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REVIEW ARTICLE

Emotions, Stress, and Maternal Motivation in Primates

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Recent research conducted with nonhuman primates confirms that adaptive emotional processes, such as maternal attraction arousability and maternal anxiety arousability, enhance and sustain female motivation to interact with infants, invest in them, and protect them during the postpartum period. Changes in these emotional processes, and concomitant changes in maternal motivation, facilitate the reduction and eventual termination of maternal investment associated with infant weaning. Although laboratory studies of rodents and socially deprived rhesus monkeys have suggested that nulliparous females are neophobic and find infant stimuli aversive, recent primate research indicates that neophobia or aversion to infant stimuli do not occur in females with normal developmental experience. Furthermore, although some rodent and human studies have shown that lactation is accompanied by physiological hyporesponsiveness to stress, other studies of rodents, nonhuman primates, and humans indicate that mothers are highly vulnerable to stress and that stress-induced dysregulation of emotions can interfere with maternal motivation and parenting behavior. It is possible that some aspects of the emotional and experiential regulation of maternal motivation and parental behavior are different in different mammalian species. However, variation in the environments in which subjects are tested and in their developmental experience may also be responsible for the some discrepancies between the results of different studies. Am. J. Primatol. 73:516–529, 2011. © 2010 Wiley-Liss, Inc.

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INTRODUCTION

Female parental care is the rule among the over 300 species of nonhuman primates, the exceptions being a few socially monogamous species in which fathers carry their infants. Social monogamy and paternal care are mainly concentrated among New World monkeys and associated with particular reproductive or ecological characteristics (e.g. the production of twins in marmosets and tamarins) [Snowdon & Suomi, 1982]. Among the Old World monkeys and the apes, females typically give birth to one infant at a time, feed their offspring with milk for 1 year or more, and in some cases continue investing in them for the rest of their lives with little or no contribution from males. During the period of infant dependence, maternal care manifests itself mainly as breastfeeding, carrying, and protecting the infant. Among great apes, mothers also play with their infants and share solid food with them. Primate maternal behavior is generally comparable, in terms of its basic characteristics, to that of many other mammalian species, although primate infants are generally carried more by their mothers than other mammalian young.

In mammalian species with a short life span (e.g. many rodents), first-time mothers exhibit a full repertoire of maternal behavior from the moment their offspring are born and are generally successful in raising their litters without any prior maternal experience. In fact, in some of these species, nulliparous females avoid any contact with other females' pups or kill them and cannibalize them, at least in the laboratory [e.g. Fleming & Orpen, 1986]. In rodents, maternal responsiveness and behavior are probably under relatively strong genetic control and are regulated by a combination of hormonal changes induced by pregnancy and lactation along with sensory stimulation from the offspring [e.g. Fleming & Orpen, 1986]. Unlike rodents, Old World monkeys, apes, and humans have relatively long life spans, and in these species, many aspects of maternal behavior depend, in part, on experience acquired during development. For example, nonhuman primate mothers need experience to learn how to carry their infants properly, to allow infants to maintain nipple contact long enough to obtain their necessary

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nourishment, to protect infants from unwanted attention from other conspecifics, and to encourage infant independence and weaning [e.g. Pryce, 1996].

In rhesus monkeys, newborn infants spend a great deal of time nursing or sleeping on their mother's chest. During this time, they are cradled and groomed by mothers. Mothers carry their infants while they travel for several months. During time devoted to resting or social activities, however, infants spend increasing amounts of time out of contact with their mothers, in order to explore the environment or to play with other infants. Mothers may restrict and control their infants' activities by physically restraining them and by making contact with them frequently. During the first few weeks of infant life, mothers are almost entirely responsible for maintaining contact and proximity with their infants. For example, infants tend to break contact and walk away from their mothers, while mothers follow them and reestablish contact. During the second or third month of infant life, however, responsibility for maintaining contact and proximity shifts to infants. Therefore, mothers frequently break contact and walk away from their infants, while infants follow their mothers and make contact with them. Mothers encourage their infants' independence by breaking contact with them frequently and physically rejecting their infants' attempts to make contact and gain access to the nipples. The frequency of maternal rejection increases steadily with infant age, peaking when infants are approximately 6 months old, when the mating season begins and mothers return into estrus.

Although these basic features of maternal behavior are observed in all rhesus monkey females, individual mothers differ greatly from one another in the frequency with which they cradle or groom their infants, make or break contact with them, or restrain or reject them. Individual differences in maternal behavior are consistent over time and across different infants. These differences are accounted for by sociodemographic characteristics of the mothers (e.g. their age, previous maternal experience, or dominance rank), those of their infants (e.g. age or sex), and those of the surrounding environment (e.g. availability of food, risk of predation, risk of aggression or infant kidnapping by other group members). Among the mothers' characteristics that affect their motivation to take care of their infants and the quality of their maternal care, their personality or temperament are very important. Emotional reactivity, in general, plays a fundamental role in the regulation of maternal behavior in mammals, and this is especially true for primates including humans [Dix, 1991; Maestripieri, 1999; Pryce, 1992]. Emotions can be powerful elicitors of maternal behavior and play a crucial role in mediating the impact of the surrounding environment on the mother–infant dyad. Adaptive emotional processes can enhance maternal motivation and facilitate the expression of adaptive behavior. Stress-induced dysregulation of emotions and their physiological substrates, however, can alter maternal motivation and cause maladaptive parenting behavior.

Pryce [1992] proposed a systems model of the regulation of maternal motivation in mammals, in which emotional processes play a central role (Fig. 1). The model was based mainly on research conducted with laboratory rats, sheep, and socially deprived rhesus monkeys. In this model, there are some inputs, some outputs, and some intermediary processes. The main inputs to the system are infant stimuli. The outputs are maternal motivation and maternal behavior. Crucial intermediary processes are previous maternal experience, female hormonal state, and an emotional system called maternal arousability. The maternal arousability system comprises four different subsystems: maternal attraction arousability, maternal anxiety arousability, maternal aversion arousability, and novelty-fear arousability. Attraction and anxiety arousability have positive influences on maternal motivation, whereas aversion arousability and novelty-fear arousability inhibit maternal motivation.

