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REPORT

The immunological function of allosuckling

Alexandre Roulin and Philipp Heeb
Department of Zoology, University of Bern, CH-3032 Hinterkappelen, Switzerland.
E-mail: aroulin@esh.unibe.ch

Abstract

Young mammals are unable to mount an efficient immune response against invading pathogens. Until their immune system is mature mothers transmit to their young immunological compounds during lactation. Given that genetic and foster mothers can assume this protective role, we propose that young mammals may gain immunological benefits by suckling more than one nursing female, a behaviour referred to as "allosuckling". This hypothesis has so far not been considered as a potential explanation for the propensity of young mammals to suckle foster mothers. However, pathogen transmission through milk during allosuckling may reduce the immunological net benefit that young gain, and furthermore allosuckling may increase pathogen transmission between foster and genetic mothers implying costs of allosuckling for all participants. Here, we develop the immunological function of allosuckling hypothesis (IFA) as a potential explanation for intra-and interspecific variation in allosuckling frequency. We present published experimental evidence for the assumption that immunological benefits of allosuckling depend on the immunological status of the offspring, the foster and the genetic mothers. Finally, we give predictions arising from the IFA hypothesis and propose that the IFA may provide a new explanation as to why neonates suckle various females and why foster females often refuse to nurse nonoffspring.

Keywords

Alloparental care, allosuckling, antibody, human, immunology, lactation, mammal, parent–offspring conflict, pathogen

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INTRODUCTION

In a number of mammalian species, neonates suckle milk from females that are not their genetic mothers, a behaviour called "allosuckling". In a review of nonoffspring nursing, Packer *et al.* (1992) found that allosuckling took place in 68 out of 100 species, and in some of them the amount of suckling on the foster mother was as frequent as on the genetic mother. Ekvall (1998) also observed that within a population of fallow deer, *Dama dama*, females varied in the extent to which they accepted to nurse nonoffspring. There thus appears to be ample inter- and intraspecific variation in the frequency of allosuckling. The key problem in understanding the evolution of allosuckling is to determine what are the costs and benefits associated with this behaviour. Lactation in mammals is energetically costly, leading to a reduction of the residual reproductive value of the nursing females (Prentice & Prentice 1988; Clutton-Brock *et al.* 1989). Theory of parent–offspring conflict over parental investment suggests that mothers are reluctant to transfer the total amount of milk that their own offspring, and particularly nonoffspring, request to grow at maximal rate (Trivers 1974; Rogowitz 1996).

Several explanations have been proposed for the widespread nonoffspring nursing behaviour of females. Packer *et al.* (1992) reported that, in mammalian species having only one offspring, allosuckling was apparently the result of the young stealing milk from the foster mother. Allosuckling may thus be seen as a case of social parasitism by the young (Ekvall 1998). An alternative hypothesis proposes that foster mothers may obtain inclusive fitness benefits by providing energetically rich milk to related nonoffspring (Wilkinson & Baker 1988; Packer *et al.* 1992; Pusey & Packer 1994). For instance, in the house mouse, *Mus musculus*, sisters pool and rear their litters in a communal nest (König 1994). Allonursing by lactating females to unrelated offspring is also common (Packer *et al.* 1992; Wilkinson 1992), and it has been proposed that females reciprocate with unrel-ated females by nursing each others offspring (Packer *et al.* 1992; Ekvall 1998). No experimental tests of these different

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hypotheses have yet been conducted, and the fitness benefits obtained by foster mothers due to allosuckling remain unclear (Pusey & Packer 1994; König 1997).

So far, evolutionary ecologists considered that neonates gain extra energetically rich food by suckling foster mothers (Riedman 1982; Packer *et al.* 1992) given that milk contains large amounts of proteins, lipids and carbohydrates (Prentice & Prentice 1988; Clutton-Brock 1991). However, this explanation does not consider the vital immunological benefits of lactation for the young. Young mammals are unable to mount an efficient immunological response against invading pathogens. Until their immune system is mature the mother provides the necessary immune compounds during lactation (Watson 1980; Newman 1995).

