Behavioral Endocrinology of Male Rats with Periodic Sexual Contacts with Exclusive or Varied Females (42991)

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Abstract. **Sexual contact keys a profound series of acute and chronic changes in males that, presumably, are orchestrated by acute pulsatile release of hormones. An experimental paradigm is reported in which male rats were paired periodically with either the same or different estrous females to receive identical amounts of copulatory experiences. Results confirmed the hypothesis that exposure to an unfamiliar female would induce a different endocrine response which would be reflected in various androgen-sensitive systems. The "successively polygynous" males showed more sexual behavior than "monogamous" males, and their respective females solicited the males differently, as well. Circulating levels of testosterone were higher immediately after sexual contact with an unfamiliar than with a familiar female partner. There were no differences in testosterone titers among the groups when the animals were killed at either 2 or 7 weeks after the final copulatory experiences. Yet, necropsies at 2 weeks postcopulation revealed that primary and secondary sex structures from polygynous males clearly were larger. Differences between the two experimental groups were reduced after 7 weeks of sexual rest, yet, polygynous males continued to show a different structural profile than the other groups. Conclusions were that males may experience greater activation of androgen-sensitive behavior and physiology following qualitatively different sexual contacts.** [P.S.E.B.M. 1989, Vol 192]

The behavior, physiology, and morphology of sexually experienced males differ dramatically from virgin males (1). For example, an experienced rat shows greater interest in the odors of a receptive female (2), she has more interest in his odors (3), and the pair initiates copulation sooner (4). Physiologic changes are concentrated in peripheral structures specific to reproduction and can be more or less permanent (5). Modifications in morphology may be more ubiquitous because changes with sexual contact may lay dormant for long periods of time before being expressed as a disease state (6–8). The quantity and quality of sexual contact may affect all of these processes.

It seems that only a few copulatory experiences are necessary to induce acute and chronic behavioral and physiologic changes in males, (3, 9), and further increases in number of experiences may elevate fecundity in a dose-response fashion (10). A period of sexual rest, on the other hand, can modify male behavior (11), spermiogenesis (12), and primary sexual structures (13). Qualitative variation in sexual contact that is influenced by factors such as individual differences among females also can have a substantial impact on behavior and endocrinology of the male (14, 15).

Indeed, the presumed mechanism underlying the heterogeneous changes in the experienced male is a modified endocrine milieu with copulation. Pulses of gonadotropin and testicular hormones are released into circulation with exposure to a receptive female (16). Hormone-sensitive systems are activated with these acute pulses (17). The endocrine response habituates to a familiar female but is restored with the introduction of a new female (18).

The suggestion is that similar numbers of sexual contact with varied females or with a single female may provoke a different endocrine response with different behavioral, physiologic, and morphologic consequences. Because there is considerable contemporary interest in the health consequences of different forms

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of sexual contact (19), an experimental paradigm is proposed as an animal model of sexual behavior-pathogenesis relations. This study served as an initial empirical test of the paradigm by examining acute changes in behavior and physiology of male rats exposed successively to different females.

Materials and Methods

Animals. The rats were 36 Wistar males, 120–180 days of age, that were sexually inexperienced when they were obtained at 2 months of age from a supplier (Hannover). Each animal was housed individually in solid bottom opaque plastic Makrolon III cages with wire lids. Individually housed females of the same strain and ages were ovariectomized under ether anesthesia. Food and water were freely available to each animal; temperature (20–22°C) and humidity (50%) were controlled automatically in both colony and experimental rooms. Lighting was on a 12-hr light:12-hr darkness cycle. Observations of behavior were conducted during the initial 3 hr of the light cycle.

Materials. Home cages of the males were used for observations of sexual behavior, and stop clocks were used to record latencies. Hormones to induce the ovariectomized females to estrus were purchased from Sigma Chemical (Mannheim, Federal Republic of Germany).

