Hormones and Behavior 60 (2011) 666–675

Contents lists available at SciVerse ScienceDirect

Hormones and Behavior

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

Acute effects of corticosterone injection on paternal behavior in California mouse (*Peromyscus californicus*) fathers

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ARTICLE INFO

Article history:
Received 1 July 2011
Revised 3 September 2011
Accepted 6 September 2011
Available online 14 September 2011

Keywords:
Corticosterone
California mice
Peromyscus
Paternal care
Acute
HPA
Stress
Glucocorticoid
Body mass
Trade-off

ABSTRACT

Glucocorticoids are thought to mediate the disruption of parental behavior in response to acute and chronic stress. Previous research supports their role in chronic stress; however, no study has experimentally tested the effects of acute glucocorticoid elevation on paternal behavior. We tested the prediction that acute corticosterone (CORT) increases would decrease paternal behavior in California mouse fathers and would lead to longer-term effects on reproductive success, as even short-term increases in CORT have been shown to produce lasting effects on the hypothalamic-pituitary-adrenal axis. First-time fathers were injected with 30 mg/kg CORT, 60 mg/kg CORT or vehicle, or left unmanipulated. Interactions between the male and its pup(s) were recorded 1.5–2 h after injection and scored for paternal and non-paternal behavior. Treatment groups were combined into control (unmanipulated + vehicle, n = 15) and CORT (30 mg/kg + 60 mg/kg, n = 16) for analysis based on resulting plasma CORT concentrations. CORT treatment did not alter paternal or non-paternal behaviors or any long-term measures (male body mass or temperature, pup growth rate, pup survival, interbirth interval, number or mass of pups born in the second litter). Fathers showed a significant rise in body mass at day 30 postpartum, followed by a decrease in body mass after the birth of the second litter; however, this pattern did not differ between the CORT and control groups. In summary, acute elevation of plasma CORT did not alter direct paternal behavior, body mass, or reproductive outcomes, suggesting that acute CORT elevation alone does not overtly disrupt paternal care in this biparental mammal.

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Introduction

The glucocorticoids, steroid hormone end-products of the hypothalamic-pituitary-adrenal (HPA) axis, play a major role in mediating the physiological and behavioral changes that occur in response to stressors. These hormones, which include cortisol and corticosterone, are known to affect multiple homeostatic and organismic systems (e.g., blood glucose levels, mood, cognition, metabolism; McEwen, 2005; Sapolsky et al., 2000) as well as several types of behavior, including reproductive behavior (both sexual and parental; see Wingfield and Sapolsky, 2003 for a review). Therefore, numerous authors have hypothesized that increased glucocorticoid concentrations in response to stress, both acute and chronic, may signal parents to invest in themselves over their offspring, thus mediating the trade-off between self-maintenance and reproduction (Breuner and Hahn, 2003; Ricklefs and Wikelski, 2002; Wasser and Barash, 1983; Wingfield and Sapolsky, 2003; Wingfield et al., 1998). Under adverse and energetically challenging ecological or organismic circumstances, decreasing investment in offspring might increase a parent's chances of survival and its lifetime reproductive success at the expense of current reproductive effort (Breuner and Hahn, 2003; Silverin, 1986, 1998; Wingfield and Sapolsky, 2003; Wingfield et al., 1998).

Experiments designed to test the effects of glucocorticoids on parental behavior have typically utilized chronic stress or chronic glucocorticoid manipulation. Findings from these studies suggest that chronic stress can negatively impact parental care and that this effect is mediated, at least in part, by persistent increases in glucocorticoid concentrations. Effects of chronic glucocorticoid implantation on parental behavior by both mothers and fathers (maternal and paternal care) have been studied most extensively in birds. Data from the avian literature indicate that prolonged circulation of high glucocorticoid concentrations results in decreased parental effort (Breuner et al., 2008). For example, glucocorticoid implantation in mothers and/or fathers in several species led to decreased time on the nest (Kitaysky et al., 2001), less time spent in the territory (Breuner and Hahn, 2003), decreased feeding of young and/or nest abandonment (Silverin, 1986, 1998; Spée et al., 2011). For mammalian species no data are available on the effects of chronic stress or glucocorticoid elevation in fathers; however, studies of female mammals have yielded similar findings to those obtained in birds. Data from female rats (*Rattus norvegicus*), for example, suggest that various forms of chronic stress, such as wet bedding and forced foraging (Léonhardt et al., 2007) or decreased nesting material (Ivy et al., 2008), can decrease maternal behavior. As in birds, this effect appears to be mediated, at

