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Maternal and offspring effects influence provisioning to mixed litters of own and alien young in mice

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In communally nesting species such as mice, nursing females may be confronted with alien and own young in mixed litters, and offspring may be fostered by either own or alien mothers. Because of the costly nature of maternal investment and offspring solicitation behaviour, maternal provisioning is expected to favour own young. While previous studies have investigated kin recognition between mother and pups with inconclusive results, it remains unexplored whether any such ability yields a fitness advantage for own pups when nursed in a mixed litter. Moreover, nursing females may have evolved strategies to effect a reduction in fitness costs associated with nursing alien pups, for example, reducing their maternal effort. In this study, we show that young mice procure an advantage by gaining relatively more weight than alien pups when nursed together in a mixed litter by their own mothers. However, we did not detect an effect of offspring or maternal genotype on this difference in weight gain. Furthermore, we show that mothers provide overall fewer resources to mixed litters than to unmixed litters and that two mouse strains differ in the magnitude of this reduction. We suggest that a combination of sibling competition and maternal strategies to reduce costs of nursing unrelated young may be the underlying causes of these findings.

Keywords: communal nursing; kin recognition; maternal provisioning; mice; *Mus musculus*; parent-of-origin-dependent effects; sibling competition

Many rodent species are known to nest cooperatively and are characterized by multiple breeding females per group (Manning et al. 1995; Solomon & Getz 1997; Hayes 2000). In many of these communally breeding species, including house mice, females may participate in the care of unrelated young, often in the form of allo-nursing (i.e. provisioning of milk to alien young; König 1997; see Packer et al. 1992 and Roulin 2002 for reviews on communal nursing). Lactation is energetically very demanding for the female and, as a consequence, providing milk to unrelated young is likely to incur fitness costs (Clutton-Brock et al. 1989; König 1989; Elwood 1991). Females are thus expected to distinguish pups in a communal nest and to favour their own over alien young (Elwood 1991; Jacquot & Vessey 1994; Roulin & Hager 2003). Previous studies investigating the extent to which mothers can discriminate kin have yielded inconsistent results. While the ability to distinguish kin from nonkin in adult mice has been reported in several studies (e.g. Kareem & Barnard 1982; Barnard & Aldhous 1991; Dobson et al. 2000; Heth et al. 2003), it remains unclear whether lactating females are able to distinguish own from alien young. For instance, Chantrey & Jenkins (1982) and Yamazaki et al. (2000) showed that female mice preferentially retrieve own pups within a short period of 3–10 min, whereas Ebensperger et al. (2006) report no difference in retrieval behaviour towards own versus alien pups by lactating females.

It seems rather more relevant to focus on potential effects of discrimination during lactation since the underlying rationale for an investigation of maternal discrimination are fitness costs incurred by directing resources to unrelated young (i.e. the effects of indiscriminate nursing) rather than the ability to discriminate per se. In this regard, König (1989) found no difference in pup weight comparing absolute bodyweight of own and alien

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young on 6 days during lactation, while a study by Hager & Johnstone (2005) showed a growth advantage of own young over a 6-day period only during late lactation (day 15–21), but not before. It seems reasonable to assume that over longer periods of time differences in weight gain between own and alien young may be due to multiple factors including differential nursing, differences in development, and effects of sibling competition. Therefore, looking at changes in weight over longer periods may convey only limited insight into whether mothers are able to preferentially nurse or whether there are other potential strategies by which females reduce costs of nursing alien young in communal nests. In addition, recognition of kin may not only be possible on the part of the mother but also by offspring who recognize their mother (Bateson 1979; Jäckel & Trillmich 2003) and offspring and maternal traits may be co-adapted to yield high offspring fitness (Wolf & Brodie 1998; Wolf & Hager 2006). Generally, such behaviour may be beneficial in situations in which young are expected to monitor the mother's state (Bateson 1994) or when there is the chance that parents accidentally accept or nurse alien young, for example, in communal nests.

