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Costs of pair-bonding and paternal care in male prairie voles (*Microtus ochrogaster*)

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ABSTRACT

The direct costs of paternal care are relatively well documented in primates, however little research has explored these effects in monogamous rodents. The present study examines the long-term effects that pairing and parenting have on male prairie voles. We hypothesized that there would be a significant weight loss over the course of pairing and parenting, presumably from the energetic demands that accompany these changes in social condition. In a longitudinal study, we followed ten male prairie voles through being housed with their brother; paired with a female; and caring for three consecutive litters. We found a significant drop in bodyweight across time, with maximum weight loss near the weaning of the first litter. At that same time, feeding increased, leading to possible recovery in weight; however, leptin levels dropped precipitously across time and did not recover. Corticosterone did not change significantly across time points, and overall activity levels also did not vary significantly over the course of the study. In addition, newly paired males showed a significant increase in preference for a 2% sucrose solution during a three-hour test, indicating a metabolic need for more calories. A cross-sectional study confirmed leptin and corticosterone findings, and showed significant loss of subcutaneous (inguinal) fat in males that had cared for a litter of pups, when compared to males housed with their brothers or newly paired males. These results suggest that cohabitation with a female, and caring for pups, all have costs for male prairie voles.

1. Introduction

Monogamous mammals display a suite of behaviors, including pair-bonding, intrasexual aggression, and parental care by fathers [1–3]. Paternal care in monogamous rodents includes direct behaviors, such as caring for the offspring through huddling, retrieving to the nest and grooming, and indirect behaviors, such as ensuring the continued investment of the female in her litter. Consequently, paternal care in monogamous rodents is often crucial, or at least beneficial, for survival of the offspring [4,5]. In prairie voles (*Microtus ochrogaster*), fathers display a suite of parental behaviors very similar to mothers [6]. In addition, females may lose pregnancies if their mates are not present [7], pups with both parents are left alone in the nest less often [8], and pups in groups with more adults have higher survivorship [9]. In studies of prairie voles where direct benefits of father presence were *not* found, authors have suggested that environmental conditions were not particularly challenging [8,10]. However, there are still presumably energetic costs associated with the parental care given by fathers, just as there are for mothers [11,12]. It is intriguing that wild, adult male prairie voles have higher survivorship when living singly than when living in male–female pairs, which suggests a possible survivorship consequence of pairing and parenting [10].

Food availability is clearly one of the primary factors limiting reproduction in both males and females. Gestation, lactation and infant care are all energetically expensive [11], and males as well as females have shown reduced ability to reproduce when under food restriction [13,14]. The current "metabolic fuels" hypothesis [15,16], which is based on rat studies, suggests that effects of food availability on reproductive readiness and feeding behavior are more immediately reliant on glucose levels, rather than stored fat reserves. However, monogamous male rodents are in a fairly unusual situation for a male mammal. Once mated, female prairie voles may give birth every three weeks, given a successful postpartum estrus. Therefore, male prairie voles are constantly caring for infants and may more heavily rely on longer term energy reserves and a regulatory system that integrates long-term energy signals (e.g., leptin) in order to meet the demands of this important behavior.

Although there is little research on the costs associated with paternal care in monogamous rodents, this topic has been addressed in monogamous primates. Schradin and Anzenberger [17] found that both male and female common marmosets (*Callithrix jacchus*) had lower leaping ability while carrying infants, although the carriers did not lose weight during the period of infant care (thus the lessened leaping ability was presumably due to the extra weight of the infants). Both common marmoset and cotton-top tamarin (*Saguinus oedipus*)

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males gained significant amounts of weight prior to the birth of their infants, presumably to prepare for the energetic demands of carrying [18]. Male cotton-top tamarins lost up to 11.3% of their pre-birth weight during the carrying of their offspring or non-littermate infant siblings [19]. In cotton-top tamarins, there was also a correlation between weight lost and time spent carrying the infant, with those animals that provide the most care losing the most weight [20]. In male fat-tailed dwarf lemurs (*Cheirogaleus medius*), which are also socially monogamous, fathers tended to have less stored fat in their tails than non-fathers during the period of infant care [21].

Male canids also perform many paternal care behaviors which would appear to be energetically expensive (ex. regurgitation of food, provisioning of solid food to young), and presumably beneficial to young [22,23]; however there are also documented cases of single canids raising young successfully [24].

Although the energetic demands associated with investing in parental care might tax energy reserves, decreases in energy reserve might also result from reductions in energy intake. Infant care in primates has been shown to decrease time spent foraging for food, foraging efficiency (food gained per unit time), time locomoting, and time spent in social activities [25,26]. This effect on foraging is even more prominent in animal species that rely on crypticity to avoid predation versus animals with other anti-predation strategies [27]. In this study we sought to explore costs associated with long-term energy balance of male prairie voles of engaging in a pair bond and participating in infant care. Furthermore, we tested the hypothesis that changes in these behaviors were related to two metabolically important hormones, corticosterone and leptin.

