

Motherhood

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Abstract

Motherhood is fundamentally the state of being a mother. In mammals this manifests as behaviorally nurturing and physiologically nourishing one's young. The state of motherhood requires substantial and dramatic changes in the mother's behavior, brain, and body. Moreover among humans, motherhood occurs within a familial, socioeconomic, and cultural context. Among many animals, to become a mother marks the transition to a new stage of life, from a period dedicated to growth and development to a period of sexual maturity and productivity. Considering trade-offs within and across the stages of the life course, known as *life history theory*, is essential to understand motherhood. Moreover, the interests of the mother and the infant overlap, but are not identical, leading to conflicts of interest. Here we will consider established and emerging topics of investigation into motherhood—from the neuron to the society—and directions for the future.

INTRODUCTION

In 1952, John Bowlby and his colleague James Robertson presented a short film entitled "A Two-Year-Old Goes to Hospital." Over the course of an eight day hospital stay, the infant deteriorated in the absence of maternal care despite nutritional and medical support. This dramatic interruption of the mother-infant dyad served as a window into the infant's psychological processes in light of separation from the mother. From expanded studies by Bowlby, cross-cultural investigations of mothers and infants by Mary Ainsworth, and rhesus macaque experiments by Harry Harlow, Steve Suomi, and colleagues, the mid-twentieth century laid a foundation for Attachment Theory and established a framework for evaluating the mother-infant dynamic, the role of the mother, and the consequences for infants. Maternal behavioral care was demonstrated to be an important contribution to species-typical behavioral development and physiological regulation. This expanding research into the importance of maternal love was a crucial repudiation of the conventional "wisdom" of regimented infant care recommended by many prominent physicians between WWI

and WWII. Prior to these empirical studies, mothers were cautioned against excessive affection—such as cuddling and soothing—directed toward the infant (Lewis, 1982).

Notably, studies of mothers were, and remain to this day, mostly infant-centered, that is to say, predominantly designed to investigate infant outcomes. Progeny are the principle currency of natural selection, attracting the interests of evolutionary biologists and behavioral ecologists. Piagetian psychologists, Batesian linguists, and Barkerian DOHaDians¹ are motivated to understand how early environment and experiences influence cognitive development, language acquisition, and physiological function into childhood and adulthood. Parents, clinicians, and public health advocates are particularly motivated to optimize infant outcomes.

However, mothers, and their experience of motherhood, are more than merely inputs into infant developmental trajectories. Depending on the social, behavioral, or life science lens through which motherhood is assessed, one can approach it as a state, a stage, and a construct. Fundamentally, motherhood is the state of behaviorally caring for young—after either producing one's own biological young as is typical, or occasionally in the case of humans, through adoption of a nonbiological infant or child. Among many animals, to become a mother marks the transition to a new stage of life, from a period dedicated to growth and development to a period of sexual maturity and productivity. Considering trade-offs within and across the stages of the life course, known as *life history theory*, is essential to understanding motherhood. Across species, motherhood involves substantial changes in behavior—not only in direct care of the infant, but also indirectly by changed interactions with other individuals. Motherhood precipitates a cascade of neurobiological and physiological changes that mediate infant care and nourishment as well as transitions to the next reproductive effort. Among humans, motherhood is also a feature of personal identity—a construct of self, as well as a cultural construct. Here we will explore recent studies that provide new information about motherhood and identify future directions that enhance the translational utility of scholarly studies of motherhood.