In the present paper, we propose that besides a gain in nutrients by suckling various females, young mammals may simultaneously improve their immunocompetence. In this context, we first describe the mechanisms of immunity derived from maternal milk. Second, we present experimental evidence that foster mothers can supply immunity to nonoffspring. Third, we examine the possibility that pathogen transmission during lactation may reduce the immunological net benefit of allosuckling. Finally, we propose that the transmission of both immunological compounds and pathogens during allosuckling could potentially account for variations in the frequency of allosuckling within and among species. We call this novel hypothesis the "Immunological Function of Allosuckling" hypothesis, or "IFA" in short.

IMMUNOLOGY OF LACTATION

Maternal milk contains many immunological compounds participating in the protection of the offspring against pathogens (Newman 1995). Antibodies (Ab) or immunoglobulins (Ig) are the most studied and probably the most important immunological components in milk (e.g. Gustafsson *et al.* 1994, 1996). For simplicity, hereafter we will refer mainly to Ab. In some mammalian taxa the mother transfers Ab to the foetus through the placenta (Watson 1980). In all taxa, mothers transfer to offspring, shortly after delivery, large amounts of Ab in the colostrum and, up to weaning, low Ab-concentrated milk (Butler 1979; Watson 1980; Berthon & Salmon 1993). Because allosuckling usually takes place when young are able to move towards lactating foster mothers (Ekvall 1998), we will focus here on the immunological aspects of milk rather than colostrum.

The gastrointestinal and respiratory tracts of young mammals are invaded by a wide range of parasites including worms, bacteria, viruses, fungi and protozoa (hereafter all referred to as pathogens), which draw resources from the young and cause cell lysis (Abbas *et al.* 1994). Ultimately these pathogens depress the fitness of their host (Arnold & Lichtenstein 1993; Roelke-Parker *et al.* 1996). To complete growth and maturation of tissues, young have therefore to eliminate or keep under control the proliferation of pathogens (Behnke *et al.* 1992; Sams *et al.* 1996). Before the immune system of the suckling young is mature, the mother assumes this protective role by transferring Ab during lactation (Gillin & Reiner 1983; Villalpando & Hamosh 1998). For instance, in humans, breast-fed infants appear to be less susceptible to pneumonia and gastroenteritis than bottle-fed infants (Liu & Wang 1995; Wright *et al.* 1998).

Mother and offspring live in the same environment, and therefore have a high probability of sharing similar pathogens. Pathogens display on their surface a wide range of antigens inducing the production of specific maternal Ab (Abbas *et al.* 1994). After having been transferred through milk into the offspring, these Ab react with the same category of antigens (Newman 1995). The ingested maternal Ab can have therapeutic effects when transferred at the time of infection. For instance, maternal IgA protects the gastrointestinal tract of the suckling young by blocking the initiation of bacterial or viral infections, neutralizing enterotoxins, opsonizing bacteria or facilitating their phagocytosis (Reiter 1978; Watson 1980). The ingested maternal IgG are absorbed through the intestines of the neonate, enter the bloodstream and can be transported up to peripheral body sites from where pathogens are spreading (Watson 1980). Moreover, it has been shown that neonates are better protected from diseases when provided with milk containing high rather than low concentrations of Ab (Gustafsson *et al.* 1994). Ingested specific maternal Ab can also have prophylactic effects when they have a subsequent immunological activity, at the time of first pathogen infestation (Gustafsson *et al.* 1994; Villalpando & Hamosh 1998).

Most Ab present in milk are not produced by the mammary tissue but transported from blood to the mammary gland (Watson 1980). The amounts of milk produced as well as the concentration of Ab vary throughout the lactation period and among teats (Klobasa & Butler 1987; Hoy *et al.* 1995; Weaver *et al.* 1998). Because the production of specific Ab following an infection is limited in time, a mother needs to be re-immunized if she is to confer immunity to offspring during the whole suckling period. Moreover, because the production of specific Ab packed in milk is induced by pathogens displaying specific antigens (Dimitrijevic *et al.* 1995; Abbas *et al.* 1994), previous contact with a given pathogen will determine whether a female can transmit to her progeny Ab directed specifically against this pathogen. Mounting of a specific immune response can take several days (Goldblum *et al.* 1975) to several weeks (Roitt *et al.* 1996), a period too long to protect offspring efficiently against virulent pathogens (Andrews & Hewlett 1981). Thus, mothers can vary in

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their ability to transfer immunity to offspring if they differ in their past exposure to pathogens.