While it seems reasonable to assume that communally nursing females should direct resources preferentially to own young, few suggestions have been made to possible alternative strategies by which females could reduce costs of nursing alien young. Assuming females are able to distinguish own from alien offspring, one obvious way to achieve cost reduction would be preferential nursing of own young (Elwood 1991; Jacquot & Vessey 1994; Roulin & Hager 2003). However, it may be that mothers have only limited discriminative abilities or that it may be difficult to differentially nurse in a communal nest. For example, preventing alien pups from sucking may not be possible when there are more teats available than own young were born, which is often the case in house mice with five pairs of nipples and an average litter size of five to eight (Hummel et al. 1975). A maternal strategy that indirectly reduces costs of provisioning to unrelated young might be to decrease their overall maternal effort when faced with mixed litters.

In polygynous species, such as house mice, males and females are in conflict over the level of maternal provisioning to young because males benefit from higher maternal investment to the current litter than is optimal for the female, who needs to consider her residual reproductive success (e.g. Trivers 1972; Parker et al. 2002). This situation has been assumed to lead to the evolution of parent-of-origin-dependent gene expression at loci affecting resource transfer between mother and offspring (Haig & Graham 1991; Haig 1997; Roulin & Hager 2003). Several lines of empirical investigation highlight the importance of parent-of-origin-dependent effects such as genomic imprinting and maternal effects in determining the amount of maternal investment: for example, gene targeting studies showing a positive effect on resource transfer of paternally (but not maternally) expressed genes (DeChiara et al. 1991; Li et al. 1999). Prior work in the strains used in this study showed that provisioning depended on an interaction between the offspring's maternally derived genes and the mother's genotype (Hager & Johnstone 2003). Thus, additional insight into the underlying causes of which parent determines the amount of maternal provisioning may be gained by considering parent-of-origin-dependent effects on provisioning (Hager & Johnstone 2006a).

The objective of this study was first to investigate whether own young benefit from maternal provisioning to a mixed litter, for example, by obtaining more maternal resources. Second, we aimed to assess whether any such effect is due to offspring and maternal genotype or parent-of-origin-dependent interactions between them. Finally, we aimed to determine whether mothers alter their level of provisioning in response to the presence of alien pups in a litter, which could be indicative of different maternal strategies to reduce fitness costs from nursing unrelated young in communal nests.

METHODS

Subjects and Experimental Design

We conducted our experiments using mice, *Mus musculus*, of the CBA/Ca and C57Bl/6 strain (hereafter denoted CBA and B6) obtained from Harlan, U.K. These strains differ in key life history parameters such as the number of young produced per litter, and previous work has shown that cross-fostering within and between these strains is possible, making them an ideal model system to study maternal provisioning to both related and unrelated young and the role of parent-of-origin-dependent effects (Hager & Johnstone 2003, 2006a). All animals were housed in standard mouse cages (North Kent Plastics, 'M1', 33 × 15 cm and 13 cm) with wood shavings as bedding material ('Goldshavings', Lillico, Surrey), which contained one male and one female during mating or one female and one litter during the experiments. The animals were kept on a reverse dark:light cycle with red light between 0800 and 2000 hours, and the temperature was held constant at 21°C with a relative humidity between 55% and 65%. Food ('B&K 001E', standard expanded mouse diet) and water were provided ad libitum.

The parental mice were sexually mature (5–7 weeks of age) at the start of the experiment. We synchronized female cycles by adding bedding from the male cages to the female cages 3 days prior to the pairings. Males and females were mated to yield offspring of all four possible combinations: B6B6, B6CBA, CBAB6, CBACBA (dam strain/sire strain). For example, CBAB6 offspring were obtained by mating a CBA female with a B6 male. The two heterozygous offspring types are genetically identical but they differ with respect to the parent-of-origin of their paternally and maternally derived genes. The distinction of the two heterozygotes is essential for any investigation of potential parent-of-origin-dependent effects on provisioning (e.g. Wolf & Hager 2006). Once females were visibly pregnant males were removed from the cages. On the day litters were born, we first created mixed litters consisting of pups differing with respect to their mother's strain because our prior work showed that only the offspring's maternally derived genotype affected the level of provisioning to unmixed