WORLD RABBIT SCIENCE

ANALYSIS OF SEXUAL BEHAVIOUR IN MALE RABBITS ACROSS SUCCESSIVE TESTS LEADING TO SEXUAL EXHAUSTION

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ABSTRACT: Various parameters of sexual behaviour were studied in 10 male rabbits daily tested with sexually receptive females (ovariectomized, given estradiol benzoate s.c. 5 µg/d). The aim of this study was to analyse rabbit sexual behaviour during successive tests leading to sexual exhaustion. We allowed copulation *ad libitum* and determined if sexual satiety was reached within 1 d and sexual exhaustion across several days. The pair was allowed to copulate freely until the male failed to show sexual interest in that female for 30 min. The female was then removed and replaced by another; this procedure was repeated using as many does as needed, until the male showed no interest in any female for 2 h. Scent-marking (chinning) was also recorded, before and after the copulation test. This whole procedure was repeated daily until the male showed no sexual behaviour at all on a given day. Within a test, copulation *ad libitum* led to a gradual increase in the time interval between successive mounts and ejaculations, regardless of the day of testing. Such increments predicted that the buck was reaching sexual satiety. The "miss" rate (i.e., the proportion of mounts that did not culminate in ejaculation) significantly increased from a median of 25 on the 1st d to 55 on the last day of testing. The mean time to reach copulatory inactivity decreased from 4 h on the 1st d to 1 h on the last day. The total number of ejaculations within a test decreased from an average of 22 to 6 (first *vs.* last day, respectively) and the number of chin marks was reduced by 69% compared with pre-mating values, regardless of the day of testing. All bucks eventually stopped copulating after a variable number of days (range=2-15 d). We concluded that, following copulation *ad libitum* with several females, male rabbits reach sexual satiety (i.e., they are unable to continue copulating on the same day) and, after several days, they also attain sexual exhaustion, a state in which copulation is totally arrested for at least 24 h. Some behavioural parameters can be used as reliable predictors that a buck is approaching sexual satiety and sexual exhaustion.

Key Words: male sexual behaviour, sexual satiety, copulation, ejaculation, rabbit, chinning.

INTRODUCTION

Male sexual behaviour in rabbits consists of the execution of a single mount that is followed by a series of pelvic thrusts, during which intromission occurs, and generally results in ejaculation (Beyer *et al.*, 1980; Contreras and Beyer, 1979; Rubin and Azrin, 1967). The exposure of a male to a succession of receptive females allows copulation *ad libitum,* during which a buck will display a large number of mounts, intromissions, and ejaculations until sexual activity ceases. At this point it is assumed that the buck has reached sexual satiety. However, few studies have

explored the characteristics of sexual activity across a test leading to sexual satiety, such as the time required to reach this state, the number of mounts, intromissions, and ejaculations displayed therein, the interval between successive mounts, etc. (Fuentes *et al*., 2005). One criterion used to establish that sexual satiety has been reached in males copulating *ad libitum* is the absence of mounting towards a new female for 4 min after the last ejaculation (Fuentes *et al.*, 2005; Villagrán *et al.*, 2003). To reach this point, bucks in those studies performed 6 to 8 mounts, although the authors did not report whether they culminated in ejaculation or not. Another study reported that bucks were able to perform 6 ejaculations in 30 min, the first one occurring within 19 s after the doe was presented (Melin and Kihlström, 1963). Another study (Rubin and Azrin, 1967) reported that, when the total number of copulations was measured across 8 h, mating took place in groups or "runs" with a great individual variability, ranging from 5 to 40 matings in the first 5 h and approaching zero matings after 6 h. No distinction was made between mounts alone and those culminating in ejaculation. As a whole, the above studies show that, if allowed to copulate freely with a series of receptive does, male rabbits reach sexual satiety within 1 d. However, it is not known if after successive days of copulating to satiety: a) bucks reach sexual exhaustion, i.e., a state during copulation is totally arrested for at least 1 d; and b) specific parameters of male sexual behaviour are modified.

