TEMPORAL PATTERNS OF SEXUAL BEHAVIOR IN RABBITS AS DETERMINED BY AN AUTOMATIC RECORDING TECHNIQUE¹

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Sexual behavior between rabbits was automatically recorded by means of electrodes attached externally to the unrestrained animals. Current flowed only when the animals came into physical contact; the duration and amplitude of the current flow provided a means of automatic differentiation between sexual and other types of physical contact. Various temporal aspects of sexual behavior were revealed: (1) copulation was preceded by a series of thrusts that occurred at a constant frequency of 13 to 14 thrusts per sec; (2) the duration of a copulation was about 1.5 sec and could be as brief as 0.3 sec; (3) copulation was much more likely during the hours between dusk and dawn despite constant illumination; (4) copulations occurred in groups or "runs" characterized by many copulations within a few hours; (5) each run began with a high rate of copulation that often decreased over time; (6) between runs, several hours or days passed with little or no sexual activity; and (7) a run of copulations was noted at the end of every 16- to 20-day period (which corresponds to the known period of pseudopregnancy in rabbits) whether or not other runs occurred within this period.

Research in the area of sexual behavior has relied heavily upon visual observation for recording the copulatory response. This has been true whether the research was done in the field (*e.g.* Carpenter, 1942), in the zoo (Crandall, 1964), or on the farm (Hafez, 1962).

Some laboratory investigators have attempted to improve observation techniques. For example, a glass-bottomed cage and mirror has been used to achieve a standardized ventral view (Beach and Rabedeau, 1959). High speed cinematography has been used to study duration of contact (Stone and Ferguson, 1940; Bermant, 1965). Small amounts of monitored current have been passed through pairs of subjects to corroborate visual observations of sexual contacts (Peirce and Nuttall, 1961; Bermant, 1965). The number of copulatory plugs of rats (vaginal obstructions produced by the coagulation of semen) deposited daily in the drop pan has been used to deter-

mine the number of copulations occurring in 24-hr periods (Lisk, 1966).

These laboratory techniques constitute major improvements over simple visual observations. The ventral viewing procedure permitted direct observation of penile-vaginal contact. The cinematographic technique permitted slow-motion representation of copulation, as well as allowing repeated viewing at the observer's convenience. The method of recording current flow resulting from physical contact provided an objective measure of number and duration of copulations when used as an adjunct to visual observation. The vaginal plug method provided an objective measure of number of copulations and eliminated the need for visual observation unless information about the temporal parameters of copulation was required.

The present study sought to develop a method of measuring sexual behavior that did not rely on visual observation but which would provide information about the exact moment of copulation. This method, which was similar to that of Peirce and Nuttall (1961) where monitored current was passed through a pair of animals, required an apparatus which would: (1) accurately discriminate the current flow resulting from penile-vaginal contact from that resulting from other

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physical contacts such as genital licking, biting, mounting, thrusting, *etc.*; (2) maintain its electrical characteristics over extended periods of time without deterioration; (3) resist damage from gnawing, scratching, urine, feces, *etc.*; and, (4) allow free movement of the subjects.

Subjects

Domestic rabbits of the American Dutch breed were purchased from commercial suppliers and maintained in individual living cages. They were sexually mature at the start of the experiment; their exact age and sexual experience were unknown. Their weight ranged from 1100 to 2500 g.

Apparatus

Electrodes. Each electrode consisted of a gold wire 2 in. in length and 0.025 in. in diameter. The gold wire was implanted subcutaneously in the nape of the neck, using minimal local anesthesia, by raising a loose fold of skin and taking a single stitch with a surgical needle threaded with the gold wire. Two electrodes were implanted in each subject about 2 in. apart, as shown in Fig. 1. This procedure did not appear to discomfort the animal and was routinely performed within 5 min. Of 86 implants no electrode "grew out" or developed an unusually high resistance in less than 60 days. After 60 days some electrodes had to be replaced, although some were satisfactory for as long as six months.

Harness and connections. A harness was designed that provided an insulated, bite-proof

electrical connection to the subjects without imposing undue physical restraint. The harness was constructed from a sheet of $5\frac{1}{2}$ by $2\frac{1}{2}$ by $\frac{1}{8}$ in. Plexiglas cut to the pattern shown in Fig. 2. The patterned Plexiglas was heated and formed around a $2\frac{1}{4}$ -in. diameter cylinder until it assumed a "U" shape. The resulting size and shape provided a satisfactory fit for all of the rabbits used. A leather strap and a bead chain (enclosed in a rubber tube) held the harness in place. As seen in Fig. 1, this harness arrangement provided electrically insulated protection of the entire area of electrode placement.

Figure 1 also shows a metal plate $1\frac{3}{4}$ by $\frac{3}{4}$ by $\frac{1}{8}$ in. which was attached to the top of the harness and formed a rigid base for the physical and electrical connections to the animal. Attached to the metal plate was a "dog collar" ring which served as a connector for the protective spring which enclosed the connecting wires. The spring (a 20-in. long "spring sash rod" purchased at a local hardware store) absorbed most of the force produced by the rapid movements of the subjects. The wires were made 2 in. longer than the spring (via a loop) in order to permit the spring to expand without placing strain on the wires.

