

Regulation of social contact by the female rat during the postejaculatory interval

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Mating behavior of male and estrous female rats was observed in a large cage through three ejaculatory series. Movement, 22-kHz ultrasonic vocalizations, sexual behavior, and distance between animals were studied during the postejaculatory interval (PEI) to help establish how copulatory contact is maintained and reinitiated for successive ejaculations. Females moved more than males throughout the three series. The duration of vocalization by the male during the PEI increased in the presence of an experienced female. During the male's vocalization, the rats exhibited a period of immobility that usually began with the experienced female's terminating contact by moving away from the male and ended when the female reinitiated contact by moving toward the male. Virgin females did not show this pattern of movement. Experienced females maintained a greater distance from the male during the PEI than did virgin females. We conclude that the behavior of the experienced estrous female assures both considerable spatial separation during the male's refractory period and the reinitiation of contact.

Calhoun (1963, p. 123) noted long ago that rat colonies coordinate periods of activity and inactivity. His suggestion that vocalizations were involved in the temporal regulation of social behavior has gained recent support (Adler & Anisko, 1979; Barfield, Auerbach, Geyer, & McIntosh, 1979). Following each ejaculation, rats cease copulatory activity; however, the male and female later resume copulation if they reinitiate contact successfully, and the process is repeated through several ejaculatory series. This study elucidates the processes by which contact is maintained across copulatory sequences.

A mating male and female rat modify their activities to reduce contact following ejaculation. During the first quarter of the postejaculatory interval (PEI), both sexes show decreased locomotion (Dewsbury, 1967). During this quiescent period, the male emits a 22-kHz vocalization (Barfield & Geyer, 1972, 1975). Various aspects of male behavior during the PEI are well studied, whereas the female's activities are little understood.

Both neuroendocrine and genetic factors exert specific effects on sexual responsiveness of females. Gonadal hormones affect the pacing of sexual con-

tacts by female rats. In the presence of estrogen, females given progesterone exhibit accelerated pacing of intromissions and increased darting (Gilman & Hitt, 1978; reviewed by Madlafousek & Hlinak, 1977). Strain differences influence the frequency of ear wiggling (Hlinak, 1975; Madlafousek & Hlinak, 1978), and domestication of females appears to modify intromission intervals (McClintock & Adler, 1978).

Part of the influence of the female may be due to a refractory state, since the barpress latency of an estrous female to release a male increases with copulatory stimulation and successive ejaculatory series (Bermant & Westbrook, 1966). Reduced latencies to release a male following ejaculation occur if no copulatory plug is present. A female stays away from three males longer following increased copulatory stimulation (Peirce & Nuttall, 1961). Females also exhibit less running following ejaculation (Dewsbury, 1967).

With appropriate stimulation, females exhibit enhanced proceptivity (Beach, 1976). Ultrasonic vocalizations associated with copulation both prime (Geyer, McIntosh, & Barfield, 1978) and elicit (McIntosh, Barfield, & Geyer, 1978) darting by female rats. In turn, males are sexually facilitated by the females' proceptive patterns, especially sexually inexperienced males who have difficulty initiating copulation with nondarting females (Hlinak & Madlafousek, 1972).

In two recent studies of the female's contribution to the temporal pattern of copulation (Fadem, 1977; Krieger, Orr, & Perper, 1976), a female was given limited access to a restricted male. Ejaculations resulted in a decline in proceptivity of the female. Another study used a large testing environment in

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which copulatory intervals were longer, thereby allowing detailed observations of solicitation patterns during copulation (McClintock, 1974). The female was shown to have an important role in adjusting the temporal patterning of intromissions via solicitation (McClintock & Adler, 1978).

Although there has been considerable study of male and female copulatory behavior, dynamic interplay during the PEI has received little attention. The major objective of our study was to characterize the male/female interactions during the PEI, particularly the maintenance and pacing of contact. We chose to observe copulation during the first and second mating test of the female. Contrasts of interest were (1) female and male behavioral differences in regulating spatial separation, and (2) changes in behavior of the female as she gains experience. Another objective was to determine the relationship, if any, between the 22-kHz postejaculatory vocalization and the movements of the male and the female.

METHOD

Subjects and Apparatus

Ten 4-month-old female rats (Long-Evans strain, Charles River Farms) were subjects. They were mated with 10 sexually experienced males of approximately 12 months of age.