Our overarching hypothesis was that paternal males, like mothers, would experience an energetic cost to raising infants and that this cost would be associated with indices of long-term energy balance. We predicted that throughout the process of pair-bonding and parenting, males would demonstrate higher metabolic needs (“costs”) than unpaired males. We hypothesized that as males underwent these changes in social behavior, body weight and fat reserves would drop and activity levels would increase. Plasma leptin might be expected to drop along with body weight; we included its analysis to give us information about whether or not weight loss was due to loss in fat reserves. Since sucrose is calorically dense and highly lipogenic, we also expected sucrose intake to increase during pairing and parenting as a possible response to increased metabolic need. The alternative hypothesis was that males, unlike females, do not experience sufficient costs of social behavior that reflect changes in any of these behavioral or energetic measures. We first addressed these questions in a longitudinal study in which we followed males through different social conditions. We followed up with a second, cross-sectional experiment, in which we examined whether or not losses in body weight and leptin levels observed in the longitudinal experiment might be due to losses in body fat. To our knowledge, this is the first time that these questions have been addressed in monogamous rodents.

2. Methods

2.1. Experiment I: Longitudinal study of effects of male pairing and parenting

2.1.1. Subjects

Subjects were ten laboratory-bred adult male prairie voles (*M. ochrogaster*), descended from a colony originally captured in Illinois. Subjects were housed with parents in large polycarbonate cages (44 cm long × 22 cm wide × 16 cm high) for the first 21 days after birth, and then housed with same sex siblings in standard mouse cages (27 cm long × 16 cm wide × 16 cm high) until being used for this study. All subjects were maintained on a 14 hour light:10 hour dark cycle, with lights on at 0600 and lights off at 2000 h. Voles were housed in a colony room with an average temperature of 68–72°. Cotton was provided as nesting material, and food (Purina high-fiber rabbit chow) and water were available *ad libitum* throughout the study. All procedures were approved and annually reviewed by the Institutional Animal Care and Use Committee of the University of California, Davis.

2.1.2. Treatments

Male prairie voles were removed from small polycarbonate cages and placed in a large breeder cage one month before the first data collection point to control for activity levels and weight fluctuations due to available space. During this time, they were housed with another male (either a sibling or unrelated male that they had been housed with since weaning). During this time, they were exposed to 2% sucrose dissolved in distilled water for 48 h in order to acclimate them to sucrose. For all ten males, data were collected at five time points: males housed with sibling, three days after being paired with a female, 17 days post-pairing and therefore before the birth of the first litter, 17 days after the birth of the first litter and therefore before the birth of the second litter, and 17 days after the birth of the second litter and therefore shortly before the birth of the third litter. The 17 day time point was chosen to represent a time point in which the majority of male investment had already gone into a litter, but which was not so close to the birth as to be disruptive (average days to first litter for voles in this colony, 29.9 ± 2.5 days; average days between litters, 24.1 ± 1.3 days; Stone and Bales, unpublished data). At each time point, there were three days of testing during which body weights were recorded, blood samples were taken, 24-hour activity levels were recorded, and males received a three-hour sucrose preference test.

2.1.3. Data collection

On the first day of testing for each time point, behavior was recorded for 24 h on time-lapse video. All members of the cage were placed in a clean cage with new bedding. The male was collared for identification on the video, and placed in the cage before the rest of the members of the cage. The video was later scored for motor behavior, feeding, and drinking behavior using Behavior Tracker 1.5 (www.behaviortracker.com). The tape was run for 24 h straight at a compression of 0.2 to 1. Activity levels were quantified by separating the cage into 4 sections, and quantifying the number of times the subject's front paws crossed into a new section. Durations of feeding and drinking behavior were also recorded. For the first 3 h of the tape, we also quantified social behaviors including nest-building, grooming, and huddling with the mate and/or offspring. Red lights were placed behind the cage so that during the dark period of the day behaviors may still be recorded on the video. Low intensity red light was used in order to avoid interfering with normal nighttime behavior and circadian rhythm as circadian responses to light appear to be highest in the middle of the color spectrum (Provencio and Foster, 1995). At the end of the 24 hour period the collar was removed, the males were weighed, placed back in the cage and the cage was placed back in the animal room until the next test.

On the second day of testing for each time point, each male received a sucrose preference test. A clear separator, with small holes to allow touch and social interaction, was placed between the male and other occupants in the cage (ex. female and offspring when present). However, only the male had access to the sucrose and water bottles on his side of the cage. The male was given two bottles, one containing 200 ml of distilled water, and the other containing 200 ml of 2% sucrose by weight in water. The subject was allowed to consume as much of either liquid as desired for 3 h, at which point the bottles and the cage divider were removed. The amount of each liquid consumed was recorded.

On the third day of testing at each time point, a blood sample (300 µl) was taken from each male via a supraorbital bleed. The vole