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The effect of intrauterine position on the survival, reproduction and home range size of female house mice *(Mus musculus)*

William J. Zielinski[1,*], Frederick S. vom Saal[2], and John G. Vandenbergh[1]

[1] Department of Zoology, Box 7617, North Carolina State University, Raleigh, NC 27695-7617, USA
[2] Division of Biological Science, 213 Lefevre Hall, University of Missouri, Columbia, MO 65211, USA

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Summary. In laboratory studies using albino house mice, a female's prior intrauterine position can affect many postnatal physiological, morphological and behavioral characteristics. Females flanked by males in utero (2M females) exhibit more aggressive dominance than females flanked by females (0M females). Thus, wild 2M females may be most successful during peak population densities when their aggressive nature would allow them to displace other females from limited resources. 2M and 0M females and males delivered by cesarean section were individually marked and released as young adults on two occasions onto a "highway island" (the area enclosed by exit and entrance ramps at an interchange) to determine whether 2M females have a competitive advantage over 0M females in the field. Males were included to create realistic population structure; their intrauterine position was not a treatment. Feeding stations afforded individuals an opportunity to exhibit their dominance by maintaining home-ranges at or near the stations. The populations were monitored by periodic live-trapping and reproductive success was determined using field body weights and by post-mortem examination for uterine implantation scars. Survival and capture rates were estimated, using a modified Jolly-Seber mark-recapture program, for each of four intervals between trapping occasions over the course of 7 weeks. There were no overall differences in survivorship between 2M and 0M females, neither type of female was caught more frequently at feeding stations and they did not differ in measures of reproductive success. However, 2M females had significantly larger home-range sizes than 0M females and thus space use may be a trait "masculinized" by prior intrauterine position. Although there are a number of life-history characteristics that differ between 0M and 2M females in the laboratory that we did not test specifically in the field, our findings and other features of wild house mouse biology suggest that prior intrauterine position does not have a strong effect on survival and reproduction in the wild.

* *Present address:* U.S. Forest Service, Redwood Sciences Laboratory, 1700 Bayview Dr., Arcata, CA 95521, USA

Offprint requests to: W.J. Zielinski at the present address

Introduction

The position of female and male fetuses, relative to the sexes of their intrauterine neighbors, affects the physiological, morphological, or behavioral characteristics of house mice (*Mus musculus*), rats (*Rattus rattus*), gerbils (*Meriones unguiculatus*), and hamsters (*Mesocricetus auratus*) (vom Saal and Bronson 1978; Clemens et al. 1978; vom Saal 1981, 1989; Vomachka and Lisk 1986; Clark and Galef 1988). For example, female albino house mice that were located between two males in utero (2M females) have higher plasma testosterone levels during fetal life, are more aggressive as adults, have longer estrous cycles, are less sexually attractive to males, and have a shorter reproductive life than 0M females. In virtually all characteristics measured, 2M females are phenotypically more masculine than 0M females. 2M females also have longer anogenital distances than 0M females, an observation that has become a common bioassay for the masculinizing effects of prenatal androgen exposure on females (vom Saal and Bronson 1978; vom Saal and Bronson 1980). During embryonic development perineal tissue responds to endogenous androgens such that females display a shorter anogenital distance (AGD) than males (Rugh 1968; Gupta and Goldman 1986). However, androgens transported from adjacent males can lengthen female AGD. Thus, AGD at birth is a good predictor of adult behaviors influenced by prenatal androgen exposure (vom Saal and Bronson 1978; vom Saal 1989).

It has been suggested that intrauterine position may affect an individual's ability to survive and reproduce in natural populations (vom Saal 1981, 1984). In the laboratory, 2M females establish dominance over 0M females in paired encounters in neutral arenas and lactating 2M females exhibit more aggressive behavior toward intruders than do lactating 0M females (vom Saal 1981). These differences in aggression may endow 2M females with an advantage in high-density populations where they may be capable of dominating or displacing 1M and 0M females. Further, size of home range may also be affected by intrauterine position in females. Males in polygynous mammal species usually have larger

home ranges than females (eg. DeLong 1967; Harestad and Bunnell 1979). If this difference is due to sexual differences in prenatal testosterone exposure, it may also be that 2M females have larger home ranges, and access to more resources, than 0M females. Thus, the probability both of surviving and of successfully reproducing should be greater for 2M females when density is high. Indirect support for this hypothesis comes from work on voles (*Clethrionomys rufocanus*) where females from male-biased litters (where 2M females would be most common) were most successful at establishing themselves on an island where space was limiting (Ims 1987). In an another field study, testosterone-treated females survived high densities better than oil-treated controls (Zielinski and Vandenbergh 1991), suggesting that females with higher plasma androgen levels excel in interference competition. It is unknown, however, how females that differed in their level of endogenous exposure to androgens during fetal life, via their intrauterine position, vary in their ability to survive in the wild.