EVOLUTIONARY CONTEXT

LIFE HISTORY THEORY

Before evaluating maternal behavioral care and physiological investment, we must consider life history theory and parent-offspring conflict. All biological organisms face trade-offs for allocating energy among competing

1. A reference to key scholars influencing their disciplines: cognition and Jean Piaget, linguistics and Elizabeth Bates and Developmental Origins of Health and Disease and David P. Barker.

processes. Drawing a parallel with Economics 101 and the “guns versus butter model,” capital is finite and money supporting the manufacture of one commodity is no longer available for another commodity. Such is energy for the biological organism; a calorie can only be burned once. Organisms have finite resources, such as energy, that are allocated to somatic maintenance, development, and reproduction (Stearns, 1992). For examples, among mammals, maintenance includes the physiological processes of immune function, digestion, and endothermic thermoregulation. Development includes growth, neurogenesis, and skeletal ossification. Reproduction requires mating, gametogenesis, and for females—pregnancy and lactation. Mobilization of stored fat on the mother’s body for milk synthesis is fat that is no longer available for the mother’s thermoregulation or future reproduction. She must recover those stores before resuming estrus and the next reproductive event (Valeggia & Ellison, 2009). As such, motherhood occurs within a framework of necessary trade-offs. Natural selection favored traits that produced adaptations that underlie contingencies for allocating energy among behavioral activity and physiological processes to maximize lifetime reproductive success (Clutton-Brock, 1991). Reproductive success is measured as the number of offspring produced that reach reproductive maturity across an entire reproductive career. As a result of these many factors and constraints, mammalian mothers are expected to vary their effort and investment in individual offspring in relation to the mother’s own condition, the offspring’s condition, and the time point in her reproductive career (Clutton-Brock, 1991). The many moving parts of the mother-infant dynamic complicate greatly studies of motherhood. This is particularly true when one considers that the mother and infant may have, to some extent, divergent interests when they interact.

PARENT-OFFSPRING CONFLICT

Natural selection has not only acted on adaptations in mothers. The infant plays an important role within the mother-infant dynamic. Just as mothers face trade-offs between maintenance and reproduction, so infants face trade-offs between maintenance and growth (Stearns, 1992). Moreover the interests of the infant and the mother are not perfectly aligned. Mothers are equally related to each of their offspring, as offspring inherit 50% of their genetic material, on average, from their mother. All else being equal, mothers are predicted to allocate resources equally among their offspring. But infants are 100% related to themselves, only 50% related to their mother and only 25–50% related to their mother’s other offspring, depending on whether they share a father in addition to sharing a mother. Invoking Hamilton’s rule, Trivers (1974) argued that this difference between self and relative would

generate parent-offspring conflict of interest over the amount and duration of investment from the mother and adaptations in offspring to extract greater investment from the mother. The mother-infant dynamic is therefore shaped by an essential tension as the mother and offspring negotiate behavioral care and physiological investment between their respective optima (Hinde, 2014). Negotiation of these divergent interests are further complicated as within the infant, genes of paternal origin and genes of maternal origin are also potentially in conflict (Haig, 2014). The complexity and nuance embedded within the “symbiosis of parent–offspring interactions” are therefore a particularly challenging area of research in the social and behavioral sciences (Rosenblum & Moltz, 1983).

THE BEHAVIORAL BIOLOGY OF MOTHERHOOD

MATERNAL BEHAVIOR

A suite of behaviors are generally associated with motherhood and can include protection, vigilance, nourishment, transporting, physical comforting of the young and in socially complex species, mothers may intervene on their offspring’s behalf during social encounters. The form of these behaviors will vary across species—for example, nourishment can take the form of mother’s milk or provisioned foods. Physical comforting can be licking, grooming, and huddling. Mother–infant interactions have been one of the most prevalent and enduring research areas in anthropology, psychology, and primatology. Primate and rodent models have been particularly useful in understanding maternal behavior (Champagne, 2014; Champagne & Meaney, 2001; Dettmer, Suomi, & Hinde, 2014; Phillips *et al.*, 2014). From these studies, we have a deep appreciation that mothers display substantial individual variation in their behavioral care of infants. In a diversity of animal taxa, variation in maternal care has been associated with social rank, social environment, ecological conditions, genetic predispositions, and prior experience rearing young (Champagne & Meaney, 2001; Fairbanks, 1993; Fairbanks & Hinde, 2013; Hrdy, 2009; Maestripieri & Mateo, 2009; Meaney, 2001). Long-term assessment of maternal care in free-ranging rhesus macaques on Cayo Santiago showed that females had consistent “mothering styles,” mother infant interactions of proximity, contact, and rejection were consistent across age periods and between infants (Berman, 1990). Cross-fostering experiments have been conducted with rhesus macaques at Yerkes that demonstrate that maternal–infant interactions are genetically coadapted (Maestripieri, 2004). More rejecting mothers produce infants that are more inclined to make contact and vice versa (Maestripieri, 2004). In a