All animals were housed individually in 30 × 18 × 18 cm cages with Purina Rat Chow and water available continuously. They were kept under a reversed 12:12-h schedule (lights off 9:30 a.m.-9:30 p.m.). Mating tests were conducted in a cage (104 × 52 × 29 cm) having quadruple the area of our typical testing cage and a center post. The slate floor was marked in an 8 × 4 grid with plastic tape. The cage floor was wiped with water-dampened paper towels following each test.

Sexual behavior was scored manually on a keyboard that operated a 20-channel Esterline-Angus recorder, including: for the male, mount—mount with pelvic thrusts; intromission—mount with pelvic thrusts followed by a deep thrust and rapid dismount; and ejaculation—vigorous mounting followed by a deep thrust with a slow dismount; and, for the female, darting—bilateral planting of the feet on the substrate, usually preceded by running or hopping. Locomotion, which altered the cage grid location, was continuously scored for each animal. The number of grid square spaces of separation between the male and female was continuously recorded. Ultrasonic vocalizations at 22 kHz and at 50 kHz were scored separately. In addition, the location of the male in the cage during each PEI was logged.

Ultrasonic vocalizations were audibly monitored with a Holgate ultrasonic receiver set at 50 kHz during the copulatory series and at 22 kHz during the PEI. Both the audible output and a visible oscilloscope output were utilized to confirm the presence and frequency of ultrasonic emissions. The ultrasound detector sensitivity was excellent for detecting 22-kHz pulses. Since some 50-kHz pulses may not have been detected (due to a relatively large cage, short pulse durations, and low sound pressure), we describe only the 22-kHz vocalizations in this report.

Virgin females were ovariectomized at approximately 4 months of age. Females were injected with 30 µg of estradiol benzoate during anesthesia recovery and with 500 µg of progesterone 48 h later.

Two weeks after ovariectomy, females were brought into artificial estrus with injections of estrogen (30 µg) and progesterone (500 µg) 54 and 6 h, respectively, before the time of a 20-min acclimation period alone in the testing cage.

At each of two subsequent 2-week intervals, each female was

brought in artificial estrus and given mating tests. Females, being sexually naive, were virgins prior to the first test, and "experienced" prior to the second test. Females were tested with a different male on each test. Males were tested at intervals of 1 week or longer.

Tests were carried out between hours 4 and 8 of the dark phase of the light/dark cycle. Tests were performed in a room illuminated by two 60-W red bulbs placed 2 m directly above the cage. During tests, the observer sat on a stool overlooking the cage, which was on the floor. Prior to the mating test, the male was given a 5-min acclimation period in the cage before the female was introduced. Mating was observed until the first intromission following the third ejaculation. Only one pair was tested at any one time.

Data Analysis

Measures of sexual behavior and the postejaculatory vocalization extracted from the strip chart record included: intromission latency (IL)—elapsed time from the pairing to the first intromission; ejaculation latency (EL)—time from the first intromission to ejaculation; intromission frequency (IF)—the number of intromissions prior to ejaculation; vocalization latency (VL)—duration from ejaculation until the initiation of vocalization; vocalization termination (VT)—duration from ejaculation until the termination of 22-kHz vocalization; duration of vocalization—total number of seconds in which 22-kHz vocalization were emitted during the PEI. These data were statistically analyzed using a two-way analysis of variance, with series and female experience as factors.

To evaluate utilization of space by the male and female, the number of seconds spent with each separation distance between the animals was transcribed, on a scale of 1 to 4, where each unit was 20-25 cm. Maximal distance was designated as 4 separation units, and the minimal distance was defined as 1 unit or less.

To measure movement, the percentage of time each rat moved during the ejaculation latency period was calculated for the three ejaculatory series. The duration of movement by rats during the three PEIs was also determined. These measures were tested as factors.

Several measures were used to describe nonmovement periods and the movements that immediately precede and follow them. Following intromissions and ejaculations, the female runs away from the male and then stereotypically freezes before resuming movement. The latency to resumption of movement was determined for each ejaculation and for the preceding intromission. Additionally, the PEI is characterized by extended periods of inactivity by the male and female. To evaluate these, the longest single segment of time during each PEI in which each individual did not move was determined and termed its immobility period, while the shared immobility period was the longest portion of time in which neither animal moved. Movements directly preceding and following the shared immobility period of the male and female were categorized to identify the direction of movement and the sex of the moving rat. These data were pooled across series and tested statistically with chi square for significant effects of movement directionality and female sexual experience.

