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The effects of increasing number of strange male mice on the Bruce effect

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ABSTRACT

This study investigated whether the increasing number of strange male (SM) mice influences the Bruce effect. Thirty females and 27 males were used. The females were divided into 6 groups of 5 each. Of the 27 males, 12 were introduced, 2 each to the 6 female groups as mating males (MM). The remaining 15 males, which were SM, were divided into graded numbers of 5, 4, 3, 2, 1 and 0 for groups A-F females. Two days after any female was mated, it was transferred to the cage of the corresponding SM. Within both the first round of matings and the second round of matings, the following parameters were assessed: the number of matings before conception or the number of matings through the duration of the study, the length of time before conception, gestation length, litter size at birth, litter weight at birth and average weight of new-borns at birth. The results showed a significant ($P<0.05$) number of SM-dependent increases in the number of matings before conception or the number of matings through the duration of the study for both the first round of matings and the second round of matings. There was also a number of SM-dependent significant ($P<0.05$) increases in the length of time before conception for the first round of matings. In the second round of matings, only group F showed a significantly ($P<0.05$) reduced length of time before conception. Litter size at birth, litter weight at birth and average weight of new-borns at birth for group F were only significantly ($P<0.05$) higher than those of group D in the first round of matings, and all the groups in the second round of matings. Considering primarily the result of the number of matings before conception and probably that of the length of time before conception, it was concluded that increasing the number of SM mice exhibited an enhancing effect on the Bruce effect.

Key words: mice, mating, strange male, Bruce effect

Introduction

The ability of animals to distinguish individual conspecifics influences many aspects of their behaviour, including choice of mate, territorial marking and mother-offspring interactions. The reproductive success of many animals depends on these factors, which

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are more subtle than food availability and housing condition. These social stimuli have therefore been discovered to be important contributors to the regulation of reproductive events in all mammals, including humans (VANDENBERGH, 1994; OCHIOGU et al., 2009). In many mammals, urine carries pheromones, being deposited discretely as a social response and influencing the behaviour and reproductive state of conspecifics (BRUCE, 1960; REYNOLDS, 1971; HURST, 1990). Specifically, male mouse urine contains a complex mixture of chemosignals that exert powerful effects on the reproductive biology of female mice, as exposure to male urine accelerates puberty in pre-pubertal females (VANDENBERG, 1969), induces oestrus in grouped anoestrous females (WHITTEN, 1956) and blocks the pregnancy in newly mated females (BRUCE, 1959).

There is evidence that pheromones are the main facilitator of these effects (BRONSON, 1971). The pheromones involved in these effects are excreted in the urine of intact adult males and their production is androgen-dependent (MARSDEN and BRONSON, 1964; DOMINIC, 1965; GANGRADE and DOMINIC, 1984). The active urinary substances can therefore elicit these varieties of endocrine responses in the female mice (VANDENBERGH et al., 1975; MARCHLEWSKA-KOJ, 1977; JEMIOLO et al., 1986). These male originating substances appear to act with a high degree of specificity in altering the secretory patterns of luteinizing hormone and prolactin and of the steroids whose secretion is regulated by those two trophic hormones (JEMIOLO et al., 1986).

The Bruce effect is a well-established fact, where urine-associated pheromones from strange male mice block or disrupt the establishment of pregnancy in freshly mated female mice. Or more precisely, the Bruce effect is a phenomenon whereby the exposure of a recently inseminated female to pheromones from an unfamiliar male conspecific causes the termination of her pregnancy. This effect has been most extensively studied in laboratory mice, but has also been reported to occur in wild mice and a few other rodent species (DOMINIC, 1966a). The neuroendocrine mechanism underlying pregnancy failure involves an oestrus-inducing pheromone present in male urine, which inhibits prolactin secretion from the anterior pituitary of females. This results in a decline in progesterone release from the corpora lutea and the consequent return to oestrus (DOMINIC, 1966b; BRENNAN et al., 1990). Although all males produce the pregnancy-blocking pheromones, the female is able to recognize those of her mate and prevent them from eliciting the termination of his own pregnancy (BRENNAN and PEELET, 2003; OCHIOGU et al., 2009).

