Acceleration and deceleration of sexual maturation by social cues in a tropical rodent *Zygodontomys brevicauda*

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The effects of social cues from adult conspecifics on the rate of sexual maturity were studied in a tropical rodent, the cane mouse (*Zygodontomys brevicauda*), in the laboratory. Several aspects of the biology of this species have suggested that it might be atypical in that young females may not accelerate or decelerate their rate of reproductive development in response to social cues. This hypothesis was tested by housing 16-day-old females with an adult male, an adult female, or alone, and reproductive development was assessed periodically, beginning when the mice were 20 days old. Young females paired with males underwent more uterine growth and matured markedly earlier than did isolated controls. Young females paired with adult females exhibited less uterine growth than did isolated controls. Thus, social cues both accelerate and decelerate reproductive development in females of this species, and the hypothesis that social cues have no effect on reproductive development in young females was rejected. The evolutionary conditions that favour unresponsiveness of young females to social cues appear to be restrictive, and may be rare in mammals.

Introduction

An important component of the strategy an individual mammal uses to maximize its reproductive fitness is the timing of reproductive maturity (Cole, 1954; Lewontin, 1965). Every species must have some theoretical minimum age of reproductive maturity that may be modified by environmental conditions. The age at which an individual actually matures depends upon a variety of nutritional, social and other factors (reviewed by Bronson, 1989). Under permissive nutritional conditions in the laboratory, reproductive maturity can be delayed or accelerated in many species by social cues from conspecifics. In many species, exposure of individuals to adults of the opposite sex accelerates sexual maturity while exposure to adults of the same sex delays puberty (reviewed by Drickamer, 1986; Vandenberg, 1989; Bronson, 1989; Sawrey and Dewsbury, 1991). A number of studies have provided evidence that these social cues can also play significant roles in the regulation of reproductive maturity in natural populations (Massey and Vandenberg, 1980, 1981; Heske and Nelson, 1984; Coppola, 1986; Coppola and Vandenberg, 1987; Vandenberg, 1987). The effects have been reported in so many species (Bronson, 1989) that they appear to be the norm among rodents, and are at least common in other mammalian orders.

This study was prompted by laboratory and field observations suggesting that female cane mice, *Zygodontomys brevicauda*, fail to accelerate or decelerate reproductive maturity in response to social cues. In the wild on the Llanos of

Venezuela, reproduction is nonseasonal in this species (Vivas, 1984; O'Connell, 1989). The Llanos has severe wet and dry seasons, and August (1984) suggested that the seasons are so extreme that there may not be an optimum season for reproduction in cane mice. Laboratory data demonstrate that maturity in *Z. brevicauda* is not delayed or accelerated when they are exposed to either long or short photoperiods (Heideman and Bronson, 1990). Experimental treatments that can unmask reproductive photoresponsiveness in other rodents fail to do so in cane mice (Bronson and Heideman, 1992). Laboratory-bred female cane mice can become sexually mature very early, as 21-day-old, newly weaned females can become pregnant within days of pairing with a male (Voss *et al.*, 1992). Characteristics of oestrous cycles were not affected by the presence of a male on the other side of a wire partition (Voss *et al.*, 1992). All of these observations suggested that cane mice might ignore external cues, both seasonal and social, during reproductive development, resulting in rapid maturation limited only by nutritional status. The experiments in this paper test the hypothesis that social cues do not affect the rate of reproductive development in female *Z. brevicauda*.

Materials and Methods

Two experiments were conducted. In both, the animals used were approximately the eighth laboratory generation of an outbred colony originally established by R. S. Voss at the American Museum of Natural History, New York, from a wild stock obtained at Hato el Frio, Estado Apure, Venezuela (7°N, 68°44'E; elevation approximately 60 m; Voss, 1991; Voss *et al.*, 1992). All animals were maintained at $24 \pm 1^\circ\text{C}$. Animals used in the experiments were kept under the same light schedule as

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Table 1. Body weight (mean $\pm$ SEM) and reproductive characteristics of female cane mice (*Zygodontomys brevicauda*) housed with adult males or in isolation

Characteristic	Isolate	Male-paired	Probability
20 days old			
Body weight	23.7 $\pm$ 0.8	22.6 $\pm$ 0.1	NS
Uterine weight	19.1 $\pm$ 2.0	52.8 $\pm$ 8.6	< 0.01
Percentage with large, tertiary follicles or corpora lutea	0	10	NS
30 days old			
Body weight	28.4 $\pm$ 1.2	32.2 $\pm$ 0.9	< 0.05
Uterine weight	47.0 $\pm$ 8.2	Not applicable ^a	Not applicable ^a
Percentage with large, tertiary follicles or corpora lutea	10	100	< 0.05

^aAll of the females at this stage of treatment carried fetuses at the time of autopsy.

NS: not significant.

the breeding colony (13 h light:11 h dark with lights on at 08:00 h). There is no evidence that photoperiod affects reproductive status in this species (Heideman and Bronson, 1990; Bronson and Heideman, 1992). Individuals and pairs were housed in polyethylene cages measuring 29 cm $\times$ 18 cm $\times$ 12 cm containing pine shavings to a depth of approximately 3 cm. All were given food (Purina Formulab 5008, Ralston-Purina Co., St Louis, MO) and water *ad libitum*.

