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Physiological and behavioural responses to weaning conflict in free-ranging primate infants

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Weaning, characterized by maternal reduction of resources, is both psychologically and energetically stressful to mammalian offspring. Despite the importance of physiology in this process, previous studies have reported only indirect measures of weaning stress from infants, because of the difficulties of collecting physiological measures from free-ranging mammalian infants. Here we present some of the first data on the relationship between weaning and energetic and psychological stress in infant mammals. We collected data on 47 free-ranging rhesus macaque infants on Cayo Santiago, Puerto Rico, showing that faecal glucocorticoid metabolite (fGCM) concentrations were directly related to the frequency of maternal rejection, with fGCM concentrations increasing as rates of rejection increased. Infants with higher fGCM concentrations also engaged in higher rates of mother following, and mother following was associated with increased time on the nipple, suggesting that infants that experienced greater weaning-related stress increased their efforts to maintain proximity and contact with their mothers. Infants experiencing more frequent rejection uttered more distress vocalizations when being rejected; however, there was no relationship between rates of distress vocalizations and fGCM concentrations, suggesting a disassociation between behavioural and physiological stress responses to weaning. Elevated glucocorticoid concentrations during weaning may function to mobilize energy reserves and prepare the infant for continued maternal rejection and shortage of energetic resources.

According to parent–offspring conflict theory (Trivers, 1974), offspring should demand a disproportionate amount of parental resources for themselves rather than share them equally with their siblings. In contrast, parents are equally related to all their offspring and are therefore selected to invest their resources equally among offspring. As a result, there should be conflict between parent and offspring over the amount of parental investment as well as the duration of the investment period, with individual offspring being selected to demand more investment from their parents than their parents are selected to give (Trivers, 1974).

In nonhuman primates, as in many other mammals, maternal investment is mainly expressed through the production and transfer of milk and through energetically costly infant carrying (Maestripieri, 2002). In most species of anthropoid primate, mothers carry their infants continuously and provide unrestricted access to the nipple during the first few days of lactation. As infants grow older, maternal carrying and nursing are gradually reduced as the survival benefits to the infant decrease and the costs to the mother increase (baboons: Altmann & Samuels, 1992; macaques: Hinde, 1977; Hinde & Atkinson, 1970). However, across mammalian species there are clear benefits to the offspring in extending maternal investment such as increased body weight (e.g. piglets: Bøe, 1991; Jarvis et al., 2008; lambs: Watson & Gill, 1991; primates: Lee, Majluf, & Gordon, 1991; ungulates: Lee et al., 1991), decreased parasite load and increased immune function (e.g. lambs: Watson & Gill, 1991) and decreased infant mortality (e.g. vervet monkeys: Lee, 1984).

In primates, mother–infant behavioural conflict over time spent in contact and infant access to the nipples is observable throughout the first year of an infant's life (e.g. Hinde & Spencer-Booth, 1967, 1971; Maestripieri, 1994a), and weaning conflict is particularly intense when mothers resume cycling and mating (e.g. Berman,

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Rasmussen, & Suomi, 1993). Mothers reject their infants' attempts at making bodily contact or gaining access to their nipples, and infants respond with distress calls and temper tantrums and by increasing their attempts to maintain contact or proximity. Although weaning conflict is readily observed in many species of primates and other mammals (e.g. deer: Gauthier & Barrette, 1985; sheep: Berger, 1979; macaques: Maestripieri, 1994a; apes: Codner & Nadler, 1984), the direct consequences and physiological response to this conflict are rarely measured in infants.

The lack of data on the direct effects of weaning are unfortunate as maternal rejection is likely to induce both energetic and psychological stress in the infant. In reaction to a social or ecological stressor, mammals mount a multifaceted stress response across different physiological systems (Romero, Dickens, & Cyr, 2009), including an endocrine response via activation of the hypothalamic–pituitary–adrenal (HPA) axis and the sympathetic nervous system (SNS). Activation of the HPA axis and SNS causes the release of glucocorticoid hormones and catecholamines, which in turn promote responses necessary to respond to or escape from the stressor and reduce nonessential functions (McEwen, 2001; Sapolsky, Romero, & Munck, 2000). From a monkey infant's perspective, weaning conflict and denial of access to the food resources of the nipple are likely to be both an energetic and a psychosocial stressor. Therefore, examining changes in infant glucocorticoid hormone (GC) concentrations in response to maternal rejection is important to understand both the energetic and the psychological aspects of infant responses to weaning stress.