In addition to the main olfactory system found in most mammals, mice possess a vomeronasal system that is specialized in detection and transmission of pheromonal information (ARON, 1979). A great deal of research has been carried out on the effect of these pheromones on mice reproduction, but the effects of increasing the number of strange male mice in the same enclosure with a female already mated by a familiar male has not been investigated. This study was therefore designed to investigate the effects of

increasing the number of strange males on the Bruce effect. The study is interesting and important because it gives us a better understanding of the behaviour of this animal, and of course will help those in the breeding industry to know the possible consequences of introducing strange males into a breeding stock.

Materials and methods

The experimental animals for this study were outbred adult albino mice bred at the Laboratory Animal House of the Faculty of Veterinary Medicine, University of Nigeria, Nsukka. They were 57 in number, comprising 30 females and 27 males and were aged 14-15 weeks at the commencement of the study. Out of the 27 males, 12 were mating males (MM), which were of the same stock as the 30 females. The remaining 15 males were strange males (SM) and they were of different stock from the 30 females and the 12 MM. Throughout the duration of the study, they were kept in standard clean mice cages and were fed *ad libitum* with pelletized feed (Grand Cereals and Oil Mills Limited, Jos-Nigeria), containing 16% crude protein. They were also provided freely with clean drinking water.

Initially, the 30 females were kept in a single cage, the 12 MM in another single cage and the 15 SM in a single cage different from the first two, for a period of 3 weeks before they were divided into groups. The above 3 cages containing 3 sets of mice (females, MM and SM) were kept in 3 different rooms at a minimal distance of 20 metres from one another for this three-week period. Thereafter, the 30 females were randomly distributed into 6 groups (A-F), such that each group contained 5 females. The 12 MM were then brought from their room and distributed randomly in pairs among the 6 female groups. The 15 SM, still in their original room, were also divided into 6 groups with graded numbers of 5, 4, 3, 2, 1 and 0 for groups A, B, C, D, E and F females respectively. The 6 cages containing the SM were kept at a minimal distance of 5 metres from one another. Each of the mice was identified with an indelible marker.

After distribution and identification of the mice, evidence of successful mating in the females was checked daily using the vaginal plug method of BENNETT and VICKERY (1970), and VOSS (1979) as modified by OCHIOGU et al. (2006). This procedure was carried out at 6.00 am and 6.00 pm daily.

After the presence of a vaginal plug was accessed for each female mouse, a two day interval was given before moving the females that recorded positive for mating to the appropriate cages containing the SM. Mated females of group A were moved to cage A with 5 SM; mated females of group B to cage B with 4 SM; mated females of group C to cage C with 3 SM; mated females of group D to cage D with 2 SM; mated females of group E to cage E with 1 SM; and mated females of group F to cage F with no SM. The mated females moved to the appropriate SM cages were moved back to their original cages

containing the MM after a two-day interval, and testing for evidence of mating continued. This process continued until there was obvious evidence of pregnancy, and the day of the last mating that resulted in the pregnancy was recorded as day 0 of the pregnancy for that individual mouse. Pregnancy in each mated female was followed up individually until delivery. Just prior to delivery, the pregnant females were isolated individually in another cage to enable accurate determination of gestation length, litter size and litter weight at birth, and average weight of new-borns at birth.

The parameters determined were the number of matings before conception or the number of matings throughout the duration of the study, the length of time before conception (days), gestation length (days), litter size at birth and litter weight at birth (g), and average weight of new-borns at birth (g). The number of matings before conception was determined by counting the total number of matings the individual mouse had before it conceived, while the length of time before conception was determined by calculating the total number of days the individual females stayed before they became pregnant following the introduction of the MM. Gestation length was determined by calculating the total number of days between the day of the last mating that resulted in pregnancy and the day of delivery. The litter size at birth was determined by counting the number of young delivered by one female mouse, while the litter weight at birth (g) was determined by using an electronic weighing balance to determine the collective weight of the litter. Finally, the average weight of newborns was determined by dividing the litter weight at birth with the litter size at birth.

