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Mechanisms of maternal investment by communal prairie voles, *Microtus ochrogaster*

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Communal rearing enhances the quality of offspring weaned by some social vertebrates. Previously, we observed that prairie vole pups reared in groups containing two or more breeding females (plurally breeding groups) gained significantly more body mass than did pups reared by solitary mothers, but not more than pups reared in groups containing only one breeding female (singularly breeding groups). In this study, we tested three hypotheses that might explain these differences. We tested the enhanced thermoregulation hypothesis by determining the nest temperatures experienced by pups and the time that pups were left unattended during 6-h observations, and the core body temperature of pups. To test the enhanced tactile stimulation hypothesis, we determined the time that pups were licked or groomed by adults during 20-min observations. To test the milk quality hypothesis, we determined the total solids found in milk collected from mothers with 3- and 9-day-old pups. To test the increased milk volume hypothesis, we determined an index of milk intake for 4-, 8- and 13-day-old pups. Pups reared in plurally breeding groups were left alone less by caregivers and ingested more, but not higher-quality, milk than did pups reared by solitary mothers. Pups reared in singularly breeding groups experienced greater tactile stimulation and were left unattended less, but did not ingest more or higher-quality milk than did pups reared by solitary mothers. Pups reared in plurally breeding groups experienced slightly less tactile stimulation and similar thermal conditions, but ingested more milk than did pups reared in singularly breeding groups. Our results suggest that plural breeding enhances two forms of parental investment, thermoregulation and milk volume, that contribute to the enhanced weight gain of pups in plurally breeding groups.

Communal rearing, the shared rearing of offspring by multiple individuals or mothers in a single nest, occurs in many vertebrates, including fish (Taborsky 1984), birds (Koenig & Dickinson 2004) and mammals (Riedman 1982; Packer et al. 1992). Adaptive hypotheses for communal rearing predict that offspring reared in communal groups benefit from greater protection from nest intruders, warmer nests and greater access to food and other forms of parental care compared to offspring reared by independently breeding females (Gittleman 1985; Lewis & Pusey 1997; Cockburn 1998). As a result of these benefits, communal breeders may experience greater direct fitness than conspecifics that independently rear their offspring (König 1997; but see Wolff 1994). Communal rearing may improve the inclusive fitness to individuals when groups are composed of close relatives (Hamilton 1964; Cockburn 1998; Koenig & Dickinson 2004).

In social mammals, there is some evidence suggesting that communal rearing of offspring improves maternal care and fitness of lactating females. In some mammals, females rearing offspring communally experience reduced energetic demands during lactation (Scantlebury et al. 2002; Russell et al. 2003), allowing them to maximize their investment in offspring without a significant cost (Hayes & Solomon 2004). By maximizing investment in offspring, mothers increase the weight gain of their offspring, an important factor affecting maternal fitness in some species (Lindström 1999; Festa-Bianchet et al. 2000). Heavier offspring are more likely to survive overwinter (Harding et al. 2005) or during the period between weaning and reproductive age (Solomon 1991). Heavier offspring also become reproductively active at an earlier age and are more likely to be chosen by a potential mate than lighter offspring (König et al. 1988; Sheridan & Tamarin 1988; Solomon 1993; Mappes et al. 1995; Koskela

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1998). There is also evidence that heavier females defend their offspring against infanticide better than lighter females (Jonsson et al. 2002). Consequently, increased weight gain during postnatal development may increase the reproductive success of communally reared offspring later in life (e.g. Festa-Bianchet et al. 2000), improving the direct fitness of their mothers.

Among the mammals, communal rearing is common in the rodents, occurring in more than 40 species (Solomon & Getz 1997; Hayes 2000; Ebensperger & Cofré 2001). Several laboratory studies suggest that communal rearing improves the quality of rodent offspring (herein referred to as pups). For example, the weight gain of house mouse, *Mus domesticus*, pups is significantly greater when the ratio of mother to pups is 1:3 than when the ratio is 1:1 (Sayler & Salmon 1969). In some species, including prairie voles, nonbreeders assisting with the care of pups also contribute to enhanced weight gain in those pups (Solomon 1991). Recently, we determined that the weight gain of prairie vole pups reared by mothers given limited food is sensitive to the type of communal breeding unit to which mothers belong (Hayes & Solomon 2004). Pups reared in plurally breeding groups (i.e. groups in which more than one female reproduces; Brown 1987) gained significantly more weight during the first 2 weeks after birth than did pups reared by solitary mothers (i.e. females rearing young with no other adult present; Hayes & Solomon 2004). However, the weight gain of pups reared by singularly breeding groups (i.e. groups in which only one female reproduces; Brown 1987) was intermediate to that of pups reared by solitary mothers and those in plurally breeding groups. Thus, it is likely that pups reared in plurally breeding groups experience greater reproductive fitness than pups reared by solitary mothers and possibly, singularly breeding groups.