According to Pryce's model, immature mammalian females are exposed to infant stimuli before they are reproductively mature; they store these stimuli in memory and gain practical experience with them. Memory and experience of infant stimuli gained early in a female's life will facilitate the recognition of these stimuli later in life and enhance motivation to interact with them via the influence of positive arousability intermediary processes. Infant stimuli can be passive (e.g. visual or olfactory characteristics) or active (e.g. facial expressions, vocalizations, or motor behavior). When females reach puberty and conceive, hormonal changes during pregnancy and around the time of parturition enhance maternal motivation and facilitate the expression of maternal behavior. Maternal arousability is the most direct intermediary variable regulating maternal motivation and is itself regulated by three input factors: infant stimuli, previous experience, and neuroendocrine state.

The maternal attraction arousability subsystem processes passive, visual and olfactory stimuli and is enhanced by sensory recognition of the infant and by neuroendocrine changes occurring during pregnancy and parturition. These stimuli include the shape of infant faces, the configurations of their bodies, or their odors. These stimuli are attractive to females and serve as incentives for maternal motivation and behavior. The maternal anxiety arousability subsystem processes active, behavioral stimuli (e.g. some infant facial expressions and distress vocalizations, or infant-initiated separation from the mother) and is enhanced by sensory recognition of the offspring, classical conditioning between auditory and visual infant stimuli, and by neuroendocrine changes. These stimuli induce anxiety in the mother. Maternal

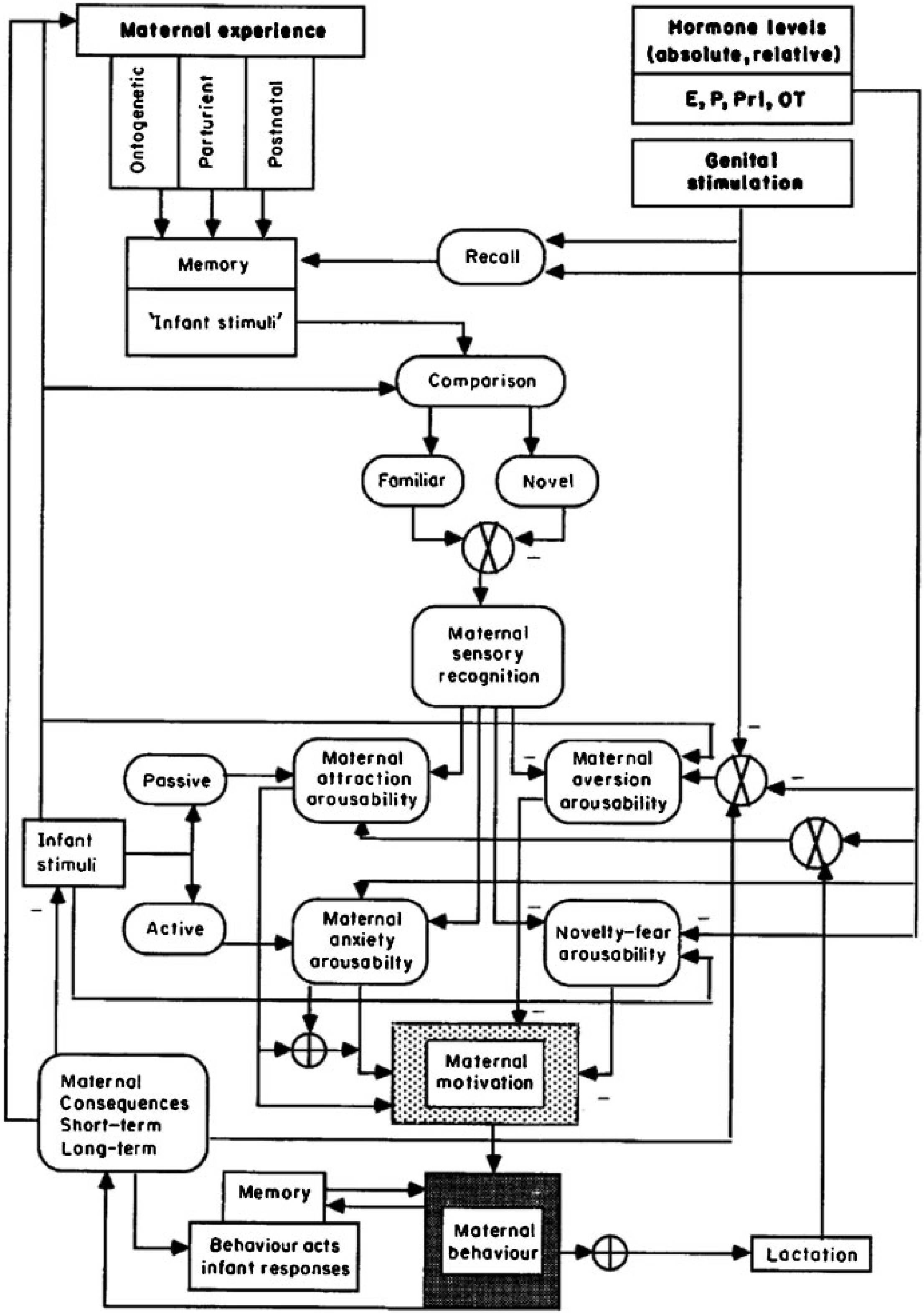

Fig. 1. Pryce's [1992] model of the regulation of maternal motivation in mammals. Figure reprinted with permission.

motivation is enhanced in an attempt to reduce anxiety. Thus, the maternal anxiety arousability subsystem is an example of homeostatic feedback.

Aversion and novelty-fear arousability reduce the overall level of maternal arousability and have an inhibitory effect on maternal motivation. Maternal aversion arousability responds particularly to infant olfactory stimuli; habituation with these stimuli is necessary to reduce aversion arousability through increased sensory recognition of the offspring. Tactile stimulation from infants could also increase aversion arousability and reduce motivation to interact with them. Periparturitional neuroendocrine changes may contribute to the reduction of aversion arousability. Novelty-fear arousability processes all unfamiliar infant stimuli, passive and active. The outcome of this information processing is infant-directed fear and inhibition of maternal behavior. According to Pryce's model, novelty-fear arousability is high in adult females but low in juveniles, thus allowing them to obtain the necessary maternal experience with infant stimuli. In adult females who give birth, both hormonal changes and sensory recognition of offspring reduce novelty-fear arousability. Therefore, the experiential and neuroendocrine state of the parturient female is such that the positive arousability factors override the negative ones, so that the mother is motivated to take care of the infant and maternal behavior is expressed.