The second round of matings to achieve the second pregnancy was achieved by returning the females together with their litters to their original mating cages immediately after delivery so as to enable them to have access to the MM, as was the case in the first round of matings. The mated females in the second round of matings were also transferred to the appropriate cages containing the SM after a two-day interval of mating. All the parameters determined in the first round of the study were also determined in the second round.

The data generated were subjected to analysis of variance (ANOVA) and variant means separated using the least significant difference. The results were presented as the mean ± standard error of the mean.

Ethics. The housing, handling and welfare of the laboratory animals (mice) used in this research were in accordance with the Ethics and Regulations guiding the use of research animals as approved by the "University of Nigeria, Nsukka" where the study was carried out.

Results

The number of matings before conception or number of matings throughout the duration of the study. The mean number of matings before conception or the number of matings throughout the duration of the study for the first round of matings showed significant differences ($P<0.05$) dependent on the number of SM with the lowest recorded in group F (0 SM) and the highest in group A (5 SM). Moreover, during the first round of matings all the adjacent groups showed significant difference ($P<0.05$) except groups D and E which did not differ significantly ($P>0.05$) from each other (Table 1). During the second round of matings, almost the same number of SM-dependent effects were expressed as group A showed a significantly higher ($P<0.05$) number of matings before conception or number of matings throughout the duration of the study when compared with group B; and groups B, C, D and E had a significantly higher number of matings before conception or number of matings throughout the duration of the study compared to group F (Table 2).

Length of time before conception. For the first round of matings, there was a number of SM-dependent differences in the length of time before conception, as group A was significantly higher ($P<0.05$) than group C, group C significantly higher ($P<0.05$) than group E, and group E significantly higher ($P<0.05$) than group F (Table 1). However, for the second round of matings, only the females of group A had a significantly longer ($P<0.05$) mean length of time before conception than the females of Group F (Table 2).

Gestation length. The mean gestation length for group F (control) mice in the first round of matings was significantly higher ($P<0.05$) than those of groups C, D and E, which had 3, 2 and 1 SM respectively. However, there was no significant difference ($P>0.05$) between the control group (F) and groups A and B with 5 and 4 SM respectively during the first round of matings (Table 1).

Litter size at birth. The females of group F had a significantly higher ($P<0.05$) mean litter size at birth from the first round of matings than the females of group A (Table 1). The LSB of all the other groups did not differ significantly ($P>0.05$) from that of the control group (F) (Table 1). For the second round of matings, the mean litter size at birth of the group F mice was significantly higher ($P<0.05$) than that of all the other mice groups (Table 2).

Litter weight at birth. Apart from group A females, which had a significantly lower ($P<0.05$) mean litter weight at birth than the females of group F (controls), those of the remaining groups did not differ significantly ($P>0.05$) from the control group in the first round of matings (Table 1). However, in the second round of matings, all the mice groups had a significantly lower ($P<0.05$) mean litter weight at birth than group F mice (Table 2).

