Animal Models and Psychological Inference

Frank A. Beach

"When I use a word," Humpty Dumpty said, in a rather scornful tone, "it means just what I choose it to mean—neither more nor less."

"The question is," said Alice, "whether you can make words mean so many different things" (Lewis Carroll, Alice Through the Looking-Glass, Chapter 6).

Humptydumptyism is endemic during interdisciplinary discourse in which different kinds of specialists use the same words to mean quite different things. Attacks of this disease are difficult to diagnose, because those afflicted with it often are misled by what Quine has termed "the implicit assumption of a mutual understanding." The dangers are acute in a congregation of travelers from lands so distinct ecologically as sociology, anthropology, psychiatry, biology, and psychology. The antibodies of one population afford little protection against the viruses of another.

As a comparative psychologist I live in a border zone between biology and psychology, and am particularly sensitive to dangers inherent in using the same vocabulary to describe behavior of different species. For example, the word sex can and should mean the same thing in relation to all species that reproduce sexually; but sexuality and gender are terms applicable only to Homo sapiens (Beach, 1974). This is no mere semantic quibble. Language is more than a tool for describing the world. It is a means of creating the world.

A powerful semantic device is the metaphor, and one form of the metaphor currently popular in behavioral science is

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the so-called animal model, which plays an increasingly important role in such diverse fields as sociobiology (Wilson, 1975) and psychiatry (McKinney, 1974).

Animal models for human behavior are seductively easy to fabricate. Many have been constructed without adequate empirical foundation, and in violation of the simplest rules for analogical reasoning in comparative science. I propose to illustrate the relevance and importance of such foundations and rules to the topic of this volume by analyzing one of the many comparisons that have been made between animal and human sexual experience—namely the phenomenon of female orgasm, which serves as a convenient example. The issues I shall raise are equally applicable to all interspecific comparisons of behavior. I believe they deserve first priority because "simple" comparisons between behavior of different species lie at the heart of evolutionary interpretations of human sexuality and, in fact, constitute the raw material of all sociobiological theories.

Constraints on Interspecific Comparisons
If building behavioral models is to amount to anything more than arm-chair theorizing, it must conform to two simple requirements: (1) Intraspecific analysis must precede interspecific generalization. Before we can make comparisons between two species we must possess a reasonably complete knowledge of the behavior of those species considered separately. (2) Intraspecific analysis demands understanding of causes and consequences as well as external patterns of response. To analyze behavior means not only to describe its formal properties, but also to discover the factors that evoke it, the mechanisms that mediate it, and the functions it serves.

How do these generalizations apply to behavioral models? The proposal that $x$ shall serve as a model for $z$ implies three things: (1) $x$ is "understood" or has been "analyzed" as indicated above; (2) there are similarities between $x$ and $z$; (3) application of the model will increase our understanding of $z$. To what extent are these implications realized in comparisons between "orgasm" in women and in nonhuman females? The example is unusual in that human behavior is represented as the model, and reactions of nonhuman species are the phenomena to be interpreted. Nevertheless, the basic issues involved are identical to those raised
the so-called animal model, which plays an increasingly important role in such diverse fields as sociobiology (Wilson, 1975) and psychiatry (McKinney, 1974).

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by more common attempts to create animal models for human behavior.

We can best answer the question by examining separately (1) the overt responses involved, (2) the interpretation that has been placed upon them, and (3) the suggestions or assumptions made with respect to their functional significance.

**Behavioral Manifestations**

The most detailed descriptions of physiological or behavioral responses to sexual stimulation in human females have been provided by Kinsey, Pomeroy, Martin, and Gebhard (1953), and by Masters and Johnson (1966). These authorities are in close agreement in their answers to the first of our three questions, which is to say they list essentially the same physiological reactions as indicators of a woman's climactic response. However, there is disagreement regarding identification of these responses as "orgasm."

The position of Kinsey and his collaborators is as follows:

The explosive discharge of neuromuscular tensions at the peak of sexual response is what we identify as orgasm. . . . There are . . . several advantages in restricting the concept of orgasm to the sudden and abrupt release itself, and it is in this sense that we have used the term (pp. 627-628).