In rodents, particular measures have been developed to investigate how male sexual behaviour is modified across tests leading to sexual satiety. Such measures have taken into account the characteristic copulatory pattern observed in such mammalian group. For instance, in rats, male sexual behaviour consists of a series of mounts and intromissions, preceding ejaculation, called a "copulatory series" (Larsson, 1979). Thus, investigators have used measures like: "interval between intromissions", "mount frequency" and "hit rate" –defined as the number of mounts with intromission/(number of mounts alone+number of mounts with intromission)– to determine how the sexual behaviour of male rats varies under specific experimental conditions (Sachs and Meisel, 1988). If given sufficient time, a rat may achieve 8 to 12 ejaculations before being sexually exhausted (Larsson, 1956; Larsson, 1979). During this period, the number of intromissions decreases while the latency to ejaculate, the number of mounts, and the duration of post-ejaculatory periods increase (Beach and Jordan, 1956; Larsson, 1956). These are signs that the rat is approaching sexual satiety (Larsson, 1979). Indeed, when tested 24-48 h later, only 29-30% of rats are capable of performing a single ejaculatory series, thus indicating that approximately 70% of males have reached sexual exhaustion (Beach and Jordan, 1956; Rodríguez-Manzo and Fernández-Guasti, 1994).

In contrast to rats, the effect of copulating to satiety in a test on specific measures of sexual behaviour has not been explored in rabbits. Moreover, the possibility that bucks can reach sexual exhaustion after copulating to satiety in successive tests has not been determined. Because the sexual behaviour of bucks differs markedly from that of rats, investigating how specific copulatory parameters are modified within and across successive tests will enrich our understanding of rabbit reproduction and allow a comparison of the ways by which mammals regulate male sexual activity. To this end, in an experimental setup that allowed a "maximal" display of sexual behaviour (i.e., a continuous provision of sexually receptive females) the following parameters were quantified: a) the number of mounts displayed in a test; b) the "miss rate", i.e., the proportion of mounts that did not culminate in ejaculation; c) the duration of intervals between successive ejaculations. We also determined if scent-marking, which decreases after 1 ejaculation (González-Mariscal *et al.*, 1997), is inhibited more intensely after copulation *ad libitum* within a test and across successive daily tests.

MATERIAL AND METHODS

Animals and housing

Ten adult (10-12 mo old), sexually active, New Zealand white male rabbits, born in our colony, were used as experimental animals. Seven adult ovariectomized New Zealand white does (6 mo old), given estradiol benzoate (5 µg/d; s.c. in 0.1 mL sesame oil) to induce sexual receptivity, were used to investigate the copulatory activity of bucks. All animals were housed individually in wire-mesh cages (52 cm long by 42 cm wide by 41 cm high) and given water and food (Purina rabbit pellets) *ad libitum*. They were kept under controlled light (14 h light:10 h dark) and natural temperature (18-23°C) conditions. Throughout this work, animal care and handling complied with the Law for the Protection of Animals (Mexico).

Drugs

Estradiol benzoate was obtained from Sigma (St. Louis, Missouri, USA).

Experimental design

A male was placed in the mating wire-mesh arena (1 m in diameter by 43 cm high) 5 min before introducing the sexually receptive female. The buck was allowed to mate *ad libitum* until no interest in the doe was shown for 30 min. At this point the female was removed and replaced by another one, and so on, until the male showed no interest in any female for a period of 2 h (criterion used to establish sexual satiety). This change of sexually receptive females was done to maximize the display of the buck's copulatory activity. In rats, an apparently satiated male is capable of resuming copulation if a novel, sexually receptive female is introduced (the so-called "coolidge effect"; Wilson *et al.*, 1963). This whole procedure was repeated every day until the male showed no sexual behaviour at all on a given day (criterion used to determine sexual exhaustion).

