be defined as the production of young that themselves reproduce. So, two generations of sexual behavior are required for any single individual to be considered successful in its reproductive efforts. Reproductive success depends upon appropriate and synchronized sexual behaviors which have functions other than simply coordinating the meeting of the gametes. That is, the behavior of each individual affects the physiology, and thus the behavior of other individuals, thereby synchronizing the complex physiological and behavioral events that culminate in fertilization. Everything is geared toward this moment, and for this reason Michael Ghiselin states ‘we have evolved a nervous system that acts in the interest of our gonads, and one attuned to the demands of reproductive competition’.

The variety of reproductive patterns are enormous, yet relatively little is known about the mechanisms that underlie these different processes and forms. Thus, it is important to

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**Fig. 2.** The three major components of the reproductive process in vertebrates are the gametes (sperm and ova), the steroid hormones produced by the gonads, and the behaviors associated with mating. In species in which the pattern of gonadal activity is associated temporally with mating, as occurs in many mammals and birds, these elements are functionally associated. This has led to the paradigm that mating behavior is activated by increasing levels of gonadal steroid hormones in the circulation. However, there is no intrinsic functional association among these elements. Indeed, studies indicate that the dependence of mating behavior on sex hormones depends upon the reproductive pattern exhibited, which in turn, depends upon various ecological, phylogenetic, developmental, and physiological constraints. The solid line indicates the only functional association shared by all living vertebrates, indicating that it is the primitive or ancient characteristic. The dashed lines represent the various functional associations that have evolved in different lineages. Whether these derived associations evolved independently, and therefore are analogous, or in a common ancestor and therefore are homologous, in vertebrates will only be determined through comparative analysis.
Fig. 3. Three types of reproductive patterns exhibited by vertebrates. Gonadal activity is defined as the development of eggs and sperm and/or increased sex steroid hormone secretion. Individuals exhibiting the associated reproductive pattern (solid line) live in temperate regions where seasonal cycles are regular and prolonged; in such species, the gonads are fully developed at the time of mating and circulating levels of sex hormones are maximal. Individuals exhibiting the dissociated reproductive pattern (dashed line) live in extreme environments in which seasonal changes are regular, but the length of time available for breeding is limited; in such species, the gonads are small and sex steroid hormone levels are low at the time of mating. Individuals exhibiting a constant reproductive pattern (hatched line) live in harsh environments where breeding conditions are completely unpredictable; in such species, the gonads are maintained at nearly maximal development so that when breeding conditions do arise, breeding can occur immediately. Just as the reproductive cycles have adapted to the environment, so too have the neuroendocrine mechanisms subserving breeding behavior.

keep in mind that we only understand what we study. When coupled with the marked tendency to study only what we know, there often is the unfortunate sequelae that we see only what we know. For example, it is a fact that early this century a variety of animals were studied by behaviorists, anatomists and physiologists. But with advances in knowledge came a sharp reduction in the species utilized in biomedical research such that, by the 1950s, inbred rodents and some primates were the preferred animal models. The tacit assumption is that the mechanisms observed in laboratory preparations are similar to those of humans. But too often this leap of faith has proven fallacious.

Fig. 4. Fixed versus flexible sex ratios in vertebrates. In genotypic sex determination (bottom panel), the sex ratio is fixed at 1:1, whereas in environmental sex determination (top panel), the sex ratio is responsive to environmental conditions and can vary anywhere between all-male or all-female sex ratios.
D. Crews

Fig. 5. Different mechanisms of sex determination in vertebrates. In vertebrates with sex chromosomes (male or female heterogamety), gonadal sex is fixed at fertilization by the union of specific chromosomes. Only after the gonad is formed do hormones begin to exert an influence, sculpting specific structures that eventually will differ between the sexes. Research on reptiles with temperature-dependent sex determination indicates that sex determination in such species is fundamentally different in at least one way. Gonadal sex is not irrevocably set by the genetic composition inherited at fertilization, but rather depends on which enzymatic and hormone receptor genes are activated during development by temperature. Incubation temperature modifies both the temporal and spatial sequence of enzymes and hormone receptors such that sex-specific hormone milieus created in the urogenital system of the developing embryo determine gonad type. Research on fish with behavior-dependent sex determination suggests that social stimuli encountered by the adult leads to sex change via the brain, acting first on hypothalamic neurons that secrete hormones which, in turn, act on neurons that project to the gonads. The activity of these neurons modifies the endocrine environment within the gonad, bringing about gonadal transformation. In such species alternative forms of sexual differentiation may exist.