Procedure: Behavioral Interactions. Animals were assigned at random to one of three groups, $n = 12$. Experimental males received sexual experience with the same (Monogamous Group) or different (Polygynous Group) females. A third group served as a control condition and remained sexually inexperienced (Virgin Group). The latter males were individually housed throughout the experiment and had no contact with females. The males to receive sexual experience were paired with receptive females twice each week for 4 weeks.

Males were allowed three ejaculations during each copulatory session. An ovariectomized female was induced to estrus with 100 μg of estradiol benzoate and, 48 hr later, with 400 μg of progesterone. Both hormones were injected sc in a 0.2-ml olive oil vehicle. The female was introduced into the home cage of the male, and times of each intromission and ejaculation were measured by the experimenter. In addition, total frequencies of female solicitations were recorded daily as a measure of her response to a familiar or unfamiliar male. Solicitation behaviors by a female rat include darting, hopping, and ear wiggling (20).

The only difference between the two groups of experimental males was that a male in the monogamous group had the same, whereas a male in the polygynous group had a different, female partner for each session. To minimize female differences as a confounding factor, all females were well-experienced sexually prior to the experiment. Females assigned to the polygynous group were exposed to several males each week, but only one male per day, and both groups of females had the same number of sessions over the course of the experiment.

Endocrine Analyses. Circulating levels of testosterone were determined twice for each male. Animals in the experimental groups were lightly ether anesthesized immediately following the second copulatory session of Week 3, and 2–3 ml of blood were collected by cardiac puncture from each male. Blood was collected from the control males during the same week and with the same technique. Serum was obtained by centrifugation and was frozen at −20°C until analyzed for testosterone using a procedure described in our earlier research (21). Blood was collected again with the same technique immediately before the males were killed for physiologic analyses. Half of the males were chosen at random from each of the three groups and killed 2 weeks after the final copulatory session of the experimental groups. The other males were killed 5 weeks later, or 7 weeks after the final exposure to females.

Physiologic Examination. Wet weights of penis, preputials, seminal vesicles, ventral prostate, testes, and epididymides were used as markers of interactions of circulating neuropeptide and steroid hormones with target tissues. The logic is that enlargement indicates hyperactivity in these highly hormone-sensitive structures (22). In addition, adrenal and pituitary glands were excised for measurement of activity in the hypophyseal-adrenocortical axis (23). Wet weights were obtained, and sections were prepared for histopathologic analysis (21).

Sperm numbers are an excellent measure of reproductive capacity (24), and epididymides were prepared for sperm counting using a procedure described earlier (25). The organ was minced to release sperm and 5 ml of 5.3% (w/v) NaCl were added. An aliquot was examined with a light microscope (40×), and sperm were counted with a hemocytometer.

Statistical Analyses. Behavioral data were analyzed with a series of 2 × 4 analyses of variance with the main factors of groups, monogamous or polygynous, and weeks of testing as a repeated measure. A mean value for each measure was calculated for each male from the two copulatory exposures each week. Those data include latencies to first intromission and first ejaculation. Interejaculation intervals (26) were determined by calculating the mean time between the first to second and second to third ejaculations for each animal. An intromission frequency score was calculated by totaling the numbers of intromissions during each observational session for each male. A single behavioral score for each female was calculated by totaling the frequencies of the various types of solicitation.

The control group was included in the physiologic analyses. A series of 3 × 2 analysis of variances were performed with main factors of groups, either monogamous, polygynous, or virgin, and time of examina-

tion, either 2 or 7 weeks after the final copulatory session by the experimental groups. Wet weights of organs and glands were calculated as mg/100 g body wt. Testosterone titers in circulation were expressed as ng/100 ml serum, and sperm were calculated as 10^6/g epididymis.

With a statistically significant interaction between main factors, simple main effects were used to examine the interaction in more detail (27). Tukey's honestly significant difference (HSD) test ($P < 0.05$) was used to make paired comparisons of group means. Finally, a post hoc chi-square test was employed to examine different frequencies of cysts found during histopathologic diagnosis.