Behavioural measurements

On the 1st d of testing we quantified the following parameters of male sexual behaviour displayed towards the 1st female, to eliminate possible effects on copulatory activity derived from the execution of previous sexual behaviour: a) duration of test with the 1st female, i.e.: time elapsed between introduction of the female and execution of the last mount with such female; b) total number of ejaculations performed with that female; c) interval between copulatory events (i.e., between 2 successive mounts, 2 successive ejaculations, or 1 mount and 1 ejaculation); d) "miss rate": total number of mounts that did not culminate in ejaculation, calculated by the formula: (number of mounts/number of mounts+number of ejaculations)×100. If the buck showed no interest in the doe for 30 min a new one was introduced and, from then until the end of testing, the following parameters were quantified: a) total duration of test, i.e.: time elapsed between introduction of the 1st female and the last mount performed by the male towards the last female; b) total number of mounts and ejaculations in test: we counted the number of mounts that culminated in ejaculation and the number of mounts that did not; c) interval between copulatory events (see above); d) interval between ejaculations, i.e.: time elapsed between one ejaculation and the next one; e) "miss rate" (see above). In addition, a specific form of scent-marking characteristic of rabbits (chinning) was quantified before and after copulation *ad libitum*, as described previously (González-Mariscal *et al.*, 1997). The male was placed in the round wire-mesh arena and 3 terracotta brick piles were placed inside it. The number of times the male rubbed its chin onto any of the brick piles was counted over 10 min. The bricks were then removed and the stimulus

female was introduced to begin the sexual satiety test. The chinning frequency was determined again at the end of the sexual satiety test.

Statistical analysis

Interval between copulatory events towards the first female on the first test day: Within 1 d, individuals varied in the amount of sexual activity exhibited, yielding uneven amounts of behavioural records for most of them. Unequal sample sizes violate the assumptions of repeated measures tests (our test of choice, see below) (Sokal and Rohlf, 1981). The total number of behavioural records of each individual within 1 d was therefore divided into 3 cohorts of equal size. The mean of the intervals between copulatory events of every cohort was then determined for each individual. We obtained 3 non-independent events (3 repeated measures) for data on the ejaculation intervals for each individual throughout 1 d. The $\log_{10}$ transformed data on ejaculation intervals (see below) were used as the within-subject effect (interval) in a repeated measures general linear model (GLM). Further differences between intervals were investigated using the least significant difference (LSD) test.

Interval between copulatory events considering all the females used in a test: Following a similar procedure to the one described above, we obtained 3 non-independent events (3 repeated measures) of activity for each individual throughout 1 d. This procedure was carried out for the first and last day of testing only. However, 2 individuals produced only 1 behavioural record for the last day of experiments. These individuals were therefore excluded from this analysis, which produced a sample size of 8 individuals. The data were used as the within-subject effect (interval) in a repeated measures GLM and the day of experiments (first or last) was used as the between-subject effect (day). The interaction term interval×day was tested in our model. Further differences between the intervals between copulatory events were tested using the Least Significant Difference test.

Interval between ejaculations considering all the females used in a test: We followed the same procedure as above, thus eliminating differences in the number of behavioural records shown by individuals and producing 3 repeated measures per individual. Nonetheless, only 6 individuals produced enough data to test for differences in this parameter. Data on ejaculation events were used as the within-subject effect (interval) in a Repeated Measures General Linear Model while day of experiments (first or last) was used as the between-subject effect (day). The interaction term interval×day was tested in our model. Further differences between the intervals between ejaculation events were tested using the LSD test.

Duration of test considering all the females used in it: Data from the first and last day of testing were compared using a paired samples *t*-test, since the data were normally distributed (Shapiro-Wilk *W*=0.923, *P*=0.114).

Interval between copulatory events across days considering all the females used in the tests: To test for differences, a repeated measures ANOVA was used (the data were normally distributed, Shapiro-Wilk *W*=0.946, *P*=0.166).

"Miss" rate considering all females used: Differences between the first and last day of testing were compared using a Wilcoxon Signed Ranks test, since the data did not follow a normal distribution (Shapiro-Wilk *W*=0.867, *P*=0.011).