Understanding the specific ways in which communal females enhance their investment in pups is critical to understanding how natural selection affects the behaviour of social rodents. To date, our understanding of how communal mothers increase their investment in pups is limited to only a few studies. Powell & Fried (1992) observed that pine vole, *Microtus pinetorum*, pups reared in singularly breeding groups are left alone less than pups reared by a mother and her mate. Likewise, in two species of social rodents, pups reared in plurally breeding groups are left unattended less often than pups reared by solitarily breeding females (*M. musculus*: Sayler & Salmon 1971; *Octodon degus*: Ebensperger et al. 2002). Previous studies have been limited to comparisons between solitarily breeding females and females breeding in plurally breeding groups or between solitarily breeding females and females breeding in singularly breeding groups. In this study we tested multiple hypotheses to explain: (1) why pups reared in plurally breeding groups gain significantly more body mass between birth and 13 days of age than do pups reared by solitary mothers, but not more than pups reared in singularly breeding groups, and (2) why pups reared by singularly breeding groups gain a similar amount of body weight as pups reared by solitary mothers (Hayes & Solomon 2004). We used prairie voles in this study because they occur in single-female units (36.8% of social units, Getz et al. 1993), singularly breeding groups (29% of social units, McGuire & Getz 1995) and plurally breeding groups (19% of social units, McGuire et al. 2002) in the wild.

Enhancements of several forms of maternal investment could explain the pattern of pup weight gain observed by Hayes & Solomon (2004). Increased contact with mothers and alloparents (i.e. individuals providing care to nondescendant offspring) in singularly breeding and plurally breeding groups could provide thermoregulatory benefits. The 'enhanced thermoregulation' hypothesis predicts that pups reared in singularly breeding and plurally breeding groups are left alone less, experience a warmer nest and have warmer core body temperatures than pups reared by solitary females (Sayler & Salmon 1969). Caregiving females remaining in contact with pups would limit heat loss to the environment by pups (Cutrera et al. 2003) because pups would be touching a warm body rather than being exposed to ambient conditions. Consequently, pups reared in communal groups could be maintained at body temperatures that are optimal for digestion and growth (sensu McConnachie & Alexander 2004). In rodents that produce altricial pups, including prairie voles, this mechanism may be particularly important because pups are unable to maintain endothermy when they are unattended (Hill 1992).

Increased contact with mothers and alloparents in communal groups could also increase the tactile stimulation of pups. The 'increased tactile stimulation' hypothesis predicts that pups reared in singularly breeding and plurally breeding groups are licked and groomed more than pups reared by solitary mothers (Solomon & Getz 1997). Increased licking and grooming would facilitate a greater release of enzymes and hormones in pups that affect somatic growth (Schanberg et al. 1984) and reduce parasite loads of pups (Johnson et al. 2003). To date, no one has determined the amount of tactile stimulation received by rodent pups reared in plurally breeding groups.

Assistance with the care of offspring by an alloparent or another mother may reduce the costs of lactation to mothers (Scantlebury et al. 2002), improving their physical condition. Mothers that are in better physical condition are most likely able to allocate more assimilated nutrients from ingested food to milk, increasing the quality of milk that they produce (but see Sayler & Salmon 1971). The 'enhanced milk quality' hypothesis posits that singularly breeding and plurally breeding mothers can allocate more energy to milk production and, thus, produce milk of higher quality than solitary mothers. In plurally breeding groups, communal nursing may reduce the energetic demands to females (Scantlebury et al. 2002), increasing the amount of milk that mothers produce. Pups reared in plurally breeding groups may also have greater access to lactating females than do pups reared in singularly breeding groups. In contrast to singular breeding, pups reared in plurally breeding groups may have opportunities to suckle even when one female has left the nest. Thus, the 'increased milk volume' hypothesis posits that pups reared in plurally breeding groups receive