One end of the spring was clipped to the ring on the harness; the other end was permanently fastened to a swivel. Three swivels

Fig. 1. Harness and electrical connections to the rabbit. The bite-proof spring containing the connecting wires is clipped to the ring on the harness.

Fig. 2. Harness pattern cut from $5\frac{1}{2}$ by $2\frac{1}{2}$ by $\frac{1}{8}$ in. Plexiglas. When formed to a "U" shape around a $2\frac{1}{4}$ -in. diameter cylinder, the harness provided a satisfactory fit for rabbits in a 1100 to 2400 g weight range.

were used in a manner which allowed free movement of either animal in any direction without tangling the springs. (R. R. Hutchinson designed the swivel arrangement, which is now commercially available from Lehigh Valley Electronics.)

In addition to allowing unrestrained movement of the subjects, the three-swivel complex served as a commutator making electrical connections to the subjects. The upper swivel contained four concentric channels, each 0.5-in. deep and filled with mercury; each of the pair of lower swivels contained two mercury-filled channels 1.5-in. deep. The four channels provided four independent electrical contacts, one for each electrode. The low electrical noise level of the mercury contacts was especially valuable because of the low voltages used.

The connecting wires from the swivel terminated in a miniature, two-prong plug (Switchcraft Inc. "Little Plug" No. 410) which was cemented to the lower end of the spring. (Before being cemented to the spring, the plug was modified by cutting off 0.5 in. of its length and attaching its leads perpendicular to its prongs). The plug was covered with epoxy cement to protect it against gnawing. The female connector for this plug (Switchcraft Inc. "Extension Jax" No. 810) was modified in the same way as the plug and was fastened to the metal plate on the harness. The lead wire from the connector went through the metal plate and harness and was connected to the

implanted electrodes by solderless wire connectors. All exposed metal portions of the electrodes, connectors, and wires were covered with shrinkable-tubing insulation (Allied Electronics Cat. No. 49Z938C).

Experimental space. The experimental chamber, shown in Fig. 3, was constructed entirely of electrically insulating Plexiglas and was 24 by 24 by 18 in. high. The chamber was enclosed in an exterior box lined with sound-absorbing insulation. The floor was constructed of $\frac{3}{8}$ -in. parallel plastic rods spaced $\frac{3}{4}$ in. center to center. This "grid" prevented the rabbits from contacting the metal drop pan, and precluded the accumulation of urine, feces, or other material which could serve as an electrical conductor. A water bottle and food dish (attached to a wall) were always present in the enclosure. A closed-circuit TV camera mounted on the outside of the exterior box permitted visual observation of the subjects from an adjacent room.

Copulation detection circuit. A schematic drawing of the copulation detection circuit is shown in Fig. 4. The voltage source was 100

Fig. 3. Experimental chamber. Interior chamber was constructed entirely of Plexiglas; the exterior chamber was constructed of wood and lined with sound absorbing material. The "chimney" on top of interior chamber provided an opening for the connecting wires, but prevented any escape by the subjects.

Fig. 4. Schematic drawing of the copulation detection and electrode test circuits. The copulation detection circuit continuously monitored current flow through both subjects. The electrode test circuit was used to measure momentarily the current flow through the two electrodes in a given subject.

T1—Constant Voltage Transformer Sola #20-06-015

T2—115 v ac "Powerstat" Superior Electric Type 10B

T3—115 v ac "Powerstat" Superior Electric Type 10B

T4—Transformer 115 v ac pri 6 v ac Sec

S1—Switch DPDT Spring Return

S2—Switch DPST Spring Return

CR1—Diode RCA #1N3195

CR2—Diode RCA #1N3195

CR3—Diode RCA #1N3195

CR4—Diode RCA #1N3195

M1—Meter 0-3 v ac Simpson #8720

M2—Meter 0-100 μ a ac Weston #302 ac M1C

M3—Meter-Relay 0-50 μ a dc Simpson #3324XA.

mv ac (later raised to 150 mv) and was obtained from a constant voltage transformer in series with a variac. This current was passed through one electrode in each of a pair of subjects. Current flow through the pair of subjects was monitored by a 0 to 50 μ a dc meter-relay. Alternating current was used to prevent polarization, but was rectified in that part of the circuit that included the dc meter-relay. The lower section of Fig. 4 shows the test circuit used to estimate the resistance of the electrodes and to test the integrity of the electrical connections to each subject. This circuit, which could be activated by closing switch S2, imposed 200 mv ac across the two electrodes in one subject. The position of switch S1 determined which subject was being tested. The amount of current flow in the test circuit was displayed on meter M2. All intensities of current used were well below the perceptual threshold of electric shock.

EXPERIMENTAL ANALYSIS OF THE AUTOMATED METHOD

I. Discrimination of Copulations

A series of observations determined if the copulation detection circuit would differentiate copulations from other physical contacts.

Method. The subjects were 16 rabbits divided into eight male-female pairs. The males were vasectomized to prevent fertilization of the females.