In this species, vaginal opening and other external reproductive characteristics are poor indicators of reproductive maturity; these mice have typical oestrous cycles of about 4–7 days (Voss, 1991; Voss *et al.*, 1992). Uterine weight and the ovarian condition were therefore used as indicators of reproductive development. Because *Z. brevicauda* ovulate spontaneously (Voss *et al.*, 1992), the presence of corpora lutea or large tertiary follicles (diameter > 2 mm, similar in size to corpora lutea) was considered to be evidence of reproductive maturity. Uterine weights were measured immediately after uteri were removed, opened and drained of any fluid, and blotted gently on a paper towel. Test females were housed directly with stimulus animals rather than separated using a barrier to include the effects of tactile as well as other potential cues (Bronson and Maruniak, 1975; Drickamer, 1977; Carter *et al.*, 1987). Individuals were weaned 16 $\pm$ 1 days after birth and immediately placed into their respective treatment group. Treatment groups in each experiment were matched for bodyweight, because bodyweight may affect reproductive development and responses to social cues in rodents (Bronson and Desjardins, 1974; Bronson and Macmillan, 1983). Changes in bodyweight were recorded to test for the effects of treatment on somatic growth. Body and uterine weights were compared across treatments (male-paired versus isolated groups and female-paired versus isolated groups) and ages using a separate two-way analysis of variance for each experiment, and were compared at particular ages using Student's *t* test.

Experiment 1

This experiment examined the effects of unfamiliar adult males on female reproductive development. Eight groups of

9–10 females aged 16 $\pm$ 1 days and weighing 16–24 g were formed and siblings were assigned to different treatment groups. Young females in four of the groups were housed alone (isolates), and females in the other four groups were paired with adult males (male-paired). One group of isolates and one group of male-paired females were autopsied at 20, 30, 40 and 55 days of age.

Experiment 2

Expt 2 was conducted simultaneously with Expt 1 and shared the mice in the isolated groups that were autopsied at 30, 40 and 55 days of age in Expt 1. In Expt 2, the effect of unfamiliar adult females on female reproductive development was examined. Groups of 9–10 females aged 16 $\pm$ 1 days and weighing 16–24 g were formed and siblings were assigned to different treatment groups. Young females in four of the groups were housed alone (isolates), and females in the other four groups were paired with adult females (female-paired). Isolate and female-paired female groups were compared at 30, 40, 55 and 70 days of age.

Results

Experiment 1

Uterine development in weanling females paired with adult males was accelerated significantly compared with that of isolated females. At 20 days of age, after 4 $\pm$ 1 days of exposure to a male, uterine weights were more than double those of isolated females (Table 1; $P < 0.01$). Isolated females required an additional 10 days to approach the uterine weights of male-paired females (Table 1). At 30 days of age, the ovaries of only one of ten isolated females had corpora lutea or large tertiary follicles, while those of all 30-day-old male-paired females had corpora lutea or large tertiary follicles. Eight of ten male-paired females were pregnant at 30 days of age, as were eight of ten male-paired females at 40 days of age. Data on the 55-day-old male-paired females, 60% of which delivered pups at 46 days of age, were used to determine the age of

Table 2. The effect of both age and treatment on the uterine size (mean $\pm$ SEM) of young female cane mice (*Zygodontomys brevicauda*) comparing isolated and female-paired treatments

Characteristic	Isolate	Female-paired	Probability
30 days old			
Body weight	28.4 $\pm$ 1.2	31.9 $\pm$ 4.2	0.06
Uterine weight	47.0 $\pm$ 8.2	44.2 $\pm$ 9.3	NS
Percentage with large, tertiary follicles or corpora lutea	10	0	
40 days old			
Body weight	37.5 $\pm$ 5.6	43.0 $\pm$ 5.1	0.05
Uterine weight	57.7 $\pm$ 7.9	34.9 $\pm$ 7.4	0.05
Percentage with large, tertiary follicles or corpora lutea	40	10	
55 days old			
Body weight	37.7 $\pm$ 10.7	41.7 $\pm$ 6.4	NS
Uterine weight	74.7 $\pm$ 8.4	59.5 $\pm$ 13.4	NS
Percentage with large, tertiary follicles or corpora lutea	30	30	
70 days old			
Body weight	46.4 $\pm$ 5.7	43.9 $\pm$ 6.4	NS
Uterine weight	83.6 $\pm$ 9.2	53.3 $\pm$ 8.0	0.03
Percentage with large, tertiary follicles or corpora lutea	40	0	

NS: not significant.

fertilization. Cane mice have a mean gestation period of 25 days (Voss *et al.*, 1992), indicating that most females were impregnated, and therefore reproductively mature, between about 19 and 23 days of age. Isolated females of this age had immature uteri and small ovaries without large tertiary follicles or corpora lutea. Overall, body weight was similar in the two groups ($F = 2.19$; $P > 0.10$). Results for treatments lasting 40 and 55 days are not presented in Table 1 because almost all male-paired females were pregnant with advanced embryos.

