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Effect of testosterone and melatonin on social dominance and agonistic behavior in male *Tscheskia triton*

Dawei Wang[a,b], Jianxu Zhang[a,**], Zhibin Zhang[a,*]

[a] State Key Laboratory of Integrated Management of Pest Insects and Rodents in Agriculture, Institute of Zoology, Chinese Academy of Sciences, 1 Beichen West Road, Beijing 100101, China

[b] Key Laboratory of Integrated Pest Management in Crops, Ministry of Agriculture, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Yuanmingyuanxi Road, Beijing 100193, China

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ABSTRACT

Social dominance and agonistic behavior play important roles in animal societies. Melatonin and testosterone are closely related to social dominance and agonistic behavior in rodents, but interactions between both of them remain unknown. In this study we investigated the effects of testosterone and melatonin by manipulating photoperiod and castration on social dominance and agonistic behavior in male *Tscheskia triton*. Castration significantly decreases social dominance of both short- and long-day males, suggesting that testosterone benefits social dominance of males in both breeding and non-breeding seasons. In intact conditions, long-day males tended to dominate short-day males, suggesting that the effect of testosterone on social dominance was a little stronger than melatonin. However, castrated short-day males became dominant over their castrated long-day opponents meaning that high melatonin levels obviously benefit social dominance in males. Hormone implantation indicated that testosterone had no effect on non-breeding condition, but that melatonin was important during the breeding season. Our results indicate that both testosterone and melatonin are important in determining social dominance in male hamsters, and the effect of testosterone appears to be stronger than melatonin. Testosterone is responsible for aggression and social dominance in male hamsters during the breeding season, while melatonin regulates behavior during non-breeding, probably due to the different seasonal secretory patterns of the hormones.

1. Introduction

Agonistic behavior and social dominance play important roles in maintaining social stability in animal societies. Agonistic behavior is necessary for conspecifics to form social structures, for optimum population densities, and for territory and resource defense (Albers et al., 2002; Arregi et al., 2006). Social dominance is established and maintained via agonistic behavior; for example, aggressive behavior is usually observed in dominant animals and defensive and submissive behavior observed in subordinate individuals (Blanchard et al., 1993). The factors known to influence agonistic behavior and social dominance are numerous. Studies of rodents have tended to focus on photoperiod and hormones linked to photoperiod, such as gonadal hormones and melatonin in rats (van de Poll et al., 1986), mice (Compaan et al., 1992; Edwards, 1969; Kriegsfeld and Nelson, 1998; Kudryavtseva et al., 2004; Oyegbile and Marler, 2005), hamsters (Demas et al., 2004; Jasnow et al., 2000, 2002), gerbils (Christianson et al., 1972; Razzoli et al., 2003) and voles (Bowler et al., 2002; Demas et al., 1999; West and Dublin, 1984).

Photoperiod is viewed as the most important proximate factor used by seasonally breeding nontropical rodents to predict seasonal shifts and to mediate social behaviors such as agonistic behavior and social interactions (Albers et al., 2002; Nelson et al., 1990). Seasonal changes in behavior are complex and different across species. For example, short days (non-breeding condition) increases aggression in male solitary Syrian hamsters (*Mesocricetus auratus*) (Jasnow et al., 2002; Garrett and Campbell, 1980) and Siberian hamsters (*Phodopus sungorus*) (Jasnow et al., 2000) possibly to aid in food and burrow guarding, but decreases aggression in social voles during winter to avoid wasting energy (West and Dublin, 1984). Studies into mechanisms behind the effect of

* Corresponding author at: State Key Laboratory of Integrated Management of Pest Insects and Rodents in Agriculture, Institute of Zoology, Chinese Academy of Sciences, 1 Beichen West Road, Chaoyang District, Beijing 100101, China.
Tel.: +86 10 64807096; fax: +86 10 64807099.
** Corresponding author at: State Key Laboratory of Integrated Management of Pest Insects and Rodents in Agriculture, Institute of Zoology, Chinese Academy of Sciences, 1 Beichen West Road, Chaoyang District, Beijing 100101, China.
Tel.: +86 10 64807206; fax: +86 10 64807896.
E-mail addresses: zhangjx@ioz.ac.cn (J. Zhang), zhangzb@ioz.ac.cn (Z. Zhang).

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photoperiod have focused on physiological factors such as testosterone and melatonin which also display annual cycles and seasonal variation (Albers et al., 2002; Badura and Nunez, 1989; Nelson et al., 1990; Schultz and Kay, 2003).

Testosterone is produced in the testes, is involved in spermatogenesis and reproductive behavior, and affects male agonistic behavior and social dominance in many rodents (Campbell et al., 1978; Morin and Zucker, 1978; Siegel, 1985). Male aggression and social dominance are positively correlated with testosterone levels, weakened by castration and restored by testosterone replacement in rats (*Rattus norvegicus*) and house mice (*Mus musculus*) (Brain and Haug, 1992; Compaan et al., 1992; Edwards, 1969; van de Poll et al., 1986). However, exceptions have been reported in wild seasonal breeding rodents. For example, castration does not decrease male aggression in Mongolian gerbils (*Meriones unguiculatus*) (Christianson et al., 1972) and prairie voles (*Microtus ochrogaster*) (Demas et al., 1999). Short-day conditions do not affect aggression in dusky footed wood rats (*Neotoma fuscipes*) (Caldwell et al., 1984), and even elevate aggression in Syrian and Siberian hamsters in spite of testicle regression and testosterone decline (Jasnow et al., 2000, 2002; Garrett and Campbell, 1980). Furthermore, higher testosterone replacement did not result in increased aggression in male Syrian hamsters (Romeo et al., 2003). These studies suggest that the relationship between testosterone, aggression and social dominance varies between species.