Number of mounts alone and with ejaculation considering all females used: A repeated measures GLM was made using the total number of mounts on the first and last days of testing as the within-subject effect (mounts). We further specified whether the mounts culminated in

ejaculation or not, using a 2 level between-subjects factor (status). We tested the interaction term mounts×status. Further differences between the estimated marginal means of the first and last days of experiments within the between-subjects factor were assessed by calculating the 95% confidence intervals (CIs). Two estimated marginal means were considered to differ if their 95% CIs did not overlap.

Chinning frequency: On the first and last day of testing, we determined if chinning frequency (chin marks/10 min) changed after copulation with respect to baseline. To test for differences, a Repeated Measures GLM was constructed using the transformed data on chinning behaviour (see below) as the Within-subjects effect (status) and day of testing (first or last) as the between-subjects effect (day). The interaction term status×day was tested and retained in our model.

Data on i) the interval between copulatory events towards the 1st female on the 1st test day, ii) the interval between copulatory events considering all the females used in a test, iii) the interval between ejaculations considering all the females used in a test, iv) the number of mounts alone and with ejaculation considering all females used, and v) chinning frequency, violated the assumptions of the normal distribution (Shapiro-Wilk tests, $P<0.05$ in all cases); these were therefore adjusted to normality using the log_{10} transformation. Following transformation, we used the new, transformed values in our analyses, although the relevant figures (1-3, 6 and 7) illustrate raw values, in order to facilitate interpretation.

Statistical analyses and figures were made with the SPSS software, version 17 (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

The number of females required for a male to reach sexual exhaustion ranged from 1 to 3 across all days of testing. On the 1st d all bucks but 2 needed more than 1 female to achieve sexual satiety. The number of ejaculations, duration of the test (min)and the "miss rate" determined on the 1st d of testing towards the 1st female ranged 2-29, 6.6 -82 and 0-63, respectively.

Interval between ejaculations towards the 1st female on the 1st d of testing

Figure 1 shows that the interval between ejaculations differs among cohorts ($F_{2,16}=9.139$, $P=0.002$). Specifically, cohort 3 is significantly different from the other two (LSD test; $P=0.006$, $P=0.05$, respectively) and cohorts 1 and 2 are different from each other ($P=0.043$). The slope among cohorts reveals that the interval between ejaculations increases linearly over time ($\beta=0.248$, $P=0.002$).

Figure 1: Interval between ejaculations (minutes; i.e., time elapsed between two successive ejaculations) as determined on the first day of testing, with the first female provided. The number of ejaculations of each individual was divided into three equal cohorts for analysis

Interval between ejaculations considering all females

On the first and last days of testing there were significant differences in the intervals between ejaculations displayed across the
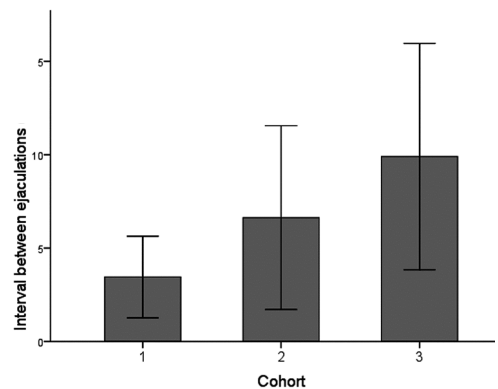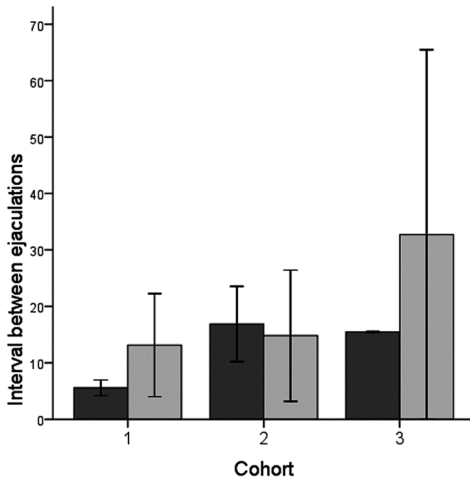
Figure 2: Interval between ejaculations (min) determined on the first and last days of testing. The total number of ejaculations of each individual in a day was divided into three equal cohorts for analysis. ■ First day and ▨ Last day, bars correspond to standard deviation.
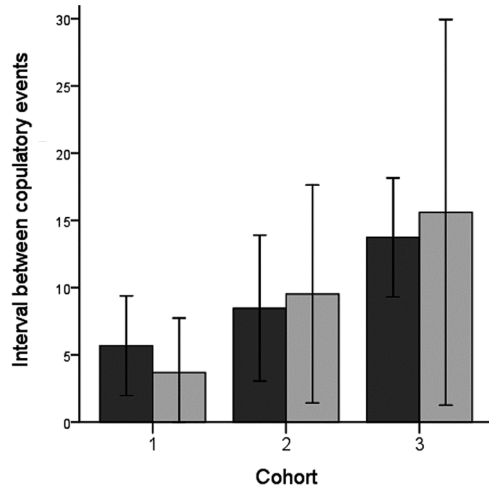
Figure 3: Interval between copulatory events (min; i.e., regardless of whether they were mounts only or mounts culminating in ejaculation) as determined on the first and last days of testing. The total number of copulatory events of each individual on a given day was divided into three equal cohorts for analysis. ■ First day and ▨ Last day, bars correspond to standard deviation.