The revival of the comparative approach has yielded new insights and prompted new research into questions important to human health. A characteristic of these new studies is a renewed appreciation for evolution. Let us take, for example, the study of behavior. It long has been recognized that behavior is the leading edge of evolutionary change (Mayr, 1963), but only recently has it been realized that reproductive behaviors, in particular, have a ‘disproportionate influence on brain evolution’ (Bullock, 1984). Studies of various organisms representing other evolutionary trajectories and inhabiting various environments have given us a glimpse at what may actually be fundamental to reproductive behavior (Crews, 1989, 1992, 1993).

A case in point is the functional association among the three basic components comprising vertebrate reproduction: gametes, steroid hormones, and behavior (Fig. 2). For years it was assumed that a fundamental linkage existed between the production of
gametes, the secretion of gonadal steroid hormones, and the expression of sexual behavior. However, of the six relationships possible among these three elements, only one can be regarded as fundamental, namely that gametes cannot be produced independent of steroid hormone secretion (Crews, 1984, 1987). 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 a number of studies into the ecological, phylogenetic, developmental, and physiological constraints that have given rise to the wide variety of neuroendocrine mechanisms that subserve sexual behavior among vertebrate animals (Fig. 3). Such comparative research has revealed that the areas in the limbic forebrain involved in the regulation of social and sexual behaviors are ancient and conserved among vertebrates. It has also revealed that differences in the distribution of sex steroid concentrating neurons are rare, but differences in the distribution of steroid hormone receptors as well as differences in the regulation of steroid hormone receptors are common. Further, species differences in plasma levels of sex hormones are paralleled by differences in behavioral sensitivity to these hormones as well as by differences in the regulation of genes coding for steroid hormone receptors.

**DIVERSITY OF MECHANISMS OF SEX DETERMINATION**

Another discovery of great importance for human health concerns the discovery of alternative sex determining systems in the higher, or the amniote, vertebrates (the mammals, birds, and reptiles) (Bull, 1983). We all are familiar with the fact that in a genotypic sex determining system, the secondary sex ratio, or the number of males to females at birth, approximates 1:1 (Fig. 4). However, this is not fixed at unity as evidenced by the fact that significantly more eggs are fertilized by Y-bearing sperm, resulting in a primary sex ratio, or the number of males to females in utero, being significantly

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**Fig. 6.** The organizational concept (top panel) postulates that the female is the neutral or the default sex, whereas the male is the organized sex. This paradigm emphasizes how males and females differ. The organizational concept does not apply to vertebrates lacking sex chromosomes. An alternative paradigm (bottom panel) focuses more on the common origin of male, namely a single fertilized egg. Since males evolved only after the evolution of self-replicating (= female) organisms, the female can regarded as the ancestral sex, whereas the male is regarded as the derived sex.
Fig. 7. All vertebrates display complementary sexual behavior patterns. However, they accomplish this by different means. Illustrated are the paths to the display of sexually dimorphic behaviors in the various forms of reproduction exhibited by vertebrates. Even in unisexual species pseudosexual matings are seen. 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 the width of the arrows connotes early organizational effects of sex hormones on the probability that sexual receptivity (female-typical behaviors) and mounting and intromission (male-typical behaviors) will be shown by the breeding adult. Since comparable information is not available for the other forms of reproduction, all lines in other modes of reproduction are of equal width.
Evolutionary Antecedents to Love

Fig. 8. The evolution of the parthenogenetic whiptail lizard, *Cnemidophorus uniparens*. The all-female, parthenogenetic whiptail arose from the hybrid mating between two sexual species.

male-biased. Recently it has been established that a number of factors, including the hormonal condition of the parents, the timing of insemination relative to ovulation, social rank, and even the age difference of the parents can skew the secondary sex ratio. The mechanisms underlying this manipulation are unclear, but may involve the differential mobility of X- and Y-bearing sperm or differential investment in male or female zygotes in utero leading to higher miscarriage rate of one or the other sex.