At the time Pryce's [1992] model was published, the regulation of maternal motivation in laboratory rats and sheep was already well understood, but the regulation of maternal motivation in nonhuman primates was just beginning to be investigated. After almost two decades of additional research on primate maternal motivation and behavior, it is important to assess whether the findings of this research are consistent with the assumptions of Pryce's model or whether the model needs revision. Although some central assumptions of Pryce's model are based on studies of rhesus monkeys conducted in the 1950s and 1960s, these studies were conducted in highly artificial laboratory conditions, e.g. with socially deprived and individually housed individuals. Recent research on the neuroendocrine regulation of primate maternal behavior, however, has been conducted with individuals living in social groups in naturalistic or semi-naturalistic conditions [Saltzman & Maestripieri, 2011]. Therefore, it is necessary to assess whether or not the findings of early laboratory studies of rhesus monkeys, on which Pryce's model is based, have been confirmed and validated by more recent studies.

The goal of this article is to explore the role of emotions in the regulation of primate maternal motivation, and in particular the maternal arousability system and its subsystems proposed by Pryce [1992] in light of new research conducted in the last two decades [Saltzman & Maestripieri, 2011]. The primary focus of the article will be on rhesus macaques, although evidence from other primate species will be discussed as well. A number of questions will be raised and addressed about each of the four maternal arousability subsystems. With regard to the *maternal attraction arousability subsystem*, is it true that primate females are attracted to infants and aroused by them? What determines infant attractiveness and what modulates female arousability? Do female arousal and attraction to infants enhance maternal motivation and facilitate the expression of adaptive maternal behavior? With regard to the *maternal anxiety arousability subsystem*, what determines maternal anxiety and what are its modulating factors? Does maternal anxiety enhance maternal motivation and maternal behavior, as predicted by the model? Finally, with regard to the *maternal aversion* and the *novelty/fear arousability subsystems*, do infants represent novel and aversive stimuli for nulliparous females and does fear of novelty inhibit maternal motivation, as in rodents? Is lactation associated with lower reactivity to novelty and stress in primates, as in rodents? And finally: can stress inhibit maternal motivation and impair the expression of adaptive maternal behavior?

MATERNAL ATTRACTION AROUSABILITY

Female Attraction to Infants and Arousal

In rhesus macaques, females of all ages are highly attracted to infants and show visible signs of arousal in their presence. They approach other females' infants, use particular facial expressions and vocalizations to get their attention, and engage in various types of social interactions with them, which are collectively referred to as infant handling [Maestripieri, 1994a]. In most cases, infant handling consists of brief touching, holding, or grooming the infant. Rough infant handling (e.g. pulling, hitting, or dragging the infant) is sometimes referred to as infant harassment. Interactions in which infants are taken away from their mothers and prevented from being reunited with them are referred to as infant kidnapping.

Infant stimuli that seem to drive female attraction include: the shape of the face, body configuration and pelage coloration, coo vocalizations, and possibly olfactory, and motor characteristics [Gerald et al., 2006]. An experimental study involving digitized images of faces of newborn and 6-month-old infants showed that adult rhesus females find these faces equally attractive and that the pink coloration of the newborns' face is not an additional attractive stimulus [Gerald et al., 2006; but see Higley et al., 1987].

In rhesus macaques, a strong sex difference in interest in infants, expressed in rates of infant handling, emerges by the end of the first year of life and persists through the prepubertal years and beyond [Herman et al., 2003; Lovejoy & Wallen, 1988; Maestripieri, 2005a]. In the first year of life, males and females are not treated any differently by their mothers or other group members [Maestripieri, 2004]. Furthermore, male and female yearlings spend similar amounts of time in proximity to their mothers, and mothers do not encourage or discourage any social activities differentially in their sons and daughters. Therefore, greater female interest in infants early in life is unlikely to be the result of socialization and could reflect genetic predispositions or prenatal hormonal exposure [see Berenbaum & Hines, 1992; Gibber & Goy, 1985; Herman et al., 2003; Leveroni & Berenbaum, 1998, for humans].

After approaching other females' infants and engaging in visual or tactile interactions with them, rhesus females of all ages show behavioral signs of arousal. The main one is a dramatic increase in the rate of self-scratching. Scratching is the most common displacement activity in primates and may reflect arousal, excitement, or anxiety depending on the circumstances [Maestripieri et al., 1992]. Females also lip-smack and present their hindquarters to infants. Finally, they emit two specific vocalizations that are likely to reflect increased arousal: grunts and girneys. Female grunts given in the presence of infants have been described as brief bark-like atonal sounds, with an abrupt start and average length of about 0.2 sec, which occur in a series and with short intervals between units, and are produced with lip protrusion but negligible lip separation [e.g. Rowell & Hinde, 1962]. Girneys have been described as soft, low frequency, nasal or ''singing'' noises that are produced through lip protrusion, minimum lip separation, and rapid lip movement, as if the animal is chewing [Green, 1975; Hauser, 1993]. Both grunts and girneys are likely to reflect female arousal elicited by the sight of an infant or its behavior (e.g. walking independently), and are accompanied by other signs of arousal such as tail-wagging [Whitham et al., 2007]. In conclusion, recent studies confirm that in rhesus macaques, females of all ages find other females' infants attractive, get aroused by them, and actively attempt to engage in interactions with them.