corresponding test (Repeated Measures GLM, $F_{2,20}$=11.057, P=0.001; Figure 2). Specifically, the intervals between ejaculations became longer as the copulation series progressed (all cohorts differed, LSD test, P<0.046 in all cases; Figure 2). A non-significant interaction term interval×day ($F_{2,20}$=1.384, P=0.274) indicates that this pattern was similar between the first and last day of testing.

Interval between copulatory events considering all females

The means on the first and last days of testing differed across the copulatory series ($F_{2,28}$=23.340, P=0.001; Figure 3). On the first and last days of testing, the intervals between copulatory events (regardless of whether they were mounts only or mounts culminating in ejaculation) became longer as the number of successive matings increased (all thirds differed, LSD test, P<0.001 in all cases; Figure 3). A non-significant interaction term interval×day ($F_{2,28}$=1.386, P=0.267) indicated that this pattern did not differ between the first and last days of testing.

Duration of test and "miss rate" considering all females

There was a significant difference in the duration of the sexual satiety tests between the first and the last day (t_9=5.693, P=0.001; Figure 4). In all cases, the first trials lasted longer than the last ones.

The *"miss" rate* was lower at the beginning of the experiment than on the last day of testing (Wilcoxon Signed Ranks Z=2.090, df=9, P=0.037; Figure 5).
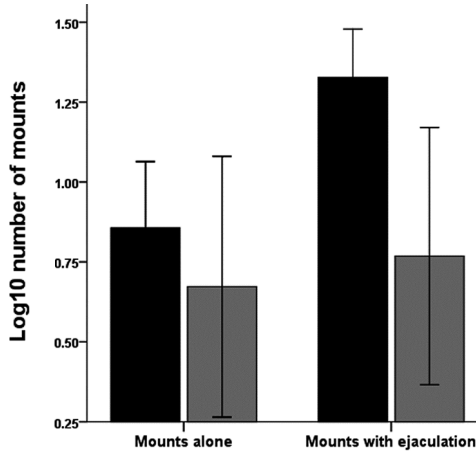
Figure 4: Total duration of the tests performed on the first and the last day. ■ First day and ▢ Last day, bars correspond to standard deviation.
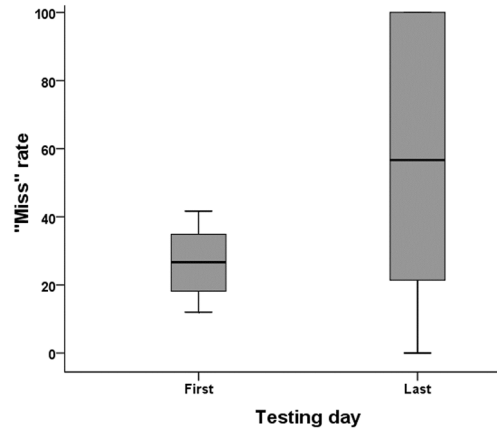

Figure 5: "Miss rate", i.e., proportion of mounts that did not culminate in ejaculation, as determined on the first and last days of testing. Figure shows medians and lower and upper quartiles. Bars correspond to standard deviation..

