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Pregnancy Blockage Following Multiple-Male Copulation or Exposure at the Time of Mating in Deer Mice, *Peromyscus maniculatus*

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Summary. Pregnancy blockage resulting from multiple-male copulation or exposure around the time of mating was studied in three experiments on deer mice, *Peromyscus maniculatus*. First, significantly more females were pregnant after copulating, either with or without disturbance and a delay, with one male than after receiving the same total number of ejaculations from two males. Second, when females received three ejaculations from one male and then were immediately exposed to either a blonde male or a wild-type male for 2 h, the pregnancy rate was lower than when they were exposed to an empty cage. Third, when immediately after mating females were placed for 2 h in the cage of a strange male they were less likely to deliver a litter than when placed in the familiar male's cage. This phenomenon bears at least a superficial resemblence to the Bruce effect but either communality or difference in underlying mechanism remains to be determined. The present multi-male pregnancy block may provide a means for females in unstable social situations to defer reproduction for 4 days or longer when more stable conditions may exist and a single male prevails.

Introduction

Females of many species mate with more than one male during a single period of receptivity (e.g. Allison 1977; Bertram 1976; Calhoun 1962; Parker 1970; Hanken and Sherman 1981). An understanding of the dynamics and consequences of such multiple matings is critical to understanding the evolution of mating strategies and mating systems. For example, the composition of resulting litters is affected in different ways by the order in which the males mate in different species (Dewsbury and Baumgardner 1981). The effects of multiple mating on the probability that a litter will be delivered and, if so, upon litter size, are also important (e.g., Beatty 1960; Sakaluk and Cade 1980).

Deer mice, *Peromyscus maniculatus*, are an ideal species for the study of the consequences of multiple mating because multiple paternity of litters has been demonstrated in females inseminated in the field (Birdsall and Nash 1973), thus providing ecological validity. In studies of sperm competition in deer mice, Dewsbury and Baumgardner (1981) found that females mated or exposed to more than one male appeared less likely to deliver a litter than those mated with and exposed to just one male. Whereas the majority of females receiving two ejaculations from one male (and no other exposure or mating) became pregnant, only one of 31 females became pregnant after mating for two ejaculations with one male and subsequently refusing to mate with a second male in whose cage they were placed. Further, females mating for two ejaculations with each of two males had lower probabilities of pregnancy than those mating for four ejaculations or to satiety with one male (Dewsbury 1979b; Dewsbury and Baumgardner 1981). Such data suggest the possibility of a pregnancy block following multi-male exposure. Such a phenomenon would differ from the much studied Bruce effect (e.g. Bruce 1959) in that it is triggered by events occurring at the time of mating rather than some days later. However, the data just discussed were from several different experiments and their comparisons are complicated by a number of missing controls and differences among the experiments compared. The objective in the present research was to investigate systematically both the possibility and the characteristics of multi-male pregnancy block.

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Materials and Methods

Subjects. Two genotypes of deer mice, *Peromyscus maniculatus*, were studied. Twenty-two males and 28 females were drawn from a colony of *P.m. bairdi* established with stock trapped near East Lansing, Michigan, in the early 1970's and into which wild-trapped stock has been bred on several occasions. Fifty males and 83 females were of a blonde mutant genotype (BL) that originated at Michigan State University (Robbins 1979). Both lines breed true, with the wild genotype dominant to the BL (Dewsbury and Baumgardner 1981).

Animals were 5–14 months old at the beginning of experimentation. Those in the first experiment had previously served in a study of sperm competition (Dewsbury and Baumgardner 1981). Some of the animals in the second experiment were pretested for fertility by housing an adult male and female together and noting the birth of a litter; others received no pretesting. Animals in the third experiment had served in a previous experiment dealing with the effectiveness of males in initiating pregnancy with two successive females.

