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Physiological mechanisms, behavioral and psychological factors influencing the transfer of milk from mothers to their young

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ABSTRACT

This article is part of a Special Issue "Parental Care".

Producing milk to support the growth of their young is a central element of maternal care in mammals. In spite of the facts that ecological constraints influence nursing frequency, length of time until weaning and the composition of milk, there is considerable similarity in the anatomy and physiology of milk production and delivery across mammalian species. Here we provide an overview of cross species variation in nursing patterns and milk composition as well as the mechanisms underlying mammary gland development, milk production and letdown. Not all women breastfeed their infants, thus in later sections we review studies of factors that facilitate or impede the initiation and duration of breastfeeding. The results of these investigations suggest that the decisions to initiate and maintain breastfeeding are influenced by an array of personal, social and biological factors. Finally, studies comparing the development of breastfed and formula fed infants as well as those investigating associations between breastfeeding, maternal health and mother/infant interaction are reviewed. Leading health agencies including the World Health Organization and CDC advocate breastfeeding for at least the first 6 months postpartum. To achieve these rates will require not only institutional support but also a focus on individual mother/infant dyads and their experience.

Introduction

Providing milk for their young is the defining characteristic of mammalian females. The energetic demands of lactation itself, as well as the need for ample food supply to support the growth of weanlings, mean that the timing of reproduction, the length of lactation and patterns of nursing are closely tied to species ecology (Hayssen, 1993). The basic elements of the mammary gland, its development during pregnancy and the processes of milk synthesis and letdown show considerable similarity across species, however, as do the hormonal mechanisms that control them (Lincoln and Paisley, 1982). In the first part of this paper we present a brief overview of cross species variation in lactational strategies and in the second we describe the mechanisms underlying milk synthesis and letdown. Technological advances have freed women in some societies from many of the ecological constraints, e.g. large seasonal fluctuations in food availability, imposed on other species. In addition, the development of nutritionally adequate substitutes for breast milk has made breastfeeding optional rather than obligatory for large numbers of women. The variations in behavior that this has produced have allowed the investigation of those factors that influence the decision to initiate breastfeeding and its duration, as well as the association between breastfeeding and wellbeing of both members of the mother infant dyad.

Cross-species overview of lactation

A mammary gland comprising alveoli and a duct system is seen in all mammals but other aspects of gland morphology vary across species. For example, the mammary glands of goats and cows contain cisterns where milk collects, whereas in other species the milk is stored in the alveoli and ducts (Lincoln and Paisley, 1982). In most mammals milk ducts exteriorize through a nipple structure although the extent to which ducts converge varies (Anderson et al., 2007) and in monotremes there is no nipple structure and the milk ducts simply open onto the skin (Oftedal, 2002). The gross anatomy of the mammary gland is not the only element of lactation that shows cross-species variation, milk composition, the frequency at which young are nursed and the duration of lactation are also species specific.

Milk composition

The gross energetic content of milk varies dramatically across species, as does the macronutrient content. In general, species in which mothers fast for all or part of lactation, such as some seals as well as

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bears and baleen whales, produce milk that is high in fat and lower in sugar a composition that reflects the use of maternal energy stores to support milk production (Oftedal, 2000). Fur seals, for example, secrete milk that has a cross energy content of 516 kcal/100 g and comprises approximately 53% fat by weight, whereas the fat content of rat milk is only 9% and its gross energetic value is 131 kcal/100 g (see Jenness, 1986for review).

It has been suggested that there is an association between the fat content of maternal milk and nursing frequency (Ben Shaul, 1963; Jenness, 1986). Thus, milk high in fat is associated with long maternal absences (Sharp et al., 2006) whereas the "on demand" nursing pattern seen when mothers and their young stay in close contact for long periods of time is associated with milk that is higher in carbohydrate and low in fat (Oftedal, 2000).

Milk composition varies not only between species but also as the young develop. For example, in marsupials milk composition changes with the age of the young so that carbohydrate content of the milk increases over the first six months of nursing (Messer and Green, 1979). Since nursing two offspring, one continuously attached to a nipple and the other fully mobile although still returning to the pouch to nurse, is common in these animals they have developed the capacity to produce milk of different composition from each nipple (Messer and Green, 1979). Studies of bonnet macaques (*Macaca radiate*) have shown an increase in milk lipid and protein content as well as concentration of electrolytes with offspring age a pattern similar to that seen in other monkeys as well as in humans (Laudenslager et al., 2010). In some species both milk composition and milk yield have also been shown to vary with the sex of offspring and these differences may be programmed by intra uterine factors (Hinde, 2009; Hinde et al., 2013, 2014).

Experimental studies in rodents have demonstrated that variations in nutritionally adequate maternal diets can also influence milk composition. For example, rat dams fed a high saturated fat diet produced milk higher in saturated fats than rats eating a diet high in unsaturated fat (Priego et al., 2013). Further, Walker and her colleagues have shown in rodents that maternal diet effects on milk composition can have longlasting consequences for the phenotype of the offspring. They demonstrated that feeding rat mothers a high fat diet increased the fat content of their milk and resulted in offspring that showed higher circulating concentrations of the metabolic hormone leptin as early as Day 10 postpartum, as well as alterations in the stress axis, both in infancy and adolescence (Trottier et al., 1998).