Masters and Johnson propose a more inclusive definition:

Physiologically [orgasm] is a brief episode of physical release from the vasocongestive and myotonic increment developed in response to sexual stimuli. Psychologically, it is subjective perception of a peak of physical reaction to sexual stimuli (p. 127).

Here, then, is an excellent example of the same word being used to mean two different things. For Masters and Johnson, human orgasm is a "psychophysiological experience" or a "potpourri of psychophysiological conditions and social influence." For Kinsey and his co-authors, it is only the reflexive contraction of smooth and striped muscles plus the neural impulses responsible for them.

With this degree of variance in definitions of human orgasm, how can we expect to identify an analogous event in other species? The customary procedure is to focus on physiological consequences of sexual stimulation. To examine the logic involved,
let us therefore compare the physiological aspects of orgasm in human females with behavior that has been taken to indicate occurrence of orgasm in nonhuman primates.

The relevant evidence is summarized in Table 1, and resemblances are almost totally lacking except in the case of one experiment (Burton) that involved strapping a female rhesus to a metal frame and stimulating her vagina with a mechanical penis. Even in this case no "orgasm phase" as defined by Masters and Johnson could be identified, and the only "positive" results consisted of a few vaginal and anal contractions elicited from two females upon two or three occasions. Furthermore, the investigator expressed serious doubt that even these responses would be expected to occur in normal intercourse because of the brief duration of the male's insertions.

It would appear that, even if we restrict our comparison to overtly observable behavior, there is little basis for accepting a woman's orgasmic response as a model for orgasm in female monkeys. But there are other dimensions to be considered.

**Psychological Aspects of Orgasm**

Masters and Johnson's insistence that the definition of orgasm must include an individual's perception of the crucial physiological reactions, and Kinsey's exclusion of this dimension of awareness, amounts to disagreement concerning the importance of cerebral events associated with sexual stimulation and its outcome. According to one interpretation, the sensations of orgasm are evoked by proprioceptive feedback to the brain from effectors involved in the peripheral events; and according to the other, the brain is not involved. Nothing could make this distinction clearer than the following quotation.

When the human paraplegic receives genital or pelvic stimulation, he does not feel the stimulation or the consequent physiologic changes in those areas . . . and is not conscious of sexual satisfaction when he has coitus . . . even though he may come to erection and reach orgasm (Kinsey et al., p. 696).

In other words, after complete transection of the spinal cord, a human being may have orgasm without perceiving it, a conclusion that Kinsey further emphasizes by citing several authorities to the effect that the "true paraplegic" is unable to perceive
Table 1
Observable Reactions Associated with (Presumed) Orgasm

<table>
<thead>
<tr>
<th>Human Female Reactions According to Masters and Johnson</th>
<th>Nonhuman Primate Female Reactions According to Various Observers</th>
</tr>
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<tbody>
<tr>
<td>Contractions of outer two-thirds of vagina (&quot;orgasmic platform&quot;).</td>
<td><strong>Rhesus macaque</strong></td>
</tr>
<tr>
<td>Hyperextension including carpopedal spasm.</td>
<td>Female mounting another female. In 5 of 3,837 episodes (&lt;.001%) mounting individual &quot;appeared to reach a sexual climax [showing] small but obvious rhythmic contractions of thigh muscles and around the base of the tail&quot; (Michael, Wilson, and Zumpe, 1974).</td>
</tr>
<tr>
<td>Hyperventilation.</td>
<td>Forcibly restrained female stimulated with artificial penis occasionally uttered &quot;low pitched grunting sounds&quot; and showed a few vaginal and anal contractions. Second female showed vaginal contractions plus &quot;spasmodic arm reflex&quot; on one occasion (Burton, 1971).</td>
</tr>
<tr>
<td>Tachycardia.</td>
<td><strong>Stumptail macaque</strong></td>
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<tr>
<td>Maximal sex-flush.</td>
<td>During 14% of observed copulations female showed rhythmic expiration vocalization and &quot;characteristic facial expression.&quot;</td>
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<td>All of foregoing culminate in general release of vasocongestion and myotonia within a space of a few seconds.</td>
<td>When mounted on another female, the mounting female thrusts, shows body contractions and other reactions resembling those of male during his ejaculation (Chevalier-Skolnikoff, 1973).</td>
</tr>
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</table>