Another source of variation in the production of specific Ab is differences in genetic make-up between females (Abbas *et al.* 1994). Selection experiments with mice have demonstrated that the ability to produce large amounts of Ab is heritable (da Silva *et al.* 1998). Thus, females can vary in their efficiency to control parasite infection, for instance because they have different alleles allowing them to produce different amounts of specific antibodies in response to antigenic challenge (Roitt *et al.* 1996). Genetic variation also occurs at other genes than those controlling humoral immunity. For example, variation in the activity of macrophages can have a genetic component (Roitt *et al.* 1996), and macrophages are transmitted through milk into offspring (Newman 1995). Genetic variation also occurs at the major histocompatibility complex (MHC), which are molecules displayed at the cell surface of lymphocytes, and used for immune recognition (Abbas *et al.* 1994). Different MHC-alleles confer resistance to different parasites (Apanius *et al.* 1997). Given that lymphocytes are passed on from mother to offspring during lactation (Newman 1995), MHC may play a role in the immunological protection of neonates.

Finally, poor nutritional condition and stressful environments tend to inhibit the maternal production of Ab (Ader & Cohen 1985; Gorczynski 1992; Weaver *et al.* 1998) and females in different phenotypic condition may vary in their ability to transfer immunocompetence to offspring (Sams *et al.* 1996). Females in poorer condition can produce a smaller amount of milk (Brussow *et al.* 1996) or milk with lower Ab concentrations (Weaver *et al.* 1998).

IMMUNOLOGICAL BENEFITS OF ALLOSUCKLING

Experimental evidence that foster mothers can confer immunity against pathogens to foster offspring have been provided using knock-out laboratory mice lacking functional B cells. Gustafsson *et al.* (1994) showed that immunodeficient mice raised by immunodeficient foster mothers successfully completed their development only in pathogen-free environment. In nonsterilized conditions immunodeficient mice survived and grew normally only when suckling immunocompetent foster mothers. In nonsterilized environments phenotypically normal mice survived and grew normally only if raised by immunocompetent mothers. In another experiment, Gustafsson *et al.* (1996) showed that mice nursed by immunodeficient mothers grew normally when artificially administered monoclonal Ab, whereas offspring not provided with Ab grew at a slow rate and died more often. Two conclusions for the IFA hypothesis can be made from Gustafssons' experiments. First, immunological compounds supplied by foster mothers *per se* improved the growth and the survival prospect of immunodeficient foster offspring. Second, the benefits young obtained from suckling foster females depended on the immunological status of the young, the genetic mother and the foster mother (Fig. 1).

IMMUNOLOGICAL COSTS OF ALLOSUCKLING

Determining the immunological costs of allosuckling might help explain why allosuckling often does not occur. Milk is not only a way for immunological compounds to be transferred from mother to offspring but it also constitutes the milieu where pathogens can be transmitted among hosts. For instance, women infected by syphilis, hepatitis B, or HIV can infect their babies during lactation (Fildes 1988; Ewald 1994; Kreiss 1997; Vochem *et al.* 1998). Thus, an allosuckler runs the risk of contracting

