

Females of the communally breeding rodent, *Octodon degus*, transfer antibodies to their offspring during pregnancy and lactation

María Inés Becker^{a,b}, Alfredo E. De Ioannes^{a,c},
Cecilia León^d, Luis A. Ebensperger^{d,*}

^a Departamento de Investigación y Desarrollo, BIOSONDA, Chile

^b Fundación Ciencia y Tecnología para el Desarrollo, Chile

^c Departamento de Microbiología y Genética Molecular, Facultad de Ciencias Biológicas,
Pontificia Universidad Católica de Chile, Chile

^d Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile and
Centro de Estudios Avanzados en Ecología & Biodiversidad, Casilla 114-D, Santiago, Chile

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Abstract

Females in numerous rodent species engage in communal nesting and breeding, meaning that they share a nest to rear their young together. One potential benefit to communally nesting mothers is that infants improve their immunocompetence. Thus, suckling from two or more females might provide newborns with a more diverse array of antibodies and defensive cells. As a first step toward testing the immunocompetence hypothesis, we assessed whether female degus (*Octodon degus*), a communally nesting and breeding caviomorph rodent, transfer immunoglobulins to their young through the yolk sac or placenta while in the uterus and, during lactation, through milk. With this aim, adult degu females were immunized with four antigens, including two mollusk hemocyanins from *Concholepas* and *Megathura* (CCH and KLH, respectively), porcine thyroglobulin and tetanus toxoid. Specific antibodies against the experimental antigens were used to track the origin of antibodies in the young. To establish the presence of specific antibodies of IgG and IgA isotypes in sera and milk of animals, an indirect enzyme-linked immunosorbent assay (ELISA) was developed. Degu females produced specific antibodies against antigens not found in their natural environment, and mothers were able to transfer the induced antibodies to their litters during pregnancy (IgG) and during lactation (IgA). However, we recorded only limited evidence of degu offspring acquiring antibodies from lactating mothers other than their own, giving little support to the increased immunocompetence hypothesis.

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1. Introduction

Individuals of numerous rodent species engage in group-living, meaning that they share an area of activity,

a nest (or den), and interact more frequently with group members than with individuals from other groups. When group members share a nest during breeding and rear their young together, they are regarded as communal breeders (Hayes, 2000; Lewis and Pusey, 1997; Solomon and Getz, 1997). Under these conditions, female breeders may incur a cost of providing milk to less related or totally unrelated offspring (Hayes, 2000). The provision

* Corresponding author. Tel.: +56 2 6862733; fax: +56 2 3542621.
E-mail address: lebensperger@bio.puc.cl (L.A. Ebensperger).

of milk to unrelated offspring is costly, given that lactation represents the most energetically expensive cost of breeding rodents and mammals (Thompson, 1992), and lactating females pay a fitness cost in terms of subsequent survival and reproductive success (Clutton-Brock et al., 1989). Providing milk and other parental resources to unrelated offspring may involve additional short-term costs such as increased transmission of internal and external pathogens to mothers and pups (Roulin and Heeb, 1999). Therefore, explanations for the occurrence of communal breeding tend to rely on direct and indirect benefits that compensate such drawbacks, including protection of young from infanticide or predation, improved thermoregulation of young, improved growth of young through enhanced milk intake, reduction of maternal energy costs and adoption of young whose mothers die (Hayes, 2000; Lee, 1989; Lewis and Pusey, 1997; Riedman, 1982; Roulin, 2002). Potential benefits, however, include the possibility that infants improve their immunocompetence (Roulin and Heeb, 1999). Thus, suckling from two or more, genetically different, lactating females might provide newborns and young with a more diverse and polyvalent population of immunoglobulins and defensive cells (macrophages, dendritic cells and lymphocytes).

Evidence that young improve immunity through the milk of foster mothers is well known in humans, laboratory primates and mice. Thus, human milk is known to have several cells and molecules that enhance protection from microbes and parasites (Gillin and Reiner, 1983; Newman, 1995). More importantly, protective cells (e.g., leukocytes) and immunoglobulins can resist digestion and cross the intestinal epithelium of neonates (Xanthou, 1998; Van de Perre, 2003). As might be expected, breast-fed infants experience less illness and mortality than formula-fed infants (Dewey, 1998; Villalpando and Hamosh, 1998). In mice, B-cell deficient neonates nursed from B-cell normal foster mothers develop higher levels of serum IgG and splenic B cells (Arvola et al., 2001). More importantly, neonatal mice nursed from immunoglobulin-deficient mothers grow relatively less and suffer high mortality early in life (Gustafsson et al., 1994). The only available study on free-living wild rodents demonstrated that maternal antibodies postpone hantavirus infection and enhance breeding success in the bank vole *Clethrionomys glareolus* (Kallio et al., 2006).

In contrast to that in humans and a few other animal models, very little is known of free-living wild species (Kallio et al., 2006) and communally breeding species in particular. In this study, experiments were designed to investigate whether female degus (*Octodon degus*), a caviomorph rodent from central Chile, are able to achieve

passive transfer of humoral immunity to their litters, therefore, protecting them from pathogens. In particular, we examined whether specific antibodies are acquired through the yolk sac or placenta by young while in uterus, during lactation through the milk, or both. Evidence from mice and rats indicates that some immunoglobulins can be transferred to young through both ways (Carlier and Truysens, 1995). Differing from humans, where most IgG are transmitted to the fetus from amniotic fluid through the vascular system present in the placenta, mice and rats acquire most IgG from colostrum and milk (Rojas and Apodaca, 2002). Furthermore, immunoglobulin transport in rodents, bovines, cats and ferrets takes place across the intestinal epithelium into the neonatal circulation (Van de Perre, 2003). This transfer is carried out by enterocytes located in intestinal crypts and on the surface of villi that express surface membrane FcRn receptors that bind IgG to facilitate their transcytosis (Rojas and Apodaca, 2002).

Degus are social rodents where a variable number of females (one to four) and one or two males share one or more underground burrow systems (Ebensperger et al., 2004; Fulk, 1976). More importantly, communally nesting groups include simultaneously lactating females (Ebensperger et al., 2004), and allonursing of young has been observed among captive individuals (Ebensperger et al., 2002). More recently, establishment of communal litters and allonursing were all recorded in captivity under conditions resembling natural settings, including a limited supply of food, but under an unlimited supply of nest boxes, i.e., burrows (Ebensperger et al., 2007). Intriguingly, this study revealed that some females within communal nests pay an immediate direct fitness cost in terms of reduced growth and survival of their pups to weaning age (Ebensperger et al., 2007). Therefore, the possibility that communally breeding females accrue other long-term fitness benefits, such as the enhancement of immunocompetence, to their offspring needs to be examined.

With this aim, we immunized adult degu females with four protein antigens, including two mollusk hemocyanins (one from *Concholepas concholepas* or CCH, and one from *Megathura crenulata* or KLH), tetanus toxoid (TT) and porcine thyroglobulin (TYG). We selected these antigens based on hemocyanins being powerful immunogens due to the absence of similar molecules in mammals, their large size and repeated subunit structure (Harris and Markl, 1999; Van Holde and Miller, 1995). Current applications of hemocyanins include their use as carriers for vaccines against pathogens and cancer (Markl et al., 2001; Moltedo et al., 2006), and in contraceptive vaccines to control wild animal populations

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