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The effect of alloparental experience and care on anxiety-like, social and parental behaviour in adult mandarin voles

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Social experiences, especially during early development, have profound effects on the brain and behaviour in later life. We examined whether the provision of alloparental care by older siblings affects anxiety, sociability and parental behaviour at adulthood in both them and the younger siblings for which they care. Using mandarin voles, *Microtus mandarinus*, we kept the older litter in the parents' cage at weaning where they provided alloparental care to younger siblings of the next litter. We found that mandarin voles that had cared for younger siblings displayed significantly more locomotor activity in a novel environment and engaged in more social investigation of unfamiliar same-sex individuals. Females of this group also provided more parental care compared to control voles. Individuals cared for by older siblings demonstrated lower levels of anxiety and aggression, and higher levels of parental investment at adulthood, compared to control animals. These results suggest that providing alloparental care increases locomotor activity, social investigation and maternal care in adulthood, and that receiving alloparental care reduces levels of anxiety and aggression and increases biparental care in adulthood. Giving and receiving alloparental care has clear benefits in this species and suggests that alloparental care may increase the inclusive fitness of both givers and receivers.

Many studies have established that various early postnatal social experiences at different developmental stages exert different long-term or transient influences on brain function and behaviour, including anxiety and sociability (Rutter & O'Connor 2004; Levine 2005; Jia et al. 2009; Curley et al. 2011). In mammals, some species live in an extended family unit that includes the mother, father and offspring from different litters and they exhibit a cooperative breeding system (Wang & Novak 1994). Within these social units, older juvenile offspring may provide care-giving towards younger siblings and this is considered as a form of alloparenting (Solomon & French 1997). The effect of maternal and paternal care on offspring behaviour has been investigated and reported in many species (Jia et al. 2009; Curley et al. 2011); however, the effects of alloparental care as an important early social experience remain poorly understood.

According to inclusive fitness theory, alloparenting or helping to care for younger siblings by older juveniles may alter both indirect and direct fitness (Hamilton 1964). Helpers may be contributing to their indirect fitness when they care for younger siblings, who are more likely to survive with the presence of helpers (Hamilton 1964; Emlen & Wrege 1989; Emlen et al. 1991). They also benefit indirectly if breeders that receive assistance have higher survivorship because of decreased workload (Rood 1990; Bales et al. 2000), and subsequently breeders produce more litters or have shorter interlitter intervals (Solomon 1991; Powell & Fried 1992; Bales et al. 2001; Russell et al. 2003). Helpers acquire direct benefits if their alloparental experience allows them to become more successful parents (Lancaster 1971; Snowdon & Cronin 2007). This alloparental experience can improve nest-building skills and enhance other parental behaviours (Margulis et al. 2005; Stone et al. 2010), and increase survival rate and weight gain of offspring (Salo & French 1989; Margulis et al. 2005; Stone et al. 2010). Pubertal alloparenting experience is thus a positive social interaction, and the diversity of social contact with siblings during juvenile development can also induce shifts in adult behavioural phenotypes associated with multiple changes in monoamine pathways (Neumann 2009; Curley et al. 2011). Although several lines of evidence have established the beneficial effects of alloparenting on the reproductive success of helpers, whether this early social

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experience exerts any effect on anxiety-like and social behaviour in helpers at adulthood remains unclear.

Variations in parental care can induce different behavioural and neuroendocrine consequences for offspring particularly for emotional, social and parental behaviours (Champagne & Curley 2005; Branchi 2009). For example, offspring whose mothers display high levels of licking and grooming exhibit more modest hypothalamic–pituitary–adrenal responses to stress, increased levels of hippocampal glucocorticoid receptor expression (Liu et al. 1997), reduced fear (Caldji et al. 1998), enhanced cognitive ability (Liu et al. 2000; Champagne et al. 2003) and increased parental care of their own offspring (Francis et al. 1999; Fleming et al. 2002; Champagne et al. 2003). In contrast, reduction of maternal care suppresses or impairs the parental behaviour of offspring including licking, nursing, crouching and retrieving their own pups (Gonzalez et al. 2001; Lovic et al. 2001; Kikusui et al. 2005). Fathers also play an important role in offspring development in some social rodents (Ovtscharoff et al. 2006). In California mice, *Peromyscus californicus*, paternal grooming promotes the development of novel object recognition (Bredy et al. 2004). In contrast, minimizing paternal care can increase anxiety and reduce sociality and levels of parental behaviour of adult mandarin voles, *Microtus mandarinus* (Jia et al. 2009, 2011). In some rodents, older juveniles that spend as much time in the nest with pups as do parents in an extended family provide alloparental care to sibling pups via pup licking, pup retrieval and huddling over pups (Wang & Novak 1994; Solomon & Getz 1997). The presence of these juvenile helpers is beneficial to the development of pups (Solomon 1991, 1994); however, whether alloparental care provided by older juvenile helpers exerts a long-term effect on anxiety-like, social and parental behaviour in younger siblings is unknown.