Neuroendocrine Factors Modulating Female Attraction Arousability

A longitudinal study of group-living captive pigtail macaques reported that the frequency of female infant handling increased during late pregnancy and peaked the week before parturition [Maestripieri & Zehr, 1998]. The increase in infant handling during late pregnancy was correlated with an increase in the concentrations of plasma estradiol and in the estradiol to progesterone ratio. This correlational evidence that hormones can affect caregiving motivation was corroborated by experimental manipulations of hormonal variables. Rhesus macaque females whose ovaries had been removed increased significantly their frequency of interactions with other females' infants after the administration of estradiol in doses similar to those of middle-late pregnancy [Maestripieri & Zehr, 1998]. Further correlational evidence of a relation between infant handling and periparturitional changes in estrogen, progesterone, and also cortisol has been obtained in Japanese macaques and in baboons [Bardi et al., 2001, 2003a,b,c, 2004; Ramirez et al., 2004]. These findings obtained with Old World monkeys confirmed previous results obtained with common marmosets, in which nonpregnant females treated with estrogen and progesterone in concentrations similar to those of late pregnancy showed a significantly higher motivation to interact with infant stimuli (they pressed a bar in order to simultaneously gain visual access to a replica of an infant and turn off an audio recording of infant distress vocalizations) than nontreated females [Pryce et al., 1993; see also Pryce et al., 1988]. Pregnancy and lactation hormones, such as estrogen, progesterone and prolactin, probably do not affect maternal motivation directly but do so through their effects on brain neurochemical systems [Saltzman & Maestripieri, 2011].

The brain opioid system may provide one of the mechanisms through which females find infant stimuli attractive and rewarding. The role of the opioid system in regulating maternal motivation has been investigated in three studies of rhesus macaques producing conflicting results. In one study, the opioid system was pharmacologically manipulated after mother–infant separation and reunion [Kalin et al., 1995]. Morphine decreased clinging with the infant during the first 30 min of reunion, whereas the opioid receptor blocker naltrexone increased clinging. In a study of socially living rhesus mothers and infants, however, naloxone (another opioid receptor blocker) reduced both maternal grooming and maternal restraining of the infant, suggesting decreased rather than increased attachment to the infant [Martel et al., 1993]. In this study, however, the effects of naloxone on affiliative interactions between mothers and other adults were also contrary to the expectations. In fact, the mothers treated with naloxone showed reduced number of grooming solicitations and reduced amount of grooming received from other individuals. Finally, in another study of rhesus macaques, naltrexone had no significant effects on any aspects of maternal behavior, including abusive parenting [Graves et al., 2002]. Although some of these inconsistencies may be due to methodological differences between studies, further research is needed before any firm conclusions can be drawn regarding the relationship between opioids and maternal motivation.

The neuropeptide oxytocin is another primary candidate as a mechanism through which primate females find infant stimuli rewarding. The role of oxytocin in the regulation of maternal motivation in primates, however, is only beginning to be investigated. In a pilot experiment conducted with two nulliparous rhesus macaque females, Holman and

Goy [1995] examined whether an intracerebroventricular injection of oxytocin affected responsiveness to infants. The two females were exposed to an unfamiliar infant in a cage 10 min after the injection of oxytocin or saline. The females sat near the infant, and watched, touched, and lipsmacked to the infant more frequently following oxytocin compared with saline administration. In no case, however, was more intense caregiving behavior observed, perhaps because of the environment in which the animals were tested. In another study, CSF levels of oxytocin measured in ten multiparous rhesus females before, immediately after parturition, and 7 days postpartum were not correlated with mother–infant behaviors such as contact or grooming [Cooke et al., 1997]. Finally, Boccia et al. [2007] reported that the administration of a human uterine oxytocin receptor blocker reduced the frequency of lip-smacking, approaching, and touching a stimulus infant in one 4-year-old nulliparous rhesus macaque female. Although the effects of oxytocin receptor blockade on infant-directed behavior in one subject were suggestive of a relation between oxytocin and maternal motivaiton, the authors of this study acknowledged that other explanations for their results were also possible.

Do Female Attraction to Infants and Arousal Enhance Maternal Motivation and Facilitate the Expression of Adaptive Maternal Behavior?

Most, if not, all primate research on female attraction to infants and arousability has been conducted using other females' infants as stimuli. There is virtually no research on maternal arousability in response to a female's own offspring. Work on postpartum mother–infant bonding in rhesus macaques, however, is consistent with Pryce's [1992] suggestion that arousal and attraction to one's own infant provide the motivational basis for postpartum bonding and maternal behavior in the first few weeks of infant life [Maestripieri, 2001]. After the first few postpartum weeks, maternal motivation decreases steadily, in part due to a reduction in maternal attraction arousability. This is because there are changes in the value of infant stimuli (infants probably become less attractive to their mothers as they grow older) and changes in maternal neuroendocrine variables that reduce responsiveness to these stimuli. Little or no research on this topic, however, has been conducted.

Evidence that female attraction to infants, in general, enhances maternal motivation and facilitates the development and expression of maternal behavior is provided by the observed relationship between infant handling early in life and quality of maternal behavior in adulthood. Several lines of evidence suggest that developmental experience with other females' infants and with one's own offspring is important for the expression of competent maternal behavior in primates. For example, among macaques living in naturalistic social groups, first-time mothers are generally more likely than multiparous mothers to neglect and abandon their infants or to show clumsy maternal behavior such as carrying infants upside down [Maestripieri & Carroll, 1998a,b; Schino & Troisi, 2005]. The probability of infant abandonment is greatly reduced as females give birth to successive infants, and the quality of maternal care typically increases as well [Maestripieri & Carroll, 1998b; Schino & Troisi, 2005].

Important experience for learning maternal behavior can be acquired by primate females during interactions with their own mothers in infancy, through observation of interactions between their mothers and younger siblings or between other females and their infants during the juvenile period, through direct interaction with younger siblings or other females' infants during the juvenile period, and through direct interactions with their own offspring. Young females who are aroused by infants are highly motivated to interact with them, and those who do so become better mothers in the future. Research with vervet monkeys has shown that interactions with younger siblings or other females' infants during the juvenile period affect the quality of maternal care and the probability of infant survival of first-time mothers. Specifically, first-time mothers who had greater infant handling experience with infants as juveniles were more likely to be competent mothers and their infants had a higher probability of survival than females with less juvenile experience with infants [Fairbanks, 1990]. Interest in infants in the juvenile years and motivation to engage in extensive social interactions with them probably represent a developmental adaptation that has been best documented in nonhuman primates and humans [Maestripieri & Roney, 2006], but which may be present in other mammalian species as well, especially those with relatively long lifespans and complex patterns of maternal care.

