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Anogenital Distance and Dominance Status in Male House Mice (*Mus domesticus*)

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Factors influencing the tendency to be aggressive were investigated in male house mice using a series of paired encounters. Body size, body length, body temperature, age, and anogenital distance were measured on all males. Paired encounters were conducted using a standard mouse cage as an arena. Across 64 males involved in 224 encounters, the tendency to be dominant and win encounters was significantly correlated only with anogenital distance ($r = 0.383$). These findings suggest that there are significant behavioral effects in male mice that could parallel the intrauterine position and related prenatal hormone effects that have been elucidated in female house mice and other rodents. © 1995 Wiley-Liss, Inc.

Key words: house mice, aggression, anogenital distance, intrauterine position, *Mus domesticus*

INTRODUCTION

Among mammals, aggression and related phenomena involving mating systems, access to food resources, and establishment and maintenance of living areas have been studied in such diverse groups as ungulates [Clutton-Brock et al., 1982], mongooses [Rasa, 1986], pinnipeds [Le Bouef, 1974; Renouf, 1991], and primates [Hall, 1964; Zuckerman, 1981]. Rodents have been studied very extensively with regard to aggression [Scott and Fredericson, 1951; Barnett, 1963; Lagerspetz, 1964; Sachser and Prove, 1984; Siegel, 1985].

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Success in aggressive encounters, resulting in differences in dominance status, has been related to reproductive success and mate choice in a variety of mammals, including red deer [*Cervus elaphus*, Clutton-Brock et al., 1982], elephant seals [*Mirounga angustirostris*, Le Bouef, 1974], and house mice [Oakeshott, 1974; Parmigiani et al., 1982; Drickamer, 1992]. Aggressive interactions influence other behavior, including sexual behavior [Oakeshott, 1974; Dewsbury, 1981]. Outcomes from dominance encounters also influence reproductive hormones (FSH and LH) [Bronson et al., 1973], although endocrine changes often do not persist for as long as behavioral changes.

A number of factors can influence aggression in the proximate sense. Such factors include early experience [Kahn 1954; King and Gurney 1954], genotype [Scott, 1966; Lagerspetz and Lagerspetz, 1971; van Oortmerssen et al., 1985], litter size [Ryan and Wehmer, 1975], isolation versus group housing [Valzelli, 1969; Mugford and Nowell, 1972], residency status (encounter staged in home area or in unfamiliar surroundings) [Charpentier, 1969], pheromonal cues [Mugford and Nowell, 1970, 1971], and population density [Southwick, 1958]. Also, for white-footed mice (*Peromyscus maniculatus*), dominance may be related to metabolic rate [Farr and Andrews, 1978].

Intrauterine position, another proximate factor, is related to activity [Kinsley et al., 1986; Yousif et al., 1991] and to aggression [vom Saal, 1983] in male mice. Males located in utero between two males are less active [Kinsley et al., 1986] and show less investigative and less social and sexual activity, but are more aggressive than males located between a pair of females [Yousif et al., 1991].

There is a relationship between intrauterine position and some combination of levels of testosterone and/or levels of sensitivity of the brain and reproductive organs to circulating levels of testosterone in adult male mice and gerbils. This, in turn, influences aggressiveness and other behavior patterns as well as the functioning of reproductive organs [Clark et al., 1992; Even et al., 1992; Nonneman et al., 1992]. Aggression in male mice appears to be mediated in part by prenatal exposure to androgen and estrogen, postnatal exposure to androgen, and experience in aggressive interactions [Scott and Fredericson, 1951; Edwards, 1969; Maruniak et al., 1977; vom Saal, 1983]. Significant positive relationships between testosterone levels in adulthood and various components of aggression have been reported in adult male mice by a number of investigators [Beeman, 1947; Bronson and Desjardins, 1968; van Oortmerssen et al., 1987].