Until recently all of the data on intrauterine position effects in house mice had been collected in the laboratory using laboratory strains of albino mice. However, the recent observation that 2M female wild-type house mice had longer AGDs than 0M females (Zielinski et al. 1991) provides justification for investigating the role of intrauterine position on the behavior of mice in the wild. The purpose of the present experiment was to compare the survival, reproduction and home range size of 2M and 0M female house mice in the field.

We recognize that embryo position can be classified using other schemes (Meisel and Ward 1981; Houtsmuller and Slob 1990) and that some controversy exists about the transport mechanism of intrauterine steroids. However, we chose to classify the animals on the basis of contiguity since it is sufficient to explain most of the position variation in steroid levels and behavior (vom Saal and Bronson 1980; vom Saal et al. 1989).

Methods

Subjects and laboratory procedures. The subjects were descendants of wild house mice caught near Alberta, Canada (Perrigo and Bronson 1985). Virgin females were mated with proven breeder males, had their pups removed immediately after parturition, and were mated during their first post-partum estrus by the same male. Because females are usually impregnated within 18 h of parturition, the second litter reliably occurs 20 days later. We did not check cycling females for plugs because this procedure stresses wild-type females and can cause pregnancy termination. Between 0600 and 1000 hours on Day 19 of gestation (conception equals day 1) the pups were delivered via cesarean section and the intrauterine position (0M, 1M, or 2M) of the females was noted. Each pup was resuscitated using either vacuum suction or by rubbing its nose gently on a paper towel, and was allowed to recover under a heat lamp. Females were individually marked as to intrauterine position using a dermal ink prick and the entire litter was cross-fostered to a lactating albino laboratory female.

At 25 days of age all animals were weaned to individual cages and 0M and 2M females and all males were toe-clipped for individual identification and then weighed at 30–35 days of age. Males were to be released along with females to simulate natural social structure but their intrauterine position was not a treatment variable. Because of the rarity of 0M and especially 2M females (vom Saal 1981) we had difficulty breeding enough females to produce them in sufficient numbers for the field experiment. The sample was augmented by adding to the 0M and 2M groups a minority of 1M females that either had extremely short or extremely long AGDs, respectively. 1M female pups were selected that had AGDs either 1 SD greater than or 1 SD less than the mean for 1M females and can be considered respectively more and less masculinized than the typical 1M female. Thus, the two groups of females are best thought of as either "masculinized" or "non-masculinized". In the "non-masculinized" group 10 females (21.2%) were short-AGD 1M females and 37 (78.8%) were true 0M females. In the "masculinized" group 9 females (20.0%) were long-AGD 1M females and 36 (80.0%) were true 2M females. For convenience we will continue to refer to the two treatment groups as 0M and 2M females.

Field procedures. Our study site was a "highway island" (0.9 ha of unmowed area) formed by the exit and entrance ramps at a highway interchange (Massey and Vandenbergh 1980; Massey 1982; Coppola and Vandenbergh 1987). A highway island was used because many include habitats preferred by wild house mice and because mice released onto the islands emigrate from them at a low rate (Massey 1982; Coppola 1986).

The particular island we used was developed and seeded 8 years prior to this study and the vegetation is typical of an old-field community 5–10 years after abandonment (Keever 1950). Dog-fennel (*Eupatorium canadense*), goldenrod (*Solidago* sp.), blackberry (*Rubus* sp.), broomsedge (*Andropogon* sp.) and isolated loblolly pines (*Pinus taeda*) are the dominant native species. However, several species of Korean lespedeza (*Lespedeza* sp.) and fescue (*Festuca* sp.) that were established during construction are also widespread.

Competition among females was promoted by (1) introducing a total number of animals on each island that was 3–6 times higher than the typical densities of natural house mice populations recorded on similar sites (Massey and Vandenbergh 1980; Coppola and Vandenbergh 1987; Zielinski personal observation) and (2) by establishing a number of feeding stations on each island. We assumed that competitively dominant animals would defend areas around permanent supplies of food (Stueck and Barrett 1978; Ims 1987). Cracked corn and sunflower seeds were provided, every 10 days, under the cover of 1×1-m wooden boards supported by bricks.