A male and a female subject were connected to the copulation detection circuit. Two observers independently reported all oral, mounting, thrusting, and copulatory contacts made by the pair from that time when the subjects were placed in the experimental space until the copulation detecting circuit indicated that a copulation had occurred. One observer viewed the subjects through the plastic door of the experimental chamber; the other viewed them on a TV monitor in an adjacent room.

Each observer had a panel of four switches, one for each kind of physical contact. Each switch deflected a different pen on an event recorder. The pens remained deflected as long as the switch was closed. The observers operated the "oral contact" switches when the muzzle of one animal made any physical contact with the body of the other; they operated the "mount" switches when the male placed the front part of his body on the back of the

female, his pelvis covering her hind-quarters; they operated the "thrust" switches when the male rapidly oscillated his pelvis while in a mounted position; and they operated the "copulation" switches when the male made a characteristic backward lunge, falling off the back of the female. (For a complete description of copulations by rabbits, see Worden and Leahy, 1962, pp. 402-424 or Macirone and Walton, 1938, pp. 131-132.) The two observers were in perfect agreement as to the occurrence of a contact; they only differed, and then slightly, in the duration of a contact. Because of this agreement, only one observer was used in the last four pairings.

Concurrent with the visual observations, a polygraph recorded the current flow through the subjects during the entire session. The adjustable meter-relay contacts were preset to provide an impulse only when the current flow exceeded 15 μ a. A timer was placed in series with the meter-relay and was preset to provide an impulse only when the contacts of the meter-relay had been closed for at least 250 msec. When these criteria were met, a mark was made on the polygraph record of the current flow.

Results. The lower curve in Fig. 5 shows a sample record of the current flow which occurred during one session. The other curves represent one observer's reports of specific physical contacts. The observer's report of a contact always lagged behind the record of

Fig. 5. Sample recording of sexual behavior of one pair of rabbits. The four upper tracings were produced by an observer who closed a switch to indicate the occurrence of a specific physical contact. Closing a switch resulted in the upward deflection of the appropriate pen. The lower tracing was produced by the current flow between the two rabbits and was recorded directly from the copulation detection circuit by a polygraph. The arrow indicates the moment when an output was obtained from the meter-relay that was part of the copulation detection circuit.

current flow, presumably because of his "reaction time error".

The first deflection on the current flow record was produced by an oral contact. This contact resulted in a flow of $10\ \mu\text{a}$ of current for about 200 msec. Oral contacts frequently occurred when the male was mounted on the female and seemed to consist of a bite at the female's back or neck. Mounting alone did not result in a flow of current, presumably because of the high resistance of a contact of fur against fur.

Thrusts, however, resulted in a current flow of about $30\ \mu\text{a}$ for a duration of less than 100 msec per thrust, and were probably produced by physical contact between the erect penis and the vulva. These contacts are indicated by the oscillating tracing in the center of the current flow record. The pen did not drop to the zero baseline during the breaks in contact between thrusts because of recorder inertia. (The fact that the breaks occurred was visu-

ally corroborated by examination of high-speed motion pictures of the behavior). The short duration contacts of thrusts preceded every intromission (penetration of the vagina by the penis). The intromission itself can be identified on the current flow record by its steady flow of current for a period of about 1 sec at an intensity of about $30\ \mu\text{a}$. The impulse from the copulation detection circuit is indicated by an arrow on the current flow record.

The current flow pattern shown in Fig. 5 is typical: (1) an initial low-intensity flow accompanying biting or oral contact; (2) high-frequency, short-duration pulses accompanying pelvic thrusting; and (3) steady, long-duration flow accompanying intromission and terminated with the backward lunge.

Figure 6 shows the duration and amount of current flow for every physical contact made by all eight pairs of rabbits during the observational sessions. It can be seen that each

Fig. 6. Amount and duration of current flow resulting from every physical contact made by each of eight pairs of rabbits during one session. The physical contacts were classified by visual observation. Amount and duration of current flow were read from a polygraph record. The dotted lines indicate the minimum duration and intensity of current flow necessary to differentiate copulations from other physical contacts.

copulation resulted in a current flow intensity greater than $15 \mu\text{a}$; no oral contact did. Each copulation resulted in a current flow duration greater than 250 msec; no thrust did. These data indicated that copulations could be differentiated from oral contacts only by the amount of current flow, and from thrusting contacts only by the duration of current flow. An accounting of both parameters, therefore, was necessary to discriminate automatically a copulation from the other types of physical contact.

The copulation detection circuit required a minimum duration of current flow (250 msec) and a minimum intensity of current flow ($15 \mu\text{a}$) before producing an impulse. These criteria were met eight times during the course of the experiment, and corresponded with the eight occasions that the observer reported a copulation. Thus, the copulation detection circuit and the observer were always in perfect agreement on the occurrence of a copulation.

II. Validity of the Automated Method

A series of observations determined the extent to which the electrical changes correlated with physical evidence of ejaculation, *i.e.*, the presence of sperm.

Method. Two fertile male and 14 female rabbits were observed in 15 pairings; one male was paired with 10 females, the other with four females. (One pair was observed twice, five days separating the sessions.) The apparatus was the same as above except the polygraph was disconnected.