Table 1. Mean reproductive parameter values in the first round of matings ± SEM

	Group A	Group B	Group C	Group D	Group E	Group F (Control)
Number of matings before conception or Number of matings throughout the duration of the study	23.80 ± 1.74[a]	19.20 ± 1.66[b]	14.60 ± 1.63[c]	9.80 ± 0.37[d]	8.00 ± 0.55[d]	1.80 ± 0.37[e]
Length of time before conception (days)	92.80 ± 11.28[a]	71.20 ± 11.20[ab]	60.80 ± 13.51[b]	38.60 ± 5.05[bc]	25.20 ± 3.17[c]	3.00 ± 0.55[d]
Gestation length (days)	20.20 ± 0.37[ab]	20.20 ± 0.37[ab]	19.60 ± 0.68[a]	19.00 ± 0.32[a]	19.60 ± 0.40[a]	21.20 ± 0.58[b]
Litter size at birth	2.60 ± 1.60[a]	6.80 ± 0.49[b]	6.40 ± 0.75[b]	4.60 ± 0.75[ab]	5.20 ± 0.37[ab]	6.60 ± 0.51[b]
Litter weight at birth (g)	3.80 ± 2.15[a]	7.96 ± 0.34[b]	9.34 ± 1.24[b]	8.72 ± 1.39[b]	8.46 ± 0.75[b]	9.42 ± 0.32[b]
Average weight of new-borns at birth (g)	0.64 ± 0.41[a]	1.26 ± 0.12[b]	1.46 ± 0.09[bc]	1.94 ± 0.17[c]	1.66 ± 0.05[bc]	1.46 ± 0.10[bc]

[abcd] Different superscripts in a row indicate significant difference between the means. ($P<0.05$). Group A - 5 strange males; Group B - 4 strange males; Group C - 3 strange males; Group D - 2 strange males; Group E - 1 strange males; Group F - no strange male.

Table 2. Mean reproductive parameter values in the second round of matings ± SEM

	Group A	Group B	Group C	Group D	Group E	Group F (Control)
Number of matings before conception or Number of matings throughout the duration of the study	19.00 ± 3.90^{a}	10.40 ± 3.79^{b}	11.60 ± 1.89^{ab}	11.00 ± 1.58^{ab}	15.00 ± 2.95^{ab}	6.60 ± 1.81^{c}
Length of time before conception (days)	76.80 ± 20.99^{a}	45.80 ± 17.11^{ab}	56.20 ± 14.68^{ab}	44.80 ± 6.58^{ab}	53.40 ± 11.29^{ab}	20.40 ± 5.42^{b}
Litter size at birth	0.00 ± 0.00^{a}	0.00 ± 0.00^{a}	1.60 ± 1.60^{a}	1.60 ± 1.60^{a}	1.20 ± 1.20^{a}	7.60 ± 0.24^{b}
Litter weight at birth (g)	0.00 ± 0.00^{a}	0.00 ± 0.00^{a}	2.50 ± 2.50^{a}	2.40 ± 2.40^{a}	1.92 ± 1.92^{a}	9.78 ± 0.68^{b}
Average weight of new-borns at birth (g)	0.00 ± 0.00^{a}	0.00 ± 0.00^{a}	0.32 ± 0.32^{a}	0.30 ± 0.30^{a}	0.32 ± 0.32^{a}	1.36 ± 0.07^{b}

^{abc} Different superscripts in a row indicate significant difference between the means. ($P<0.05$). Group A - 5 strange males; Group B - 4 strange males; Group C - 3 strange males; Group D - 2 strange males; Group E - 1 strange males; Group F - no strange male.

Average weight of new-borns at birth. In the first round of matings, the mean average weight of new-borns for group A was significantly lower ($P<0.05$) than those of the other groups, which did not show any significant difference ($P>0.05$) from one another (Table 1). For the second round of matings, all the groups (A, B, C, D and E) had a significantly lower ($P<0.05$) mean value than the controls (group F) (Table 2).