series of landmark studies, Rosenblum and colleagues manipulated foraging demands on mothers to understand how it changed their behavioral interactions with their infants and other monkeys in the social group. The researchers created three foraging conditions; (i) high foraging demand (HFD) 90–100 monkey biscuits were hidden in 1000 food holes (110% of their normal diet), (ii) low foraging demand (LFD) 600 biscuits were hidden in 1000 food holes, and (iii) variable foraging demand (VFD) in which food was provided either the HFD or LFD condition on a 2-week cycle. The VFD condition seemed to be psychologically demanding for mothers. These mothers were less attentive to their infants, broke contact with their infant significantly more frequently, and infants expended greater effort to reestablish contact than in the HFD or LFD groups. Among the adults in the VFD condition, including mothers, there were more hierarchical interactions (e.g., aggression, displacement) and less grooming. These studies provide strong evidence that unpredictable environmental conditions are particularly difficult on mothers even though the foraging demands were intermediate between the HFD and LFD. The variable aspect of the VFD condition was more stressful and had a greater affect on maternal care than even the condition in which foraging demands were always high (Rosenblum & Andrews, 1994; Rosenblum & Paus, 1984). This pioneering work continues to this day, revealing that individuals reared under VFD conditions have deficits in adulthood and transmit variable foraging demand consequences across generations (Coplan *et al.*, 2001; Coplan *et al.*, 2006; Kinnally *et al.*, 2013). Increasingly, studies of maternal behavior have expanded beyond ethology to understand the neurobiology and physiology of motherhood (Clancy, Hinde, & Rutherford, 2013), or rather the maternal brain and the maternal body.

THE MATERNAL BRAIN

The mother-infant bond is established shortly after birth via neurobiological mechanisms. The dopaminergic and oxytocinergic neuroendocrine pathways underlie the mother-infant bond—neurobiologically motivating and rewarding mothers for maternal care. Naturally occurring variation in the production, reception, and distribution of dopamine and oxytocin within the maternal brain, among other neurotransmitters, can contribute to variation in maternal responsiveness, attachment, and behavioral care (Carter, Lederhendler, & Kirkpatrick, 1999; Feldman, Gordon, Schneiderman, Weisman, & Zagoory-Sharon, 2010; Insel & Young, 2001; Saltzman & Maestripieri, 2011; Strathearn, Fonagy, Amico, & Montague, 2009). Most research into the maternal brain has occurred in the rodent model because of ethical, experimental, and logistical considerations. Much less is understood in

the primate brain, including humans, although new imaging technologies are affording researchers more options for investigating brain changes as a function of motherhood. In human mothers, the brain undergoes morphological changes in the weeks and months after giving birth. Specifically, the amount of grey matter, rich with neuronal cell bodies, increases in regions of the brain that are critical for sensory perception, emotion processing, and motivation (Kim *et al.*, 2010). These morphological changes are consistent with functional imaging showing increased oxygen utilization and glucose uptake in these same regions during the early months of motherhood (reviewed in Kim *et al.*, 2010). Most intriguingly, mothers who self-reported the most positive thoughts about their baby at the outset of the study showed the greatest increases in grey matter months later (Kim *et al.*, 2010). This result suggests that perceptions of motherhood and mother-infant dynamics may positively feedback, enhancing maternal behavior, but this remains speculative in the absence of more data. Higher circulating oxytocin in human mothers has been associated with increased maternal bonding behaviors, such as gazing at, checking on, and speaking to the infant, as well as affectionately touching and positive affect regarding the infant (Feldman, Weller, Zagoory-Sharon, & Levine, 2007; Gordon, Zagoory-Sharon, Leckman, & Feldman, 2010). Although not directly measuring the maternal brain, they still provide insight into the physiology of motherhood. Moreover, many of the hormones that mediate behavioral care in the brain also exert important peripheral effects that are critical for mothers during lactation. Particularly important, prolactin stimulates milk production while oxytocin triggers milk letdown for transfer to the infant (Lincoln, 1983) and among mammals, milk is a particular marker of motherhood.