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doi:10.1016/j.yhbeh.2011.09.001

least in part, by chronic glucocorticoid elevations. For example, repeated injection of synthetic glucocorticoid in common marmoset (*Callithrix jacchus*) mothers caused mothers to carry their infants less than vehicle-injected mothers (Saltzman and Abbott, 2009).

Much less is known about the effects of acute stress or glucocorticoid manipulation on parental behavior: very few studies have investigated this relationship in mothers, and to date no studies have been conducted on fathers. Acute stressors have been shown to disrupt maternal behavior in female rats (Roth and Sullivan, 2005; Sukikara et al., 2010; Yamada et al., 2002) and pigtail macaques (*Macaca nemestrina*; Maestripieri and Carroll, 1998). The mechanism by which this occurs is not known, but glucocorticoids are a likely candidate.

In a recent review of the trade-off between self-maintenance and reproduction under stressful conditions, Breuner et al. (2008) emphasized the need for more data on acute manipulations. They argued that drawing an ecologically relevant line between what constitutes acute vs. chronic stress in a free-living organism can be difficult, and that an acute paradigm more closely mimics natural stress reactivity (Breuner et al., 2008). They further suggested that future studies should include more direct measurements of reproductive output and survival combined with manipulation of acute glucocorticoid elevation, as "exogenous glucocorticoid treatment should be one of the best ways to test relationships between acute stress reactivity and performance measures" (Breuner et al., 2008, p. 293), and should more directly test for a trade-off between self-maintenance and reproductive effort/outcome in the face of stress.

In this study, therefore, we aimed to 1) experimentally determine the effects of acute glucocorticoid elevation on parental behavior, separate from effects of acute stress, and 2) measure any possible longer-lasting fitness effects. Due to the lack of data on male mammals, and because paternal care is practiced by 6–10% of mammalian species, including humans (Kleiman and Malcolm, 1981), and can be important for survival and development of offspring (e.g., Ovtscharoff et al., 2006; Piovanotti and Vieira, 2004; Schradin and Pillay, 2004), we chose to manipulate glucocorticoid levels in first-time fathers of the monogamous, biparental California mouse (*Peromyscus californicus*). In this species, care by both parents maximizes offspring survival, accelerates offspring development, and increases parents' reproductive success both in the lab and in the field, especially under challenging conditions (Bester-Meredith and Marler, 2001; Bredy et al., 2004; Cantoni and Brown, 1997a,b; Dudley, 1974; Frazier et al., 2006; Gubernick and Teferi, 2000; Gubernick et al., 1993; Wright and Brown, 2002). Therefore, if parental care by either the mother or the father is disrupted, decreases in offspring quality and survival, as well as in parental fitness, are likely to occur.

To determine the effects of acute glucocorticoid elevation we injected corticosterone (CORT) or vehicle, or performed no manipulations, in first-time California mouse fathers, and characterized the acute effects on paternal care and general activity. In order to quantify possible longer-term fitness effects of acute CORT treatment, we characterized changes in the male (body mass over time, body temperature), the female pairmate (interbirth interval, second litter size), and their offspring (body mass over time, survival to weaning). We chose these specific long-term measures because recent studies have suggested that even a single acute stressor can have persistent effects on the HPA axis (Lynn et al., 2010; Malisch et al., 2010), and CORT is known to exert metabolic effects that can be manifest as changes in body mass (Baxter, 1976; Strack et al., 1995). In addition, if CORT caused a reduction in male parental care, it is possible that the pups would grow more slowly, or that the female pairmate would compensate by investing more in care, possibly resulting in a longer interbirth interval or a decrease in the number of pups born in the second litter. This study, to our knowledge, is the first to experimentally test whether glucocorticoids inhibit paternal behavior in mammalian fathers, and to measure the effects of an acute increase in glucocorticoids in a male mammal on longer-term reproductive outcomes.