Glucocorticoids are essentially metabolic hormones. The release of GCs leads to a stimulatory and preparatory metabolic response by decreasing appetite and mobilizing energy stored in tissues, enabling an individual to cope with temporary food restriction (Sapolsky et al., 2000). In addition, GCs act in a preparatory manner by minimizing energy expenditure and increasing glycogen storage in the liver, readying an individual to cope with a continued lack of food (Sapolsky et al., 2000). Release of GCs in response to the deprivation of expected food (e.g. when an infant attempts to nurse but is prevented) can be characterized as an adaptive response that enables the body to deal with decreased resources and prepares it for the possibility that resources will be limited in the future. Although previous studies have examined the effect of prolonged mother–infant separation on GCs (e.g. piglets: Colson, Orgeur, Foury, & Mormède, 2006; Poletto, Steibel, Siegford, & Zanella, 2006; rhesus macaques: Gunnar, Gonzalez, Goodlin, & Levine, 1981; squirrel monkesy: Levine, Wiener, & Coe, 1993), infant GC response to naturally occurring maternal rejection behaviour as it occurs in real-time has yet to be quantified in any mammalian species.

In addition to shedding light on the functional, adaptive value of GCs on metabolism during the weaning period, studying and quantifying infant physiological stress in response to naturally occurring maternal rejection is important for understanding the psychological consequences of weaning. In nonhuman primates, infants sometimes display behavioural resistance to maternal rejection, such as screams or tantrums (e.g. baboons: Altmann, 1980; DeVore, 1963; langurs: Jay, 1963), and there are often strong individual differences in infant reaction to maternal rejection and separation (e.g. rhesus macaques: Hinde & Spencer-Booth, 1970). For example, some infants may show 'protest' or 'distress' in response to maternal separation or rejection and vocalize frequently (e.g. rhesus macaques: Berman et al., 1993; baboons; Altmann, 1980; DeVore, 1963; great apes: Codner & Nadler, 1984), while others may react with depression and not vocalize at all (e.g. rhesus macaques: Berman et al., 1993). Studies on captive squirrel monkeys in which infants were experimentally separated from their mothers reported that while infant vocalizations and behavioural agitation habituated over time or multiple separations, cortisol levels remained elevated, suggesting that behavioural and physiological indicators of stress sometimes operate on different timescales and thus do not always correlate (e.g. Hennessy, 1986; Levine et al., 1993). To understand the multiple ways in which infants are affected by a reduction in maternal resources, it is necessary to measure changes in both infant GC concentrations as well as infant behaviour across the period of peak mother–infant conflict.

In this study we investigated the relationship between naturally occurring maternal rejection behaviour and GCs in free-ranging infant rhesus macaques on the island of Cayo Santiago, Puerto Rico. We observed mother–infant pairs when infants were 5–12 months of age, encapsulating the period of peak weaning conflict (Hinde & Spencer-Booth, 1967; Maestripieri, 1994a), and measured faecal glucocorticoid metabolite (fGCM) concentrations as a proxy for circulating levels of GCs (e.g. Heistermann, Palme, & Gaswindt, 2006). fGCM concentration provides an integrated measure of adrenocortical activity (i.e. stress), allowing for analysis of a basal HPA axis activity (over a period of days), as opposed to acute HPA reactivity to stress assessed by measuring hormone concentrations in blood or saliva (over a period of minutes). Thus, our approach allowed us to examine weekly changes in GC concentration in response to weekly variation in behaviours and interactions.

We tested the hypothesis that maternal rejection is energetically and psychologically stressful, predicting that maternal rejection would be (1) accompanied by a GC response in infants, such that high rates of maternal rejection behaviours would be temporally associated with elevated concentrations of fGCMs and (2) associated with behavioural indicators of anxiety. To our knowledge, this is the first study to use noninvasive endocrine assessment to quantify real-time changes in GCs and infant behaviour in relation to maternal rejection during the weaning period in mammalian infants.

METHODS

This study was conducted on Cayo Santiago, a 15.2 ha island located 1 km off the east coast of Puerto Rico (Rawlins & Kessler, 1986). The Cayo Santiago colony contains approximately 1000 free-ranging rhesus macaques; macaques on Cayo Santiago are provisioned with monkey chow and rainwater, but also forage naturally on vegetation. Behavioural and physiological data were collected in Groups R and S, which contained approximately 250 and 115 individuals, respectively, at the time of data collection. Rhesus macaques are seasonal breeders (Gordon, 1981), with the majority of births on Cayo Santiago occurring between August and October (per Caribbean Primate Research Centre census records). Data were collected for the present study from March through August 2012 on infants born in the previous (2011) birth season. March–August encompasses the period of peak weaning conflict, as determined by infant age during this period (Maestripieri, 1994a; Hinde & Spencer-Booth, 1967).

Behavioural Data Collection

Infants were observed between 0700 and 1430 hours, 5 days a week, using continuous focal animal sampling (Altmann, 1974). Behavioural data were collected from 47 infants when the infants were approximately 5–12 months of age (27–56 weeks). Infants were observed for one 30 min period each week using a hand-held event recorder, the Psion Workabout (www.psionteklogix.com) loaded with 'Behaviour' software (Syscan International Inc., Montreal, Quebec). The order of focal animal sampling was randomized and behavioural data were converted into mean hourly frequencies (event behaviours) or mean hourly durations (state behaviours) for