THE MATERNAL BODY

The synthesis of milk by mammary glands is the defining characteristic of our mammalian class. Unfortunately, we still know relatively little about postnatal maternal physiological investment. For example, much more research effort has been dedicated to understanding pregnancy than aspects of lactation, particularly breast milk composition (Figure 1). Mother's milk consists of hundreds, possibly thousands of bioactive constituents, including numerous fats, proteins, sugars, vitamins, minerals, immunofactors, and hormones as well as water that hydrates the neonate (Hinde & Milligan, 2011; Neville *et al.*, 2012). How mothers pay the costs of lactation vary according to life history theory. Mothers energetically support lactation via a diversity of tactics and strategies that vary across individuals and species. Lactation can be supported by mobilizing body reserves (Oftedal, 2000); basically mothers dissolve parts of themselves to feed their young. Others rely to a greater

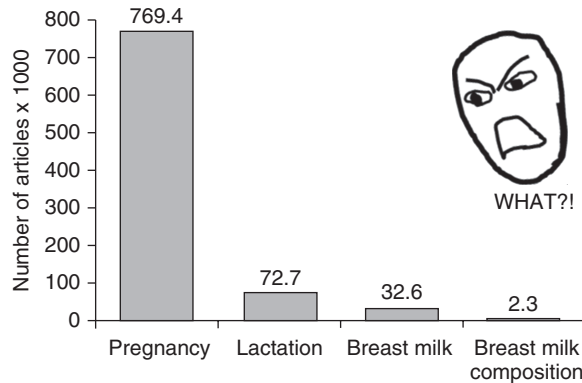


Figure 1 The number of articles returned as a result of keyword searches in PubMed, a database maintained by the United States National Library of Medicine (NLM) at the National Institutes of Health. Key word search conducted on June 1, 2014.

extent on dietary intake to sustain lactation. Conceptually these approaches can be characterized as “capital” and “income” breeding (Jönsson, 1997). However in practice most species exhibit multiple tactics to sustain lactation, relying on the mobilization of maternal reserves and dietary intake, as well as behavioral compensation and metabolic efficiencies (Gittleman & Thompson, 1988; Speakman, 2008). The tactics utilized to sustain lactation can therefore influence interbirth interval and consequently lifetime reproductive success. In baboons, chimpanzees, and humans, weight loss from mobilizing bodily reserves to sustain lactation, suppresses ovulation and subsequent conception is contingent on maternal recovery (Emery Thompson, 2013).

Given that mothers face trade-offs and rely on different tactics during lactation, substantial variation in milk synthesis is to be expected. Indeed a growing body of literature evaluating mother’s milk from an evolutionary perspective, demonstrates that mother’s milk varies across time, across individuals, across populations, and across species (Hinde & Milligan, 2011; Neville *et al.* 2012; Oftedal & Iverson 1995; Skibieli, Downing, Orr, & Hood, 2013). First-time mothers generally produce lower volumes of milk during lactation than do experienced, multiparous females in humans, monkeys, pinnipeds, rodents, and bovids (reviewed in Hinde, Carpenter, Clay, & Bradford, 2014; Hinde, Power, & Oftedal, 2009). Maternal diet can also predict milk composition (Hinde & Milligan, 2011; Milligan & Bazinet, 2008; Skibieli *et al.*, 2013). Maternal parasite load is associated with lower milk production in cows (Perri *et al.*, 2011) and milk fat concentration in rhesus monkeys (Hinde, 2007). Moreover, although mothers synthesize milk, accumulating evidence suggests that sometimes milk differs between