An experimental replicate consisted of releasing equivalent numbers of approximately 35-day-old 0M and 2M females, and a number of males roughly equal to the total number of females, on the island. Two replicates were run at two different times of the year on the same island. On 10 October 1989 23 2M females and 24 0M females plus 40 males (87 animals; 96/ha) were released and on 10 May 1990 22 2M and 23 0M females plus 45 males (90 animals; 100/ha) were released. The long- and short-AGD 1M females were included in the second replicate only. Three weeks before mice were released the traps were set to capture and relocate all the native small mammals on the island. These were checked twice a day for at least 3 days each week. The same trap distribution was used to remove these animals as was later used to recapture the experimental house mice. Single $7 \times 7 \times 25$-cm Sherman live-traps were placed at 30-m intervals along traplines located 30 m apart and two traps were placed at each feeding station, totalling 77 traps.

The experimental animals were released at the center of the island in the late afternoon. Mice were recaptured at four occasions during the 7 weeks that followed their release. Each occasion included three consecutive nights of trapping where traps were set in the late afternoon, checked at dawn, closed for the rest of the day and reopened again in the afternoon. The first morning of each of the four recapture occasions occurred 7, 20, 35, and 50 days after each release resulting in four between-capture intervals of 7, 10, 13, and 13 days respectively.

Analyses of survivorship, dominance, space use, and reproduction. The initial analysis of survivorship was conducted by comparing the number of 0M females, 2M females, and male mice that were captured at least once with the number that were never captured, using χ^2 contingency tables. Animals that were never captured were assumed to have either died or dispersed from the island and thus did not "survive". However, differences in capture rates may merely reflect differences in behavior toward traps or different activity levels, so we also estimated survival rates independent of capture rates using the Jolly-Seber capture-recapture model (Jolly 1965; Seber 1965) as included in the software program RELEASE (Burnham et al. 1987). RELEASE was developed to distinguish capture from survival probabilities for fish that are exposed to different levels of treatment, released at one point in time and recaptured at several possible downstream locations. However, the model is applicable to experiments where the survival and capture probabilities of two or more treatment groups of any species released at the same time are to be compared (eg. starlings; Krementz et al. 1989). All test statistics in RELEASE are distributed as χ^2 and tests are in the form of contingency tables. We applied the model separately to the 0M females, 2M females, and males to obtain independent estimates of survival probability (Φ_i) for each of the four between-capture intervals, and capture probability (p_i) for each of the four capture occasions. Replicates were compared for statistical equivalency before the data from both were pooled.

Dominance was also assessed by comparing the number of 0M females, 2M females, and male mice caught at feeding stations. Dominant animals were presumed to establish home ranges near feeding stations. The area that an individual used was calculated for each mouse that was captured a minimum of three times. Although an animal with only three captures was included, the mean number of captures per animal included in the analyses were 6.4 (SD=2.2) for females and 6.2 (SD=3.2) for males. The location analysis program MCPAAL (Stüwe and Blohowiak 1982) was used to calculate minimum polygon areas for 0M and 2M females and males separately for each replicate. Mean home range areas were compared using *t*-tests. Body weights, measured during recapture, were an index of reproductive activity and general health. Females that both weighed ≥ 27 g *and* had a conspicuously large abdomen were assumed to be pregnant (Zielinski unpublished data). All females captured on the last occasion were returned to the laboratory and sacrificed. Their uteri were removed and placental scars were counted as an index of fecundity (Davis and Emlen 1948; Kirkpatrick 1980).

Results

The fall and spring data were pooled because the survivorship of 0M ($\chi^2=7.98$, $P=0.33$), 2M ($\chi^2=4.31$, $P=0.37$) or male mice ($\chi^2=5.15$, $P=0.64$) did not vary with season. A total of 47, 45, and 85 0M female, 2M female, and male mice, respectively, were released. At the first recapture episode, 7 days after release, 37.3% of the animals were recaptured. Seven weeks after release, at the end of the experiment, 19.8% of the animals were captured. Analyzed simply on the basis of whether an individual was either caught or not caught after release, there were no differences in the persistence of 0M and 2M females on the islands ($\chi^2=2.22$, $P>0.10$). In addition, the probability of capturing a male at least once after release was no different than capturing either type of female (Table 1).