Housing and testing were in a windowless, air-conditioned room that was maintained on a reversed 16L:8D cycle of fluorescent light. Males were housed in clear plastic cages measuring 48 x 27 x 13 cm, with females in cages measuring 29 x 19 x 13 cm. Wood shavings were provided as bedding and water and Purina laboratory rodent chow were available at all times.

Testing Procedures. Tests were conducted on the first day of virtual disappearance of leukocytes from the vaginal smear of a female (proestrus or estrus). Smears were taken each morning from each female throughout the period of experimentation, except when a female had a litter present. A thin wire loop and tap water were used in taking smears.

Tests were conducted in the home cage of the male. The cages were moved to a designated shelf and the food-hopper lid was replaced with a flat metal lid well before the beginning of testing in order to permit adaptation by the males. Females were introduced to the males' home cages and the occurrence of copulatory behavior was noted and recorded with an Esterline Angus operations recorder. The males were permitted to obtain a predetermined number of ejaculations before beginning the experimental manipulations described below. Where a female was to be placed across from a strange male, the target male was housed in a cage that permitted the insertion of a wire-mesh barrier that would divide the cage in half during the period that the female was present. If a female was to mate with two successive males, she was introduced into the home cage of the second male approximately 3 min after the designated ejaculation by the first male.

If a female delivered a litter conceived during a test the gestation period, litter size, and paternity were determined. Results were categorized as 'no response' if there was a return to a proestrous or estrous vaginal smear within 7 days or less or as 'pseudopregnant' if the return to a proestrous or estrous vaginal smear required 8 days or longer (generally 12–15 days).

Behavioral Measures. Behavioral measures used were as defined by Dewsbury (1979a). Copulatory behavior in deer mice includes *mounts* (with pelvic thrusting but no vaginal insertion), *intromissions* (with brief vaginal insertion but no sperm transfer), and *ejaculations* (with insertion and sperm transfer). These events occur in organized ejaculatory series, with each series including at least one intromission, ending with ejaculation, and separated from other series by postejaculatory refractory periods. The following standard measures were used: mount latency (ML)-time (s) from the start of a test until the first mount or intromission, intromission latency (IL)-time (s) from the start of a test until the first intromission, ejaculation latency (EL)-time (s) from the first intromission of a series until ejaculation, intromission frequency (IF) – the number of intromissions in a series, mount frequency (MF) – the number of mounts in a series, mean interintromission interval (MIII) – the mean interval (s) separating the intromissions of a series, and postejaculatory interval (PEI)-time (s) from an ejaculation until the first intromission of the next series. When associated with an arabic number, the measure refers to the designated series (e.g., IF-3).

Results

Effects of Multi-Male Mating on Pregnancy Initiation

First it was determined whether mating with two males would result in a lower probability of pregnancy than would mating for the same number of ejaculations with just one male. Each of 36 blonde females completed three tests – one in each of three conditions. Six of the females were tested in each of the six possible running orders. In one condition (B3), a blonde male and a blonde female were permitted to copulate for three complete ejaculatory series with no disturbance. In a second condition (B2W1), the female mated with a blonde male for two ejaculatory series and then was placed in the home cage of a wild-type male for one ejaculatory series. The latter two groups differ not only with respect to the number of males mating with the female but also with respect to disturbance created by handling the female during the change of cages and the time between series (because the initiation of copulation by a male generally takes longer than the time of the second PEI). The third condition (20P) represented an effort to control for these factors. A blonde male and blonde female mated for two ejaculations, whereupon the female was returned to her home cage. Twenty min later, the female was returned to the cage of the original male and permitted to mate for a third ejaculation.

The percentages of females pregnant were 50, 53, and 28 for the B3, 20P, and B2W1 conditions respectively (see Fig. 1). This difference was found to be statistically significant with a Cochran *Q* test ($Q=7.30$, $df=2$, $P<0.5$, 2-tailed). Using binominal tests it was found that significantly more 20P than B2W1 females were pregnant ($P<0.006$, 1-tailed) and that significantly more B3 females than B2W1 were pregnant ($P<0.058$, 1-tailed). The B2W1 and 20P females showed no difference. There were no differences among groups with respect to gestation period or litter size in this experiment or the two described below. Genotypes were determined for 8 of the 10 litters conceived in the B2W1 condition; there were 25 blonde pups and 19 wild-type pups.