Discussion

Within 4 days of introducing the MM (2 each to a group of 5 females) to the 6 groups, all the females were mated at least once. This was an indication that the males used for mating were potent and that the females were cycling and therefore receptive. SCHARMANN and WOLFF (1980) reported that when oestrus is synchronized in mice, 50-70% of the females can conceive on a single mating or night. In this case, only group F (without SM) conformed to this report with a mean number of matings before conception of 1.80 ± 0.37 and mean length of time before conception of 3.00 ± 0.55 days. There were therefore a number of SM-dependent increases in the number of matings before conception or the number of matings throughout the duration of the study, showing that the SM did not only induce the Bruce effect (BRUCE, 1959) but also had an enhancing effect on the Bruce effect. It was discovered initially that the SM disrupted pregnancies that would have resulted from the females' matings with the familiar MM without the SM mating them, but as the study progressed the females also became familiar with the SM. This resulted in the SM mating with the females in addition to blocking the pregnancies that would have been established as a result of the females' matings with the normal MM. Apart from the fact that when matings from a familiar or normal MM were blocked from resulting in pregnancies and as a result of this the females returned to cycle and were mated again by the familiar MM, resulting in an increased number of matings before conception or number of matings throughout the duration of the study, the eventual matings with the SM also added to the increase.

In the first round of matings, groups A-E (with varied numbers of SM) had a mean of 8.0 ± 0.55 to 23.80 ± 1.74 number of matings before conception or number of matings throughout the duration of the study, which increased with the number of SM. All of them were far from the 1.80 ± 0.37 number of matings for group F (with no SM). For the second round of matings, the mean number of matings before conception or number of matings throughout the duration of the study for group F was higher (6.6 ± 1.81 days), with mean length of time before conception of 20.4 ± 5.42 days. This was evidence that they underwent an oestrus cycle after the first delivery (post-partum oestrus). Delayed pregnancy among the group F females in the SRM (second round of matings) therefore, may be attributed to the large number of litters from the first pregnancy which the females

were suckling at the time of these matings. According to ENDERS (1970) this causes implantation and pregnancy failure in mice. The groups with SM had almost similar patterns of increases in the number of matings before conception or number of matings throughout the duration of the study in the second round of matings, ranging from 10 ± 3.59 to 19 ± 3.89 days, with the longest being obviously less than the longest obtained in the first round of matings. This decrease was because most of the females that conceived did so late in the first round of matings and some did not even conceive at all, and so had less time to mate and possibly conceive before the end of the study. The length of time before conception for first round of matings also increased with the number of SM. However, in the second round of matings, only the females of group A had a significantly higher ($P<0.05$) length of time before conception than group F. However, during the course of this study, three females from group A and one from both groups B and C did not conceive at all in either the first or second rounds of matings, but their total number of matings were determined and the number of days the study lasted was recorded as the length of time before conception in their case. Groups B, C, D and E had far higher lengths of time before conception than group F, which were not statistically significantly different, probably because of their high standard error of mean. It is conceivable that since the females were constantly switched between the MM and the SM, a point was attained where some of the mated females that conceived in both rounds of matings learnt the pregnancy blocking chemo-signals of all the males (both SM and MM). In this way, these females were able to recognize as familiar the chemosignals from all their male associates and this made it impossible for the chemosignals from the SM to block a pregnancy sequel to the MM (BRENNAN and PEELET, 2003; OCHIOGU et al., 2009).

Though all the group F females conceived in the second round of matings, most of the females did not conceive in the second round of matings with SM and so had no gestation length. Therefore, only the mean gestation length for the first round of matings was determined. Using the gestation length of the few (one each from groups C, D and E, and none from groups A and B with SM) that littered the second time to find the mean gestation length of the groups would definitely give a wrong impression of the effect of increasing the number of SM on gestation length. For the first round of matings, the gestation length from Group A to group F ranged from 19 ± 0.32 to 21.2 ± 0.58. Even though there was a significant difference between these groups, they were all within the normal range of gestation (19-21 days) for mice (HENDRICKS and HOUSTON, 1970).

Since a few of the females did not conceive at all in either the first or second rounds of matings with SM and the majority of them also did not conceive in the second rounds of matings, the mean litter size at birth, litter weight at birth and average weight of newborns were obviously affected. In the first round of matings, group A had a significantly lower ($P<0.05$) mean litter size at birth, litter weight at birth and average weight of new-borns at

birth than most of the other groups. This could be a result of the fact that only two females from this group were able to conceive in the course of this study. In the first round of matings, however, there was no significant difference ($P>0.05$) between the control group F and the rest of the groups with SM.