However, this measure of success does not distinguish between the probability of *survival* and the probability of *capture* (i.e. individual or treatment-specific responses to traps) and does not test for a change in relative survivorship over time. Program RELEASE allowed us to address both of these problems. The survival rate of 0M and 2M females differed only for the second between-capture interval, where the survivorship of 2M females exceeded that of 0M females (Table 2; Fig. 1). This would mean that for those 2M and 0M females that were alive at the first capture episode, fewer 0M females survived to be caught at the second episode. However, the estimate of *capture* rate of 2M females exceeded that for 0M females during this same period (Table 2), indicating that 2M females were more "capturable" during this period. This could be due to an

Table 1. Numer of 0M females, 2M females and males either caught at least once or never caught after release

	Fall 1989			Spring 1990			Pooled		
	0M	2M	Male	0M	2M	Male	0M[a]	2M[b]	Males
Caught	10	7	19	15	10	20	25	16	39
Not caught	14	16	21	8	12	25	22	29	46
Total number released	24	23	40	23	22	45	47	45	85

[a] 0M v 2M ($\chi^2=2.22$; $0.10<P<0.20$, NS)
0M v males ($\chi^2=0.4$; $0.50<P<0.70$, NS)
[b] 2M v males ($\chi^2=0.9$; $0.30<P<0.50$, NS

The data are presented separately for the two replicates and for replicates pooled

Table 2. Survival (ϕ_x) and capture (p_x) rate estimates[1]

	Females		Males
	0M	2M	
Survival rates			
$\phi(1)$	0.85 (0.25)	0.40 (0.08)	0.53 (0.08)
$\phi(2)$	0.28 (0.11)[a]	0.71 (0.12)[b]	0.45 (0.09)[a,3]
$\phi(3)$	0.89 (0.11)[a,b]	1.0 (0.0)[a]	0.69 (0.11)[b]
$\phi(4)$ p(4)[2]	0.90 (0.09)	0.92 (0.07)	0.84 (0.10)
Capture rates			
$p(1)$	0.42 (0.14)	0.76 (0.12)	0.75 (0.10)
$p(2)$	0.73 (0.13)[a]	1.0 (0.0)[b]	0.93 (0.07)[a]
$p(3)$	0.90 (0.09)	0.90 (0.09)	0.92 (0.08)

[1] x for survival refers to the between-capture interval and x for capture refers to capture occasion (eg. $\phi(1)$=survival rate from release to the first capture occasion and $p(1)$=capture rate at the first capture occasion)
[2] Neither the survival rate for the final between-capture interval ($\phi(4)$) nor the capture rate for the final capture occasion ($p(4)$) can be estimated independently. They are combined here to yield an approximate estimate of survival rate for the final between-capture
[3] Difference between males and 2M females is marginally significant ($P=0.08$)
[a,b] Different letters, within a row, designate statistical differences at $P<0.05$. Absence of letters indicates lack of statistical differences. Standard errors are given in parentheses

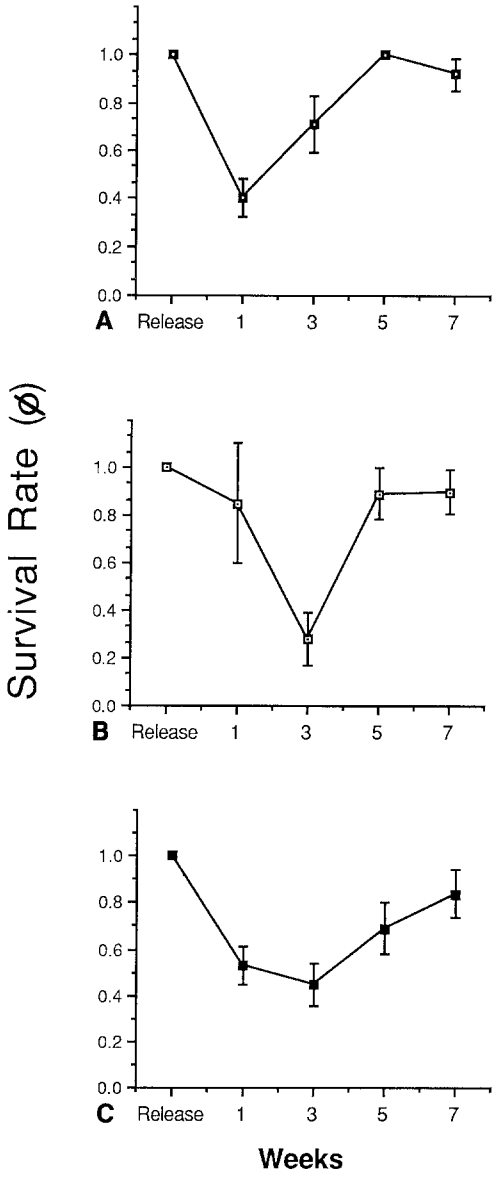

Fig. 1a–c. Survival rates (±1 SE) of 2M (**a**) and 0M (**b**) females and males (**c**) for each between-capture episode during the 7-week experiment. These are estimates of the probability of surviving the subsequent between-trapping interval provided the animal was alive at the previous trapping session. The survival rate at release was standardized at 1.0