Anogenital distance, a morphological trait, is affected by intrauterine position of females and can serve as a possible bioassay of the position occupied by a mouse when it was in utero. We raise the possibility here that this is also the case in males. We also tested whether other characteristics of male mice, in addition to anogenital distance, correlate with their aggressiveness and winning or losing in paired encounters. While some investigators have examined body size (as either body mass or some linear measure of body dimensions) with regard to social dominance interactions, neither body temperature nor anogenital distance have been examined with respect to their effects on outcomes of interactions. From data on several other mammalian species (e.g., red deer, *Cervus elaphus*, [Clutton-Brock et al., 1982], Syrian hamsters, *Mesocricetus auratus* [Payne and Swanson 1970]) we predict that body size could be an important factor in house mouse aggressive interactions, with larger animals expected to be winners more often [Robitaille and Bovet, 1976]. There is some evidence from white-footed mice (*Peromyscus maniculatus*) that dominance is positively related to metabolic rate

[Farr and Andrews, 1978]. If we assume body temperature is an indirect measure of general metabolic activity, then we would predict that for house mice, higher body temperatures should be associated with winning more often in encounters with other males. We tested the age of males as a possible factor in determining winners in aggressive encounters, because in a variety of mammals and from our own unpublished data we know that body size increases as a positive function of age.

Lastly, in the literature regarding intrauterine position effects on social and sexual behavior in rodents [vom Saal, 1981, 1989; Clark and Galef, 1988], there is evidence that a) anogenital distance in males can be affected by hormones during intrauterine development [Kinsley and Svare, 1987; Zielinski et al., 1991] and b) differences in aggressive behavior can be related to intrauterine position for male mice [vom Saal, 1983; Yousif et al., 1991]. We tested whether variation in anogenital distance, whatever its proximate causes, could be related to variation in aggressive behavior in male mice. Since previous findings suggest that larger anogenital distances may be associated with higher levels of intrauterine exposure to androgens in males, we predicted that males with larger anogenital distances would be the aggressors more often in encounters with other males.

MATERIALS AND METHODS

Subjects and Husbandry

We used two stocks of wild house mice, each treated identically. One stock consisted of first generation laboratory progeny from mice captured at the Swine Farm of Southern Illinois University, Carbondale, IL. The other stock was established from wild mice originally captured at Fort Collins, CO, bred in the laboratory of Dr. Sarah Lenington at Rutgers University, Newark, NJ, and crossed with an inbred laboratory strain (LT/MA); progeny used from this stock were several generations removed from the wild at the time of testing. Mice of both stocks were bred by placing a single male with a single female. Litters were weaned at 23–25 days of age and housed in unisexual groups of 4–5 individuals until they were approximately 90 days of age. Throughout rearing and development, mice were housed in standard shoebox polypropylene mouse cages on a bedding of wood shavings in an animal colony room at 20–23°C with overhead fluorescent lights on a 14 hr light:10 hr dark daily cycle. At the beginning of March 1993, 2 weeks prior to testing, all males were separated into individual cages. At this time they were moved to an enclosed barn where they were exposed to current external ambient conditions of temperature and daylength. At that time of the year the external conditions involved between 12 and 13 hr per day of daylight, temperatures ranging from lows of 3–10°C to highs of 14–23°C, and relative humidity of 40–60%. In addition to a bedding of wood shavings, each male was given a cotton square (2.8 × 2.8 × 0.3 cm thick; Nestlets made by Ancare Corp., Belmont, NY) with which to make a nest. The mice were moved to the barn because of a larger field study in which they eventually were released into outdoor enclosures.

Apparatus and Procedures

Two weeks after being placed in the barn, each mouse was measured for body mass (g) using a Pesola spring scale; for body length (cm), defined as the distance from the tip of the nose to base of the tail, by holding the mouse down on a metric ruler; for body temperature (°C) using a Physitemp Model BAT-12 Digital Thermometer with a RET-3 rectal probe; and for anogenital distance (cm), defined as the minimum distance between the posterior base of the penis and the anterior lip of the anus using Calipputer calipers. Interobserver reliability values for the measurement of body mass, body length, and anogenital distance were obtained by having two individuals make each set of measurements. The Spearman rank correlation [Siegel, 1956] interobserver values were all ≥0.92.

We conducted the encounters in a standard opaque polypropylene mouse cage (15 cm × 28 cm × 15 cm deep) with a flat hardware cloth lid. The cage was cleaned between each encounter. Mouse measurements were made by LCD, encounters involving mice from Illinois stock were conducted by LMM, and encounters involving mice from Colorado/New Jersey stock were conducted by CC. Other than possible interactions with cagemates during early development, none of these males had any previous fighting experience.

We tested 32 males of each stock; males within each stock were divided into four groups of eight males each such that no brothers (mice from the same rearing cage) were in the same group of eight. Thus, there were a total of eight groups of eight males. Within each group of eight males a complete series of round robin encounters was staged for a total seven encounters per male and 28 encounters per group. That is, each male was paired with each of the other seven males in his group. Order of testing in each group was randomized. No male was used in more than one encounter per day and the entire encounter testing procedure was completed in a period of 10 days. Encounters lasted 10 min, or were terminated as described below when one male established clear aggressive superiority prior to the end of time period.

