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Sexual Cyclicity in Captive Lowland Gorillas

Abstract. *Oppositely sexed pairs of gorillas exhibit some behavior indicative of higher cognitive functioning, such as individual partner preferences and varied copulatory positions, but also mate in a cyclic manner closely related to the degree of female genital swelling. The latter finding is contrary to predictions based on their advanced position in phylogeny.*

Nearly 30 years ago Beach (*1*) proposed that animals with relatively larger forebrains and, consequently, greater cognitive abilities were less dependent on gonadal hormones for the regulation of their sexual behavior than were animals with smaller forebrains. Evidence in support of this hypothesis has appeared over the years, but relatively little systematic data have been obtained on the more advanced species, in particular the higher primates (*2*). In a study of the sexual behavior of gorillas, I obtained evidence contrary to Beach's hypothesis in that the behavior of these apes, close taxonomic affiliates of man, was rather closely related to the phase of the female's sexual cycle.

My primary objective was to evaluate periodicity in sexual behavior and female genital swelling of gorillas for evidence that the behavior was hormone-dependent. The female gorilla does not possess a sex skin as extensive as that of the chimpanzee or baboon, but it does exhibit tumescence of the perineal labia with a cycle (*3*) comparable to that of these other species and presumably under similar hormonal control (*4*). The subjects were four male and nine female lowland gorillas (*Gorilla gorilla gorilla*), ranging in age from 7 to 10 years at the beginning of the study in 1971. The animals were housed in cages consisting of an inner compartment 2.3 m by 2.3 m by 2.1 m high and an outdoor compartment 2.3 m by 4.1 m by 2.7 m high, interconnected by a guillotine door. When they were not being tested, the females were caged in isosexual pairs and the males were caged alone. Oppositely sexed pairs were tested approximately daily throughout the sexual cycle of the female. Before each test the male was confined to the outer compartment of his home cage (the test cage) and the female was introduced into the inner compartment. The test was begun after the door separating the compartments was raised and the female had entered and was confined to the outer compartment. The test was terminated after 30 minutes had elapsed without the occurrence of copulation. The labial tumescence (LT) of the female was rated on a scale of 0, 1, or 2, corresponding respectively to detumescence, minimal tumescence, or maximal tumescence, as previously described (*3*).

I paired the 13 gorillas in 20 different combinations for approximately 2000 tests over a 3-year period. All nine females copulated with at least one male partner, but only seven females from nine pairs copulated on a regular basis and were involved in copulation that culminated in ejaculation. For 4 of the 11 pairs that did not copulate or copulated very infrequently, the females failed to exhibit tumescence of the perineal labia, suggesting hormonal inadequacy as the basis for the lack of sexual activity. However, in the seven remaining infrequently copulating pairs, the female did exhibit cyclic fluctuations in LT. Since the females in these latter pairs did copulate when tested with different males, their differential responsiveness may be an example of individual partner preferences. My interpretation of this finding is that some factor other than hormonal, presumably a higher cognitive variable, exerted an important influence on the sexual behavior of these animals (*5*).

A clearer indication of higher cognitive capabilities in the gorilla was found in the varied copulatory positions taken by the subjects. Of the seven females that copulated regularly, four used the dorsal-ventral position exclusively, one used the ventral-ventral position exclusively, and two used both positions. Of the four males, two used only the dorsal-ventral position and two used both positions. Moreover, a number of variations of the two major positions were also seen. These data indicate that the primary copulatory position for these animals was dorsal-ventral, but that a considerable amount of variability was exhibited within and between positions. This type of variability in copulatory positions contrasts with the relatively invariable, stereotyped performance characteristic of species below the level of the apes and appears to represent a prerogative related to the latter's pronounced degree of encephalization.

Another conspicuous feature of the gorilla's sexual interactions was related to the different roles played by the male and female before copulation. The male was quite unobtrusive in soliciting copulation, his positive responses before copulation consisting primarily of approaches to the female and occasional touches with the back of the hand. The female, on the other hand, was very assertive, backing forcefully into the male, frequently pushing him against a wall, and actively rubbing her genitalia against the male by rhythmically raising and lowering her rump while emitting a soft, high-pitched fluttering vocalization. The male also vocalized during copulation and in a pitch similar to the female's, but his vocalization consisted of a short burst rather than the prolonged refrain of the female.

The most significant finding, however, was the relationship between various measures of sexual behavior and the female's labial condition (Table 1). Since the tests were conducted approximately daily throughout the female cycle, the proportion of tests conducted at each degree of LT reflects the proportion of days each degree of LT was represented in the cycle. Based on a cycle of 31 or 32 days (*3*), LT ratings of 0, 1, and 2 were obtained on 19,

Table 1. Sexual behavior of captive lowland gorillas for different labial tumescence (LT) ratings of the females. The female success ratio is defined as 100 times the number of copulations per test divided by the number of female presentations per test; N is the total number of tests.