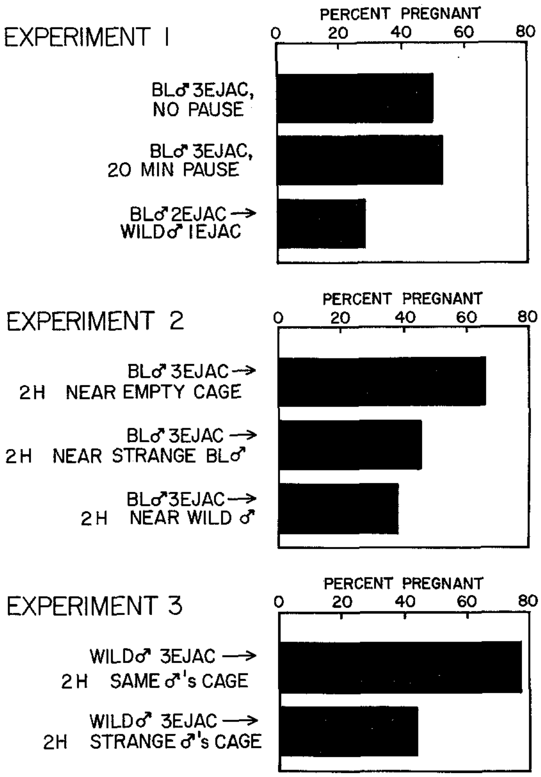

Fig. 1. Percentage of females pregnant as a function of treatment in three experiments of effects of multi-male mating or exposure

Analyses of variance were used to compare the parameters of copulatory behavior among the three groups. Paired comparisons were made with the Newman-Keuls method (Winer 1962). There was a significant difference ($F_{2,70} = 71.91$, $P < 0.001$) in the interval following the second ejaculation; that for group 20P (1449 s) was longer than that for either the B2W1 group (873 s) or B3 group (522 s); the latter two groups also differed significantly. The only other differences were for MF-3 and MIII-3. The three groups did not differ significantly with respect to the number of intromissions received ($F_{2,70} = 0.58$).

Analyses of variance revealed no consistent trends for differences in copulatory behavior for each of the three conditions as a function of the result (pregnant versus pseudopregnant versus no response) in this experiment or those described below.

Effects of Multi-Male Exposure on Pregnancy Initiation

To determine whether mere exposure to a strange male (and his bedding), without copulation, would lower the probability of pregnancy, a total of 29 blonde female deer mice completed tests in each of three conditions. Four or five females completed testing in each of the six possible orders. In each condition the females mated for three complete ejaculatory series with a single blonde male without disturbance. Females were then placed for 2 h in one half of a divided cage. In the first condition (B3/E) the other half of the cage was empty and the bedding in both sides was fresh. In the second condition (B3/B) the cage was that of a strange blonde male; the male was in the other half of the cage and the bedding in both sides was that in which the male had been living. The third condition (B3/W) was identical to the second except that the strange male was of the wild genotype.

The percentages of females pregnant were 66, 45, and 38 for females exposed to the empty cage, blonde male, and wild male respectively (Fig. 1). The difference is significant ($Q = 6.12$, $df = 2$, $P < 0.05$, 1-tailed). Using one-tailed binomial tests it was found that more B3/E females than B3/B ($P < 0.035$) or B3/W ($P < 0.038$) were pregnant; the remaining comparison revealed no significant difference. There were no reliable differences with respect to either gestation period or litter size.

