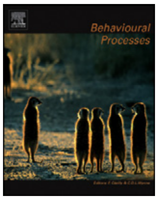
Behavioural Processes 82 (2009) 119–125

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Do male house mice (*Mus musculus*) discriminate between females that differ in nutritional status?

Aron Keith Costello*, Joshua David Pultorak[1], Douglas Bradford Meikle

Department of Zoology, Miami University, Oxford, OH 45056-1400, USA

ARTICLE INFO

Article history:
Received 6 February 2009
Received in revised form 11 May 2009
Accepted 17 May 2009

Keywords:
Body weight
Female traits
Male preference
Mate choice
Mice
Nutritional status
Sexual selection

ABSTRACT

Most studies of mate choice have focused on female preference for male traits because it is generally assumed that since males provide less parental investment they are not choosy. However, if males suffer missed opportunity costs by mating with lower quality females, selection should favor males with the ability to discriminate among females. We tested the hypothesis that male house mice (*Mus musculus)* discriminate between females that differ in nutritional status (non-food-deprived versus food-deprived). We recorded the time males spent investigating either type of female and used that to determine preference (spending $\geq$55% of their total investigation time with one female). We also examined the effects of female nutritional status and female preference status (preferred versus non-preferred) on the reproductive success of males. Males did not display a preference for non-food-deprived females nor did their reproductive success vary with nutritional status or preference status of females. Interestingly, males spent more time investigating females that were closest to the male's own weight. In addition, pairs that were closer in weight were more likely to produce a litter. These results suggest that male house mice are capable of discriminating among females and that such discrimination may influence their reproductive success.

1. Introduction

In most mammal species, males and females typically provide different amounts of parental investment (PI) and this difference has been hypothesized to play a primary role in the evolution of different mating strategies between the sexes (Bateman, 1948; Trivers, 1972). In general, there is competition among individuals of the sex that provides less PI for access to the sex that provides more PI (Trivers, 1972). Males usually provide less PI and have evolved characteristics that increase their likelihood of gaining access to females (Cunningham and Birkhead, 1998; Qvarnström and Forsgren, 1998), while females usually provide more PI and have evolved characteristics that may enable them to assess the quality of potential mates (Bateman, 1948; Andersson, 1994). Since the lifetime reproductive success of females depends, in large part, on the quality of their mates, the majority of studies have focused on female mate choice (e.g., Lenington, 1983; Shapiro et al., 1986; Coopersmith and Lenington, 1992; Eklund, 1998; Drickamer et al., 2000; Ehman and Scott, 2002; Kavaliers et al., 2003; Spritzer et al., 2005).

In promiscuous species, in which males contribute very little PI (e.g., *Mus musculus*), it is generally assumed that males do not discriminate among females (Parker and Simmons, 1996; Cunningham and Birkhead, 1998). However, if there is variation among females based on their quality (e.g., nutritional status) there may be the possibility for males to suffer a missed opportunity cost (i.e., missing the opportunity to mate with a potentially higher quality female). If males mate with lower quality females then they may miss the opportunity to mate with higher quality females due to costs associated with producing ejaculate (Dewsbury, 1982) and because females are also promiscuous (Potts et al., 1991; Dean et al., 2006; Firman and Simmons, 2008). Potts et al. (1991) found that in seminatural enclosures 52% of litters resulted from females mating with males outside of their social mate's territory and Dean et al. (2006) reported that 20% of wild-caught litters showed evidence of multiple paternity. These results indicate that females are also promiscuous and suggest that males that choose to mate with one female may lose the opportunity to mate with another potentially higher quality female. Therefore, selection should favor males with the ability to discriminate among females based on their attractiveness as potential mates (Altmann, 1997). A few studies have shown that male rodents can discriminate among females based on estrous state (e.g., Taylor and Dewsbury, 1990), mating history (e.g., Ferguson et al., 1986), quality of diet (e.g., Ferkin et al., 1997), nutritional status (e.g., Pierce et al., 2005), infection status (e.g., Kavaliers and Colwell, 1993, 1995; Gourbal and Gabrion, 2004), MHC alleles

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* Corresponding author.

E-mail addresses: costelak@muohio.edu (A.K. Costello), pultorak@wisc.edu (J.D. Pultorak), meikled@muohio.edu (D.B. Meikle).

[1] Present address: Department of Zoology, University of Wisconsin-Madison, WI 53706, USA.

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doi:10.1016/j.beproc.2009.05.001

(e.g., Yamazaki et al., 1978; Egid and Brown, 1989; Potts et al., 1991) and genetic compatibility (e.g., Ryan and Altmann, 2001). Therefore, males that discriminate among females may have a greater lifetime reproductive success than males that do not discriminate.

Gowaty et al. (2003) reported that male house mice (*M. musculus*) mated to their preferred (P) females sired more litters and produced more viable offspring than males mated with their non-preferred (NP) females. The results of Gowaty et al. (2003) suggest that males show preferences for females and those preferences may affect the reproductive success of males, however, the characteristics of females on which males based their preferences were not examined. The goal of our study was to determine whether male *M. musculus* show preferences for females based on their nutritional status and whether female nutritional status influences the reproductive success (RS) of males.

Nutritional status and diet quality have been reported to affect characteristics associated with mate choice in a number of taxa including birds (e.g., Ohlsson et al., 2003), fish (e.g., Fisher and Rosenthal, 2006) and arthropods (e.g., Kvarnemo and Simmons, 1999). A few studies have reported that diet quality influences preference for odors of potential mates (e.g., Walkden-Brown et al., 1994). Diet quality has also been shown to influence life history characteristics of mammals (e.g., Rissman and Johnston, 1986) and male and female mate choice (e.g., in meadow voles by Ferkin et al., 1997).