Results

Behavior. Findings for sexual behavior are reported in Table I. Weeks of testing were statistically reliable for latency both to first intromission and first ejaculation ($P < 0.01$). Only the latter measure was significant when the data for each group were collapsed over all weeks ($P < 0.05$). Polygynous males were faster to show the typical (4) decrease in latency to initiate and conclude a copulatory bout. Analyses of simple main effects were made of the statistically significant interactions ($P < 0.05$) between main factors both for the frequency of intromission and interejaculation interval measures. Only the polygynous males showed a pattern of shorter intervals between ejaculations over weeks and increased numbers of penetrations from the earliest to the last sexual contacts of the experiment.

Examination of the statistically significant interaction obtained for female scores revealed more solicitations over weeks by "familiar" females with their monogamous males ($P < 0.01$). There were no similar changes in solicitations by unfamiliar females for polygynous males. These differences were not a product of the slightly longer periods of time required by the monogamous partners to complete their sexual contact criterion. Solicitations typically were concentrated during the beginning of the interaction.

Physiology. Findings at necropsy (Table II) indicated statistically significant differences for epididymal sperm numbers and in weights of various androgen target structures, including seminal vesicles, epididymides, prostate glands, preputials, and ventral spongiosus muscle ($P < 0.05$). The pattern that emerges from the acute comparisons is clearly greater physiologic activation in primary and secondary sex structures of polygynous than monogamous males. Although the two experimental groups were more similar during chronic examination, polygynous males continued to have heavier seminal vesicles, ventral spongiosus muscles, and preputial glands than monogamous males.

Both hypophysis and adrenal glands from experimental groups were heavier at acute than at chronic examination, but weights of the same glands changed similarly in the control group ($P < 0.01$). To clarify these findings, histologic examination was made of sections from pituitary and adrenal cortex. Glands were fixed in formalin, sectioned, and stained with eosin and hemotoxylin as described in our earlier work (28). Two pathologists in the histodiagnostic division of the German Cancer Research Center (DKFZ) independently examined tissue sections without knowledge to which group the animals belonged.

Light microscopic examination of the adrenals revealed no morphologic differences among the groups. Examination of the pituitary, on the other hand, showed small cysts as a pathologic change in pars distalis of 7 of 36 rats, and 4 (57%) were from the polygynous group examined at 7 weeks ($P < 0.05$). The remaining three pathologic samples were from males from three other subgroups.

Endocrine Status. Data were obtained immediately after a copulatory session during the third week of behavioral observations (Table III). Both sexually experienced groups had higher testosterone values than

Table I. Sexual Behaviors of Male Rats and Female Solicitations of the Male, Over 4 Weeks of Weekly Testing either with Same (Monogamous) or Different (Polygynous) Females

Measure	Monogamous				Polygynous			
	Test 1	Test 2	Test 3	Test 4	Test 1	Test 2	Test 3	Test 4
Male								
Latency first intromission (min)	4.2 ± 0.7a	2.3 ± 0.4b	1.5 ± 0.3c	0.8 ± 0.2c	4.9 ± 0.8a	1.1 ± 0.2c	0.9 ± 0.2c	0.6 ± 0.1c
Latency first ejaculation (min)	24.2 ± 1.3a	16.6 ± 1.3b, c	16.4 ± 1.5b, c	14.7 ± 1.2c	20.6 ± 1.4a	15.3 ± 1.0b, c	14.1 ± 0.9c	13.2 ± 1.0c
Frequency of intromission	37.6 ± 2.0a	35.8 ± 2.8b	37.2 ± 2.4b	38.0 ± 2.6b	37.7 ± 2.6b	53.0 ± 3.0a	53.6 ± 2.8a	57.3 ± 2.9a
Interejaculation interval (min)	17.4 ± 2.0a	13.8 ± 1.5b, c	14.7 ± 1.1b, c	16.1 ± 1.3a, b	16.1 ± 1.0a, b	12.3 ± 0.9b, c	12.0 ± 0.7c	9.9 ± 0.6d
Female								
Solicitation	20.1 ± 1.9b	22.3 ± 1.5b	33.1 ± 1.5a	37.9 ± 1.0a	22.0 ± 1.6b	20.6 ± 1.6b	21.9 ± 1.4b	23.2 ± 1.4b

Note. Values are mean ± SE. Values with different letters differ significantly, Tukey's HSD ($P < 0.05$).