A male and a female subject were connected to the copulation detection circuit. An observer viewed the subjects' behavior through the Plexiglas door of the chamber. He closed one switch to report a mount, another switch to report a copulation. These reports were recorded on an event recorder simultaneously with the signals from the copulation detection

circuit. The copulation detection circuit criterion for indicating a copulation was the same as above, *i.e.*, $15 \mu\text{a}$ current flow for 250 msec.

A vaginal smear was taken from the female just before she was placed in the experimental chamber with the male; no sperm were found in any of those smears. Thereafter, as soon as the observer reported that the male had mounted, thrust, and dismounted, the female was removed from the chamber and another vaginal smear taken. The technician taking the smears was seated directly in front of the chamber, and the entire procedure of removing the subject, taking a smear, and replacing the subject, required less than 1 min. The procedure was repeated after every mount by the male, including those mounts which the observer reported as resulting in a copulation. The session was terminated after the report of a copulation or after 12 reports of mounts without a copulation.

Results. Table 1 shows the results of these observations. One hundred and twelve mounts were recorded from the 15 pairings of the subjects. Nine of these mounts (from nine different pairings) resulted in copulations. The observer and the copulation detection circuit always agreed on the moment of occurrence of a copulation. Sperm were always present in the female's vagina after the copulation detection circuit and the observer reported that a copulation had occurred. Sperm were never found after any of the 103 mounts that did not activate the copulation detection circuit.

These data, in addition to giving evidence for the validity of the method, also support the suggestion that ejaculation accompanies every intromission by male rabbits (Macirone and Walton, 1938).

III. Variability of the Automated Method

The data shown in Fig. 6 indicate that the amount of current flow resulting from a copulation varied between pairs of subjects. (The

Table 1
Comparison of Observer and Automatic Indications of Copulation after Mount

	Copulation Detection Circuit		Observer	
	Copulation	No Copulation	Copulation	No Copulation
Sperm present	9	0	9	0
Sperm absent	0	103	0	103

current flow resulting from eight copulations ranged from 20 to 33 μ a.) To determine if the current flow varied within a pair of subjects, the amount of current flow resulting from several copulations was recorded.

Method. The subjects were five vasectomized male and five female rabbits. Four pairs of subjects were observed during one 90-min session. The fifth pair was observed for two sessions. The second session followed a 24-hr separation of the pair. The apparatus was the same as in the previous experiment except that the source voltage of the copulation detection circuit was increased to 150 mv.

Procedure. A male and female subject were connected to the copulation detection circuit. The comparative resistance of the pair of electrodes in each subject was evaluated by activating the electrode test circuit. This circuit imposed 200 mv across the two electrodes in each subject. The electrodes of all subjects met a criterion of allowing more than 40 μ a of current to flow. The deflection of the meter-relay resulting from the current flow during the first copulation was observed, and the meter-relay contacts were then set and maintained at 90% of this value.

An observer visually monitored the behavior of the subjects on the closed-circuit TV monitor. The observer also recorded the amount of current flow, as indicated by the deflection of the meter-relay, for every copulation occurring during the session.

Results. Table 2 shows the results of these observations. The amount of current flow during any copulation always exceeded the minimum setting of the meter-relay *i.e.*, all copulations were detected by the copulation detec-

tion circuit. There was very little intra-pair variability of current flow during a copulation; the average deviation from the mean was always less than 3% of the mean. As can be seen from the data of the pair observed for two sessions (Pair #3 in Table 2), this low variability did not increase even after an interval of 24 hr.

There was also very little inter-pair variability of current flow during copulation. The range of every pair overlapped, and only 5 μ a separated the extremes. The meter-relay setting for any one pair would have been adequate to detect a copulation made by any other pair. This low inter-pair variability appears to contradict the data presented in Fig. 6, where the amount of current flow resulting from copulations from eight pairs of animals ranged from 20 to 33 μ a. In the present experiment, however, the electrode resistance of every subject met a specific criterion (40 μ a current flow at 200 mv). The electrode resistance of some of the subjects used in the prior experiment would not have met this criterion.

APPLICATION OF THE AUTOMATED METHOD

Temporal Patterns of Sexual Behavior

Temporal patterns of sexual behavior have been studied in several mammals, especially in the rat (Beach and Jordan, 1956), the guinea pig (Young, Dempsey, and Myers, 1935), and the mouse (Gresson, 1940) (also see reviews by Amoroso and Marshall, 1960; and Asdell, 1964). Attempts to measure temporal patterns of sexual behavior in rabbits (Heape, 1905; Hammond and Marshall, 1925;

Table 2
Amount of Current Flow between Subjects during Copulation

Subject Pair	No. of Copulations	Current Flow (μ a)			
		First Copulation	Range	Mean	Average Deviation
1	10	28	28-31	29.3	0.9
2	8	28	28-30	29.3	0.6
3*	11	28	28-29	28.4	0.5
3**	7	29	29-30	29.4	0.5
4	5	31	31-33	32.6	0.6
5	6	31	30-32	31.5	0.7
Total	47		28-33	29.7	1.2

*First Session.