MATERNAL ANXIETY AROUSABILITY

Expression of Maternal Anxiety, Its Determinants, and Modulating Factors

In primates, maternal anxiety is expressed with physiological changes (autonomic nervous system activation, and release of catecholamines and cortisol) and with behavioral changes such as increased vigilance and increased rates of self-directed activities such as scratching. Maternal anxiety is triggered by the perception of danger for the offspring. In the wild, it is likely that the sighting of predators or the hearing of alarm calls would trigger maternal anxiety. In addition, different aspects of separation from the offspring can trigger maternal anxiety such as: (1) forced separation and inability to regain contact with the infant, such as the experimental separation of mother and infant in a laboratory setting, or separation due to infant kidnapping by another group member; (2) infant-initiated spontaneous separation, such as for exploration of the environment. Both visual and auditory stimulation (i.e. observation of the separated infant and hearing of infant distress calls) can trigger anxiety. When young infants are out of contact with their mothers, their proximity to and interaction with dangerous conspecifics can also trigger maternal anxiety [Maestripieri, 1993a, 1995b].

Maternal Responses to Forced Separation in a Laboratory Setting

Experimental separation studies have used mothers and infants individually housed in a cage or living in a social group. When the subjects are living in a group, separation involves removal of the mother or the infant from the group, or removal of both mother and infant from the group and subsequent separation. When monkey mothers are forcibly separated from their infants, they typically display vocalizations and signs of behavioral agitation [Levine & Wiener, 1988]. Maternal vocalizations and agitation reflect efforts to locate and regain contact with the infant and they usually cease on reunion [Maestripieri & Call, 1996]. Maternal behavioral responses to separation are accompanied by physiological responses, such as increased plasma cortisol levels [squirrel monkeys: see Coe et al., 1985; Levine & Wiener, 1988, for reviews; rhesus macaques: Champoux & Suomi, 1994; Levine et al., 1985; but see Smotherman et al., 1979, for negative results]. Altogether, these studies indicate that separation from the infant is an anxiogenic event for a monkey mother. Behavioral agitation is accompanied by the activation of the hypothalamic–pituitary–adrenal axis, and both the behavioral and the physiological responses are generally enhanced if separation from the infant is associated with exposure to novel procedures or environments.

Maternal Responses to Interruption of Infant Contact in Group-Living Monkeys

Primate mothers and infants continually experience brief and repeated separations as a result of the process of infant independence. In macaques, in the first month of infant life, mother–infant contact is mainly interrupted by maternal attempts to encourage infant locomotion and by infants' early attempts to explore their surrounding environment [Maestripieri, 1995a, 1996]. Early separations are brief and usually terminated by the mother. Then, the frequency with which infants break contact with their mothers and walk away from them increases steadily with age [Hinde & Atkinson, 1970]. Interruption of contact with the infant in the first weeks of life is associated with a dramatic increase in the frequency of maternal scratching and in the rate of glancing at the infant and at other individuals [Maestripieri, 1993a,b, 1995c]. In one study, the rate of maternal scratching increased when infants were in proximity to individuals who frequently harassed and kidnapped them [Maestripieri, 1993a]. Elevated scratching rates were also observed during episodes of infant kidnapping, when infants were physically prevented from returning to their mothers by other adult females [Maestripieri, 1993c].

Maternal separation anxiety is likely to reflect both fear of infant loss and uncertainty over the action to be taken. Several findings suggest that maternal separation anxiety has a cognitive component and is not a reflexive, stereotyped response. Specifically, maternal anxiety appears to reflect both the presence of an objective risk for the infant in the social environment and the mother's subjective assessment of such a risk. Both scratching and visual monitoring of the infant and of other individuals while the infant is out of contact decrease steadily with infant age over the first 12 postpartum weeks, as infants become less vulnerable to harassment and kidnapping [Maestripieri, 1993a]. Furthermore, maternal separation anxiety is higher in species of macaques in which the risk to the infant is higher [Maestripieri, 1994b,c]. Therefore, the occurrence and developmental changes of maternal separation anxiety reflect an objective risk of infant injury or loss and the infant's vulnerability to such a risk. Although macaque mothers also display signs of anxiety when they are themselves at risk of aggression, mothers do not simply generalize the concerns they have for themselves to their infants. Rather, mothers distinguish between risk to themselves and risk to their infants, and maternal anxiety can be distinguished from social anxiety, although the two are correlated with each other [Maestripieri, 1993a, 1995b]. For example, rhesus mothers did not avoid adult females lower ranking than themselves but displayed anxiety when these individuals approached and interacted with their infants [Maestripieri, 1995b]. One explanation for this finding could be that rhesus mothers are aware that their infants' vulnerability to risks can be different from their own because of the infants' smaller size and lack of experience. Alternatively, mothers may have learned on the basis of their direct experience that certain social interactions have different consequences for themselves and their infants, and elicitation of anxiety would simply reflect these learning experiences. Consistent with this explanation, there is evidence that the mother's age and experience can influence her assessment of risk for the infant in the environment and her emotional response to separation [Maestripieri, 1993b]. Part of the variability in maternal separation anxiety, however, is not accounted for by demographic characteristics of mothers and infants, suggesting that perhaps the mother's temperament or personality may be important. Differences in temperament may also be implicated in species differences in maternal separation anxiety [see Clarke & Boinski, 1995].

Does Maternal Anxiety Enhance Maternal Motivation and Maternal Behavior?