But some animals lack sex chromosomes entirely. In such animals some aspect of the environment determines sex (Fig. 4). This can occur either early in embryonic life, forcing the embryo to become a male or a female, thereby adopting one of two mutually exclusive trajectories in life history, or can occur later in life when the individual changes sex after it has already reproduced. Examples of the former are many turtles in which sex is determined in the middle of embryogenesis by the temperature experienced during incubation. The latter would include sequentially hermaphroditic fish in which individuals are first male and then female (protandry) or first female and then male (protogyny). In both instances the individuals gonochoristic, existing either as males or females, but have the potential to adopt the other life history. The notable difference between these species and those with sex chromosomes is that the primary and secondary sex ratio can be extreme, with clutches being all-male, all-female, or anywhere in between. While environmental sex determination has been known for some time in plants, single-celled organisms,
Fig. 9. Sexual and pseudosexual behavior in whiptail lizards. The left and right panels show the mating sequence in the little stripped whiptail lizard (Cnemidophorus inornatus) and the desert grasslands whiptail lizard, (C. uniparens). In these and all sexual species of whiptail lizards, the male approaches and investigates the female with his bifid (split) tongue, presumably indicating involvement of chemical senses. If sexually receptive, the female stands for the male, allowing him to mount her back and grip with his jaws either a portion of the skin on the female’s neck or her foreleg. As the male rides the female, he scratches her sides and presses her body against the substrate. The male then maneuver his tail beneath the female’s tail, apposes their cloacal regions, and intromits one of two hemipenes. With intromission, the male shifts his jaw-grip from the female’s neck to her pelvic region, thereby assuming a contorted copulatory posture termed the doughnut. This posture, which
Evolutionary Antecedents to Love

Invertebrates, and even some fish, it was not known to occur in the higher vertebrates until about 20 years ago.

As might be imagined, the mechanisms of sex determination in species exhibiting environmental sex determination are different from those found in species with sex chromosomes (Crews, 1987, 1993) (Fig. 5). Importantly, however, the process of sexual differentiation of the phenotype appears to be similar after the gonads have formed.

THE ORGANIZATIONAL CONCEPT IS LIMITED TO VERTEBRATES WITH SEX CHROMOSOMES

The ‘organizational concept’ (Fig. 6, upper panel), developed from research with mammals, postulates that the female is the neutral or the default sex, and the male is the dominant or organized sex. This concept does not apply to vertebrates lacking sex chromosomes, however (Crews, 1993). An alternative paradigm (Fig. 6, lower panel) not only accommodates the large literature that has been gathered on sexual differentiation in animals with sex chromosomes, but also incorporates new findings on species that lack sex chromosomes.

This new paradigm hinges on the fact that males evolved only after the evolution of self-replicating (= female) organisms. Thus, the female can be regarded as the ancestral sex, and the male as the derived sex. In addition to offering an alternative view of the sexual differentiation process in the brain (Figs. 7 and 8), this perspective raises the intriguing possibility that males may be more like females than females are like males.

Four lines of evidence support this speculation: (i) the ease of masculinizing versus the difficulty of defeminizing mammals; (ii) maleness is imposed upon a female phenotype, not vice versa; (iii) recent findings that female development is an active, organized process rather than a default state; and (iv) the creation of males in parthenogenetic females, indicating that the genes of maleness are present in all-female species, but normally are suppressed. Thus, George Bernard Shaw may have posed the wrong question in his play ‘Pygmalion’ “why can’t a woman be more like a man?” A better and more interesting question may in fact be … why might males be more like females, than females like males?

THE EVOLUTION OF NOVEL NEUROENDOCRINE MECHANISMS

The neuroendocrine mechanisms that underlie complementary sexual behaviors must also differ in species that have different sex determining mechanisms. While all vertebrates display complementary sexual behavior patterns, they accomplish this by different means.

is characteristic of all species in this genus, is maintained for 5–10 min, after which he dismounts and leaves the female. *Cnemidophorus inornatus* is the maternal ancestor of the all-female desert grasslands whiptail (*C. uniparens*). The right panel depicts a similar sequence in this parthenogenetic whiptail lizard. During pseudosexual behavior, the mounting (male-like) individual will swing its tail beneath that of the mounted (female-like) individual, appose the cloacal regions and shift its jawgrip from the neck to the pelvic region of the mounted individual, forming the doughnut posture. Since parthenogens are morphologically female, there are no hemipenes and intromission does not occur.
Illustrated in Fig. 7 are the paths to the display of sexually dimorphic behaviors in the various forms of reproduction exhibited by vertebrates. Even in species lacking males altogether, such as the parthenogenetic species, complementary pseudosexual behaviors occur. This can only mean that the organization of brain process underlying these behaviors must be different from that of species with sex chromosomes.