The mean litter size at birth, litter weight at birth and average weight of new-borns at birth for the second rounds of matings were different from those of the first rounds of matings, as the groups A-E had mean value ranges of 0.00 ± 0.00 to 1.60 ± 1.60, 0.00 ± 0.00 to 2.50 ± 2.50 and 0.00 ± 0.00 to 0.32 ± 0.32 respectively, while group F (control) had mean values of 7.6 ± 0.25, 9.78 ± 0.68 and 1.36 ± 0.08 respectively. This wide variation was because all the females of the control group F conceived and delivered in the second round of matings.

All the SM were from the same stock, and before the commencement of the study were housed in one large cage for further familiarization and acclimatization for a period of three weeks before being distributed into different groups. There were no fights among the SM as they were very much familiar and acquainted with each other. The dimensions of the cages that housed each of the six groups were 80 cm long, 40 cm wide and 30 cm deep, showing that the cages were spacious. Finally, no other animals, either of the same or a different species were kept in the same room with the animals used for this study. Hence, we are confident that the Bruce effect was the focus of this study.

It could therefore be concluded that since there were a number of significant SM-dependent ($P<0.05$) increases in the mean number of matings before conception or the number of matings throughout the duration of the study, and length of time before conception, and a significant ($P<0.05$) reduction in the mean litter size at birth, litter weight at birth and average weight of new-borns at birth, increasing the number of strange males had an enhancing effect on the Bruce effect.

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SAŽETAK

U radu je korišteno 30 ženki i 27 mužjaka s ciljem da se istraži utječe li povećanje broja stranih mužjaka (SM) na Bruceov efekt kod miša. Ženke su bile podijeljene u 6 skupina po 5 životinja u svakoj skupini. Od ukupno 27 mužjaka, 12 je dodijeljeno ženkama (po 2 u svaku od 6 skupina) kao mužjaci za parenje (MP). Preostalih 15 mužjaka, koji su bili stranci (SM), podijeljeno je u skupine sa stupnjevanim brojem 5,4,3,2,1 i 0 za skupine ženki od A do F. Dva dana nakon što bi se bilo koja ženka parila, bila bi prebačena u kavez s odgovarajućim stranim mužjacima. Unutar dva kruga parenja procijenjeni su sljedeći pokazatelji: broj parenja prije koncepcije ili broj parenja tijekom cijelog razdoblja istraživanja, duljina vremena prije koncepcije, trajanje graviditeta, veličina legla pri porođaju, težina legla pri porođaju i prosječna težina novorođenčadi pri porođaju. Rezultat je pokazao značajan ($P<0,05$) utjecaj porasta broja stranih mužjaka na broj parenja prije koncepcije ili na broj parenja tijekom cijeloga razdoblja istraživanja, i to za prvi i drugi krug parenja. Također, utvrđeno je da porast broja stranih mužjaka značajno ($P<0,05$) utječe na dužinu vremenskog razdoblja prije koncepcije za prvi krug parenja. U drugom krugu parenja samo je skupina F pokazala značajno ($P<0,05$) skraćenje razdoblja prije koncepcije. Veličina legla, težina legla pri porodu i prosječna težina novorođenčadi pri porodu u skupini F bile su značajno ($P<0,05$) veće u odnosu na skupinu D nakon prvog kruga parenja i u odnosu na sve skupine nakon drugoga kruga parenja. Uzevši u obzir prvenstveno rezultat vezan za broj parenja prije koncepcije, a moguće i onaj vezan za dužinu vremenskog razdoblja prije koncepcije, može se zaključiti da povećanje broja stranih mužjaka dovodi do pojačavanja Bruceova učinka u miševa.

Ključne riječi: miševi, parenje, strani mužjak, Bruceov učinak