Table II. Physiologic Measures of Male Rats at Necropsy 2 or 7 Weeks after a Final Exposure either to the Same (Monogamous), Different (Polygynous), or No (Virgin) Female

Group measures	Virgin acute	Monogamous acute	Polygynous acute	Virgin chronic	Monogamous chronic	Polygynous chronic
Body weight[a] (g)	407.7 ± 17.5	389.7 ± 30.5	398.7 ± 25.4	428.5 ± 5.7	409.7 ± 8.8	429.0 ± 22.9
Seminal vesicle (mg/100 g body wt)	440.9 ± 15.4c	545.6 ± 50.0b	615.8 ± 29.4a	428.5 ± 10.7c	467.2 ± 20.5c	557.1 ± 10.8b
Testes (mg/100 g body wt)	862.5 ± 13.7	1014.7 ± 109.5	987.0 ± 72.7	911.5 ± 26.8	885.1 ± 16.6	939.2 ± 33.5
Epididymis (mg/100 g body wt)	325.5 ± 11.4d	430.3 ± 33.2a	437.0 ± 15.4a	351.6 ± 5.5c	378.9 ± 13.0b	403.6 ± 10.2a, b
Pituitary (mg/100 g body wt)	3.5 ± 0.4a	3.7 ± 0.3a	3.7 ± 0.2a	2.7 ± 0.2b	2.5 ± 0.1b	3.0 ± 0.3b
Adrenal (mg/100 g body wt)	23.9 ± 1.5a	23.4 ± 3.2a	25.4 ± 2.4a	19.1 ± 1.5b	19.8 ± 0.9b	18.3 ± 1.4b
Prostate (mg/100 g body wt)	120.7 ± 6.1b, c	130.5 ± 5.1b	147.7 ± 5.3a	123.3 ± 5.2b, c	122.0 ± 1.6b	113.4 ± 8.2c
Muscle Ventral (mg/100 g body wt)	294.5 ± 5.1b	313.2 ± 25.4a, b	356.7 ± 7.7a	291.0 ± 4.3b	285.7 ± 4.7b	344.5 ± 14.8a
Muscle Dosal (mg/100 g body wt)	113.2 ± 4.8	106.7 ± 8.2	120.5 ± 3.9	112.5 ± 2.3	112.3 ± 3.5	124.7 ± 7.2
Penis (mg/100 g body wt)	28.1 ± 1.0	30.4 ± 2.3	30.9 ± 2.1	27.9 ± 0.3	28.4 ± 1.5	29.4 ± 1.0
Preputials (mg/100 g body wt)	73.7 ± 2.7b	75.4 ± 4.1a, b	82.7 ± 4.2a	75.2 ± 2.1b	62.7 ± 4.1c	77.6 ± 2.1a, b
Sperm number[b] (10^6/g epididymal wt)	394.2 ± 9.9d	517.5 ± 19.9b, c	556.2 ± 15.8a	379.0 ± 16.4d	524.3 ± 14.4b	485.0 ± 18.3c

Note. Values are ± SE. Values with different letters differ significantly, Tukey's HSD ($P < 0.05$).
[a] Body weights are in g, all other organ wet weights are mg/100 g body wt.
[b] Sperm numbers are 10^6/g epididymal weight.

Table III. Serum Testosterone Values (ng/100 ml serum) of Male Rats Measured Immediately or Weeks after Copulatory Contact

Measure	Virgin	Monogamous	Polygynous
Testosterone (ng/100 ml), immediate	379.8 ± 24.9c	560.3 ± 20.7b	747.2 ± 22.4a
Testosterone (ng/100 ml) 2 weeks	416.3 ± 47.7	427.7 ± 39.6	421.5 ± 50.6
Testosterone (ng/100 ml) 7 weeks	421.3 ± 34.7	396.0 ± 29.0	402.0 ± 25.5

Note. Values are mean ± SE. Values with different letters differ significantly, Tukey's HSD ($P < 0.05$).

virgin males, but polygynous males experienced a greater concentration of androgen in circulation ($P < 0.01$). When testosterone titers were examined 2 or 7 weeks after the behavioral interactions, there were no differences among the groups.