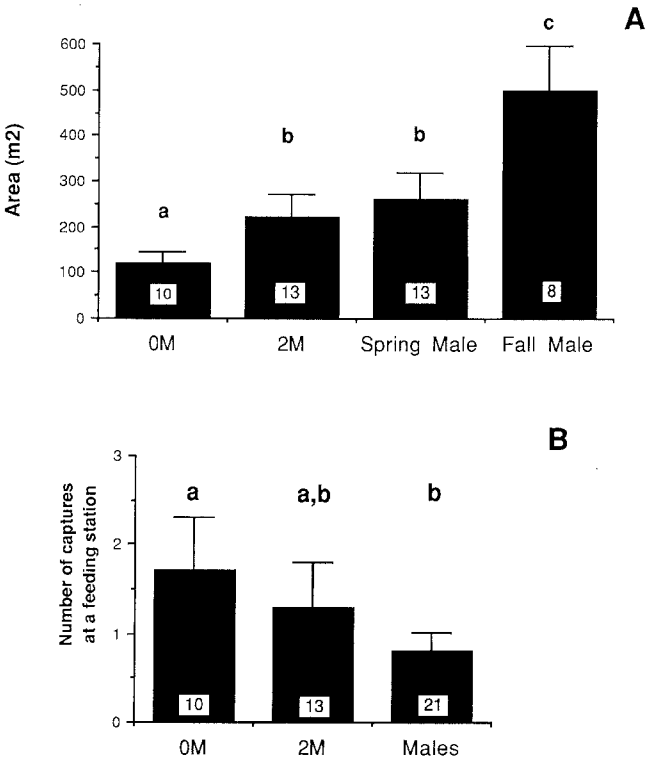

Fig. 2. A Mean home range size (±1 SE) of 0M and 2M females and of males. *Sample sizes* are imbedded in the *bars* and represent the number of animals that were captured at least 3 times during the experiment. Spring and fall data are pooled for females (there were no seasonal differences for females, see text) but significant differences for males necessitated separate presentations for spring and fall. *Letters* above bars distinguish statistically different values (*t*-tests, $P<0.05$). **B** Mean (±1 SE) number of captures at a feeding station for 0M and 2M females and males. *Samples sizes* include only those animals captured at least 3 times during the experiment; animals caught at feedings stations but that were caught only once or twice during the experiment were unlikely to have established a territory in the vicinity of the station. *Letters* above bars distinguish statistically different values (*t*-tests, $P<0.05$)

increased encounter rate with traps or greater propensity to enter an encountered trap, among other reasons. Capture rate differences confound differences in survival rates (Burnham et al. 1987), and since the only time period during which there was a significant survival rate difference was also the only time period where there was a difference in capturability the difference in survival is most likely erroneous. Therefore, there were no meaningful differences between the abilities of 0M and 2M females to survive on the islands during any of the between-capture intervals.

Analysis of space use indicated that 2M females used significantly larger areas than 0M females (Fig. 2A). Neither 0M nor 2M female home ranges differed between spring and fall ($t=0.078$; $P>0.05$ and $t=0.26$; $P>0.05$, respectively). Male ranges in the fall replicate were larger than those in spring replicate ($t=2.29$; $P<0.025$). Interestingly, the mean area used by 2M females was no different from male home range in the spring ($t=0.39$; $P>0.05$) but was significantly less than that used by males in the fall ($t=2.10$; $P<0.05$) while 0M female ranges were significantly smaller than male ranges during both seasons (spring: $t=1.85$; $P<0.05$; fall: $t=2.36$; $P<0.025$). 0M and 2M females did not differ in the mean number of captures at a feeding station, but 0M females were caught there more frequently than were males (Fig. 2B).

Ten 0M and 12 2M females were recaptured 8 weeks after release and sacrificed. The mean number of uterine implantation scars were no different and there were also no differences in the number of 0M and 2M females that weighed enough at recaptures to be considered pregnant (Table 3).