Experiment 2

The uterine development of young females paired with adult females was significantly inhibited ($F = 7.57$; $P < 0.01$; Table 2). Uterine weight also increased with age ($F = 3.80$; $P < 0.05$; Table 2), and the interaction between treatment and age was not significant ($F = 0.73$; $P > 0.50$). Female-paired young had consistently lower uterine weights than those of isolated mice (Table 2). The greatest differences between the two treatment groups occurred in the 40-day-old and 70-day-old females ($P < 0.05$; $P < 0.03$, respectively). In both groups of young females there were few large tertiary follicles and corpora lutea, but the lower frequency in female-paired young females was not statistically significant ($P > 0.10$; Table 2). There was a trend towards lower body weight in isolated females ($F = 3.16$; $P = 0.08$).

Discussion

Social cues clearly affect the timing of reproductive development in female cane mice in the laboratory. Adult males stimulated uterine growth and ovulation while adult females

inhibited uterine growth in young females. The higher body weight of female-paired females relative to isolated females suggests a possible trade-off between reproductive maturity and somatic growth, but this difference was not observed in older females. The effect of an adult male was potent, as females were capable of conceiving within days of exposure to a male beginning at 16 days of age, while isolated females retained reproductive tracts that were juvenile in appearance for an additional 10–20 days. Clearly, isolated cane mice do not mature at their maximum potential rate. Combined with the evidence of inhibitory effects of adult females on uterine development, these results demonstrate the potential for considerable flexibility in the rate of reproductive maturation.

Voss *et al.* (1992) reported that female cane mice become reproductively mature extremely rapidly in the laboratory. Our results indicate that this rapid maturation is conditional upon male exposure and the absence of adult females. Reproductive maturation in young, isolated females occurs at an intermediate rate. Rather than being insensitive to social cues, female cane mice are very sensitive to these cues, at least in the laboratory. In the wild, rates of reproductive development could vary dramatically both temporally and spatially according to local social conditions in this species. The ability to delay or accelerate reproductive maturity in response to social cues may be particularly important when populations reach high densities.

A number of hypotheses have been proposed to explain the evolution and maintenance of reproductive responses to social cues. The acceleration and deceleration of reproductive maturity in response to social cues can be interpreted as a mechanism to synchronize seasonal reproduction (Bronson, 1985), as a mechanism to protect a female from sexual maturation before dispersal (Bronson, 1979) or as adaptive responses of young individuals to local population density and

other social conditions that favour or disfavour early reproduction (Rogers and Beauchamp, 1976; Coppola, 1986; Drickamer, 1986). Actual testing of the individual hypotheses for individual species, such as cane mice, requires additional information from the laboratory and the field. The important point here is that one or more of these hypotheses could apply to virtually any species of mammal. Thus, these hypotheses provide a theoretical framework that may account for the large number of species in which social cues have been shown to modify reproductive development (reviewed by Drickamer, 1986; Vandenbergh, 1989; Bronson, 1989). Our study was prompted by observations that suggested that the cane mouse might be an exception to this generality. However, reproductive development in this aseasonally reproducing, reproductively precocial, tropical species can be affected markedly by social cues. This finding supports the hypothesis that social cues play a fundamental role in the regulation of reproductive development of mammals, and suggests that species in which social cues are unimportant may be extremely unusual.

We do not know of any mammalian species in which social cues from adult conspecifics have been demonstrated not to have a role in regulating rates of reproductive maturation. This may be related simply to the difficulty of demonstrating unresponsiveness and then publishing the negative data, but it may also reflect the ubiquity of the phenomena among mammals. It is possible that conditions that favour the evolution of a tendency in young females to ignore social cues in reproductive development are uncommon in mammals. There are five conditions that would favour individuals that ignored social cues: synchronizing reproduction with other individuals socially provides no increase in fitness (for example, if reproduction is strictly aseasonal and asynchronous, or if environmental cues such as the photoperiod synchronize reproduction); females have no difficulty encountering potential mates, and hence gain no advantage from delaying maturation until contact with a mate; insemination is the sole contribution required for successful reproduction (i.e. other resources contributed by a male, including male parental care, are unnecessary); female reproductive success is not increased by suppressing reproduction in the presence of adult conspecifics (for example, there is no harassment by older females, nor are young females more likely to lose any competition for scarce resources); and inbreeding from father-daughter matings is either unlikely or is not disadvantageous. Unless all of these conditions are met, natural selection might favour the use of social cues to modify the timing of reproductive maturity. Previous work on cane mice supported the first condition and suggested that the second and third were likely as well, but the last two conditions may not hold for cane mice. Species for which all of these conditions are met may be rare. However, we suggest that a search for species in which social cues clearly do not affect reproductive development would allow better characterization of the potential selective advantages of these phenomena, and would improve our understanding of the conditions favouring their evolution and retention.

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