**Second Session.

Friedman, 1938; Myers and Poole, 1962a, 1962b), have resulted in some conflicting reports (see reviews by Young, 1941; Worden and Leahy, 1962; and Asdell, 1964).

The primary cause of the conflicting reports appears to lie in the methods of observing the behavior. In general, if the method involved isolating a female and observing her behavior with a male during specific "trials", few, if any temporal patterns of sexual behavior were reported (Hammond and Marshall, 1925; Friedman, 1938). If the behavior of the female were observed (even for comparatively brief periods) in a situation where males were always available, temporal patterns were reported (Myers and Poole, 1962a, 1962b; Hughes and Myers, 1966).

The present method was well-suited for the measurement of very brief as well as extended temporal patterns of behavior. During the development of the method, it was noted that pelvic thrusting by the male appeared to occur at a constant frequency. Figure 7 shows

Fig. 7. Polygraph records of current flow resulting from thrusting contacts made by three different male rabbits. The numbered peaks indicate contacts between the male's penis and the female's vulva. The arrows indicate the moment of intromission.

the polygraph records of current flow resulting from pre-copulatory thrusting by three male rabbits. The peaks in these records were produced by brief contacts between the male's penis and the female's vulva. The steady 20- μ A flow of current was produced by the sustained contact during intromission. The arrows indicate the moment when intromission occurred. It can be seen that six or seven thrusts always occurred in the 0.5 sec before intromission. Figure 8 shows the rate of thrusting recorded during 11 thrusting episodes by eight pairs of subjects. In every episode, no matter what the duration, thrusting occurred at a rate of about 14 thrusts per sec. The range was 11.5 to 14.5 thrusts per sec.

Other observations during the development of the method had indicated that rabbits displayed additional temporal patterns of sexual behavior. These patterns were recorded during a series of observations.

Procedure. The subjects were eight male and 15 female rabbits paired in 23 different combinations. All the males were vasectomized. The subjects were isolated for a minimum of three days before the start of a session. Each pair was observed for one uninterrupted session of three to 11 days duration; one pair was observed for a continuous 63-day session.

Fig. 8. Frequency of thrusts occurring during 11 thrusting episodes. The number of thrusts per episode was calculated from polygraph recordings of current flow resulting from penile-vulva contacts during thrusting from four male and three female subjects paired in eight different combinations. The line designates a rate of 14 thrusts per sec.

The subjects were not removed from the chamber at any time during the session.

The apparatus was the same as in the previous experiments. The electrode resistance of each subject was measured with the electrode test circuit before the start of a session, and all electrodes exceeded a criterion of 40 μ a current flow at 200 mv. The electrode resistance was measured twice a day during each session.

The chamber was illuminated 24 hr a day by a 15-w fluorescent lamp. The environmental temperature was maintained at $75^{\circ} \pm 2^{\circ}$ by a thermostatically controlled air conditioning and heating system. Extraneous noises were excluded by isolating the sound-insulated chamber in a small room; the programming circuits and recorders were in a separate room. Extraneous visual stimulation was prevented by the opaque doors of the exterior chamber; all visual observation was done via the closed-circuit TV monitor located in the control room. The experimental space was opened for about 10 min at about 9:00 a.m. each day to refill the food and water containers and replace the drop pan. This did not appear to disturb the subjects.

The first copulation of every pair of subjects was observed on a TV monitor and its resulting current flow read from the meter-relay. The meter-relay contacts were set at 90% of that reading. The minimum duration of current flow necessary to activate the copulation detection circuit was 250 msec. If a copulation did not occur in the first 10 min of a session the female was replaced and the session restarted. (Preliminary investigation had indicated that if a pair of rabbits did not copulate within the first 10 min, they would be unlikely to copulate in the next 24 hr.)

Copulations were recorded on a Gerbrands cumulative recorder. A second Gerbrands C-3 cumulative recorder was modified to record the duration of each intromission. The stepping pen of this recorder was made "self-stepping" by removing a 40-ohm 20-w resistor from its stepping circuit. Removal of this resistor resulted in the pen stepping at a constant rate of 17 mm per sec during activation of the recorder. The recorder was activated by the copulation detection circuit; the vertical distance travelled by the cumulative recorder pen was thus an accurate measure of the duration of the intromission.

Results. The electrode resistance, as measured by the electrode test circuit, did not vary more than 5% between any two days in a session.

Fig. 9. Cumulative records of copulations by four pairs of rabbits for the first 8 hr of their sessions. Each vertical step on the curves indicates an automatically recorded copulation.

Figure 9 shows the cumulative record of copulations recorded from four pairs of rabbits during the first 8 hr of their sessions. The upper-left section shows the lowest rate of copulations recorded, five copulations in the first 5 hr of the session; the highest rate, about 40 copulations in the same period of time is shown in the lower-left section. Two records of rates of copulation between these extremes are shown in the right sections. In all four records it can be seen that the rate of copulation decreased over time, approaching zero after about 6 hr. Similar temporal patterns of copulation during the first few hours of a session were recorded from each of the 23 pairs of subjects. Copulations always occurred in a run, if they occurred at all. These initial runs were always negatively accelerated and the rate of copulation generally approached zero in about 6 hr, although in a few instances runs lasting 18 hr or longer were recorded.