Table 3. Reproductive characteristics of 0M and 2M female mice

	0M	2M
Mean (SE) number of uterine scars[1]	13.8 (1.8)	12.7 (1.4)
Number of different females that weighed ≥27 g	6	8
Number of times a female ≥27 g was captured	13	16

[1] 0M and 2Ms are not statistically different ($t=0.51$, $df=20$, $P>0.05$)

Discussion

The results of our field experiment do not support the prediction that female house mice masculinized by intrauterine proximity to males survive periods of high density any better than females that are not masculinized. There was also no difference in the number of captures of 0M and 2M females at feeding stations, indicating that if these sites were defended, neither type of female excelled at their defence. We doubt that the lack of differences in survival between the two types of females can be attributed to food provisioning. Only half of the animals had home ranges that included a feeding station and the rate at which seeds were eaten from these sites, as indicated by presence of hulls, was quite low. It is likely that during both replicates natural foods were sufficiently abundant to preclude the defense of feeding stations (Carpenter 1987). Therefore, despite the differences in aggressive behavior demonstrated between 0M and 2M females in the laboratory (vom Saal and Bronson 1978), 2M females do not appear to be capable of outcompeting 0M females for resources in the field. While Rines and vom Saal (1984) noted that the difference in aggression between the two types of females decreases with age, this seems an unlikely explanation for the lack of difference in our study since our mice were much younger than the age at which Rines and vom Saal noted the decrease.

While there were no significant differences in ability of either type of female to persist on the island, the larger home ranges of 2M females suggests that they may have the potential to exclude 0M females from some resources if the areas are defended. In other rodents, female spacing behavior has been shown to regulate female density (eg. Bujalska 1973). The fact that the size of the areas used by 2M females was no different from those used by males, at least in spring, suggests that prenatal exposure to heightened testosterone levels may induce some of the wide-ranging behavior typical of male rodents (DeLong 1967; Harestad and Bunnell 1979; Ostfeld 1986; Ims 1988; Salvioni 1988). Therefore, patterns of space use may be added to the list of behavioral and physiological attributes that are masculinized in 2M females. However, this conclusion is offered with the following caveats. First, if home range size increases with decreasing habitat quality then it may possible that the larger home ranges of 2M females reflect social subordination instead of masculinization. This is unlikely, however, because the study site has homogeneous soils and vegetation as a result of its anthropogenic origin. In addition, it would also follow that because of their generally larger home ranges that males are excluded from high quality sites by females. There is no evidence that we are aware of for house mice to support this interpretation. Secondly, space use by all animals could have been influenced by the insular setting and the results should be replicated in a setting with less impediment to dispersal.

The lack of difference between the reproductive success of 0M and 2M females was not surprising since the mean litter size has not been shown to differ in the laboratory (vom Saal and Bronson 1978). While 2M female CF-1 mice have a shorter reproductive lifespan than 0M females in the laboratory (vom Saal and Moyer 1985), our experiment probably concluded before the females were old enough to determine if any difference exists in wild mice.

The low incidence of capture of males at feeding stations is perplexing. It is possible that food resources may be more important to females whereas space resources are more important for males. Costs of lactation and gestation could be met more easily by foraging at a feeding station. It is also possible that females that are associated with feeding stations are active earlier in the evening than males and therefore enter the feeding station traps before the males encounter them. However, we have no evidence to support either of these possibilities.

In previous work knowledge of an individual's intrauterine position (IUP) has helped explain much of the morphological, physiological and behavioral variation that has historically been attributed to genetic variation (vom Saal 1989). While identifying the source of this variation is important, we did not demonstrate strong effects of IUP in a field setting. The present study did not find evidence for competitive exclusion of 0M females by 2M females. Similarly, another recent experiment, using mice from the same stock, found that the sexual attractiveness and sexual receptivity of wild-type 0M, or 1M or 2M females did not differ (Zielinski and Vandenbergh 1991). 0M females housed either alone with a male or in groups with females of other IUPs and a male did not give birth any sooner nor have any larger litter sizes than 2M females. However, there are a number of traits that vary in albino mice on the basis of IUP that were not directly tested in our field or laboratory studies using wild mice. Estrous cycle length, age at puberty, responsiveness to social cues, reproductive life span, infanticide and maternal nest defense all are affected by intrauterine position in albino mice (vom Saal 1989) but their influence on wild mice in natural settings has not been quantified. However, the differences that may occur between 2M and 0M females did not influence their survival or reproduction during the 7 weeks of our experiment.