| **Chacma baboon** | |
| During copulation female utters series of staccato grunts ("copulation call"). | During copulation female utters series of staccato grunts ("copulation call"). |
| When male ceases thrusting, female "bounds away" (Saayman, 1970). | When male ceases thrusting, female "bounds away" (Saayman, 1970). |
orgasm, and "for orgasm to be sensually appreciated the spinal connections with the brain must of course, be intact" (p. 697).

The concept of an "unfelt orgasm" that produces no "sexual satisfaction" may be logically defensible, but I am compelled to reject it on both intuitive and neurophysiological grounds. Sensory or perceptual appreciation of the neuromuscular events is an important, even vital feature in the personal experience of orgasm; and as acknowledged indirectly by Kinsey, this perception depends on brain function. Furthermore, inasmuch as "psychological" stimuli transmitted from the brain to spinal mechanisms are capable of either stimulating or inhibiting reflexes of the sex accessories, it seems inconsistent to ignore cerebral responses to stimuli returning from the same peripheral target organs.

Proximate Mechanisms, Rewards, and Evolution

The search for indications of orgasm in female animals rests on implicit assumptions regarding sexual satisfaction, even when the assumptions are not acknowledged by the searchers, and may be unrecognized by them. It is this lack of explicitness that forces Alexander, in his comments on Lancaster's paper, to complain of "a common deficiency in the [behavioral] analyses of biological and social scientists."

The deficiency . . . is the failure to recognize or take into account that proximate mechanisms exist and are maintained because in the past . . . they have served the ultimate function of reproduction. By proximate mechanisms I mean things like pleasure and pain.

It could be argued that theories of animal orgasm are immediately relevant to the issue of proximate mechanisms. Such theories always rest on unexpressed assumptions that in animals, as in ourselves, orgasm is pleasant and rewarding. Orgasm is implicitly treated as a reinforcing consequence of sexual interaction, and the concept of reinforcement traditionally is invoked as one explanation for the recurrence of behavioral responses.

Saayman (1970) suggests that female baboons in estrus prefer to copulate with mature males because the latter are especially likely to stimulate the female's putative orgasm, which Saayman infers from her behavior. Here in a nutshell is material for a theory involving proximate mechanisms, individual learning, and sociobiological or evolutionary consequences!
In this volume Lancaster writes as follows.

One of the most significant generalizations to come from the new data is that, like humans, Old World monkeys and apes do not engage in sexual activity for the sole purpose of procreation.

Why, then, do they engage in such activity? This is a question of proximate mechanisms, and I suggest that the postulation of female orgasm represents one attempted answer. An entirely different issue, but one worth mentioning although it cannot be developed here, is the effect of sexual rewards on nonsexual activities. I have discussed this important feature of primate evolution elsewhere under the topic of “socialization of sex and sexualization of society” (Beach, 1974, 1977). One aspect of the matter is reflected in Lancaster’s observation that “the stimulations and rewards of sexual behavior appear to be important mechanisms of social attachment in nonhuman primates."

Orgasm, Reinforcement, and Scientific Goals

A perfectly legitimate question is what difference it makes whether a female monkey does or does not have sexual orgasm, and as far as I can see it makes none whatsoever unless the occurrence of orgasm can be shown to exert a reliable effect upon subsequent behavior. If orgasm has reinforcing consequences that directly or indirectly increase the probability of reproduction, then it could make a very great difference indeed. But this way of asking the question restructures the entire issue and places it in a broader and scientifically more significant perspective. Furthermore, it opens the matter to experimental investigation.