To evaluate ongoing relationships between separation distance and occurrence of 22-kHz vocalizations, the PEI was divided into fifths. The initial four fifths, when vocalizing occurs, were separately evaluated. The duration spent at each of the four separation distances was then determined for PEI time intervals with and without vocalization. These data were subjected to an analysis of variance to test whether vocalization periods were characterized by greater separation distance.

RESULTS

Behavior of the Female and the Male

Previous to the first ejaculation, the male moved less than the female. Following ejaculation, the male

typically spent his quiescent period in a resting place (also reported by Anisko, Adler, & Suer, 1979), to which he frequently returned between intromissions. Following the first ejaculation, males rested in a corner square in 13 of the 20 tests, although corner squares accounted for only 12.5% of the surface area. In 12 of the 20 tests, males retained the same rest site in all three PEIs, even though a single square occupied only 3% of the surface area.

Over the course of three ejaculatory series, ejaculation latency (EL), vocalization termination (VT), and PEI all changed significantly [Table 1; series effect, $F_s(2,18)=4.79, 8.47, 17.61, p_s < .025, .005, .001$, respectively]. The first ejaculation of the inexperienced female was associated with a significantly increased intromission latency [$t(9)=2.59, p < .025$] and ejaculation latency [Series by Experience interaction: $F(2,18)=4.72, p < .025$]. Sexual experience of the female also affected vocalization termination [experience effect: $F(1,9)=5.12, p < .05$]. Other measures were unaffected by the female's experience.

The postejaculatory vocalization was significantly affected in its duration by the female's experience [$F(1,9)=40.1, p < .001$]. Mean durations of vocalization in Series 1, 2, and 3 were 104.6, 47.4, and 78.9 sec, with sexually inexperienced females, as compared with 162.2, 243.2, and 278.0 sec when the female was sexually experienced. During the second and third PEI, vocalizing by males was sharply reduced in tests in which the female was sexually naive, as reflected in a significant series by experience interaction [$F(2,18)=4.37, p < .05$].

Utilization of Space

Following sexual experience, females spent significantly more time at a maximum distance from the male and less time at a minimum distance than they did as virgins (Figure 1). Experienced females spent

significantly more time at a maximal distance from the male than they spent at the minimal distance, whereas time spent by virgin females at maximal and minimal distances did not differ statistically.

Occurrence of Movement

During all portions of the mating sequence, the females spent more time moving than the males [gender effect: $F(1,8)=67.94, p < .001$], but their movement during the ejaculation latency period declined from 41% in Series 1 to 30% in Series 2 and 28% in Series 3. Movement of males, however, remained stable at 16%, 16%, and 19% in successive series; thus, there was a significant Series by Gender interaction [$F(2,18)=10.47, p < .001$]. Following ejaculation, the males were predominantly stationary and moved less than during the time prior to ejaculation (Table 2). Females spent significantly more time moving than did males [gender effect: $F(1,9)=39.7, p < .001$].

Occurrence of Stationary Periods vs. Periods with Location Change

Following ejaculation, females run away from the male and then stop. Latency to resumption of movement following ejaculation in the three series (mean = 82.0, 167.7, 170.0 sec) was significantly greater than the latency to movement following the intromission that preceded ejaculation [mean = 22.8, 24.9, 20.3 sec; $F(1,9)=57.4, p < .001$].

The mean immobility period for males was more than twice the mean immobility period for females in all series (Table 3). The males' immobility period became significantly longer in successive series [$F(2,18)=6.69, p < .01$]. The first ejaculation was followed by prolonged immobility in experienced females as reflected in a significant series by experience interaction [$F(2,18)=18.2, p < .001$]. The single longest

Table 1
Measures of Sexual Behavior, Based on the First Two Mating Tests of 10 Females