A number of other characteristics of wild mice in natural populations make it unlikely that IUP will be of much consequence to population dynamics. The litter sizes of wild mice are much smaller than laboratory

strains. Mean litter sizes for wild mice in the field range from 4.77 to 7.0 (Smith 1954; Southwick 1958; Rowe et al. 1963; Lidicker 1966; Berry and Jakobson 1971) whereas the mean litter size of the CF-1 strain, used in IUP experiments, is 12.1 (vom Saal and Bronson 1978). Thus, the production of 2M females is less likely in wild mice. Also, as population density increases litter size can decrease (Southwick 1958), making it even less likely for 2M females to be born into a population at the time they are predicted to have the most influence.

While IUP effects may not play a direct role in population regulation, the intrauterine environment may still affect the behavior and success of males and females. Maternal stress can modify the physiology, morphology and behavior of male and female offspring (Allen and Haggett 1977; Ward and Weisz 1980; Politch and Herrenkohl 1984; vom Saal et al. 1990). In pregnant, wild-type house mice the stress of crowding can masculinize the genital morphology, and presumably behavioral traits, of female offspring (Zielinski et al. 1991). These data, and the results of experiments evaluating the effect of physical stress on pregnant CF-1 mothers (vom Saal et al. 1990), suggest that female offspring of stressed mothers have "2M-like" characteristics. If females born to stressed mothers are more aggressive and less attractive to males, *all* females born during peak populations may be competitively dominant to the female offspring of non-stressed mothers living in low-density populations. This possibility could have important consequences for population regulation in wild rodents. Future experiments, similar to those begun with voles (Ims 1990), should focus on the effect that socially-induced maternal stress has on the ability of offspring born to stressed mothers to survive and reproduce in high density conditions.

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References

Allen TO, Haggett BN (1977) Group housing of pregnant mice reduces copulatory receptivity of female progeny. Physiol Behav 19:61–68

Berry RJ, Jakobson ME (1971) Life and death in an island population of the house mouse. J Gerontol 6:187–197

Bujalska G (1973) The role of spacing behaviour among females in the regulation of reproduction in the bank vole. J Reprod Fert, Suppl 19:465–474

Burnham KP, Anderson DR, White GC, Brownie C, Pollock KH (1987) Design and analysis methods for fish survival experiments based on release-recapture. Am Fish Soc Monogr 5. Bethesda

Carpenter FL (1987) Food abundance and territoriality: to defend or not to defend? Am Zool 27:387–400

Clark M, Galef B (1988) Effects of uterine position on rate of sexual development in female Mongolian gerbils. Physiol Behav 42:15–18

Clemens L, Gladue B, Coniglio L (1978) Prenatal endogenous androgenic influences on masculine sexual behavior and genital morphology in male and female rats. Horm Behav 10:40–53

Coppola DM (1986) Reproductive status and the assimilation of introduced females into a wild population of house mice. Acta Ther 31:221–237

Coppola DM, Vandenbergh JG (1987) Induction of a pubery-regulating chemosignal in wild mouse populations. J Mammal 68:86–91

Davis DE, Emlen JT Jr (1948) The placental scar as a measure of fertility. J Wildl Manage 12:162–166

DeLong KT (1967) Population ecology of feral house mice. Ecology 48:611–634

Gupta C, Goldman AS (1986) The arachidonic acid cascade is involved in the masculinizing action of testosterone on embryonic external genitalia in mice. Proc Natl Acad Sci 83:4346–4349

Harestad AS, Bunnell FL (1979) Home range and body weight-a reevaluation. Ecology 60:389–402

Houtsmuller EJ, Slob AK (1990) Masculinization and defeminization of female rats by males located caudally in the uterus. Physiol Behav 48:555–560

Ims RA (1987) Determinants of competitive success in *Clethrionomys rufocanus*. Ecology 68:1812–1818

Ims RA (1988) Spatial clumping of sexually receptive females induces space sharing among male voles. Nature 335:541–543

Ims RA (1990) Determinants of natal dispersal and space use in grey-sided voles, *Clethrionomys rufocanus*: a combined field and laboratory experiment. Oikos 57:106–113

Jolly GM (1965) Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52:225–247

Keever C (1950) Causes of succession on old-fields of the Piedmont, North Carolina. Ecol Monogr 20:229–250

Kirkpatrick RL (1980) Physiological indices in wildlife management. In: Schemnitz SD (ed) Wildlife management techniques manual. The Wildlife Society, Washington DC, pp 99–112

Krementz DG, Nichols JD, Hines JE (1989) Postfledging survival of European starlings. Ecology 70:646–655

Lidicker WZ (1966) Ecological observations on a feral house mouse population declining to extinction. Ecol Monogr 36:27–50