Figure 10 shows the cumulative record of copulations recorded from two pairs of rabbits during their entire sessions. The upper record shows a 5-day session during which a pair of rabbits copulated about 60 times. The 60 copulations occurred in four distinct runs separated by three periods of sexual inactivity.

Each run lasted from 5 to 15 hr and contained from 8 to 25 copulations. Rate of copulation was negatively accelerated in all but the third run. The initial rate of copulation was about 5 per hr in each of the runs. The quiescent periods contained virtually no copulations and ranged from 12 to 36 hr in duration.

The lower record of Fig. 10 shows an eight-day session in which about 115 copulations occurred in five runs. The rate of copulation and duration of the runs were very similar to that in the upper record. The longest quiescent period lasted about three days; the shortest quiescent period occurred between the fourth and fifth runs and lasted only a few hours. All the runs in this session were negatively accelerated.

Figure 11 shows the entire record of the uninterrupted 63-day session. More than 200 copulations occurred in nine runs. The first two quiescent periods are examples of the longest recorded, 16 and 20 days respectively. The quiescent periods following the third run in this session had durations similar to those in the sessions shown in Fig. 10. Similar temporal patterns were found in every pair of subjects. A quiescent period always followed the first run of copulations and, if the session were long enough, succeeding runs were recorded. Quiescent periods as short as 8 hr and as long as 20 days were observed. Except

for a few instances (one is shown in the lower part of Fig. 10) copulations occurred only in runs, never singly. During the first hour of a run, rates as high as 12 copulations per hr were recorded, but rates of 5 to 7 per hr were more common. Negative acceleration of rate of copulation, always found in the initial run, was frequently found in succeeding runs.

The cumulative records indicated that most of the runs of copulations had occurred at night. Figure 12 shows the time of day when each of 217 copulations was recorded from 13 pairs of rabbits. (These data include all copulations by these pairs except those recorded during the initial run. This exclusion was necessary because the initial run occurred as soon as the animals were placed together, regardless of the time of day.) As can be seen, copulations occurred most frequently during the night hours; 72% occurred between dusk and dawn, and most of these were recorded between midnight and 6 a.m. This diurnal pattern was noted in every pair of subjects.

Figure 13 shows that the distribution of the duration of 208 intromissions recorded from 13 pairs of subjects ranged from 0.3 to 7.6 sec. As can be seen, however, most of the intromissions lasted about 1 sec. The mean duration of all the measured intromissions was 2.8 sec and the median was 1.5 sec. The comparable statistics for individual pairs of subjects were all within about 1 sec of the group statistic.

Fig. 10. Cumulative records of copulations by two pairs of rabbits for continuous five- and eight-day sessions. Each step on the curves indicates an automatically recorded copulation.

Fig. 11. Cumulative record of copulations by a pair of rabbits for a continuous 63-day session. Copulations were automatically recorded. The arrows indicate the presumed end of 16- to 20-day periods of pseudo-pregnancy.

In a few pairs of subjects, the intromissions occurring early in a run tended to last longer than those occurring later in the run. When the duration of an intromission was compared with its serial order of occurrence within a run by the Spearman Rank Correlation (Siegel, 1956), the correlation exceeded a 5% level of significance in only two of the 13 pairs of subjects. When durations were compared with serial order of all measured intromissions by the Kendall Coefficient of Concordance (Siegel, 1956), no significant correlation was found ($W = 0.3$).

DISCUSSION

Several patterns of sexual behavior in rabbits were revealed by this method. Some of these patterns were so short as to be measured in milliseconds; others were so long as to be measured in days. Perhaps it is because of the extremes of these temporal units that these patterns received little attention in studies where gross observational procedures were used (see current reviews by Young, 1941;

Amoroso and Marshall, 1960; and Asdell, 1964).

It was found that each copulation was always preceded by a series of pelvic thrusts by the male. The thrusts appeared to be probes toward the vaginal opening; penile contact with the female's body was extremely brief unless penetration of the vagina was achieved. Penetration of the vagina by the penis, or "intromission", always resulted in ejaculation. This is in contrast to some other species, *e.g.*, the rat, which require several intromissions before ejaculation occurs (Beach and Jordon, 1956; Larsson, 1956).

The rate of thrusting was found to be 13 ± 1.5 thrusts per sec. This rate was invariant both between and within subjects, and was independent of the duration of the thrusting episode. The rate of thrusting during a copulation has received little attention in the investigations of sexual behavior in other species. Stone and Ferguson (1940), however, photographed the copulatory behavior of rats with a high-speed motion picture camera. They were able to report the duration of each intromission by counting the number of frames of film from penetration to withdrawal. They also reported the number of thrusts which occurred during each intromission. When these data were converted to rate of thrusting it was found that both the mean and the median thrusting rate of rats was about 12 thrusts per sec. Their data contained much more variability than the present data (their range for rats was 6 to 19 thrusts per sec compared to 11.5 to 14.5 thrusts per sec reported here for rabbits), but this variability could be due to the difficulty in determining

Fig. 12. Time of occurrence of copulation with respect to the hour of day. Based on 217 copulations automatically recorded from 13 pairs of rabbits during continuous sessions ranging from 3 to 11 days in length. Each point designates the number of copulations during a 2-hr period.