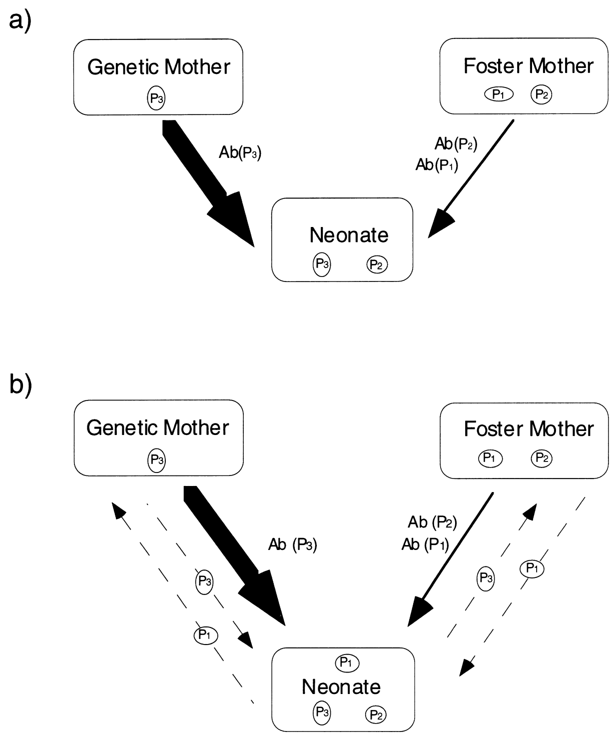

Figure 1 Immunological interactions during allosuckling. (a) No pathogen transmission takes place during lactation. The neonate gains extra milk by suckling a foster mother (thin filled arrow) which contains antibodies against pathogens P1 and P2 not present in the milk of the genetic mother (large filled arrow). The neonate obtains antibodies against P3 only from the genetic mother. (b) Pathogens are transmitted during lactation. During allosuckling the neonate not only obtains antibodies but risks being infected by pathogen P1 from the foster mother (dashed arrow). The neonate can transmit P1 to his/her genetic mother during nursing. The foster mother has a risk of being infected by pathogen P3 during allonursing.

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pathogens carried by the foster mother (Fig. 1b). Transmission of pathogens can also go from the young to the lactating mother. For example, in humans, babies carrying syphilis can transmit the disease to wetnurses (Fildes 1988). Lambs transferring bacteria to the teats of ewes (i.e. mastitis; Scott & Jones 1998) is another example. Thus, by allowing nonoffspring to suckle them, lactating females incur a risk of contracting new pathogens towards which they may not have the necessary immunological defenses. New pathogens can infect the mammary gland resulting, for instance, in a reduced milk production (Maunsell *et al.* 1998). This may reduce the current and/or future reproductive success of the lactating female and affect her propensity to nurse nonoffspring.

Maternal Ab transferred to offspring have not only beneficial effects but may also have a detrimental impact on neonatal growth. For instance, specific Ab absorbed by the offspring can bind directly to epitopes located at the surface of the pathogen and consequently decrease the stimulation and retard the maturation of the neonates' immune system (Carlier & Truyens 1995; Wold & Adlerberth 1998). Moreover, maternal Ab can react with the neonate erythrocytes leading to haemolytic diseases (Watson 1980). Despite these costs, maternally derived Ab are believed to commonly provide net benefits to offspring (Watson 1980; Carlier & Truyens 1995). In sum, under immunological costs we consider the fact that transferred Ab can have pathological effects on neonates and that the transmission of pathogens during lactation can negatively affect the health of all three participants (Fig. 1b).

PREDICTIONS OF THE IFA HYPOTHESIS

In its simplest form, allosuckling involves three participants, the allosuckler, the genetic mother and the foster mother. We expect that the frequency of allosuckling is influenced by the magnitude of the immunological benefits achieved by the allosucklers, but also by the frequency of pathogen transmission during lactation between the foster young and both the foster and the genetic mothers (Fig. 1). Below, we make three predictions based on the unexplored premises that immunological benefits of allosuckling and pathogen transmission can affect patterns of allosuckling in mammals. For clarity, we present predictions in two parts depending on whether pathogens are transmitted or not during lactation (Fig. 1a, b). This difference may be useful when considering microparasites (e.g. virus, bacteria) that can be transmitted through milk, and macroparasites (e.g. macroscopic worms, insects, acarians) that cannot. This list of predictions is nonexhaustive and is likely to grow as more knowledge on the immunological function of allosuckling and the dynamics of pathogen transmission during nonoffspring nursing becomes available.

Pathogens not transmitted during lactation (Fig. 1a)

Prediction 1. The immunological benefits of allosuckling increase with the intensity of pathogen infestation or the virulence of pathogens contracted by neonates.
Young mammals with higher burdens of pathogens or infected by virulent pathogens may benefit by obtaining Ab from other females than only those provided by their genetic mother. One assumption of this prediction is that by suckling several mothers young are able to mount a stronger immune response against pathogens, either through an increase in the amount of specific Ab or due to the presence of Ab with different paratopes for the same pathogen (for the same antigen different individuals can produce different specific Ab referred to as paratope, Roitt *et al.* 1996). It is expected that experimentally infected young will clear infections more efficiently if they are fed with milk from several mothers compared to young fed with the same quantity of milk from a single mother. Thus, allosucklers should grow better and have a higher survival rate.