Compared to other species human breast milk is relatively low in fat. Postpartum, women initially secrete a liquid, colostrum that has a relatively low level of lactose and a high concentration of immunoglobulins (Ballard and Morrow, 2013). There is a transition to mature milk production within 3–4 days postpartum. Estimates of the composition of human breast milk typically show considerable variability across individuals (Allen et al., 1991) but the averages reported across studies are quite consistent ranging from 3.2 to 4.6% of fat by weight, 0.9–1.2% protein with an overall caloric content of 65–72 kcal/100 g (Jenness, 1986; Allen et al., 1991; Nommsen et al., 1991; Wojcik et al., 2009; Ballard and Morrow, 2013). The relatively dilute nature of human milk is consistent with that reported in other primates and with an "on demand" feeding pattern (Jenness, 1986). There is a small decline in protein content between birth and 6 months postpartum in human milk whereas fat content increased slightly in late lactation (see Allen et al. (1991) for review). In general, the milk produced by mothers that give birth prematurely has a higher protein and fat content than mature milk (reviewed in Ballard and Morrow, 2013).

In human populations, as in rodents, milk composition is influenced by the nutritional state of the mother. In a longitudinal study of milk volume and composition of a group of marginally nourished Bangladeshi women, Brown et al., (1986) found that milk volume was not greatly decreased relative to reference populations although there was a further decline when the food supply was lowest. Across all seasons, however, the fat content of the milk was lower in the Bangladeshi women than in the reference group. Interestingly, mothers with greater body fat stores as reflected in skinfold thickness produced milk with a higher fat content (Brown et al., 1986). These results are consistent with those of other studies documenting a decrease in fat content of milk from undernourished populations (see Allen et al., 1991). For example, Prentice et al. (1983) compared milk production and composition between two groups of Gambian women one of which was given a nutritional supplement for 12 months postpartum and found no effect on milk volume but a significant increase in milk fat content (Prentice et al., 1983). In contrast to the effects of long-term undernourishment on milk composition in women neither acute fasting nor increased plasma insulin, in the presence of a euglycemic clamp, affects milk production or composition. Inducing hyperglycemia for 4–6 h, however dramatically increased milk glucose content (Neville et al., 1993).

Adequate nutrition for the infant depends not just on macronutrient content of the milk but also on adequate concentrations of micronutrients (Valentine and Wagner, 2013). Allen (2012) has divided these micronutrients into two groups based on whether or not their concentrations in milk depended significantly on maternal intake. Group 1 micronutrients include Vitamins A, B6, B12 and D as well as thiamin riboflavin, choline, selenium, iodine and retinol and Group 2 comprises calcium, iron, copper, zinc as well as folate (Allen, 2012). Concentrations in breast milk of the nutrients in Group 1 depend heavily on their availability in the maternal diet or maternal status whereas those in Group 2 are relatively independent of these factors. In a recent meta-analysis, Allen showed that in cases were women were clearly deficient in B vitamins, dietary supplements rapidly increased their concentration in breast milk (Allen, 2012).

Vitamin D levels in breast milk are often below recommended level and supplements are recommended both for infants and their mothers (Valentine and Wagner, 2013). Although Vitamin D is obtained through diet, synthesis in skin in response to ultraviolet light is also a major source of this micronutrient (Dawodu et al., 2015). In a study of vitamin D levels in infants across three centers in the US, Mexico and China, Dawodu et al. (2015) found that rates of vitamin D deficiency varied from a low of 12% in the US (Cincinnati) to a high of 62% in China (Shanghai). Sun exposure, season, as well as vitamin D supplementation, all contributed to the differing patterns of Vitamin D deficiency (Dawodu et al., 2015).

In addition to nutrients, milk contains a large number of other biologically active components including growth factors such as brain-derived neurotrophic factor and glial derived neurotrophic factor as well as epidermal growth factor, chemokines and cytokines (see Ballard and Morrow (2013) for review). Maternal hormone levels also influence the hormonal content of breast milk and may have long lasting effects on infant development. For example, suckling stimulates maternal secretion of cortisol (Tucker and Schwalm, 1977), which easily passes to breast milk and thus, may influence infant physiology (Pacha, 2000).

Duration of lactation

In general, across species the length of lactation positively correlates with body size (Hayssen, 1993; Langer, 2003, 2008). Within this general relationship, however, there are some distinctive outliers. For example, earless seals have a much shorter period of lactation, only 4 days (Bowen et al., 1985) than would be predicted by their body mass, perhaps because of the transient nature of the sea ice on which they nurse. Primates, marsupials and bats, on the other hand, have longer periods of lactation than would be predicted on the basis of their body size, which has been associated with a long period of postnatal development in these species (Hayssen, 1993). Langer divided lactation into two functional periods: a milk only period during which young are solely dependent on mother's milk and a transitional or weaning period during which young still receive