Behavioral Measure		Sex					
		Ejaculatory Series 1		Ejaculatory Series 2		Ejaculatory Series 3	
		Mean	SEM	Mean	SEM	Mean	SEM
Intromission Latency	V	354.4	83.2				
	E	95.4	29.1				
Intromission Frequency	V	8.6	1.4	5.3	.8	5.7	.7
	E	6.7	.7	4.8	.5	4.7	.5
Ejaculation Latency	V	2082.8	885.8	529.6	70.3	434.2	81.0
	E	458.8	115.6	284.4	57.7	284.8	83.6
Vocalization Latency	V	72.6	32.4	88.4	30.4	125.2	35.8
	E	31.2	4.6	29.4	7.0	68.2	25.0
Vocalization Termination	V	238.4	60.7	150.8	33.6	341.2	48.3
	E	229.5	27.6	291.0	42.7	400.8	27.1
Postejaculatory Interval	V	578.7	38.7	641.4	44.9	754.0	60.7
	E	481.0	49.9	564.0	48.8	680.9	60.0

Note—V = virgin female; E = sexually experienced female.

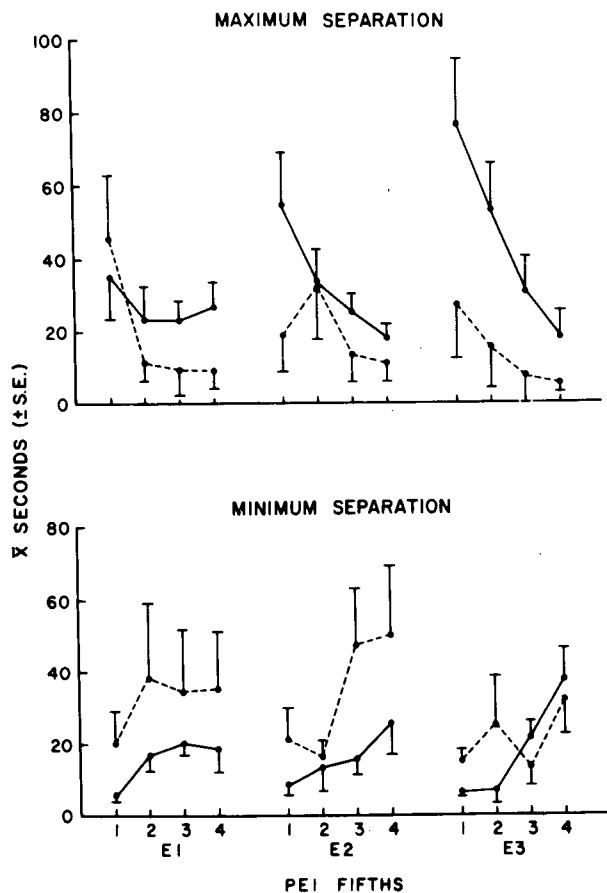


Figure 1. Effects of sexual experience by the female rat on spatial separation from the male during the postejaculatory interval (PEI). Durations of both maximal and minimal separation in the cage used are indicated by dashed lines for the first mating tests of virgin females, and data from the second mating tests following experience are shown as solid lines. Data points represent the PEIs of three ejaculatory series, each broken into fifths. The final fifth is not shown, since it typically involves resumption of copulatory attempts and includes no 22-kHz vocalization. In analyses of variance with ejaculatory series and sexual experience of the female as factors, a significant effect of female experience was found for duration at maximal separation [$F(1,9)=5.22, p < .05$] and at minimal separation [$F(1,9)=7.60, p < .025$]. In analyses of variance for experienced females, with ejaculatory series and durations at maximal vs. minimal spacing as factors, significant effects were found for maximal vs. minimal spacing [$F(1,9)=10.82, p < .01$] and for the ejaculatory series by spacing interaction [$F(2,18)=8.80, p < .005$]. A comparable analysis for virgin females yielded no significant effects.

portion of time in which neither moved, termed the shared immobility period, was significantly longer in tests with sexually inexperienced females [$F(1,9)=5.4, p < .05$].

Generally, the shared immobility period was preceded directly by a movement apart, which increased the space between the animals (42 of 60 periods), and the shared immobility period was terminated by a movement together (45 of 60 periods). This pattern characterized tests with virgin ($\chi^2=6.79, p < .01$) and experienced females ($\chi^2=19.29, p < .001$). A majority of movements beginning the shared immobility period were made by the female (44 of 60). Partners moved a maximal distance apart during the shared immobility period more often when the female had had some sexual experience (virgin: 6 of 30; experienced: 18 of 30; $\chi^2=10.00, p < .01$). This difference also held when male movements were excluded and only terminal movements made by females were considered. Thus, the occurrence of maximal separation between rats during the shared immobility period was significantly higher when the female was sexually experienced.