Rather than seeking animal analogues for human orgasm (which is too poorly understood to serve as a useful model for anything), we might better attempt to identify the variables that reinforce the occurrence of sexual behavior. Perhaps a female rhesus in copulation with a male does have vaginal and uterine contractions that give rise to pleasant and rewarding sensations and thus reinforce her tendency to engage in similar behavior on subsequent occasions. The possibility is open to experimental test, but if that particular explanation is disproved, the basic question of proximate mechanisms remains and must be answered. It is conceivable that vaginal penetration rather than any
climactic event is the essential basis for reinforcement, and this too can be experimentally verified or excluded.

My theory-hunch, or "thunch," is that there is no single source of reinforcement for a behavioral response so vital to perpetuation of the species. We shall probably discover that in animals, as in men and women, the occurrence of mating behavior normally depends upon a combination of reinforcing consequences, any one of which is dispensable as long as others remain.

However it turns out, the essential need is for explicit research rather than speculation about trivial questions. What we need to know is not whether baboons have orgasms, but why baboons (and human beings) copulate, and why they do so under conditions and in a manner that ensures perpetuation of their species. Answers to questions of this order may well contribute to an evolutionary interpretation of human sexuality.

Directions for New Research

Three major areas in which new research might be especially fruitful are (1) molecular analysis of sexual behavior, (2) comparative, physiological, and developmental study of feminine sexuality, and (3) formulation and testing of hypotheses relevant to the "new model" of evolution, which states that organisms have evolved to maximize the reproduction of their own genes.¹

Molecular Analysis of Sexual Behavior

This category includes a number of subareas, one of which is study of stimulus control of sexual responses. The common assumption that mating behavior in animals depends on simple, unisensory cues, such as odor, is gradually giving way to concepts of multisensory patterns that are perceptually organized by the receiving organism. It is clear that for males and females of many species, sexual responsiveness embodies measurable degrees of preference for particular partners. Study of individual differences in sexual attractiveness for both sexes may lead to concepts of varying degrees of "compatibility" in different heterosexual pairs.

Translated into human terms, the issue of stimulus control is

¹ These recommendations are based upon the author's discussions with Jane B. Lancaster and Richard D. Alexander.
directly related to the concept of "object choice" and therefore bears on problems of homosexuality as well as various paraphilias.

A second subcategory deals with effects of experience and learning in nonhuman species. Current evidence suggests that such effects are more likely to be exerted on the stimulus rather than the response aspects of sexual behavior. Enduring pair bonds between females and males may depend on close association in nonreproductive circumstances, and on absence or inhibition of responsiveness to "nonpartners." For some species "sexual imprinting" occurring during the equivalent of infancy or early childhood determines the nature and even the species of individual that will evoke sexual responses in adult life. The motor patterns of courtship and mating are unaffected by such early learning. This phenomenon may bear significant relations to human aberrations such as fetishism and exhibitionism (Beach, 1977).

The question of sexual reward or reinforcement is in need of exhaustive study, both because of its implications for "animal models" and because of its importance for understanding sexual behavior at the intraspecific level. We might even profit from examining the more fundamental question whether any concept of reinforcement is necessary to our behavioral analyses.

Finally, much research is needed on basic problems of neural and hormonal mediation of sexual and sex-related behavior in nonhuman species. Work in this area is proceeding apace, but a great deal remains to be accomplished.

Comparative and Longitudinal Studies of Female Sexuality

There is obvious need and opportunity for combined laboratory and field investigations of various problems relating to sexual responses of female primates. For example, physiological changes associated with mating can and must be described and measured under controlled conditions. Information provided by such study can then be utilized in more informative interpretation of field observations.

Currently available methods of measuring and manipulating hormone levels can be more broadly applied to females living in the natural environment.

Field work at the descriptive level is in need of increased emphasis and breadth. Greater attention to interspecific differences will prove especially illuminating and is badly needed as a safe-
guard against overgeneralizations purporting to describe behavior of “monkeys” or “apes” as homogenous groups.