Number of mounts alone and with ejaculation considering all females

The interaction term mounts×status was significant ($F_{1,18}$=4.689, P=0.044), thus suggesting that the total number of mounts differed if we distinguished between mounts that did not culminate in ejaculation and those that did (Figure 6). Specifically, the number of mounts that did not
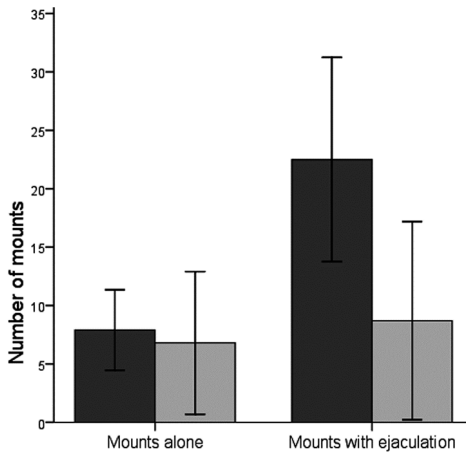

Figure 6: Number of mounts alone and mounts that culminated in ejaculation on the first and last days of testing. ■ First day and ▢ Last day, bars correspond to standard deviation.
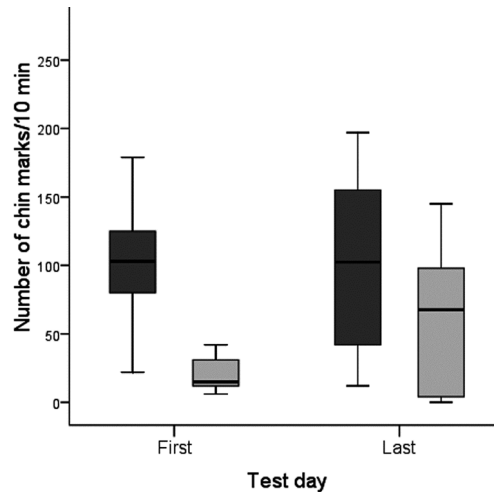

Figure 7: Chinning frequency, determined before and after copulation, on the first and last days of testing. Figure shows medians and lower and upper quartiles. ■ Before copulation, ▢ After copulation.

culminate in ejaculation did not differ between the first day (0.857±0.057; CI: 0.736-0.977) and the last day of testing (0.673±0.128; CI: 0.404-0.942). Note that the CIs largely overlap between days. In contrast, the number of mounts that culminated in ejaculation was significantly larger on the first day of testing (data estimated from raw values shown; 22.500±2.102; CI: 18.084-26.916) than on the last one (8.700± 2.338; CI: 3.789-13.611).

Chinning

Males showed a larger frequency of chin-marking during the baseline period (i.e., before copulation) than at the end of the sexual satiety test ($F_{1,18}$=41.158, *P*=0.001; Figure 7). This pattern did not differ between the first and the last day of testing, as shown by the non-significant interaction term status×day ($F_{1,18}$=1.306, *P*=0.268). That is, baseline chinning levels recovered across the time elapsed between the end of one test and the beginning of the next, but the scent-marking frequency significantly declined following copulation to satiety on a given day.