Each encounter was scored according to the outcome. If one male attacked another male five times in succession we terminated the encounter; that male was recorded as a clear winner and given a score of 3. A loser in such encounters was given a score of 0. When one male consistently displaced the other and/or made only a few attacks during the 10 min, we scored this animal as a passive winner and gave it a score of 2. Losers in these encounters received a score of 1. When two males did not attack or displace one another during 10 min, the outcome was a draw and each male was given a score of 1 [scoring system based on Lenington, 1991]. An average aggression score was computed for each male at the conclusion of his seven encounters.

Analyses

All analyses were conducted on a Macintosh SE/30 microcomputer using Statview II [1987]. We analyzed differences between the two stocks of mice using parametric t-tests. Pearson product-moment correlations were used to test relationships between individual traits and level of aggression. Lastly, a stepwise multiple regression analysis was used to determine the relative importance of the five independent parameters for predicting aggression score. Results were analyzed separately for the two stocks of mice, except that a combined analysis was also run for the stepwise multiple regression.

RESULTS

The two stocks of mice differed with respect to body mass (t 62 = 4.68; $P < 0.001$) and body length (t 62 = 6.00; $P < 0.001$), but did not differ for age (t 62 = 1.38; 0.10 <

$P < 0.20$), body temperature ($r\,62 = 0.42$; $P > 0.20$), or anogenital distance ($r\,62 = 0.25$; $P > 0.20$) (Table I).

When the individual independent measures were correlated with aggression scores within each stock, all of the values except those for anogenital distance were not significant ($P > 0.20$). The correlation coefficients for anogenital distance and aggression score were significant for both the Illinois stock ($r30 = 0.41$; $P = 0.020$; regression equation of $y = 1.54x - 0.23$) and the Colorado/New Jersey stock ($r30 = 0.38$; $P = 0.032$; regression equation of $y = 2.66x - 1.45$). When we carried out stepwise multiple regression, anogenital distance was the only variable entered into the equation by the program that accounted for a significant percentage of the variance ($\geq 1\%$) for each of the stocks analyzed separately and for the combined stocks (Table II). Additional correlation coefficients were calculated between anogenital distance and both body mass and body length within each stock of mice and no statistically significant (all $P > 0.20$) relationships were found.

DISCUSSION

The principal conclusion from these data is that there is a significant relationship between anogenital distance and the likelihood of being more aggressive and achieving dominance in interactions with other males. The length of the space separating the genital papilla and anus at birth is a function of exposure to testosterone during fetal and neonatal life in mice [Gupta, 1988; Keisler et al., 1991]. Animals with larger anogenital distances at birth also have comparatively larger anogenital distances in adulthood [vom Saal and Bronson, 1978]. This latter finding suggests that the differences in anogenital distance observed in adult male mice in the present study were a consequence of differences in exposure to testosterone during sexual differentiation of the external genitals, which occurs during the latter part of prenatal and early postnatal life [Rugh, 1968].

There is a well established relationship between exposure to testosterone during prenatal and early postnatal life and intermale aggression in mice. This relationship is based on at least two lines of evidence: 1) Experimentally increasing levels of testosterone during perinatal life in female mice results in the females showing levels of aggression toward males that are similar to those seen in male-male encounters [vom Saal, 1979]. There is a correlation between levels of testosterone

TABLE I. Mean Values (± 1 SE) for Five Independent Variables Measured on Two Stocks of Wild Male House Mice

	Stock			
	Illinois		Colorado/New Jersey	
Variable	Mean (±SE)	Range	Mean (±SE)	Range
Body mass (g)	19.6 (0.3)	18.0–24.0	21.8 (0.3)	17.5–24.5
Body length (cm)	8.6 (0.1)	7.8–9.7	9.2 (0.1)	8.6–9.8
Body temperature (°C)	36.9 (0.2)	35.7–39.1	36.8 (0.2)	35.4–38.2
Anogenital distance (cm)	1.08 (0.2)	0.82–1.30	1.09 (0.3)	0.59–1.42
Age (days)	144.5 (12.7)	111–145	149.9 (12.9)	89–150

TABLE II. Results From Stepwise Multiple Regression Analyses of Five Independent Measures for Predicting Aggression Score in Male House Mice*

Stock	R	R^2	Mean square residual
Illinois	0.410	0.168	0.837
Colorado/New Jersey	0.379	0.144	0.729
Combined	0.383	0.147	0.777

*Data were analyzed separately for each stock and in a combined analysis. Only anogenital distance was entered by the program as a significant factor affecting aggression score.

during fetal life and intermale aggression in male mice [vom Saal et al., 1983; vom Saal, 1989].

