Indiscriminate nursing in communal breeders: a role for genomic imprinting

Abstract
In several communally nesting mammal species, females indiscriminately nurse each others’ offspring. Previous hypotheses have suggested that the inability to recognize one’s own young during lactation is the result of costs incurred from recognition errors. Here, we propose an alternative hypothesis based on sexual conflict theory and genomic imprinting. In polygynous species, males copulate with several females that may later breed communally. Under such conditions, males benefit from indiscriminate nursing of all their offspring and the reduced risk of female infanticide. This may have selected for paternally expressed genes that suppress kin recognition during lactation.

Keywords
Communal nursing, genomic imprinting, kin recognition, mammals, polygyny, sexual conflict.

In communally nursing species, two or more females indiscriminately foster each others’ offspring (e.g. König 1989; Manning et al. 1995). Experiments in rodents showed that dams do not discriminate between own young and those of others during lactation (Holmes & Sherman 1982). However, after weaning, mothers do discriminate between kin and non-kin (Kareem & Barnard 1982). While the advantages of kin recognition after weaning have been interpreted in the light of inbreeding avoidance, it is not clear why mothers are unable to discriminate during lactation. Clearly, selection should favour mechanisms that enable females to preferentially nurse their own young. Previous hypotheses explaining the absence of discrimination have focused on the fitness costs incurred from recognition errors or the difficulty of controlling exclusive nursing access to own young (Roulin 2002). Here we propose an alternative hypothesis based on sexual conflict theory and recent findings of the role of imprinted genes in kin recognition.

Males and females have conflicting interests over the amount of maternal investment in offspring, with males favouring more maternal investment than is optimal for the female (Houston & Davies 1985). In the absence of lifetime monogamy, males will be selected to exploit maternal resource allocation because they will not suffer from the female’s reduced ability to successfully raise future young. Recent studies have demonstrated that imprinted genes play a key role in the resolution of sexual conflicts (e.g. Lâ et al. 1999; Haig 2000), and are also involved in kin recognition in rodent species (Isles et al. 2002).

Several rodent species are characterized by a polygynous mating system where a male may copulate with several females (e.g. Zenuto et al. 1999). Thus, offspring in a communal nest will be more closely related through the paternal than the maternal line. From the female’s point of view, she is more closely related to her own offspring than to those of other females, and hence should not invest in such offspring. In contrast, it is in the male’s interest that all of his offspring are nursed regardless of their maternal origin. Further, female infanticide is unlikely to occur when they are unable to discriminate between own and alien young because of the risk of killing own offspring. This, in turn, will prove beneficial to the male. Therefore, benefits of indiscriminate nursing to males are more likely to be greater than the costs incurred by females. However, the costs of indiscriminate nursing may be lower when females are related (Wilkinson & Baker 1988; Manning et al. 1995; Dobson et al. 2000).

Imprinted genes show parent-of-origin-specific patterns of expression in that they are either paternally or maternally expressed. While imprinted genes are passed on in a mendelian fashion, only one allele is expressed depending on the sex from which it was inherited. For instance, a paternally expressed gene is active only when inherited from a male while the maternally inherited copy remains silent. The imprint is set during gametogenesis most likely through methylation of CpG-rich domains (Feil & Khosla 1999). Imprinted genes were found to play a key role in resource transfer between mother and embryo in utero. Studies in mutant mice that carried a deactivated gene demonstrated
that paternally expressed genes such as Igf1, Peg3 and Grf1 increase resource transfer from mothers to offspring pre- and postnatally (Itier et al. 1998; Li et al. 1999). The growth-enhancing effects of paternally expressed genes have been interpreted as the result of a conflict between males and females over how much maternal investment should be given to young (Haig 2000). In addition, imprinted genes were found to affect sensitivity to maternal odour cues and a possible role in kin recognition has been suggested (Isles et al. 2002). Genes of the major histocompatibility complex (e.g. RT1.A locus) that influence kin recognition abilities were also found to be imprinted (Manning et al. 1992; Kanbourshakir et al. 1993), suggesting that imprinting may play a role in sexual conflict resolution through effects on kin recognition. Most imprinted genes are regulatory genes (Feil & Khosla 1999) and their expression may be restricted to specific periods during development (Hvid et al. 1998). Thus, paternally expressed genes that are expressed during lactation in the offspring or in females may allow males to suppress other genes involved in discrimination. After weaning the advantages of inbreeding avoidance may become more important and the expression of the paternally suppressor gene may cease. In other words, we predict that in species in which males frequently sire offspring of females over how much maternal investment should be given to young (Haig 2000). In addition, imprinted genes were found to affect sensitivity to maternal odour cues and a possible role in kin recognition has been suggested (Isles et al. 2002). Genes of the major histocompatibility complex (e.g. RT1.A locus) that influence kin recognition abilities were also found to be imprinted (Manning et al. 1992; Kanbourshakir et al. 1993), suggesting that imprinting may play a role in sexual conflict resolution through effects on kin recognition. Most imprinted genes are regulatory genes (Feil & Khosla 1999) and their expression may be restricted to specific periods during development (Hvid et al. 1998). Thus, paternally expressed genes that are expressed during lactation in the offspring or in females may allow males to suppress other genes involved in discrimination. After weaning the advantages of inbreeding avoidance may become more important and the expression of the paternally suppressor gene may cease. In other words, we predict that in species in which males frequently sire offspring of females that nest communally, paternally expressed genes suppress the expression of genes involved in kin recognition during lactation because males benefit from indiscriminate nursing of their young. In particular, future research in knock-out mutant mice (i.e. mice with one specific gene being inactivated) of paternally expressed genes should focus on effects of imprinted genes in kin recognition during lactation.

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