If the plasticity of the brain has facilitated this diversity of neuroendocrine mechanisms, can we put together a plausible scenario of how this may have occurred or, better yet, find any examples of evolution in action? A case in point is the all-female, parthenogenetic whiptail lizard *Cnemidophorus uniparens*. This species arose from the hybrid mating between two sexual species; specifically, *C. inornatus* and *C. gularis* (Fig. 8). Because representatives of both the ancestral (sexual) and descendant (parthenogenetic) species still exist, we have a snapshot of evolution in that we can compare the ancestral with the descendant species.

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**Fig. 10.** Evolution of a new neuroendocrine system. Relation among male-like and female-like pseudosexual behavior, ovarian state and circulating levels of estradiol and progesterone during different stages of the reproductive cycle of the parthenogenetic whiptail lizard. The transition from receptive to mounting behavior occurs at the time of ovulation (arrow). Also shown are the changes in the genes coding for estrogen receptor and progesterone receptor in the preoptic area and the ventromedial hypothalamus, brain areas which are involved in the regulation of male- and female-typical sexual behaviors.
The behavior and its controlling mechanism we have studied is the stereotyped courtship and copulatory behavior characteristic of whiptail lizards (Fig. 9). This was selected because even though males are no longer present, the parthenogen continues to exhibit pseudosexual behaviors that are remarkably similar to those seen in the sexual species (Fig. 9).

This phenomenon of pseudosexual behavior in an all-female species immediately raises the question of homosexuality and whether the equivalent of same-sex love in humans is common, and therefore ‘natural’, in non-human animals. If one defines homosexuality as sexual activity between individuals of the same sex, then it is common among non-human animals. This literature has been reviewed by myself and others and I refer the reader to these sources (Crews, 1987; Dagg, 1984). However, if homosexuality is defined as a sexual preference for individuals of the same sex, then it is rare among non-human animals. Thus, homosexual behavior is biological reality, but homosexuality is a human societal issue and not an issue of biology.

In *C. inornatus*, the maternal ancestral species, the courtship and copulatory behavior of the male is dependent upon testicular androgens, although there is a polymorphism in the sensitivity to progesterone. In progesterone-sensitive males, exogenous progesterone will reinstate sexual behavior in castrated males. In the descendant parthenogen, there is no circulating androgen to stimulate the male-like pseudosexual behavior, although the parthenogen retains a sensitivity to exogenous androgen. Since complementary behaviors are necessary for normal reproduction, the periovulatory surge in progesterone has been co-opted as the trigger for the transition from receptive to mounting behavior (Fig. 10). This relationship between male-like and female-like pseudosexual behavior, ovarian state, and circulating levels of estradiol and progesterone during different stages of the reproductive cycle is depicted in Fig. 10. Also shown are the changes in abundance of the gene transcript coding for estrogen receptor and progesterone receptor in the preoptic area and the ventromedial hypothalamus, brain areas which are involved in the regulation of male- and female-typical sexual behaviors.

Finally, in the sexual ancestral species, both brain areas are sexually dimorphic in a complementary fashion, but not in the parthenogen. That is, the brain is bisexual in a functional sense, but not in a structural sense. Further, there is strong evidence that the neural activity in the brain predisposes the animal to behave in a particular manner. That is, behavior is a consequence, not a cause of brain activity.

**CONCLUSION**

Reproduction is essentially an affiliative behavior. Affiliation is an essential property of the emotion we call in humans love. This essay has illustrated how the study of diverse organisms can identify what is fundamental (= evolutionarily ancient) versus derived (= recently evolved). The fact that the behavior of an individual, which emerges from its’ internal state as well as its previous experience, influences the behavior and physiology of other individual, is found in all living organisms, suggesting that it is both ancient and fundamental to reproduction.

Despite this conservation of function in the consequences of behavior, the routes to achieving this end are incredibly diverse. Study of the diversity of mechanisms that underlie the basics of sex determination and sexual differentiation can reveal much about the evolution of the mechanisms that underlie the display of these behaviors. Limbic nuclei
are an ancient part of the vertebrate brain and known to be sensitive to sex steroid hormones and involved in the regulation of social and sexual behaviors. However, evolutionary history has modified how these elements are regulated. Taking advantage of closely related species, systematic studies of one animal model system has shown how new hormone–brain-behavior mechanisms can evolve.

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