In the area of human sexuality the question of male-female differences is in serious need of extensive analysis. There exists a widespread belief that certain psychological or behavioral sex differences are, or may be, traceable to biological differences between male and female, but most of the evidence comes from Western societies in which such differences are encouraged or enforced by social training.

Other societies exist that support quite different programs of sexual training. Some of these include explicit emphasis on recognition and expression of female sexuality. Female infants are regularly masturbated, the outer labia are stretched and pulled to increase their size, and young girls are taught dances that focus on pelvic movements simulating those used in copulation. It would be most important to learn if under such conditions females grow up to be sexually more assertive, active, and independent than females in Western countries. It is conceivable that many sexual dimorphisms common in our culture would be lacking in others with different concepts of child training.

A more specific issue pertaining to female sex functions, which calls for immediate attention, is the remarkable decrease in menarcheal age that has occurred in Western countries during the last century. The average age at first menstruation has dropped approximately four years (from seventeen to thirteen) between 1870–75 and 1970–75. The causes are complex and the consequences of major social import. In this country, for example, the incidence of pregnancy in twelve- and thirteen-year-old girls is rising. Reproductive precocity is not accompanied by earlier social maturity, and the resulting disparity creates serious problems for society and potentially crippling ones for the girl and her family.

**Human Sexuality and Evolutionary Models**

Until recently the most widely accepted model of evolution hinged on the concept of group selection. According to this view, behavior of individuals evolved to preserve and perpetuate the genotype of the reproducing population.

The currently favored “new model” calls for a different

2. Comments by R. D. Alexander.
interpretation, which is that individuals behave in ways most likely to ensure the perpetuation of their own individual genotypes. In historical perspective what this model says is the following: We and our contemporaries tend to exhibit behavioral and nonbehavioral characteristics that in past generations contributed to preservation of the genes we have inherited from our ancestors. Various lines of research can be explored to test the validity of this new model as it applies to different aspects of human sexuality.

Evolution has commonly been viewed as the discipline that traces long-term changes through fossil remains and comparisons of related living forms. The more such studies focus on truly long-term changes, the less likely they are to unravel the causes of change because the environments of antiquity are inevitably so poorly known.

Another aspect of evolution, less well understood outside biology, is the use of what is known about the actual process of change, studied in living forms, to predict states of phenotypic attributes or combinations of attributes. A particularly well-studied example, relevant to this volume, is the ratio of males to females in a population.

There are similarities in sex ratios, not just across the animal kingdom, but across both the animal and plant kingdoms. Usually, they are about 1:1 in early adulthood. Even tiny shifts in sex ratio can affect sociality and sexuality. For example, one may contemplate the idea that whatever causes lie behind sex ratios might have produced one male for every ten females or vice versa. Under such conditions our sociality could scarcely have its current structure. But the sex ratio among humans also is generally about 1:1 in early adulthood. Only one explanation has been devised, and it works: An individual can maximize its reproduction in a sexual species, in which the two halves of genetic materials come from parents of the two different sexes, only by investing in the two sexes so as to produce a local sex ratio that will not cause any of its offspring to be devalued reproductively solely because of their sex (Fisher, 1958). This is what organisms appear to do, and it leads to strange predictions such as: If twice as much parental effort is required to rear a male as to rear a female then one expects a sex ratio at the end of parental care of 1:2 rather than 1:1; and things like this do happen. The major exceptions to a 1:1 investment are species in which all the females are inseminated by their brothers. Parents in those cases would be expected to
invest only enough in males to assure insemination of all of their daughters. In such species the resulting sex ratio may be 1:20 or 1:45—even though the males in some cases are tiny, crippled, blind, short-lived things that do nothing but inseminate the female and then die (Hamilton, 1966).

Philosophically, the significant idea is that individuals evolve to maximize their reproduction. This seems counter-intuitive to human views of our own motivations. We all believe that humans do countless things besides reproduce. Part of this belief is derived from our ability to define reproduction as we see fit. Nevertheless, human sex ratios suggest that we too have evolved to maximize reproduction as individuals.