Fig. 13. Duration of 208 intromissions recorded from 13 pairs of subjects. Durations were automatically recorded during continuous 3- to 11-day sessions.

the subject's pelvic position in each frame of the movie film. The similarity between rabbits and rats, and the consistency of rate both within and between individual rabbits suggest that there may be a biological constant in rate of thrusting.

The duration of intromission, which had not been previously reported for rabbits, was found to have a comparatively narrow quartile range; 75% of the intromissions had a duration of between 0.5 and 2.5 sec. This is almost identical to the time that a male rat maintains penile contact with a female during ejaculation. Stone and Ferguson (1940) and Peirce and Nuttall (1961) report that most ejaculatory intromissions by a rat have a duration of about 1 to 4 sec.

The sexual behavior of rabbits is characterized by an "all or none" phenomenon. Copulations occurred in a group or "run" where several matings took place in a few hours, or they did not occur at all. Runs were always separated by periods of sexual inactivity or "quiescence" when virtually no copulations occurred. On the rare occasion when a copulation occurred during a quiescent period, it usually preceded or followed a run by a very short period of time (see lower section of Fig. 10).

Three factors that determined when a run would occur were identified. The first was isolation of the female. Almost every time a female was removed from isolation and placed with a male, an immediate run of copulations occurred. On no occasion did a female allow one or two copulations by a male and then reject his advances. A few females refused to copulate after removal from isolation; the variables controlling this behavior are not known at this time. It is known, however, that the lack of mating was not due to the male. Every male immediately mounted and attempted to copulate with any female on their first encounter.

A second factor affecting the onset of a run of copulations was a phenomenon called pseudopregnancy. Pseudopregnancy is a physiological reaction by female rabbits to a sterile mating. The rabbit does not ovulate spontaneously at specific intervals as do many mammals from mouse to man, but rather ovulates in response to the sexual stimulation of copulation. The presence of sperm is not necessary; ovulation will occur about 10 hr

after a copulation (Heape, 1905; Hammond and Marshall, 1925). An ovulation stimulated by a sterile mating results in physiological and behavioral changes which are very similar to that of true pregnancy. A corpus luteum is formed and the mammary glands develop. Near the end of the period, which lasts from 16 to 20 days (Hammond and Marshall, 1925; Napier, 1963; Hughes and Myers, 1966), the animal pulls hair from her body and may build a nest. Many investigators (see Hammond and Marshall, 1925; Friedman, 1938; Hughes and Myers, 1966) have reported that the female will always accept the male at the termination of the pseudopregnancy period. These investigators have also reported that the female will mate at irregular and unpredictable intervals when pseudopregnant. The two-month session reported in the present study confirms the reports of mating at the end of each pseudopregnancy. Pseudopregnancy started with the first copulation in the session, and runs of copulations were recorded after each 16-20 day interval which followed. This session also emphasizes the difficulty in predicting the occurrence of mating behavior during pseudopregnancy; the same pair of rabbits, under controlled environmental conditions, did not mate during two successive pseudopregnancy periods, and yet mated almost continuously during the third (see Fig. 11). The cause of this variability (which is a major obstacle in determining an estrus or heat cycle for the rabbit) is not known.

The third factor affecting the occurrence of a run of copulations is an apparent diurnal cycle in the sexual behavior of the rabbit. Diurnal sexual cycles have been well defined in several species, *e.g.*, the mouse (Snell, Fekete, Hummel, and Law, 1940) the guinea pig (Young *et al.*, 1935), the hamster (Bruce and Hendle, 1934), and the rat (Blandau, Boling, and Young, 1941), but have been generally overlooked in the rabbit. This oversight is probably due to the fact that rabbits will mate upon initial exposure to a member of the opposite sex regardless of the time of day. Investigators who have observed rabbits over extended periods of time have suggested that there appeared to be a greater probability for matings to occur at night (see Stodart and Myers, 1964; Hughes and Myers, 1966), but the difficulties inherent in gross observation for extended periods of time made the

collecting of definitive data very laborious. The present study confirms this suggestion, and indicates that, after the initial run of copulations, the great majority of matings will occur between dusk and dawn even when illumination and temperature are constant.

All of the initial runs and most of the succeeding runs were characterized by decreasing rate of copulation over time. A run generally started with a rate of about 5 to 7 copulations per hr. This rate gradually decreased and generally approached zero in less than 12 hr. Such a negative acceleration of rate of copulation, although not previously reported for rabbits, is characteristic of the sexual behavior of mammals (see Shein and Hale, 1965). Satiation or fatigue of at least one member undoubtedly plays a part, but the phenomenon is complicated by a physiological refractory period (period of time after an ejaculation when another ejaculation cannot be elicited) which appears to increase with each succeeding copulation (see Larsson, 1956). This refractory period occurs only in the male and thus this may be one instance where a lack of sexual behavior may be attributable to the male.