Massey A (1982) Ecology of house mouse populations confined by highways. J Elisha Mitchell Sci Soc 98:135–143

Massey A, Vandenbergh JG (1980) Puberty delay by a urinary cue from female mice in feral populations. Science 209:821–822

Meisel R, Ward I (1981) Fetal female rats are masculinized by male littermates located caudally in the uterus. Science 213:239–242

Ostfeld RS (1986) Territoriality and mating system of California voles. J Anim Ecol 55:691–706

Perrigo G, Bronson FH (1985) Behavioral and physiological responses of female house mice to foraging variation. Physiol Behav 34:437–440

Politch J, Herrenkohl L (1984) Effects of prenatal stress on reproduction in male and female mice. Physiol Behav 32:95–99

Rines JP, vom Saal FS (1984) Fetal effects on sexual behavior and aggression in young and old female mice treated with estrogen and progesterone. Horm Behav 18:117–129

Rowe FP, Taylor EJ, Chudley AHJ (1963) The effect of crowding on the reproduction of the house-mouse (*Mus musculus* L.) living in corn-ricks. J Anim Ecol 33:477–483

Rugh R (1968) The mouse: Its reproduction and development. Burgess, Minneapolis

Salvioni M (1988) Home range and social behavior of three species of European *Pitymys* (Mammalia, Rodentia). Behav Ecol Sociobiol 22:203–210

Seber GAF (1965) A note on the multiple-recapture census. Biometrika 52:254–259

Smith WW (1954) Reproduction in the house mouse, *Mus musculus* L., in Mississippi. J Mammal 35:509–515

Southwick CH (1958) Population characteristics of house mice living in English carn ricks: density relationships. Proc Zool Soc London 131:163–175

Stueck KL, Barrett GW (1978) Effects of resource partitioning on the population dynamics and energy utilization strategies of feral house mice (*Mus musculus*) populations under experimental field conditions. Ecology 59:539–551

Stüwe M, Blohowiak CE (1982) Microcomputer programs for the analysis of animal locations (MCPAAL). Conservation and Research Center, Nat Zool Park, Smithsonian Inst. Unpub Mimeo

Vomachka A, Lisk R (1986) Androgen and estrogen levels in plasma and amniotic fluid of lat gestational male and female hamsters: Uterine position effects. Horm Behav 20:181–193

vom Saal F (1981) Variation in phenotype due to random intrauterine positioning of male and female fetuses in rodents. J Reprod Fertil 62:633–650

vom Saal F (1984) The intrauterine position phenomenon: effects on physiology, aggressive behavior, and population dynamics in house mice. In: Flannely K, Blanchard R, Blanchard D (eds) Biological Perspectives on Aggression. Alan Liss Inc, New York, pp 135–179

vom Saal F (1989) Sexual differentiation in litter-bearing mammals: Influence of sex of adjacent fetuses in utero. J Anim Sci 67:1824–1840

vom Saal F, Bronson F (1978) In utero proximity of female house mouse fetuses to males: Effect on reproductive performance during later life. Biol Reprod 19:842–853

vom Saal F, Bronson F (1980) Sexual characteristics of adult female mice are correlated with their blood testosterone levels during prenatal development. Science 208:597–599

vom Saal F, Moyer C (1985) Prenatal effects on reproductive capacity during aging in female mice. Biol Reprod 32:1116

vom Saal F, Dhar M, Even M (1989) Uterine blood flow, intrauterine transport of steroids, and the intrauterine position phenomenon in rats. Abstract. Conf of Reprod Behav Skidmore College, Saratoga Springs, N.Y., p. 21

vom Saal F, Quadagno DM, Even MD, Keisler LW, Keisler DH, Khan S (1990) Paradoxical effects of maternal stress on fetal steroids and postnatal reproductive traits in female mice from different intrauterine positions. Biol Reprod 43:751–761

Ward IL, Weisz J (1980) Maternal stress alters plasma testosterone in fetal males. Science 207:328–329

Zielinski WJ, Vandenbergh JG (1991) The effect of intrauterine position and social density on age of first reproduction in wild-type female house mice (*Mus musculus*). J Comp Psych 105:134–139

Zielinski WJ, Vandenbergh JG (1991) Increased survivorship of testosterone-treated female house mice (*Mus musculus*) in high-density field conditions. Anim Behav 42:955–967

Zielinski WJ, Vandenbergh JG, Montano MM (1991) Effects of social stress and intrauterine position on sexual phenotype in wild-type house mice (*Mus musculus*). Physiol Behav 49:117–123