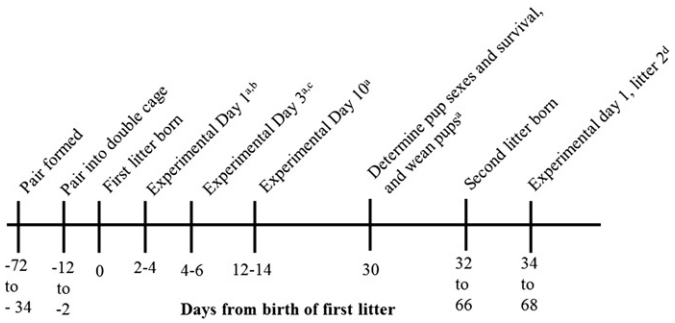
Methods

Animals

Mice were bred in our colony at the University of California, Riverside (UCR) and were descended from an original stock purchased in 2007 from the Peromyscus Genetic Stock Center, University of South Carolina (Columbia, SC). The colony was maintained on a 14:10 light:dark cycle, with lights on at 05:15 h and lights off at 19:15 h. Ambient temperature was approximately 23 °C with a humidity of about 65%. Mice were housed in standard shoe-box style, polycarbonate cages (44×24×20 cm) lined with aspen shavings; cotton wool was provided for nesting material. Food (Purina 5001 rodent chow) and water were provided *ad libitum*. Cages were cleaned once per week unless otherwise noted. In our colony, siblings are never mated with one another, and first-cousin matings are avoided whenever possible. Animals were weaned at 27–32 days of age (prior to the birth of younger siblings), ear-punched for individual identification, and housed in same-sex groups of 2–4 mice until they were pair-housed with a female for the experiment at 90–164 days of age (114.7 ± 3.4 days, mean ± SEM). Prior to the start of the experiment, beginning when animals were housed in male–female pairs, mice were weighed twice weekly to assess overall health and to detect pregnancy. UCR has full AAALAC accreditation, and all procedures were approved by the UCR IACUC and conducted in accordance with the *Guide for the Care and Use of Laboratory Animals*.

Design

The experimental design is summarized in Fig. 1. Beginning approximately 1 week prepartum, when the female showed steady weight gain (6–10 g), each pair was housed in a double cage consisting of two standard cages connected via clear plastic Crittertrail® tubing forming a z shape (35×5 cm). Animals had the opportunity to move freely between the two cages; both cages contained food, water, and aspen shavings, but initially only one side contained cotton wool. These cages allowed the male more behavioral options than standard housing (e.g., avoiding female and pups; Brown, 1993; Schradin, 2007). After each pair's first litter of pups was born, the male was randomly assigned to one of four conditions: high CORT (60 mg/kg; n = 8), low CORT (30 mg/kg; n = 8), vehicle (oil; n = 8), and unmanipulated controls (n = 7). CORT doses were based on a pilot study indicating that these low (30 mg/kg) and high (60 mg/kg) doses produced circulating CORT levels similar to the endogenous levels occurring during the circadian peak (1500–1800 ng/ml) or following acute stress exposure during lights-on (2200–2700 ng/ml) in this species, respectively (unpub. data). *P. californicus* is nocturnal, so lights-



[a]male and pup body mass, male body temp
[b]**DayE1**: injection or no manipulation (08:00h), behavioral tests, blood sample (10:00h)
[c]**DayE3**: injection or no manipulation (08:00h), blood sample (10:00h), transfer to single cage
[d]male and pup body mass

Fig. 1. Experimental timeline.

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