Melatonin, secreted by the pineal gland, is considered one of the triggers of seasonal physiological change in animals (Challet, 2007; Schultz and Kay, 2003). Melatonin is produced during darkness and reaches high levels at night. High levels of melatonin are maintained longer under short-day (winter) conditions, leading to many physiological changes such as "winter-like" conditioning in rodents and gonadal regression (Hazlerigg and Wagner, 2006; Jasnow et al., 2000, 2002). Melatonin has been found to promote aggression in several nocturnal rodent species such as house mice (Paterson and Vickers, 1981), Syrian hamsters (Jasnow et al., 2002) and Siberian hamsters (Demas et al., 2004). The removal of the pineal gland inhibits aggression in mice and female Syrian hamsters (Paterson and Vickers, 1981; Fleming et al., 1988); however, little is known how melatonin impacts upon male aggression and social dominance in wild rodents (currently only reported in the Syrian and Siberian hamsters, Jasnow et al., 2000, 2002). In seasonally breeding mammals, testosterone and melatonin may interact to determine social dominance patterns. In long-day photoperiod conditions (e.g. breeding seasons), the testosterone level should be high and melatonin level low, and vice versa during short-photoperiod conditions. Although the independent effects of these two components on social dominance have been investigated, their interactive effects remain unknown.

The greater long-tailed hamster (*Tscheskia triton*) is a solitary and polygamous rodent widely distributed across farmlands of northern China (Yang et al., 1996; Zhang et al., 2001a,b). It breeds from May to September each year and obvious gonad regression occurs in the non-breeding season (Yang et al., 1996). Males possess a pair of flank glands and a midventral gland for chemical communication. Females are philopatric and do not display stable mating associations with males (Song et al., 2005; Zhang et al., 1992, 2001a,b). Hamsters exhibit high aggression in the breeding and non-breeding season and winner-loser relationships are formed quickly and determine later dominant-subordinate relationships during male social interactions (Wang et al., 2006, 2009; Zhang et al., 2001b). Therefore, dominant or subordinate status in this species can be represented by the outcome of one social encounter (Pan et al., 2010). Our previous research found that the testes and testosterone is important for male aggression and dominance during the breeding season: castration reduces aggression and makes males subordinate, but testosterone replacement restores high aggression and elevates social rank (Zhang et al., 2001a). However, during the non-breeding season, when the testes of males have atrophied, aggression levels remain constant among males, suggesting that aggression is independent of testosterone and that other factors are responsible for these behaviors during times of non-breeding (Zhang et al., 2001b). Based on the literature we posited that testosterone may be responsible for the maintenance of aggression in male greater long-tailed hamsters during the breeding season and melatonin responsible during the non-breeding season. In addition, though melatonin and castration can affect aggression, their interactive effects on social dominance are unknown. Therefore, the purpose of this study was to test how testosterone and melatonin independently and interactively affect agnostic behavior and social dominance in male greater long-tailed hamsters.

2. Materials and methods

2.1. Animals and housing conditions

Forty healthy adult greater long-tailed hamsters (>120 g) were captured in farmlands around Beijing using live-traps made of wire mesh baited with peanuts in April 2006. Hamsters were housed individually in stainless steel cages (20 cm × 20 cm × 20 cm) containing cotton nesting material for three months prior to behavioral tests to habituate to the laboratory. The room was maintained at 20 ± 2 °C with a reverse light/dark cycle. Males were housed under natural photoperiod until the beginning of experiments. Food and water were provided ad libitum. All procedures complied with guidelines for animal use and care as required by the Institute of Zoology, Chinese Academy of Sciences.

2.2. Surgical procedures

Hamsters were anesthetized deeply using sodium pentobarbital (male: 60 mg/kg). Castration was performed through bilateral scrotum incisions, the testicles were removed and the abdominal wall and incisions were closed with sutures. Hormone capsules were made from 15 mm Silastic tubing (China Medical, o.d. 2.70 mm, i.d. 2.26 mm), which was packed with 10 mm lengths of crystalline testosterone, melatonin (Sigma, St. Louis) and sealed with 2.5 mm lengths of Medical Adhesive Silicone Type A (Dow Corning) at both ends. Capsules were implanted subcutaneously in the dorsal area of the waist. The wound was sutured with sterile sutures and treated with 75% alcohol and 2% tincture of iodine.

2.3. Experimental design

Males were randomly assigned to one of two groups and housed under a short-day (n = 20, light/dark 8:16, lights on 0000 h) or long-day photoperiod (n = 20, light/dark 16:8, lights on 1600 h). Half of the animals assigned to each photoperiod were castrated. Then, all experimental hamsters were divided into four groups: long-day intact, long-day castrated, short-day intact and short-day castrated males. Castration is known to reduce testosterone in male animals, and melatonin levels are lower under short photoperiod conditions and higher in long photoperiod conditions (Jasnow et al., 2000, 2002). Thus, castration and photoperiod manipulations help us to identify the independent and interactive effects of testosterone and melatonin on social dominance in male hamsters.

2.3.1. Experiment 1: effect of testosterone on male dominance under high or low melatonin conditions

The goal of this experiment was to test the effects of testosterone on behaviors of hamsters by observing contests between