Prediction 2. Young derive greater immunological benefits by suckling various females when their genetic mother lacks specific Ab against a pathogen or produces lower amounts of Ab.
The genetic make-up and phenotypic condition of the mother will determine her ability to mount an efficient immune response, and in turn her ability to transfer immunocompetence to offspring. Thus, it is expected that neonates of susceptible mothers infected by a pathogen are more likely to allosuckle compared to neonates of resistant mothers infected by the same pathogen. This prediction raises the possibility that females lacking specific Ab or being unable to produce sufficient amounts of Ab may promote allosuckling by their offspring.

Pathogens transmitted during lactation (Fig. 1b)

Prediction 3. High levels of allosuckling increase the rate of pathogen transmission.
In the case where allosuckling facilitates the transmission of pathogens, pathogen prevalence is expected to be higher in groups showing a higher frequency of allosuckling. This prediction should hold for both intra- and interspecific comparisons. A first corollary of this prediction states that mothers should develop stronger resistance towards nursing nonoffspring in groups infected by virulent than less virulent pathogens transmitted during lactation. A second corollary states that if the genetic mother has a risk of contracting pathogens from foster mothers through allosuckling of their young, she should prevent her offspring from suckling other females.

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CONCLUSION

The aim of this paper is to suggest the transfer of both immunological compounds and pathogens during lactation as new and potentially important aspects for understanding the evolution of allosuckling. The IFA hypothesis complements the commonly described nutrient benefits obtained by nonoffspring suckling foster mothers (Rogowitz 1996). The IFA hypothesis makes new predictions about the likely costs and benefits of allosuckling for neonates, foster mothers and genetic mothers. Because young mammals that suckle foster mothers for immunological benefits may also ingurgitate extra milk, and thus may obtain simultaneously energetical benefits from allosuckling, experiments will be required to test the relative importance of energetic and immunological benefits of allosuckling.

The IFA hypothesis may provide a functional explanation for the prevalence of wetnursing and allosuckling in human societies where mothers cross-foster babies for breastfeeding (Fildes 1988). Each woman of a cross-foster group may invest the same energy in lactation but each baby is fed on the milk of various mothers that are not necessarily related, forming so-called "milk kinships" (Fildes 1988; Khatib-Chahidi 1992). Moreover, in humans the transition in food production from hunter-gatherers to farmers led to an increase in population sizes/densities and resulted in the emergence of virulent pathogens (Diamond 1998). The IFA hypothesis would suggest that patterns of allosuckling in human societies covary with the type of food production and the related risk of pathogen infestation. Finally, the IFA hypothesis may provide an explanation for the evolution of lactation induction in nonpregnant females (Creel *et al.* 1991) where allosuckling would allow related young to gain immunological benefits from various females. In the dwarf mongoose, *Helogale parvula*, pseudopregnant subordinates suckled related nonoffspring, and litter sizes with spontaneous lactators were larger than litters without lactating subordinates (Creel *et al.* 1991).

The IFA proposes that pathogen transmission can increase the costs of allosuckling for the allosuckler, the foster mother and the genetic mother (Fig. 1b), and may thus explain why allosuckling was more frequently observed in intermediate-sized groups (Packer *et al.* 1992). In mammals, parasite prevalence, infestation intensity and parasite richness have been found to increase with group size/density (Møller *et al.* 1993; Arneberg *et al.* 1998; Morand & Poulin 1998). The optimal level of allosuckling may be achieved at intermediate group size and/or densities. For example, in large groups allosuckling may increase disproportionally the rate of pathogen transmission, whereas in small groups the cost of parasitism could be low and allosuckling may not be required to improve immunocompetence of neonates. A promising issue would be to determine whether the frequency of allonursing/wetnursing before, during and after pathogen epidemics correlates with the fitness of individuals.

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BIOSKETCH

Alexandre Roulin's main research interests are centred on sexual selection, the evolution of ornamentation signals displayed by females, and on the interactions between parents and offspring in the context of parent–offspring conflict theory.

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