Analyses of variance revealed no significant difference across conditions with respect to the total number of intromissions. There were significant differences in EI-1 ($F = 4.42$, $P < 0.02$) and IF-1 ($F = 3.53$, $P < 0.05$). Although there were fewer intromissions in the first series of females subsequently exposed to wild males, none of the paired comparisons were statistically significant.

Effects of Exposure to a Male's Bedding on Pregnancy Initiation

Having established that exposure to a strange male immediately after mating could produce a blockage of pregnancy, an experiment to determine the relevant sensory modality was conducted by exposing females only to the bedding of strange vs familiar males.

Twenty-seven wild-type females completed this experiment. Each female received two tests – one in each of two conditions. Fourteen females were tested in one running order and 13 in the other. In both conditions each female mated for three ejaculatory series with a wild-type male. She then was removed from the cage in which she had copulated and was placed alone in the home cage of either a strange male (W3/SC) or the stud male (W3/FC) for 2 h.

Seventy-eight per cent of the W3/FC females delivered litters compared to 44% of the W3/SC females (Fig. 1, $P < 0.002$, one-tailed). There were no differences in gestation period or litter size.

Analyses of variance revealed no differences in the parameters of copulatory behavior as a function of test condition. For example, females received a mean of 27.7 intromissions in the W3/FC condition and 31.0 intromissions in the W3/SC condition.

Discussion

Elaboration of Results

Dewsbury and Baumgardner (1981) suggested the possibility of a pregnancy block resulting from multi-male exposure or mating at the time of copulation. In the present study better controls were used and the suggested phenomenon was demonstrated more definitively. Mediation via a chemical cue is suggested. Effects were all-or-none; there were no effects on either gestation period or litter size in any of the experiments.

Since similar results were obtained with both blonde and wild females, the phenomenon is not limited to blonde mutuants and therefore may be applicable to animals in the field. Genotype of the strange male also had no effect on the results. Thus 'strangeness' appears important but genotype, insofar as manipulated here, appears unimportant.

Some limitations on these results should be noted. Most important is the relatively small magnitude of the differences obtained. However, relatively small differences in phenotypic characters related to genetic fitness can be of considerable importance when viewed over evolutionary time. A second limitation relates to the control used in the second experiment. In retrospect, the control might better have been run with the familiar male, rather than an empty cage, across from the female. However, as it might be expected that, when exposed to just one male, prolonged contact with the familiar male might increase, rather than decrease, the probability of pregnancy, this flaw appears to be minor.

Pregnancy initiation in deer mice is partially a function of the number of intromissions received by the female (Dewsbury 1979b; Dewsbury and Baumgardner 1981). However, differences in stimulation were not responsible for the effects observed in these three experiments. Analyses of variance indicated no significant differences across conditions regarding the total number of intromissions received. The effects might have resulted from an elevation of the threshold for pregnancy initiation in the female triggered by a strange male (Dewsbury and Baumgardner 1981). The present data do not support that possibility either. It is notable that females exposed to two males simultaneously appear to show no pregnancy blockage – at least when tested in small cages in short-term tests (Dewsbury 1981b).

The fact that appreciable numbers of female deer mice conceiving in the field deliver litters of multiple paternity (Birdsall and Nash 1973) indicates ecological validity for these experiments. However, Dewsbury and Baumgardner (1981) suggested that such field data may underestimate the number of females mating with more than one male because only about half of the females mating in the laboratory with two males and delivering a litter, delivered litters of multiple paternity. The present results suggest a further source of underestimation. Multiply-mated females have a lower probability of pregnancy than singly-mated females. Together, these two effects suggest that the incidence of multiple paternity may be greatly underestimated in field studies using electrophoretic marker genes.