DISCUSSION

The results presented show the operation of intrinsic regulatory mechanisms in the expression of male rabbit sexual behaviour. All males but 2 needed more than 1 female to achieve sexual satiety on the 1st d of testing and even those bucks never required more than 3 does. Most males engaged in sexual activity after 7 to 52 min following introduction of a 2nd female, consistent with the "Coolidge effect" described in rats (Rodriguez-Manzo, 1999a; Wilson *et al.*, 1963). Great inter-individual variability was observed in the duration of tests and in the number of copulatory events, a finding that agrees with a previous work (Rubin and Azrin, 1967) in terms of the number of copulations rabbits can perform before satiety (5 to 40) and in the number of days required to reach sexual exhaustion. Bucks were able to achieve as many as 43 ejaculations in a test before becoming sexually satiated and, when tested on the next day, all of them engaged in sexual activity and displayed several ejaculations. True sexual exhaustion occurred only after 2-15 d of copulating to satiety with numerous females. Regardless of quantitative differences among individuals in those 2 parameters, variables like the interval between copulatory events, the duration of the test, the "miss rate" and the number of ejaculations displayed within a test followed the same pattern of change across successive days as males approached sexual satiety. Thus, within a test, copulation *ad libitum* led to a gradual increase in the time interval between successive copulatory events (mounts alone or those ending in ejaculation) and this occurred regardless of the duration of the test or the total number of copulatory events displayed therein. In all bucks, ejaculations in a given test day always outnumbered the display of mounts alone, as reported by others (Villagrán *et al.*, 2003). The onset of sexual exhaustion, after a variable number of days of copulation to satiety, was predicted by a reduction in the duration of the test on the day immediately preceding exhaustion. Conversely, the "miss rate" gradually increased across successive days of testing, a finding indicating that, although the male's drive to search for a female is still present, his capacity to mount and ejaculate is decreasing.

Such patterns of change in rabbit copulatory activity across successive days of testing contrast with the performance of male rats. In this species, an ejaculation, preceded by a series of mounts and intromissions (Larsson, 1979), is followed by 4-5 min of rest before a 2nd copulatory series is started. After a 2nd period of rest (lasting a couple of minutes longer than the first one), male rats may initiate a 3rd copulatory series. If they are given sufficient time, a male rat can perform as many as 12 ejaculations before he is sexually exhausted (Larsson, 1979). If tested 24-48 h later, only 29-30% of males can achieve 1 ejaculation and the full recovery of sexual activity

occurs 15-21 d later (Beach and Jordan, 1956; Rodríguez-Manzo and Fernández-Guasti, 1994; Romano-Torres *et al.*, 2007).

The number of mounts without intromission in the rat is high during the 1st ejaculation series, decreases in the 2nd and 3rd series, and increases in the following series (Larsson, 1979). In contrast, in rabbits, the number of mounts not ending in ejaculation was not significantly different across test days, although a clear reduction in the number of mounts culminating in ejaculation was seen between the first and the last day of testing. In rats, the post-ejaculatory interval increases with every copulatory series (Larsson, 1979). A similar pattern was seen in bucks as the time between 2 successive ejaculations increased across the 3 cohorts into which the test was divided for each animal. This pattern remained unchanged between the first and last day of testing, a finding suggesting that the mechanisms regulating the ongoing display of sexual activity operate in the same way regardless of the male's sexual satiety state. Data in other species show common parameters indicative of sexual satiety: thus, in hamsters copulation *ad libitum* causes a steady increase in the lengths of the pauses that follow successive ejaculations (Beach and Rabedeau, 1959). Male guinea pigs are somewhat different as, once a male ejaculates, he does not usually reinitiate copulation within the next hour (Young and Grunt, 1951) but, as in rats or rabbits, male guinea pigs can engage in a 2nd copulation if a new female is presented (Grunt and Young, 1952; Hull and Domínguez, 2007). Macaques can achieve as many as 5 ejaculations before reaching the criterion for sexual exhaustion and post-ejaculatory interval increase after each ejaculation (Phoenix and Chambers, 1988).