sons and daughters in red deer, bank voles, cows, wallabies, rhesus monkeys, and humans (reviewed in Hinde *et al.*, 2014). Some milk bioactives, such as glucocorticoids, vary substantially among mothers (Grey, Davis, Sandman, & Glynn, 2013) and has recently been shown to reflect maternal life history (Hinde *et al.*, 2014). Better knowledge of sources of variation, especially for milk constituents linked to maternal condition can lead to more personalized clinical recommendations for mothers and their infants. Such knowledge has the potential to inform decisions about breast-feeding initiation and duration, improve replacement and supplemental formula compositions, and husbandry practices and nursery rearing of mammalian young in research or agricultural settings.

Typically the public discourse on breastfeeding among WEIRD societies [Western, educated, industrialized, rich, and democratic (Henrich, Heine, & Norenzayan, 2010)] has remained preoccupied with addressing infant outcomes: growth, obesity, health, and cognition (Colen & Ramey, 2014; Morales *et al.*, 2011; Neville *et al.*, 2012). Importantly though, breastfeeding may specifically benefit the physical and psychological health of mothers (Labbok, 1999). Breastfeeding reduces breast and ovarian cancer risk in many women (Friebel, Domchek, & Rebbeck, 2014; Luan *et al.*, 2013; Möller, Olsson, Ranstam, & Collaborative Group on Hormonal Factors in Breast Cancer, 2002). Obesity is also an established public health concern. A recent meta-analysis revealed that the relationship between breastfeeding and post-pregnancy weight loss is variable (Neville, McKinley, Holmes, Spence, & Woodside, 2014). However, in 4/5 of the most methodologically rigorous such studies, mothers who breastfed retained less of their pregnancy weight than did mothers who did not breast feed (Neville *et al.*, 2014). In the moment, breastfeeding seemingly buffers women from stress via down-regulation of the physiological stress response system (Heinrichs, Neumann, & Ehlert, 2002). Women who breastfeed may also be more protected from developing osteoporosis, type 2 diabetes, and hypertension later in life (Agarwal & Stuart-Macadam, 2003; Ryan, 2012).

Mothers, however, are more than milk. Many factors contribute to infant-feeding practices and not all mothers are able to breastfeed for a variety of economic, medical, psychological, and cultural considerations. Beyond the milk she provides, the mother's body provides an "adaptively relevant environment" for the developing infant (Hinde, 2014). Contact of mother and infant, for example, during safe cosleeping, can contribute to a physiological coregulation of mother and infant (McKenna, Ball, & Gettler, 2007). Skin-to-skin contact, also known as *kangaroo care*, influences infant regulation in the hours after birth (Ferber & Makhoul, 2004). This behavioral contact between the infant and mother's bodies, the concurrent emotional and somatosensory stimulation, likely contributes to the neurobiological

changes occurring in the maternal brain as the mother-infant bond is established.