Relationship to the Bruce Effect

The phenomenon described here bears at least superficial resemblence to the 'Bruce effect' (Bruce 1959). Such an effect has been demonstrated in deer mice (e.g., Bronson and Eleftheriou 1963). In a typical study of the Bruce effect, copulation is not observed, but is inferred from vaginal smears, and experimental manipulations are made 24–48 h later. Strange males produce a pregnancy block. Although the advantage of a Bruce effect to males appears clear, possible advantages to females appear controversial (e.g., Bronson and Coquelin 1980; Dawkins 1976; Labov 1981; Mallory and Brooks 1980; Schwagmeyer 1979). Interpretation of the Bruce effect has been constrained by experimental designs. It has been argued that if a Bruce effect occurs in the field it may be the result of a strange male's replacing a resident within a deme (e.g., Stoddart 1980) or emigration by a pregnant female (Rogers and Beauchamp 1976). Bronson and Coquelin (1980) suggested that the Bruce effect may be a laboratory artifact.

It is not yet clear whether the mechanism underlying the present phenomenon lies along a continuum with the Bruce effect or differs from it. Procedurally, the effects differ in three important ways. First, exposure to the novel male occurs shortly after copulation with the first male. Second, the duration of exposure to the first male is quite brief. Third, the duration of exposure to the second male is quite brief.

Arguing in favor of the possibility of a single underlying mechanism are results showing that the temporal parameters of studies of the Bruce effect can be manipulated through a considerable range without losing the effect (Bloch 1974; Bruce 1961; Chipman et al. 1966; Keverne and de la Riva 1982; Lott and Hopwood 1972; Milligan 1979, 1980). The possibility that the two effects are dissociable is suggested by results indicating that prairie voles show a Bruce effect (Stehn and Richmond 1975; Stehn and Jannett 1981) but apparently show no multi-male blockage (Gray et al. 1974; Dewsbury and Baumgardner 1981).

Should both effects lie along a continuum with a common underlying mechanism, the search for adaptive significance might now be shifted awasy from the narrow range of events dictated by the design of experiments on the Bruce effect to multi-male copulation, a phenomenon known to occur in nature.

Effectiveness of Multi-Male Mating

There is an appreciable literature on the effectiveness of heterospermic (more than one male) versus homospermic (single male) insemination in mammals. Most relevant research has been done with artifical insemination. Although there are some indications of improved fertility with heterospermic insemination (Beatty 1960; Hess et al. 1954; Kushner 1954), most studies have failed to reveal beneficial effects of heterospermic insemination (Beatty 1970; Napier 1961). The present results suggest a detrimental effect of multi-male mating.

Advantages and Disadvantages of Multi-Male Mating

The finding that female deer mice block pregnancies resulting from multimale copulation or exposure suggests that some selective factor may have operated to create the evolution of this response. Many potential advantages to repeated and multi-male mating have been suggested. These include (1) enhancement of genetic diversity of offspring (Byers 1978) (2) as a remedy to an inadequate mating (Boorman and Parker 1976; Byers 1978), (3) as a protection against mating with a sterile male (Oglesby et al. 1981) (4) as a source of nutrition (Byers 1978; Walker 1980), (5) as a means of enhancing male-male behavioral competition and hence producing more fit offspring (Cox and LeBoeuf 1977), (6) as a means of increasing competitive ability in the sperm of sons (Cohen 1971), (7) as being favored in terms of time, energy, and risk, over resisting large, persistent males (Gibson and Falls 1975; Parker 1970), and (8) provision of protection against predators (Walker 1980). On the other hand, prolonged copulation may produce tissue damage from excessive stimulation, waste energy, increase risk of exposure to predators, and risk loss of sperm and other constituents of the ejaculate already in the reproductive tract (Dewsbury 1981a; Oglesby et al. 1981). Further, when she mates with several males, a female may be less able to overtly control the paternity of her offspring. In addition, it has been suggested that genetic diversity in a litter may lead to deleterious competition within a litter (e.g., Hamilton 1964; Trivers 1972). Presumably, these and other influences act in the evolution of both multi-male vs one-male mating patterns and, perhaps, in the kind of pregnancy block demonstrated herein.