Consistent with Pryce's [1992] model, several lines of evidence suggest that maternal anxiety enhances maternal motivation and the expression of protective behaviors. First, behavioral expressions of maternal anxiety are immediately followed by maternal protective behaviors. For example, mothers who scratch themselves at high rates when their infant is in proximity to a dangerous group member [e.g. a female with a history of infant kidnapping) will immediately retrieve the infant [Maestripieri, 1995b]. Second, mothers who exhibit high levels of anxiety also have highly protective maternal styles. For example, in rhesus macaques, two indicators of maternal separation anxiety were better predictors of variability in maternal protectiveness than any sociodemographic characteristics of the mothers. The rate of visual monitoring of the infant was linearly related to protectiveness, whereas the rate of scratching showed an inverse U-shaped relation with protectiveness, i.e. the mothers with the highest scratching rates during separation had intermediate levels of protectiveness [Maestripieri, 1993b]. This finding was interpreted by suggesting that visual monitoring primarily reflects the fear component of maternal anxiety, whereas scratching primarily reflects the uncertainty component. Therefore, the most and the least protective mothers have only moderate scratching rates because they are strongly biased toward intervention and non-intervention, respectively [Maestripieri, 1993b]. A study of Japanese macaques, which used overall scratching frequency instead of scratching rates during separation, reported a linear relationship between scratching and maternal protectiveness [Troisi et al., 1991].

The relationship between maternal anxiety and maternal protectiveness is consistent with the notion that maternal anxiety arousability has an adaptive value in that it promotes proximity to the infant and protective behaviors such as retrieval and restraint. Insofar as maternal separation anxiety activates behaviors that promote proximity to and protection of the offspring, maternal separation anxiety can significantly increase the chances of offspring survival and the reproductive success of the parent. Therefore, maternal separation anxiety may be a specific adaptation of parenting, just as infant separation anxiety is an adaptation of the developing infant. Accordingly, maternal separation anxiety should be a phenomenon common to all animal species in which offspring survival is crucially dependent on mother–offspring contact and proximity. Therefore, the notion that maternal anxiety arousability plays a central role in the regulation of maternal motivation in mammals [Pryce, 1992] is fully legitimate.

In primates, as in humans, there is evidence that too little or too much concern over separation may be associated with dysfunctional parenting. Troisi and D'Amato [1984, 1991] presented evidence from a case of infant abuse in Japanese macaques suggesting that extreme maternal separation anxiety played an important role in the occurrence of abuse. Although these authors did not measure maternal separation anxiety with scratching or visual monitoring, the abusive mother alternated abuse with extremely possessive maternal responses, and abuse occurred when infants attempted to break contact with the mother or did not respond to her retrieval signals. Moreover, the administration of an anxiolytic drug to the abusive mother resulted in a reduction of maternal protectiveness and termination of abuse [Troisi & D'Amato, 1991]. A recent study of ten group-living rhesus mothers who physically abused their infants reported that abusive mothers did not show the typical separation-related increase in scratching during the first 2–3 weeks of life [Maestripieri, 1998]. The first weeks of infant life were also the period with the highest frequency of abuse. In the third month of infant life, however, when abuse was considerably reduced, maternal separation anxiety was higher in the abusive mothers than in the control mothers. Thus, early abuse was associated with low maternal separation anxiety, whereas a reduction in abuse and increase in protectiveness in the third month were associated with increased maternal separation anxiety. The developmental changes in abuse frequency, maternal separation anxiety, and parenting style suggest that the development of attachment between abusive mothers and their infants may be slower or delayed relative to controls.

Data on infant abuse in pigtail macaques lend further support to the notion that lack of concern over infant separation may result in maladaptive parenting. In one well-documented case of abuse, maternal abusive behavior appeared in strict temporal association with the repeated kidnapping and severe harassment of the infant by another adult female in the group, abuse being absent before the appearance of the kidnapping episodes and drastically reduced after their termination [Maestripieri, 1994d]. The abusive mother did not exhibit obvious signs of maternal separation anxiety during the forced separation from her infant nor did she attempt to prevent further kidnappings by increasing her protectiveness. Abuse occurred at reunion with the infant, often after several hours of forced separation. Maestripieri [1994d] argued that the mother's failure to cope with the stressful situation, both emotionally and behaviorally, may have been a factor precipitating abuse.

Although failure to show a maternal separation anxiety response when infants are young and vulnerable may be associated with neglectful or abusive parenting, a decrease in maternal separation anxiety as a function of increasing infant age and reduced infant vulnerability is adaptive and may facilitate infant weaning. Thus, the steady reduction in maternal motivation that leads to infant weaning over the first 6–12 months of infant life is caused not only by a reduction in maternal attraction arousability but also in maternal anxiety arousability.

At the proximate level, individual differences and developmental changes in maternal anxiety are probably the result of the activity of brain neurotransmitter systems that are involved in emotion regulation, and especially anxiety [Lonstein, 2007]. A primary candidate is the monoamine neurotransmitter serotonin. Early studies of serotonin and maternal behavior in primates reported that monkey mothers with low concentrations of the serotonin metabolite 5-HIAA in their cerebrospinal fluid (CSF) were more protective and restrictive, and that their infants spent more time in contact with them, than mothers with high CSF 5-HIAA [Fairbanks et al., 1998; Lindell et al., 1997]. Cleveland et al. [2004] found no relationship between CSF 5-HIAA and maternal behavior in the first few postpartum days, but on postpartum days 15 and 20, females with low CSF 5-HIAA broke contact and left their infants less frequently than females with high CSF 5-HIAA. A preliminary study in our laboratory reported a positive correlation between CSF 5-HIAA concentrations measured during pregnancy and maternal rejection behaviors in the first postpartum month in multiparous females [Maestripieri et al., 2005]. Our more recent work involving multiple measurements of CSF 5-HIAA during development, however, reported a negative correlation between CSF 5-HIAA and maternal rejection among first-time mothers [Maestripieri et al., 2007].

The serotonin system may also be involved in the intergenerational transmission of infant abuse. We reported that about half of the females who were abused by their mothers early in life, whether crossfostered or non-crossfostered, exhibited abusive parenting toward their first-born offspring, whereas none of the females reared by nonabusive mothers did (including those born to abusive mothers) [Maestripieri, 2005b]. Moreover, the abused females, both crossfostered and non-crossfostered, who became abusive mothers had lower CSF 5-HIAA concentrations than the abused females who did not become abusive mothers [Maestripieri et al., 2006]. Since abuse tends to co-occur with high rates of maternal rejection, our findings suggest that experience-induced long-term alterations in serotonergic function in females reared by highly rejecting and abusive mothers contribute to the manifestation of maternal rejection and abusive parenting in adulthood. It is possible that experience-induced reduction in serotonergic function results in elevated anxiety and impaired impulse control, and that high anxiety and impulsivity increase the probability of occurrence of maternal rejection and abusive parenting with one's own offspring later in life, perhaps in conjunction with social learning resulting from direct experience with one's own mother or from observation of maternal interactions with siblings [Maestripieri, 2008]. Although it is likely that serotonin affects maternal motivation through its effects on maternal anxiety arousability, it is also possible that serotonin affects maternal attraction arousability through its effects on oxytocin or prolactin release [Insel & Winslow, 1998; Numan & Insel, 2003].