Occurrence of Ultrasonic Vocalization

In a majority of tests (35 of 60 PEIs), the 22-kHz vocalization was totally within the male's immobility period. This contrasts with the proportion of vocalization occurring during each female's immobility period, in which the median scores were 33%, 25%, and 33% in successive series, respectively. An analysis within PEI fifths of time segments with and without vocalizing demonstrated an ongoing temporal correlation between vocalization and animals' separation distance (vocalization by distance interaction),¹ as animals were farther apart during vocalization than in its absence. In Figure 2, for example, percent times spent at maximal and at minimal separation are shown for time portions with and without vocalization.

DISCUSSION

Our data show clear sex differences in activity during the PEI and also in the nature of changes occurring across successive PEIs. In Dewsbury's (1967)

Table 2
Occurrence of Movement by the Male and the Female During the Postejaculatory Interval (PEI)

PEI	Male								Female					
	Total Seconds		Mean Percentage of PEI Fifths					Total Seconds		Mean Percentage of PEI Fifths				
	Mean	SEM	1	2	3	4	5	Mean	SEM	1	2	3	4	5
1	58.9	7.2	9.1	7.5	8.5	13.5	17.5	119.4	16.2	19.3	17.3	22.7	24.7	30.3
2	30.2	4.8	3.5	3.5	4.5	5.2	10.2	128.1	19.3	8.5	22.2	23.6	24.0	25.3
3	38.2	6.9	3.1	1.9	3.1	7.3	10.2	111.9	16.4	8.8	9.1	17.1	18.5	20.9

Note—N = 20 tests for each PEI.

Table 3
 Immobility Period: The Longest Segment of Time During the Postejaculatory Interval in Which the Subjects Did Not Move

Subject		Ejaculatory Series 1		Ejaculatory Series 2		Ejaculatory Series 3	
		Mean	SEM	Mean	SEM	Mean	SEM
Female	V	193.0	49.5	170.2	45.1	169.0	52.8
	E	65.2	14.2	136.6	32.9	187.6	43.4
Male	V	306.6	51.5	433.6	84.0	503.2	70.9
	E	187.6	46.5	350.0	80.5	450.0	93.8
Female and Male	V	229.4	73.0	138.6	32.1	138.2	29.5
	E	60.0	13.9	82.4	19.5	108.0	16.4

Note— $N = 20$ tests for each series. *V* = virgin female; *E* = sexually experienced female.