One other factor may be relevant specifically to the evolution of pregnancy blockage. Stable physical and social conditions generally would be expected to enhance the success of females in raising litters. A female that could predict a period of instability may be best off deferring reproduction until a later time when conditions are more favorable. In chimpanzees, females copulating in a restrictive mating pattern (i.e., either a pattern of possessiveness by one male or a consortship) appear more likely to conceive than those engaging in 'opportunistic, non-competitive mating' with several males (Tutin 1979). Female rats mating in a burrow system dominated by one male appear more likely to conceive and rear young than those exposed to numbers of males (Calhoun 1962). The multi-male pregnancy block demonstrated here may reflect the operation of similar selective pressures and may provide a proximate mechanism for the termination of reproductive effort in an unstable social situation, as indicated by multi-male mating.

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References

Allison AJ (1977) Flock mating in sheep II. Effect of number of ewes per ram on mating behavior and fertility of two-tooth and mixed-age Romney ewes run together. NZ J Agric Res 20:123–128

Beatty RA (1960) Fertility of mixed semen from different rabbits. J Reprod Fertil 1:52–60

Beatty RA (1970) The genetics of the mammalian gamete. Biol Rev 45:73–119

Bertram BCR (1976) Kin selection in lions and in evolution. In: Bateson PPG, Hinde RA (eds) Growing points in ethology. Cambridge University Press, Cambridge, pp 281–301

Birdsall DA, Nash D (1973) Occurrence of successful multiple insemination of females in natural populations of deer mice (*Peromyscus maniculatus*). Evolution 27:106–110

Bloch S (1974) Observations on the ability of the stud male to block pregnancy in the mouse. J Reprod Fertil 38:469–471

Boorman E, Parker GA (1976) Sperm (ejaculate) competition in *Drosophila melanogaster*, and the reproductive value of females to males in relation to female age and mating status. Ecol Entomol 1:145–155

Bronson FH, Coquelin A (1980) The modulation of reproduction by priming pheromones in house mice: Speculations on adaptive function. In: Müller-Schwarze D, Silverstein RM (eds) Chemical signals: Vertebrates and aquatic invertebrates. Plenum Press, New York, pp 243–265

Bronson FH, Eleftheriou BE (1963) Influence of strange males on implanation in the deermouse. Gen Comp Endocrinol 3:515–518

Bruce HM (1959) An exteroceptive block to pregnancy in the mouse. Nature 184:105

Bruce HM (1961) Time relations in the pregnancy-block induced in mice by strange males. J Reprod Fertil 2:138–142

Byers JR (1978) Biosystematics of the genus *Euxoa* (Lepidoptera: Noctuidae) X. Incidence and level of multiple mating in natural and laboratory populations. Can Entomol 110:193–200

Calhoun JB (1962) The ecology and sociology of the Norway rat. US Dept Health Educ Welfare, Bethesda, Maryland

Chipman RK, Holt JA, Fox KA (1966) Pregnancy failure in laboratory mice after multiple short-term exposure to strange males. Nature 210:653

Cohen J (1971) The comparative physiology of gamete populations. Adv Comp Physiol Biochem 4:256–379

Cox CR, LeBoeuf BJ (1977) Female incitation of male competition: A mechanism in sexual selection. Am Nat 111:317–335

Dawkins R (1976) The selfish gene. Oxford University Press, Oxford

Dewsbury DA (1979a) Copulatory behavior of deer mice (*Peromyscus maniculatus*) I. Normative data, subspecific differences, and effects of cross-fostering. J Comp Physiol Psychol 93:151–160

Dewsbury DA (1979b) Copulatory behavior of deer mice (*Peromycus maniculatus*) III. Effects on pregnancy initiation. J Comp Physiol Psychol 93:178–188

Dewsbury DA (1981a) On the function of the multiple-intromission, multiple-ejaculation copulatory patterns of rodents. Bull Psychon Soc 18:221–223

Dewsbury DA (1981b) Social dominance, copulatory behavior, and differential reproduction in deer mice (*Peromyscus maniculatus*). J Comp Physiol Psychol 95:880–895