MOTHERHOOD CROSS-CULTURALLY

Motherhood in humans, however, is further embedded within psychological and cultural constructs (Cassidy & El Tom, 2015; Hrdy, 1999, 2009). Recently, Faircloth considered intensive motherhood as “Identity Work.” In light of her work on attachment parenting among mothers in the United Kingdom, encouraged a new wave of an anthropology of parenting and consideration of a culturally constructed moral motherhood (2009). Indeed, culturally mediated and reinforced expectations of motherhood actuate manifestation of attitudes, behaviors, and identify of individual mothers. For example, among the Khmir in Tunisia, breast-feeding is seen as “evidence of *Baraka*: a life-sustaining force” (Creyghton, 1992, p. 37). *Baraka* not only bonds a mother to her child, but the life sustaining force permeates to all members of the household, so a healthy baby is perceived as a blessing on the entire family. Lactation lasts 2 years and the Khmir believe that only mother’s milk can affect the infant; if the baby is unwell it is because of milk illness due to maternal violations of expected behavior (Creyghton, 1992). Meehan compared trade-offs between subsistence work and infant caregiving among Aka and Ngandu mothers in the Central African Republic (2009). Their different subsistence patterns, the Aka are tropical forest foragers whereas the Ngandu practice slash-and-burn horticulture influenced the works demands and availability of helpers. Aka mothers were able to spend more time holding their infants than did Ngandu mothers (Meehan, 2009). Mothers may care for sons and daughters differently as reflects cultural preferences or evolutionary adaptive allocations (Margulis, Altmann, & Ober, 1993; R. Quinlan, M. Quinlan, & Flinn, 2005; Wander & Mattison, 2013). Moreover motherhood can extend well into advanced years; indeed the grandmaternal niche is a crucial human attribute and contributes to the features that characterize human cooperative breeding (Scelza, 2009). Even within a patrilocal society in which women live with or near their husband’s families, they still maintain contact with their own kin (Scelza, 2011). Among the Himba pastoralists of Namibia women maintain relationships and access to their mothers, through periodic visitation (Scelza, 2011). Indeed the cultural and cooperative context in which human mothers are rearing their infants and children is experiencing a resurgence of research effort, integrating the social transmission as well as adaptive significance of motherhood.

KEY ISSUES GOING FORWARD

Here we have considered motherhood from the perspective of the mother, rather than through the outcome of her mothering—the infant. In the coming years and decades we will benefit from the continued investigation of maternal behavior and the underlying neurobiology and physiology as well as for humans within the cultural context in which motherhood occurs. Increasingly studies are integrating multiple facets of motherhood simultaneously which has a multiplicative rather than additive affect on our understanding of motherhood. Of particular importance will be integrative studies that assess the multiple pathways of maternal input to young—their behavioral care and their physiological investment (Hinde, 2013). Such studies will have important translational potential to world health and public policy. The focus on motherhood and the importance to infants, however, risks depriving mothers of personhood. Emphasizing the maternal “exalts women as mothers and not women qua women” (Waggoner, 2013). Disentangling the maternal from the feminine is an important and emerging area of research in the fields of gender studies, the history of science, and other fields in which social science and public health intersect.

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Katie Hinde earned her BA in Anthropology from the University of Washington in 1999, MA in Anthropology from UCLA in 2003, and PhD in Anthropology from UCLA in 2008. Her post-doctoral training was in Neuroscience at the California National Primate Research Center, UC Davis from 2009 to 2011. In her Comparative Lactation Lab they investigate how mother's milk contributes to infant behavioral, psychobiological, and somatic development in socially complex taxa, particularly humans and nonhuman primates. She established descriptive values for rhesus macaque milk production across lactation, and demonstrated the effects of maternal life-history and infant sex on milk synthesis. In addition to journal publications, Hinde coedited "Building Babies: Primate Developmental Trajectories in Proximate and Ultimate Perspective" released by Springer in 2013. Her ARMMS Program (Archive of Rhesus Macaque Milk Samples) makes hundreds of milk samples available to colleagues to assay for bioactive factors. Hinde is an Associate Editor and writer for *SPLASH! Milk Science Update*, executive council member for the International Society for Research in Human Milk and Lactation (2013–2015), and showcases research on mother's milk, breastfeeding, and lactation for the general public, clinicians, and researchers on her blog "Mammals Suck... Milk!"

Links: <http://mammalssuck.blogspot.com>;

<http://www.people.fas.harvard.edu/~khinde/contact.html>.

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