REFERENCES

- Amoroso, E. C. and Marshall, F. H. A. External factors in sexual periodicity. In A. S. Parks (Ed.), *Marshall's physiology of reproduction*. London: Longman's Green & Co., 1960.
- Asdell, S. A. *Patterns of mammalian reproduction*. (2nd ed.) Ithaca: Cornell Univ., 1964.
- Beach, F. A. and Jordon, L. Sexual exhaustion and recovery in the male rat. *Quart. J. exp. Psychol.*, 1956, 8, 121-133.
- Beach, F. A. and Rabedean, R. G. Sexual exhaustion and recovery in the male hamster. *J. comp. physiol. Psychol.*, 1959, 52, 56-61.
- Bermant, G. Rat sexual behavior: Photographic analysis of the intromission response. *Psychon. Sci.*, 1965, 2, 65-66.
- Blandau, R. J., Boling, J. L., and Young, W. C. The length of heat in the albino rat as determined by the copulatory response. *Anat. Rec.*, 1941, 79, 453-463.
- Bruce, H. M. and Hindle, E. The golden hamster *Cricetus (mesocricetus) auratus*: Waterhouse. Notes on its breeding and growth. *Proc. Zool. Soc. (London)*, 1934, 2, 361-366.
- Carpenter, C. R. Sexual behavior of free-ranging rhesus monkeys (*Macaca mulatta*). *J. comp. Psychol.*, 1942, 33, 113-162.
- Crandall, L. S. *The management of wild animals in captivity*. Chicago: Univ. of Chicago, 1964.
- Friedman, M. H. Criteria for the selection of estrous rabbits. *Endocrin.*, 1938, 22, 354-359.
- Gresson, R. A. R. The effect of increased daily illumination and of reversed day and night on the oestrus cycle of the mouse (*Mus musculus*). *Proc. Roy. Soc. Edin.*, 1940, 60, 333-343.
- Hafez, E. S. E. (Ed.) *The behavior of domestic animals*. Baltimore: The Williams and Wilkins Co., 1962.
- Hammond, J. and Marshall, F. H. A. *Reproduction in the rabbit*. Edinburgh, 1925.
- Heape, W. Ovulation and degeneration of ova in the rabbit. *Proc. Roy. Soc. B*, 1905, 76, 260-268.
- Hughes, R. L. and Myers, K. Behavioral cycles during pseudopregnancy in confined populations of domestic rabbits and their relation to the histology of the female reproductive tract. *Aust. J. Zool.*, 1966, 14, 173-183.
- Larsson, K. *Conditioning and sexual behavior in the male albino rat*. Stockholm: Almqvist and Wiksell, 1956.
- Lisk, R. D. Inhibitory centers in sexual behavior in the male rat. *Science*, 1966, 152, 669-670.
- Macirone, C. and Walton, A. Fecundity of male rabbits as determined by "dummy matings". *J. Agric. Sci.*, 1938, 28, 122-134.
- Myers, K. and Poole, W. E. A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L.) in confined populations. III. Reproduction. *Aust. J. Zool.*, 1962a, 10, 225-267.
- Myers, K. and Poole, W. E. Oestrous cycles in the rabbit *Oryctolagus cuniculus* (L.). *Nature*, 1962b, 195, 358-359.
- Napier, R. A. N. Rabbits. In W. Lane-Petter (Ed.), *Animals for research: Principles of breeding and management*. London: Academic Press, 1963.
- Peirce, J. T. and Nuttall, R. Durations of sexual contact in the rat. *J. comp. physiol. Psychol.*, 1961, 54, 584-587.
- Schein, M. W. and Hale, E. B. Stimuli eliciting sexual behavior. In F. A. Beach (Ed.), *Sex and behavior*. New York: John Wiley & Sons, 1965.
- Siegel, S. *Nonparametric statistics for the behavioral sciences*. New York: McGraw-Hill, 1956.
- Snell, G. D., Fekete, E., Hummel, K. P., and Law, L. W. The relation of mating, ovulation, and the estrous smear in the house mouse to time of day. *Anat. Rec.*, 1940, 76, 39-54.
- Stodart, E. and Myers, K. A comparison of behavior, reproduction, and mortality of wild and domestic rabbits in confined populations. *CSIRO Wildl. Res.*, 1964, 9, 144-159.
- Stone, C. P. and Ferguson, L. W. Temporal relationships in the copulatory acts of adult male rats. *J. comp. physiol. Psychol.*, 1940, 30, 419-433.
- Worden, A. N. and Leahy, J. S. The behavior of rabbits. In E. S. E. Hafez (Ed.), *The behavior of domestic animals*. Baltimore: The Williams and Wilkins Co., 1962.
- Young, W. C. Observations and experiments on mating behavior in female mammals. *Quart. Rev. Biol.*, 1941, 16, 135-156, 311-335.
- Young, W. C., Dempsey, E. W., and Myers, H. I. Cyclic reproductive behavior in the female guinea pig. *J. comp. Psychol.*, 1935, 19, 313-335.

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