Dewsbury DA, Baumgardner DJ (1981) Studies of sperm competition in two species of muroid rodents. Behav Ecol Sociobiol 9:121–133

Gibson AR, Falls JB (1975) Evidence for multiple insemination in the common garter snake, *Thamnophis sirtalis*. Can J Zool 53:1362–1368

Gray GD, Zerylnick, M, Davis HN, Dewsbury DA (1974) Effects of variations in male copulatory behavior on ovulation and implantation in prairie voles, *Microtus ochrogaster*. Horm Behav 5:389–396

Hanken J, Sherman PW (1981) Multiple paternity in Belding's ground squirrel litters. Science 212:351–353

Hamilton WJ (1964) The genetical evolution of social behavior. J Theor Biol 7:1–52

Hess EA, Ludwick T, Rickard HC, Fordyce E (1954) Some of the influences of mixed ejaculates upon bovine fertility. J Dairy Sci 37:649–650

Keverne EB, Riva C de la (1982) Pheromones in mice: reciprocal interaction between the nose and brain. Nature 296:148–150

Kushner F (1954) The effect of heterospermic insemination in animals and its biological nature. Izv Akad Nauk SSSR Biol 1:1–32 (Translated by A McLaren)

Labov JB (1981) Pregnancy blocking in rodents: Adaptive advantages for females. Am Nat 118:361–371

Lott DF, Hopwood JH (1972) Olfactory pregnancy-block in mice (*Mus musculus*): An unusual response acquisition paradigm. Anim Behav 20:263–267

Mallory FF, Brooks RJ (1980) Infanticide and pregnancy failure: Reproductive strategies in the female collared lemming (*Dicrostonyx groenlandicus*). Biol Reprod 22:192–196

Milligan SR (1979) Pregnancy blockage and the memory of the stud male in the vole (*Microtus agrestis*). J Reprod Fertil 57:223–225

Milligan SR (1980) Pheromones and rodent reproductive physiology. Symp Zool Soc (Lond) 45:251–275

Napier RAN (1961) Fertility in the male rabbit III. Estimation of spermatozoan quality by mixed insemination, and the inheritance of spermatozoan characters. J Reprod Fertil 2:273–289

Oglesby JM, Lanier DL, Dewsbury DA (1981) The role of prolonged copulatory behavior in facilitating reproductive success in male Syran golden hamsters (*Mesocricetus auratus*) in a competitive mating situation. Behav Ecol Sociobiol 8:47–54

Parker GA (1970) Sperm competition and its evolutionary consequences in the insects. Biol Rev 45:525–567

Robbins RJ (1979) "Blonde" mutants. Unpublished manuscript, Michigan State University

Rogers JG, Beauchamp GK (1976) Some ecological implications of primer chemical stimuli in rodents. In: Doty RL (ed) Mammaliam olfaction, reproductive processes and behavior. Academic Press, New York, pp 181–195

Sakaluk SK, Cade WH (1980) Female mating frequency and progeny production in singly and doubly mated house and field crickets. Can J Zool 58:404–411

Schwagmeyer PL (1979) The Bruce effect: An evaluation of male/female advantages. Am Nat 114:932–938

Stehn RA, Jannett FJ Jr (1981) Male-induced abortion in various microtine rodents. J Mammal 62:369–372

Stehn RA, Richmond ME (1975) Male-induced pregnancy termination in the prairie vole, *Microtus ochrogaster*. Science 187:1211–1213

Stoddart DM (1980) The ecology of vertebrate olfaction. Chapman and Hall, London

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man 1871–1971. Aldine, Chicago, pp 136–179

Tutin CEG (1979) Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). Behav Ecol Sociobiol 6:29–38

Walker WF (1980) Sperm utilization strategies in nonsocial insects. Am Nat 115:780–799

Winer BJ (1962) Statistical principles in experimental design. McGraw-Hill, New York