Copulation *ad libitum* markedly reduced chinning frequency, in agreement with our previous report (González-Mariscal *et al.*, 1997). Thus, in all bucks at 2 h after the last ejaculation, chinning frequency was reduced by around 70%. This effect was evident in all tests, regardless of their duration or the number of copulatory events observed therein. In contrast, baseline chinning frequency was remarkably stable in all individuals across successive tests, despite the fact that a great variability was observed among experimental animals. As chinning has been reported to be closely related to the willingness of subjects to copulate (González-Mariscal *et al.*, 1992), our findings suggest that males are equally motivated to engage in sexual activity at the start of testing as they are after several days of copulation *ad libitum*, even if they are not able to reach ejaculation. Moreover, no major changes in the animals' general activity were noted following sexual exhaustion tests, a finding that supports the idea that the decrease in chinning and sexual activity are due to the activation of specific inhibitory mechanisms, rather than to a general physical fatigue.

What is the biological meaning of this remarkable capacity for sexual activity in rabbits? Some studies have found that, after 5-6 successive ejaculations, the buck has almost no sperm in the ejaculate (Ambriz *et al.*, 2002; Oshio *et al.*, 1986). This finding is at odds with our behavioural data in which the ejaculatory motor pattern can exceed 43 on a given test day. As female rabbits (which are reflex ovulators) can become pseudopregnant by an infertile mount from either another female (Marshall and Verney, 1935) or a male (González-Mariscal *et al.*, 1990), we may speculate that a possible role for this "exaggerated" sexual behaviour in a rabbit colony would be to keep females in a pseudopregnant state, thus preventing them from becoming pregnant by another male.

In summary, our results have revealed the operation of complex mechanisms that regulate the expression of male sexual behaviour in rabbits. The impact of such mechanisms is exerted at 3 levels: the ongoing copulatory series (short-term effect), the subsequent ones within the same day (mid-term effect) and the copulatory series of the next days (long-term effect). Although

in rabbits nothing is known about the neurohormonal mechanisms that regulate sexual satiety within a day or sexual exhaustion across days, some studies have shown the participation of monoamines, acetylcholine, opiates, and gamma-aminobutyric acid (GABA) on the ongoing display of copulation within a day. The dopaminergic system facilitates male sexual behaviour as the blockade of dopaminergic receptors with flupenthixol reduces the proportion of bucks displaying ejaculation as well as the number of ejaculations displayed during the test (Agmo *et al.*, 1996). In contrast, the cholinergic, opiatergic, serotonergic, and GABAergic systems exert inhibitory actions on the display of male sexual behaviour, as the administration of pilocarpine (a muscarinic receptor agonist; (Agmo, 1976), morphine (Agmo *et al.*, 1994), several serotonin agonists (Paredes *et al.*, 2000), inhibitors of GABA transaminase (Agmo *et al.*, 1991), or several GABA agonists (Paredes *et al.*, 1998) abolishes male rabbit sexual activity within a single test.

In rats, there is evidence that catecholamines reverse sexual exhaustion in a dose-response manner as the administration of agonists of dopamine (apomorphine) or noradrenaline (yohimbine) increases the percentage of rats that resume copulation after satiety (Rodriguez-Manzo and Fernandez-Guasti, 1995). Accordingly, the simultaneous injection of haloperidol, a nonspecific dopamine receptor antagonist, blocks the ability of these drugs to reverse sexual satiety (Rodriguez-Manzo, 1999b). Serotonin, in contrast, tends to inhibit male sexual behaviour in rats (Fernandez-Guasti and Rodriguez-Manzo, 1992) and mice (Rodriguez-Manzo *et al.*, 2002): injection of 5-HTP, a serotonin precursor, increases the number of mounts and intromissions preceding ejaculation, prolongs the intromission and ejaculation latencies, and increases the post-ejaculatory interval. However, the injection of 8-OH-DPAT, a potent agonist of 5-HT_{1A} receptors, promotes ejaculation or reverses sexual exhaustion (Fernandez-Guasti and Rodriguez-Manzo, 1997; Rodríguez-Manzo and Fernández-Guasti, 1994). Similar studies need to be performed in rabbits to determine if the same neurotransmitter systems operate across mammals to regulate the expression of sexual satiety and sexual exhaustion, regardless of the particular type of copulatory pattern shown by a species.

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