In almost all groups of the world’s species, including all mammals, females invest more than males in rearing their offspring. Males work harder in competition for matings. Consequently, some males in all these species reproduce more than any female. Biologists refer to such species as polygamous, whether or not the males have harems. In polygynous species, because sex-ratio selection produces about a 1:1 sex ratio in early adulthood, the male’s lifetime is a high-stakes, high-risk game compared with the female’s (Williams, 1957; Hamilton, 1966; Alexander et al., 1978). In other words, because some males inseminate many females, other males do not reproduce at all.

Humans are polygamous in the sense that I have described and share many common characteristics with other polygynous species: In these species in which the sex ratios are about 1:1, males take longer to mature and senesce more rapidly; mortality is higher in males at essentially every age. In species that compete sexually on the ground, rather than in water or in the air, males are always bigger than females. Promising juvenile males get more help from their parents than do any females, while not-so-promising males are abandoned or killed either as fetuses or later; that is also true in humans to some extent. More males are conceived, but more die while still under parental care, even though males get more parental care than females. In mammals, males are carried longer during gestation and are larger at birth. Healthy and high-ranking parents produce male-biased broods, while low-ranking and less healthy parents do not, or in some cases produce female-biased broods. There is good evidence that in stratified human societies the same effect is brought about by sex-preferential infanticide (Dickeman, 1978).
Quotes from other papers in this volume show the connections between topics like sex-ratio selection and the goals of this conference. Luria, for example, indicates that in early or middle childhood the rigidity of sex-typing falls most heavily on the shoulders of boys. She points out that parents appear to be more worried about a boy’s masculinity than about a girl’s femininity; that boys are more likely to be ostracized as sissies than girls are as tomboys; that girls fight less than boys; and that “higher education and middle-class status are associated with more relaxed gender roles.” All of these findings are consistent with what I have said about sex-ratio selection. In other words, the basic aspects of sex and gender roles derive from the effects of sex-ratio selection upon our species. Surely it is no triviality to realize this.

The consensus of authors in this volume seems to be that the reasons we are what we are and do what we do—like it or not—are mostly social. There are, of course, genetic differences between males and females, which lead to differences of appearance; but these appearances only initiate the social phenomena that cause the development, exaggeration, and diversification of gender-role differences. It seems that, historically, social contingencies have represented the most appropriate kinds of causes for achieving desired ends. How to succeed socially is the most difficult of all questions about how to succeed, because everybody else is also trying to succeed socially, and our individual goals necessarily conflict.

The sources of the effective social contingencies for the development of sex and gender roles also seem apparent in this volume. They are parents, peers, and ourselves. These are the sources of the social stimuli that put us in particular roles. An evolutionary biologist would suppose that these social influences work because parents want their offspring to succeed. But what constitutes “success” or “desired ends”? It is worth contemplating that, in terms of history, success may be defined in terms of the general theoretical approach that has developed in biology in the last ten years—namely, that attributes of organisms exist because they help those individual organisms maximize their reproduction.

This approach is a brand-new philosophy in biology. Previously we assumed that the attributes of organisms exist because they are good for perpetuating the species; but that explanation does not work. Sex ratios cannot be explained that way. Nor can senescence patterns, mating systems, sex differ-
ences and similarities, or sociality. We have thought that it is
all a matter of personal satisfaction or pleasure or the acquisi-
tion of power or of influence; but those ideas will not work
alone either. Beginning with things like sex ratios and con-
sidering others like patterns of senescence, social behavior,
nepotism, and sexual competition, the hypothesis that indi-
viduals evolve to maximize their own reproduction, and not that
of the species, does work (Alexander, 1977).

This discovery does not mean that we are bound to our
history. We are the organisms who sit and contemplate these
things. Then the contemplation itself becomes part of the
environment, which means that in the end we can do almost
anything we like. Perhaps this possibility is open to us only if
we bring the significance of our evolutionary past into our
consciousness through analysis of, and reflection on, the kinds
of considerations raised here.

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Human Sexuality

A Comparative and Developmental Perspective

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