LT rating	N	Presentations		Female success ratio	Copulations		Ejaculations	
		Percent of tests	Per test (median)		Percent of tests	Per test (median)	Percent of tests	Per test (median)
0	705	23	1.6	3	1	0.3	0	0.0
1	342	48	2.1	35	25	1.2	14	1.0
2	102	66	2.8	41	43	1.8	37	1.0
Totals	1149*	34*	2.1†	23*	12‡	1.4	7‡	1.0

*$P < .001$, Friedman two-way analysis of variance (*14*). †$P < .05$, Friedman two-way analysis of variance (*14*). ‡LT = 1 compared with LT = 2, $P < .05$, Wilcoxon matched-pairs signed-ranks test (*14*).

9, and 3 days per cycle, respectively. The females presented themselves sexually to the males during all degrees of LT, but they exhibited significant differences in the percentage of tests on which they presented for the different degrees of LT. All females presented least frequently during their detumescent condition and exhibited successive increases with successively greater degrees of LT. A similar pattern of significant differences was found for the frequency with which females presented per test and for the female success ratio. This is one of the few laboratory studies of primate sexual behavior in which a consistent relationship was found between female sexual behavior and phase of the sexual cycle (*6*).

The data on the female success ratio, a measure of female attractiveness (*7*), indicate that the females not only solicited copulation more frequently at successively greater degrees of LT, but were also more successful at those times. Examination of the data on copulation and ejaculation (*8*) supports the relationship between sexual behavior and LT. The males copulated on 12 percent of their tests (approximately 4 days per cycle) and ejaculated on 7 percent of their tests (approximately 2 days per cycle). However, they rarely copulated and never ejaculated with females in the detumescent condition, and exhibited the greatest frequency of these sexual interactions at the maximal degree of LT. However, the frequency of copulations and ejaculations per test did not differ significantly for the different degrees of LT. These data suggest that whether or not copulation and ejaculation occurred on a particular day was importantly influenced by the stage of the female's cycle, but that the frequency with which they occurred on a given day was not so influenced. In fact, although all the males exhibited multiple copulations and ejaculations on some tests, their characteristic pattern was to ejaculate on a single copulation and then to interact sexually no further.

These findings on the varied copulatory positions used by gorillas and the relatively passive and assertive roles, respectively, of males and females augment and extend the reports describing gorillas living in zoos (*9*). Those reports, based primarily on single pairs of animals, also indicated that sexual interactions occurred at fairly regular 30-day intervals and were confined to a period of 1 to 4 days. The present study of the largest group of adult gorillas in captivity confirmed those findings and also yielded data on the relationship between sexual behavior and the female's genital swelling.

The parallel changes in tumescence of the female's perineal labia, sexual receptivity, and occurrence of copulation described above represent the first systematic data of this type on gorillas and indicate that sexual behavior of this species is quantitatively different from that of the chimpanzee. Yerkes and co-workers (*10*) and Young and Orbison (*11*) reported that chimpanzees mated throughout the sexual cycle, although most copulated more frequently during the period of maximal genital swelling of the female. They concluded that hormonal influences were relatively unimportant in the sexual behavior of these apes because the expression of estrus could be altered substantially and even completely overwhelmed in any given subject by significant individual differences and social factors associated with the test situation.

Their findings supported Beach's hypothesis (*1*) in that the chimpanzee exhibited a degree of behavioral independence from hormonal control commensurate with its relatively advanced brain capacity. The gorillas of the present study mated less frequently, in general, than did the chimpanzees and their sexual interactions were more closely related to the degree of genital tumescence of the females. These data suggest that sexual behavior of gorillas is under relatively greater hormonal control than that of chimpanzees and is a reflection of the variability in behavioral regulation that exists among these higher primates. No comparable studies have been conducted on the third species of great ape, the orangutan, but limited observations of wild (*12*) and captive (*13*) specimens, as well as my own observations of four captive pairs, suggest that sexual behavior in that species shows less evidence of cyclicity than in either the gorilla or the chimpanzee.

The three great ape species, therefore, appear to comprise a continuum on which animals with similar forebrain development and intelligence differ in the extent to which their sexual behavior is regulated by hormones. Although confirmation of the hormonal mediation of the behavior observed in this study requires further research, these findings suggest that hormonal factors play a more significant role in the regulation of sexual behavior in gorillas than would be predicted on the basis of their advanced position in phylogeny.

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