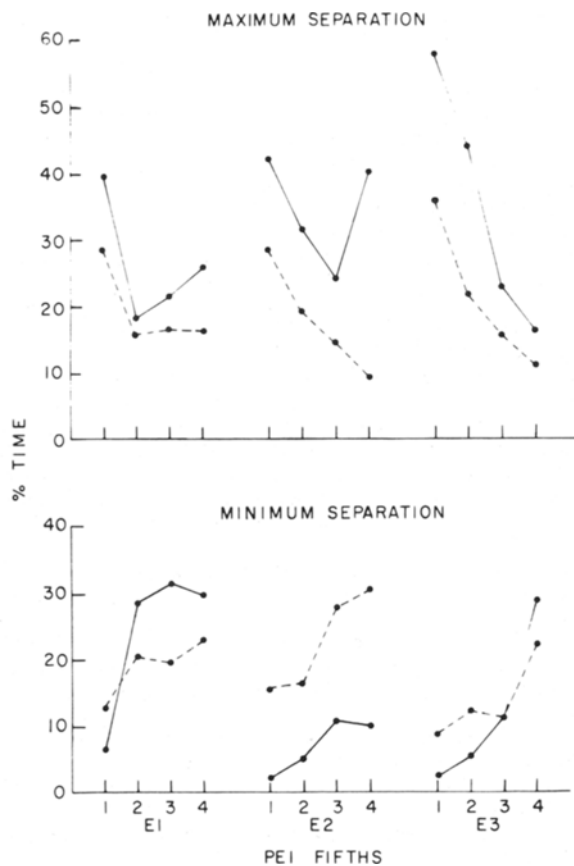


Figure 2. The relationship of ultrasonic vocalization and spatial separation between the male and female rat during the first four-fifths of the postejaculatory interval (PEI). Data are shown in solid lines as percentages of time during vocalization spent at maximal and at minimal spatial separation; data are shown in dashed lines as percentages of time without vocalization spent at maximal and at minimal spatial separation. Analysis of variance included the following factors: ejaculatory series by vocalization presence or absence by PEI fifth by grid separation. Since the final fifth of the PEI typically includes no 22-kHz vocalization, only the first four-fifths were included in the analysis. Grid separation was based on a maximum of four units. For analysis purposes, data were expressed as the absolute total number of seconds for each cell with all 20 tests pooled. The statistical test of interest, vocalization by distance interaction, was $F(3,12) = 11.91, p < .005$.

analysis of copulatory behavior during the first ejaculatory series, locomotor-exploratory behavior was exhibited by males approximately 22% and 35% of the EL and PEI, respectively, and by females 66% and 72%. Animals were tested in a small semicircular arena. Compared with our data, ejaculatory series took less time and animals spent a greater proportion of time moving. In both studies, however, females spent at least twice as much time moving during the EL and PEI as did males.

Dewsbury (1967) noted the immobility response in both sexes, especially immediately after ejaculation. We observed that the inactivity period of the male lasted several minutes, extending through the vocalization. For the female, it exceeded 2 min. This extended period of immobility occurred with a marked separation between the two animals.

Sperm transport is most readily disrupted by intromissions within the first 2 min after ejaculation (Matthews & Adler, 1977), a period in which we found the female to show prolonged immobility. The studies of sperm transport by Adler (1974) and his colleagues have shown that quiescence of the female is supportive of pregnancy induction. It therefore seems reasonable that the female has mechanisms to regulate her activity and suppress her behavior during the early PEI.

In this study, females are shown to regulate contact not only during intromissions, as reported by McClintock and Adler (1978), but also during the PEI. Since females accounted for most of the movements during the PEI, contact episodes can largely be attributed to females rather than males. Females moved away from males before the extended immobility period and moved toward them at the end of the period.

Males are known to vocalize less reliably following four or more ejaculations (Anisko, Suer, McClintock, & Adler, 1978). This is the first report of erratic postejaculatory vocalization during copulation with an inexperienced female. In several studies, we have observed that if the female nuzzles or touches the male during vocalization, he often shifts position and

stops vocalizing. We therefore attribute the short vocalization to the disruptive mating pattern of the virgin female.

Our data support the possibility that the female remains significantly distant from the male during ultrasonic calling by the male, since we found vocalization by distance interaction. Another report has shown that approach and solicitation by the female during the PEI are not diminished during vocalization bouts (Anisko, Suer, McClintock, & Adler, 1978). Taken together, these studies suggest that the post-ejaculatory vocalization may affect the distance that the female moves away from the male rather than her later approaches to the male.

During portions of time that included the post-ejaculatory vocalization, the distance between the male and female was greater than in periods in which there was no vocalization. This result is due to the female, since a majority of males did not move during the vocalization period, while females sporadically approached and withdrew during this period. It is possible that the female moves away from the male to avoid the strong auditory stimulus (at times, 80 dB or greater; Barfield & Geyer, 1972) produced by the male. For the female, ejaculation is associated with extensive exertion and sensory bombardment, including tactile, genital, auditory, and olfactory stimuli from the male, as well as the accompanying self-stimulation of an extended lordosis posture. During the first third of the PEI, the female shows an increase in sleeplike EEG (Kurtz, 1975), and it seems likely that the female might exhibit a heightened sensitivity to the vocalization immediately following ejaculation. The 22-kHz vocalization may constitute an aversion stimulus facilitating the female's temporary withdrawal from the male, particularly with increasing sexual experience. At the same time, the vocalization could serve to maintain some contact prior to the resumption of mating.

The importance of courtship activities of female rodents has been increasingly recognized in recent years (e.g., Beach, 1976; Doty, 1974). This study shows that the female rat modulates the distance and frequency of contact with the male following ejaculation. This maintenance of contact is coordinated with the male vocalization and increases the likelihood of continued copulation. We conclude that the female rat performs an important courtship pattern during the postejaculatory interval, which maintains her contact with the male during his sexual refractory period.

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NOTE

1. The final fifth of the PEI was not included in this analysis, since vocalization is ended by then and initial copulatory approaches have begun.

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