The mandarin vole is a socially monogamous rodent widely distributed across China (Tai et al. 2001; Tai & Wang 2001). This rodent has an extended family group occupying a single burrow system (Smorkatcheva 1999). It also shows a number of other traits associated with a cooperative breeding system such as the delayed dispersal of juveniles and the presence of multiple successive litters within a nest (Smorkatcheva 1999; Tai & Wang 2001). High levels of alloparental care have also been found in this species (Song et al. 2010). In captivity, juveniles provide high levels of pup licking, pup retrieval and huddling over pups. As mentioned above, paternal and maternal care can affect the anxiety-like, social and parental behaviour of offspring; it is thus hypothesized that alloparental behaviour is possibly an important early social experience that can also affect these behaviours.

Using the mandarin vole with high levels of alloparental care as an interesting model, we aimed to answer the following questions. (1) Does the alloparental experience of juvenile helpers exert a long-term effect on their anxiety and social behaviour at adulthood? (2) Does the alloparenting experience make vole helpers more successful parents than inexperienced animals? (3) Does receiving alloparental care from older siblings have positive effects on anxiety-like, social and parental behaviour at adulthood, such as attenuating emotional responses, promoting close social interaction and increasing parental investment?

METHODS

Breeding Colony

Mandarin voles at Shaanxi Normal University were laboratory reared F2 generation animals (30–34 g) that originated from a wild population. Wild voles were captured in cropland at Chengcun (212 km east of Xi'an, China; 34°41′N, 111°11′E). We conducted trapping using iron-sheet live traps (20 × 8 cm and 20 cm high) set inside burrows. Fresh carrots were used as bait and water and local dry leaves were provided as nesting material. An iron sheet was attached on the upper side of the trap as shelter to protect from predators and sunshine. Traps were checked at 2 h intervals after sunrise (0700 hours). Pregnant and lactating females were released immediately on site. Captured animals were carefully transferred to the laboratory in polycarbonate cages (44 × 22 cm and 16 cm high) containing wood shavings and cotton for nesting material. To facilitate habituation to the colony room and minimize the influence of stress following capture and transport, a 1-week acclimatization period was included before all treatments. Animals were maintained on a 14:10 h light:dark cycle (lights on at 2000 hours) and at a temperature of 25 ± 3 °C. They were allowed free access to food (carrots and rabbit chow) and water. After the end of the study, animals were retained in the laboratory and used in other experiments. Animals remained healthy during captivity. All procedures were in accordance with the Guide for the Care and Use of Laboratory Animals of China and were reviewed by the Institutional Animal Care and Use Committee at Shaanxi Normal University (SNNU IACUC Protocol No. 08–06).

Experimental Design

Thirty pairs of laboratory-bred male and female mandarin voles were used as breeding pairs for the production of subjects. After the delivery of the first litter, most of the females underwent a postpartum oestrus and copulated with their mates. Thus, the mated mother lactated and took care of the first litter. Mandarin voles generally gave birth to the second litter within 1 week of weaning the first litter. In this study, only litters containing three or more pups were used to generate our experienced and inexperienced experimental groups. In some breeding pairs, first litters were allowed to remain with their parents and provide alloparental care to younger siblings from the second litter until their weaning. Animals from the first litter formed the alloparental group (AP). Once the younger siblings of the second litter were 21 days old they were removed from the parental cage along with juveniles from the first litter and housed in same-sex/same-age sibling pairs until testing. Younger siblings from the second litter that received alloparental care from the first litter formed the YS group. Some breeding pairs did not produce a second litter until the first litter was at postnatal day 45 and so juveniles from these breeding pairs formed the control group of AP (named the AC group); these juveniles were removed from the parental cage and housed in same-sex sibling conditions until testing. For some breeding pairs the first litter was removed from the cage at the age of weaning and so second litters did not receive alloparental care from the first litter; these animals were the control group of YS (hereafter named YC) and were also removed from their natal cage at 21 days of age and housed in same-sex sibling conditions until testing (Fig. 1). All behavioural tests were performed in dark light between 0800 and 1000 hours following a sequence with the test of least stress first.

Open Field Test

When an experimental animal from each group (10 females and 10 males per group) was 70 days old, locomotor activity and anxiety-like behaviour were assessed in an open field chamber made of white glacial polyvinyl chloride (50 × 50 cm and 25 cm high). The arena was divided into 16 quadrants (four central and 12 peripheral; Fiore & Ratti 2007) and illuminated with one lamp placed 1.5 m above the box. Light intensity was approximately 200 lx in the centre of the arena. Experimental animals were placed individually into the centre of the open field and left to explore for 5 min. The time spent in the central and peripheral areas and the