Reproduction in small mammals is a very energetically demanding process and when there is not a sufficient quantity or quality of food the reproductive physiology and sexual behavior of females may be negatively impacted (e.g., Wade and Schneider, 1992; Wade et al., 1996; Temple et al., 2002; Schneider, 2004; Wade and Jones, 2004; Pierce et al., 2007). Food-deprived female rodents have been found to have lower gonadal steroid and estradiol concentrations (e.g., Wade et al., 1996; Kauffman and Rissman, 2004; Temple and Rissman, 2000), and interrupted estrous cycles and lower rates of lordosis (e.g., Wade and Schneider, 1992; Wade et al., 1996). Pierce et al. (2005) reported that 6–24 h of food-deprivation inhibited attractivity, proceptivity and receptivity of female meadow voles and males spent more time investigating the anogenital odors of females that were fed *ad libitum* than females that were food-deprived.

Food availability can not only alter the reproductive physiology and sexual behavior of females, but if quantity or quality of food is lower during gestation it may negatively impact developing offspring. Since poor nutritional status can negatively affect females in several ways, it can also have a negative impact on the RS of males that mate with them (Meikle and Drickamer, 1986; Drickamer and Meikle, 1988; Wright et al., 1988; Krackow, 1993; Meikle et al., 1995; Yakovleva et al., 1997; Meikle and Westberg, 2001a,b). In a study using house mice, Meikle and Westberg (2001a) reported that sons of mothers that were food-deprived during gestation weighed less, on average, than sons of non-food-deprived mothers (i.e., fed *ad libitum*), and Krackow (1993) reported a positive relationship between the weight of males at weaning and their reproductive success. Meikle and Westberg (2001a) also reported that sons of mothers that were food-deprived were subordinate in agonistic encounters, and had lighter vesicular-coagulating gland complexes and preputial glands than did sons of non-food-deprived mothers. Furthermore, daughters of food-deprived mothers weaned fewer pups in their second litter than did daughters of non-food-deprived mothers (Meikle and Westberg, 2001b). Sons of food-deprived females were less attractive to females than were sons of non-food-deprived mothers (Meikle et al., 1995).

Characteristics of non-food-deprived females may indicate to males that those females have access to food sources and thus may be able to devote more and better maternal care to offspring than food-deprived females. If males were to mate with food-deprived females they may have a lower RS than males that mated with non-food-deprived females, therefore non-food-deprived females may be more attractive to males than food-deprived females.

Since food-deprived *M. musculus* females produce sons and daughters of poorer quality than do females that have not been food-deprived, we tested the hypothesis that males have evolved a predisposition to mate with well-nourished females because the reproductive success of males is influenced by the nutritional status of their mates. First, we predicted that males should prefer non-food-deprived (NFD) females to food-deprived (FD) females. Second, we predicted that males that are paired with NFD females should have a higher RS (produce a litter and have more or heavier offspring at birth and weaning) than males that are paired with FD females. Third, if prediction two is not supported, we predict that males paired with preferred females (regardless of nutritional status) should have a greater RS than males paired with non-preferred females (Gowaty et al., 2003). Since the weight of some female rodents influences their RS (Wauters and Dhondt, 1989), our fourth prediction was that males should spend more time investigating relatively heavier females (most likely NFD) than relatively lighter females (most likely FD).

2. Materials and methods

2.1. Subjects

During fall, 2005, a colony of house mice was established by systematically out-breeding mice captured from three sites in Butler County, Ohio ($n = 63$). Breeding pairs were established by pairing one male and one female in a cage (15 cm × 29 cm × 17 cm) for 10–14 days. The coefficient of relatedness among all breeding pairs was <0.125. In January 2007 additional wild-caught mice ($n = 20$) from two sites in Butler County, Ohio, were added to the colony. All mice were housed in standard polycarbonate cages with stainless steel lids. Each cage contained Cell-sorb Plus bedding (Fangman Specialties Inc., Cincinnati, Ohio) and one cotton square (Nestlet; Ancare Corp.,Waupaca, Wisconsin). The colony rooms were maintained at 18–23 °C and 20–70% relative humidity with a 14:10 light:dark cycle (lights on at 08:00). Unless otherwise noted, water and food (LabDiet® no. 5010; PMI Nutrition, LLC, Brentwood, Missouri) were provided *ad libitum*.

We conducted 73 male preference trials from May to June 2007 by randomly selecting 73 males and 108 females from the colony. All mice were weaned at 24 days. Males were housed individually and the majority of females were housed in sister pairs (86.5%). The remaining 13.5% ($n = 13$) were housed individually and were balanced between the two treatment groups: non-food-deprived ($n = 6$) and food-deprived ($n = 7$). At the time of the trials, all males and females were sexually naive and were 77–122 days old ($\text{females}: \bar{x} \pm \text{SE} = 94 \pm 1.3\,\text{d};\ \text{males}: \ 94 \pm 1.8\,\text{d}$). The average difference in the age of females used during the same preference trial was 4.1 days.

2.2. Male preference

The preference apparatus (61 cm × 30 cm × 44 cm) was constructed using Lexan® that was completely surrounded by opaque material. In addition, all trials were conducted under red light during which an infrared camcorder recorded a top-down view. The apparatus consisted of two outer compartments (A and B; 23 cm × 20 cm), each containing a female held in a wire mesh cage (Fig. 1). Compartments A and B were separated by a 15 cm × 20 cm × 44 cm opaque Lexan® box, which the focal male could not enter. The remaining area of the apparatus (61 cm × 10 cm) allowed males access to both females (Fig. 1).