Discussion

The findings suggest that qualitatively different sexual interactions can generate different profiles in the behavioral endocrinology of males. Results confirmed the hypothesis of increased activity in varied androgen sensitive systems of male rats allowed the same precisely controlled number of ejaculations with multiple females as opposed to a single partner. Repeated pairing of the males with an unfamiliar female increased measures of both sexual motivation and performance. Examination of animals at necropsy at either 2 or 7 weeks after the final copulatory experience suggested greater

growth of target tissues in the successively polygynous males. A possible mechanism underlying these behavioral and physiologic changes is the different endocrine response by polygynous males to an unfamiliar female (29).

We used an experimental paradigm in which gonadally intact males were exposed twice weekly for a month to either an exclusive or one of various sexually receptive females. Over weeks, the polygynous males were faster to copulate and ejaculate than monogamous males, measures which indicate increases in both motivation and arousal, respectively, in rats (22). The polygynous males also had intromissions and shorter intervals between ejaculations (30). These data are reminiscent of the "Coolidge effect," where an apparently sexually exhausted male rat will recover quickly in the presence of a new female (31). Behavior with that experimental paradigm, however, commonly is within a single observation session (32), whereas the present paradigm exchanged females between sessions.

Solicitations of the male by the female also were measured. That the female solicited a familiar male *more* than an unfamiliar male (33, 34) is of less importance than the implications for social memory between the pairs (35). The different rates of solicitation provided additional evidence that the female rats recognized a sexual partner as familiar with only two exposures to him per week.

We also were interested in physiologic differences when the males were killed at 2 or 7 weeks after the final sexual interaction. In comparisons with virgin males, weights of various primary and secondary sex structures were elevated in males 2 weeks after sexual contact and particularly in males with multiple female partners. Increased sizes in these highly androgen-sensitive tissues suggest a pattern of greater functional activity in polygynous males. The epididymal sperm counts indicate that short-term physiologic activation may elevate fertility also (24, 36).

Findings after 7 weeks of sexual rest indicated a more complex relation of the physiologic measures with qualitatively different sexual experiences. Some gland weights (e.g., prostate) in the polygynous group returned to control values, whereas some structures remained chronically elevated (e.g., seminal vesicles and spongiosus muscles) in polygynous males over both chronic and monogamous groups. But, sperm counts were lower in polygynous than monogamous males. The conclusion from these more chronic effects, nevertheless, are consistent with the implications from acute analysis. Males with varied sexual partners exhibit a different physiologic profile than males with an exclusive partner.

The underlying mechanism for these data may be the endocrine system. Typically, exposure to a receptive female induces a brief, but high amplitude pulsatile release of gonadotropic and testicular hormones (16, 37). It is possible that the response is exaggerated with the introduction of an unfamiliar female partner (18, 29). Indeed, we found a greater elevation of testosterone in the males when blood serum was analyzed immediately after exposure to an unfamiliar female as opposed to a familiar partner. The suggestion is that the increase was short-lived (38) because circulating testosterone levels among the groups did not differ when the animals were killed some weeks later for physiologic examination.

Environmental events which induce different endocrine profiles can modify the behavior, physiology, and morphology of animals differently (39). One such event may be qualitatively dissimilar, but quantitatively similar, sexual contacts. The implications are notable for the biology of reproduction and for our interest (28) in the relation of behavioral endocrinology to structural pathogenesis. For example, we believe any benefits accrued by physiologic activation in the younger adult male with exposure to varied females may prove to be short-term gains (40, 41). In a manuscript in preparation, we report prostate nuclear chromatin changes that portend pathologic changes over the long term. Regardless, the experimental paradigm proposed here should prove useful in studies of the endocrinology of sexual behavior.

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