Taken together, the forgoing findings show that both anogenital distance and intermale aggression are related to the levels of testosterone to which males are exposed during the perinatal period of development. Thus, we propose that our present finding of a correlation between anogenital distance and intermale aggression in adult male mice is mediated, at least in part, by variation in exposure to testosterone during perinatal life.

An interesting and significant aspect of our findings is the large degree of variation in anogenital distance among adult males of both stocks (Table I). We calculated the percent difference in anogenital distance (largest − smallest/smallest). For the hybrid stock (wild Colorado mice × laboratory LT.MA strain) used in the present study, the percent difference (141%) in anogenital distance was dramatically larger than for the wild stock trapped in Illinois (59%). This latter value is virtually identical to the value for anogenital distance at birth in wild male mice derived from a founder stock of mice trapped in Alberta, Canada (57%; vom Saal, unpublished observation).

Previous findings using a number of outbred and inbred laboratory mice have provided evidence for relatively little variability among male mice in anogential distance at birth [Kinsley and Svare, 1987; vom Saal, 1979]. For example, in male Rockland-Swiss mice, the percent difference in anogenital distance at birth was 26% (vom Saal, unpublished observation), or about one-half that observed in wild mice. In studies with laboratory mice, the likelihood of finding correlations between anogenital distance at birth or in adulthood and various behavior patterns, such as intermale aggression, is unlikely, due to the low level of variability among males in anogential distance [Kinsley and Svare, 1987; Keisler et al., 1991; vom Saal, unpublished observation].

Neither body temperature nor age were significant predictors of aggressiveness, although all animals tested were adults (Table I). We also did not find any significant relationships between anogenital distance in adulthood and either measure of body size (body mass or body length) or aggressiveness and body size in either stock of mice. This latter finding is interesting in that some investigators have reported a correlation between body weight and being victorious in encounters between male rodents [Barnett, 1963; Lagerspetz, 1964; Spencer and Cameron, 1983]. We should note that body mass values for our mice ranged 6–7 g (Table I), encompassing almost the entire range for wild stock adult *Mus*. Thus, our prediction is that while perinatal levels of testosterone influence adult anogenital distance and aggressiveness, factors other than levels of testosterone during perinatal life likely influence adult body size.

Adult as well as perinatal testosterone levels influence intermale aggression and other behavior patterns in male mice. However, testosterone is released into the blood in male mice in pulses that occur at unpredictable intervals [Coquelin and Desjardins, 1982]. Thus, it is not surprising that relationships between circulating testosterone and behavior patterns such as aggression are not always found [Svare et al., 1977; Brain and Nowell, 1969; van Oortmerssen et al., 1987], since the pulsatile release of testosterone makes correlating blood testosterone levels in males with behavior possible only with frequent collection of blood samples via cannulae. We thus did not attempt, in the present study, to measure circulating testosterone and correlate this with a male's anogenital distance or aggressiveness. Average levels of circulating testosterone can be estimated by measuring testosterone in feces of some mammals [Gunther Scheffler and Toni Zeigler, personal communication), and this will be done in future studies.

Our findings suggest two lines for future research. The high variability in anogenital distance observed for wild mice, both at birth and in adulthood, suggests a much greater variability in testosterone levels during the prenatal period of differentiation of the external genitals relative to variability that has been observed in laboratory stocks of mice. One possible source of variability in prenatal testosterone levels, anogenital distance at birth, and adult behavior is the intrauterine proximity of male fetuses to male or female siblings (the intrauterine position phenomenon). Namely, males exposed to elevated levels of testosterone in utero due to being positioned between male fetuses may have the largest anogenital distances at birth and in adulthood, and they may also be the most aggressive animals. In contrast, males positioned in utero between female fetuses are exposed to the lowest levels of testosterone during fetal life and may have the shortest anogenital distances at birth and in adulthood and be the lest aggressive males [vom Saal, 1989]. A second area for future investigation involves the examination of additional correlations between anogenital distance and other behavior patterns in male mice, e.g., home range size [Zielinski and Vandenbergh, 1991], resource defence, and reproductive success.

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