In conclusion, research on maternal anxiety arousability and its neurochemical substrates conducted in the last two decades confirms Pryce's [1992] assumption that this system plays an important adaptive role in the regulation of maternal motivation in primates.

MATERNAL AVERSION AROUSABILITY

Do Infants Represent Aversive Stimuli for Nulliparous Primate Females and Does Aversion Impair Maternal Motivation?

Pryce's [1992] assumption that mammalian females without hormonal priming and/or developmental experience with infants find neonates aversive is mainly derived from laboratory studies of rodents and of socially deprived rhesus monkeys. In laboratory rats and other rodents, virgin females find pup odors aversive and will actively avoid or kill unfamiliar pups. The idea here is that pup odors elicit negative emotions (perhaps disgust?) and that such emotions reduce maternal motivation and increase avoidance or infanticidal behavior. Thus, research with laboratory rodents has shown that an important component of the elicitation of maternal behavior through pregnancy, hormonal treatment, or sensitization involves the inhibition and suppression of aversive, avoidant, and infanticidal responses elicited by pups.

Whether nulliparous females' aversion to infant stimuli is a general phenomenon shared by all mammals is uncertain. One possibility is that it is a by-product of the reproductive and social systems of rodents. Most rodents live in territorial social systems in which female–female aggression and infanticide play an important role [Maestripieri, 1992]. Mothers themselves kill and cannibalize their own offspring when their territories have been invaded by intruders and they have been unable to effectively defend their litter [Maestripieri, 1992]. Although female territoriality and competitive infanticide (i.e. killing other females' offspring) are not uncommon in other mammals, they appear to play a relatively small role in the social and reproductive strategies of extant primates, with the possible exception of common marmosets and other New World monkeys [Digby & Saltzman, 2009; Saltzman et al., 2008]. Thus, it is possible that the mechanisms underlying the induction of maternal behavior through the suppression of avoidant and infanticidal tendencies in rodents do not apply to other mammals such as primates. Another possibility is that nulliparous females' aversion to pups is common in laboratory rodents, which often do not have normal developmental experiences and live in highly artificial environments, but less common in wild rodents and other mammals living in naturalistic environments. When female rodents in the laboratory are exposed to pups and allowed to gain experience with them during early development, aversion to infants and the occurrence of infanticide later in life are greatly reduced. Finally, in some strains of mice, nulliparous females spontaneously exhibit maternal behavior without any previous juvenile parenting experience.

Laboratory studies of socially deprived rhesus monkeys showed that when females were separated at birth from their mothers, raised in conditions of social deprivation, and individually housed with their infant in a small cage, there was a high incidence of inadequate maternal behavior including infant abuse and neglect [Ruppenthal et al., 1976; Suomi, 1978]. Furthermore, the proportion of mothers displaying adequate maternal care increased with successive infants, suggesting that maternal behavior improved with experience. One study of rhesus monkeys in which individually housed nulliparous females were tested with strange infants showed that females avoided any interaction with the infants [Gibber, 1986]. Taken together, these findings have led to the notion that, similar to rodents, nulliparous monkey females find newborns aversive and need experience and/or hormonal priming to overcome their aversion. These extrapolations, however, need to be made with caution for several reasons. First, one-third of the rhesus mothers studied by Ruppenthal et al. [1976] displayed adequate maternal care with their first-born infants, suggesting that their caregiving skills had not been significantly impaired by their developmental history. Second, while the occurrence of infant neglect decreased with successive infants, the occurrence of abuse did not. This finding, along with those obtained in group-living macaques [Maestripieri & Carroll, 1998b], suggests that abuse does not result from lack of experience with infants and is not overcome through such experience. Third, most socially deprived mothers displayed maladaptive behavior in all behavioral interactions with conspecifics [Suomi, 1978], suggesting that their maladaptive infant-directed behavior could be best interpreted as one of the many aberrations induced by traumatic developmental experience rather than the result of a specific deficit in learning mothering skills. Fourth, when primate females are housed alone with an infant in a small cage, they are more likely to avoid or abuse the infant regardless of their previous experience, although young females may be more sensitive to this stressful situation than older females [Maestripieri & Carroll, 1998a]. Thus, studies of socially deprived monkeys do not offer unequivocal evidence that nulliparous females find infants aversive or that experience with infants or hormonal priming is necessary to develop adequate caregiving skills.

Nulliparous females with normal developmental experiences (i.e. who were not socially deprived) do not find infant stimuli aversive and do not show avoidant or abusive responses to them. When macaque females live in their natal social group surrounded by their family and other conspecifics of different sex and ages, they usually find newborns very attractive and not aversive. More generally, it is hard to imagine the evolutionary reasons why primate females should perceive infant stimuli as aversive and not be biologically predisposed to display some basic caregiving skills. Thus, the existence of a maternal aversion arousability system in primates is uncertain. Whether this system plays a central role in the regulation of maternal motivation in rodents and other mammals is uncertain as well, and the possibility should be taken into consideration that female aversion to infants is a prominent phenomenon in laboratory rodents mainly due to their abnormal developmental histories and artificial environments.

MATERNAL NOVELTY-FEAR AROUSABILITY

Is Lactation Associated With Lower Reactivity to Novelty and Stress in Primates?

In laboratory rodents, nonpregnant and non-lactating females are highly neophobic. It has been argued that fear of novelty reduces motivation for maternal behavior and increases avoidance or infanticidal behavior [Fleming & Luebke, 1981]. Pregnancy and lactation are characterized by reduced endocrine and behavioral reactivity to novelty and stress. Lactation, in particular, makes mothers less anxious and less fearful; this enhances maternal motivation and facilitates the expression of maternal care [Lonstein, 2007; Maestripieri & D'Amato, 1991; Maestripieri et al., 1991]. Whereas the postpartum period has been associated with lower physiological reactivity to stress in some studies of rodents [e.g. Tu et al., 2006; but not in others such as Deschamps et al., 2003, in which rat mothers showed high physiological reactivity to stress when tested in presence of their pups and pups were in potential danger] and humans [Altemus et al., 1995, 2001; but see Heinrichs et al., 2001, who showed that this is a transient effect that occurs only during breastfeeding], pregnancy and the postpartum period in primates are characterized by high emotional instability and reactivity.

Recent data obtained with free-ranging rhesus macaques on the island of Cayo Santiago strongly suggest that lactation and motherhood is characterized by heightened, not diminished, endocrine reactivity to stress. This 2-year study involved, as subjects, 70 adult females between 6 and 26 years of age. We observed their behavior as well as collected fecal samples for cortisol assays on a weekly basis. Females were captured once a year, and blood samples were collected for plasma cortisol assays. Of the 70 females, 30 were captured in the first year of the project, 18 were captured in the second year, and 22 were captured in both years. Fecal hormone metabolite concentrations were used as a measure of baseline cortisol levels while plasma cortisol concentrations measured after capture and overnight individual housing were used as indicators of endocrine responsiveness to stress. Data from the 22 females captured in both years indicated that there were significant positive correlations between measures of plasma cortisol concentrations in the 2 years [Hoffman et al., 2010]. Moreover, individual differences in plasma cortisol responses to stress were positively correlated with individual differences in baseline cortisol concentrations measured in fecal samples [Hoffman et al., in preparation]. Both between- and within-subject analyses showed that plasma cortisol concentrations in response to the stress of capture were higher when females were lactating than when they were cycling [Hoffman et al., 2010]. Moreover, higher cortisol concentrations in lactating females were also found with the fecal hormonal data [Hoffman et al., in preparation]. Higher baseline cortisol and plasma cortisol responses to stress are unlikely to reflect metabolic processes associated with lactation because, in humans, it has been demonstrated that cortisol levels return to preconception levels within 24–48 hr after giving birth (the same is true for corticosterone levels in rodents). Instead, higher cortisol levels in lactating females are likely to reflect social stress associated with motherhood. In fact, motherhood and lactation are periods of high stress and increased stress reactivity in primates and humans due to maternal concerns for infant safety, disruption of sleep and other maintenance activities, and stressful changes in social relationships with others. In our rhesus monkey study, plasma cortisol levels were also higher among low-ranking than among high-ranking females. Moreover, low-ranking females had greater increases in cortisol from the cycling condition to the lactating condition than high-ranking females [Hoffman et al., 2010]. Taken together, these results suggest that motherhood and low social status are stressful for females, and that the stress of motherhood is greater for low-ranking than for high-ranking females. Thus, as with the maternal aversion arousability system, the existence of a novelty-fear arousability system in primates is uncertain.

MOTHERHOOD AND STRESS IN PRIMATES

Although some human studies have shown that moderately high cortisol levels in the early postpartum period can be associated with greater sensitivity to infant cues and greater maternal responsiveness [Fleming et al., 1987, 1997], a large body of evidence indicates that extremely high or chronically elevated cortisol levels due to stress can impair maternal motivation and result in maladaptive parenting behavior. Specifically, it has been shown in humans that stress is a major risk factor for postpartum depression and for child neglect and abuse; in addition, stressed mothers are more likely to find infant stimuli (e.g. cries) aversive [e.g. Adamakos et al., 1986; Besser et al., 2002; Wolfe, 1987].

Preliminary evidence that dysregulation of emotion due to stress can impair maternal motivation and result in maladaptive parenting also exists for nonhuman primates. In a study of captive lowland gorillas, stress due to social disruption and abnormal housing conditions was associated with high concentrations of cortisol in fecal samples, and high cortisol, in turn, was associated with infant neglect [Bahr et al., 1998]. In pigtail macaques, maternal abuse of offspring is often precipitated by socially stressful events [Maestripieri, 1994d; Maestripieri & Carroll, 1998c]. In addition, rhesus macaque abusive mothers have neurochemical profiles similar to those of humans with PTSD, suggesting chronic stress [Maestripieri et al., 2005]. In captive baboons, Brent et al. [2002] reported that the postpartum period was associated with a significant increase in stress-related behavior, and in a related study, the same investigators showed that stressed mothers who showed abnormal behaviors also had higher levels of urinary cortisol [Bardi et al., 2004]. Finally, there is a recent experimental evidence that exogenous administration of elevated doses of cortisol in lactating female common marmosets impairs maternal motivation and interferes with the expression of appropriate maternal behavior [Saltzman & Abbott, 2009].

Although the relationship between primate maternal behavior and stress-sensitive physiological systems such as the HPA axis or the brain serotonergic system needs to be better understood [Saltzman & Maestripieri, 2011], it is becoming increasingly clear that motherhood is associated with increased stress, and that stress can impair maternal motivation. Therefore, the effects of stress need to be taken into consideration in a model of the regulation of maternal motivation in mammals, along with the possibility that the relationship between lactation and stress may be different in different mammalian species or in animals tested in the laboratory vs the wild.

In conclusion, evidence that emotions play a central role in the regulation of maternal motivation and parental behavior of mammals is overwhelming. Many assumptions and predictions of Pryce's [1992] model have been confirmed by recent studies of nonhuman primates. At the same time, these studies have suggested that certain extrapolations from studies of laboratory rodents and socially deprived monkeys, particularly with the regard to the existence and importance of a maternal aversion arousability and a maternal novelty-fear arousability subsystem, need to made be caution. Future studies are necessary to assess whether the lack of strong evidence for these subsystems in organisms other than laboratory rodents is due to differences in the regulation of maternal motivation between rodents and other mammals, or due to the abnormal developmental histories of laboratory rodents and the characteristics of their rearing and living environment. Further research is also needed to better understand the effects of stress on maternal motivation so that this variable can be effectively incorporated in future models of mammalian parenting.

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