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Reproductive asynchrony and infanticide in house mice breeding communally

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Earlier findings suggest that female house mice, *Mus musculus*, breeding communally care for each other's offspring indiscriminately in a communal nest. The ultimate explanation for this apparently altruistic behaviour is still not well understood. Communal breeding creates a situation in which deceptive behaviour may be an alternative tactic, possibly coexisting with genuine altruism. To investigate this phenomenon we studied caring behaviour and infanticide as two opposite facets of communal breeding in triplets of unrelated females, and developed a dynamic model to help interpret our results. Of the 142 litters observed, in 30 all pups were killed by adult females and in 37 only some of the litter survived infanticide. Our empirical results are in concordance with our model's prediction and show that asynchrony in reproduction has a strong nonlinear effect on reproductive success: pups of litters born in the middle of the caring period of any female in the group had the lowest expected survival probability. Females that partly or totally lost their litter tended to spend less time caring for pups that were not their own, but they still contributed considerably to the common care. These findings suggest that infanticide is an effective strategy to exploit nestmates. As house mice are unable to discriminate between similarly aged young pups, synchronous breeding (e.g. by oestrus synchronization) may be an effective counter-strategy against infanticidal conspecifics.

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Communal nesting in mammals occurs when several females care for their offspring together in a common nest (Hayes, 2000). In some species (especially among rodents), communal nesting is associated with communal caring, that is, when females indiscriminately care for pups in the communal nest, including the young of other females (Auclair, König, Ferrari, Perony, & Lindholm, 2014; Ebensperger, Hurtado, & León, 2006; Ebensperger, Veloso, & Wallem, 2002; König, 1997; Hayes, 2000; Manning, Dewsbury, Wakeland, & Poots, 1995; Packer, Lewis, & Pusey, 1992; Roulin, 2002; Weidt, Lindholm, & König, 2014; Wilkinson & Baker, 1988). The evolutionary forces maintaining this apparently altruistic behaviour are not well understood, especially in nonkin animal societies (Clutton-Brock, 2009).

In stable breeding groups of close relatives the concept of inclusive fitness may be a potential explanation for communal nesting (Gardner & West, 2014; Hamilton, 1964). Close relatives share a portion of their genes by common descent; therefore helping close relatives, given that Hamilton's rule is fulfilled, can increase an individual's inclusive fitness (the total genetic success of an individual; Hamilton, 1964). Accordingly, female mice show a strong preference for nesting with close kin over nesting with nonkin (Manning et al., 1995; Manning, Wakeland, & Potts, 1992; Sutherland, Spencer, Singleton, & Taylor, 2005). However, cooperation may evolve even in the absence of kin selection. In his seminal work, Trivers (1971) suggested that cooperation among unrelated animals may be maintained by repeated interactions in which individuals exchange resources or services reciprocally. In this case, although cooperative behaviours have temporary net costs, these are compensated by subsequent assistance by the individuals that received help earlier (Clutton-Brock, 2009). This concept, termed reciprocal altruism or direct reciprocity, has a wide range of examples, including alarm signals in white-tailed deer, *Odocoileus virginianus* (Bildstein, 1983; Hirth & McCullough, 1977; Smith, 1991), food sharing in vampire bats, *Desmodus rotundus* (Carter & Wilkinson, 2013), reciprocal grooming in chimpanzees, *Pan troglodytes* (Arnold & Whiten, 2003; Gomez, Mundry, & Boesch, 2009; Hemelrijk & Ek, 1991) and the communal nursing of unrelated offspring in rodents and carnivores (Hayes, 2000; König, 1997; Packer et al., 1992; Roulin, 2002).

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Other mutually nonexclusive explanations for communal nesting can be group defence against conspecific intruders attempting infanticide (Agrell, Wolff, & Ylönen, 1998; Ebensperger, 1998) and/or enhanced thermoregulation. Studies in mice have confirmed that pups' survival in communal nests is higher than in single-mother nests, because in the latter infanticide by intruders occurs more frequently (Gerlach & Bartmann, 2002; Manning et al., 1995; Rusu & Krackow, 2004). Solitary living may also cost more energy in small rodents as individuals in larger groups may obtain thermoregulatory benefits from huddling (Hayes & Solomon, 2006; Scantlebury, Benett, Speakman, Pillay, & Schradin, 2006; Schradin, Scantlebury, Pillay, & König, 2009). These advantages may also have led to the evolution of communal nesting in mammals living in nonkin societies.

Apart from its benefits, the formation of communally nesting groups also creates opportunities for exploitation of others' caring effort (König, 1997; Silk, 2007). To increase their own reproductive success, individuals can use various manipulative tactics like harassment, reproductive suppression, unequal share of resources or infanticide to force the others to care for their offspring (Cant & Johnstone, 2006; Clutton-Brock, 2009; Clutton-Brock & Parker, 1995; Gerlach & Bartmann, 2002).

Communal nesting in house mice, *Mus musculus*, can easily be observed under laboratory conditions (König, 1993, 1994a, 1994b; König & Markl, 1987; Sayler & Salmon, 1969, 1971). In laboratory systems a single male frequently copulates with several (usually unrelated) females that later breed and care for the young together. The dynamics of interindividual relationships among female mice can be evaluated through regular records of litters' stages (i.e. records of birth, weaning, age and number of pups and length of interlitter intervals) and behavioural observations. Therefore, communal breeding in house mice can provide a good model system to study both aspects of communal breeding: cooperation and conflict. The conflict is mainly infanticide committed by nestmates, a phenomenon that frequently occurs among female mice (Dobson, Jacquot, & Baudoin, 2000; König, 1994a; Rusu & Krackow, 2004). Males well established in a group do not kill pups (vom Saal & Howard, 1982), because they would be destroying their own offspring.

Mouse pups most frequently become victims of infanticide when they are 0–3 days old (Manning et al., 1995). On the one hand, under synchronous breeding the occurrence of infanticide can be limited because of the lowered aggression against pups around delivery (Ogawa & Makino, 1984, but see McCarthy & vom Saal, 1985; Sorokel & Terkel, 1988). This mechanism may serve to reduce the risk of infanticidal females killing their own pups since female mice are probably unable to discriminate between their own and others' pups if they are of similar age (Hager & Johnstone, 2005; Manning et al., 1995; Sayler & Salmon, 1971; but see Ostermeyer & Elwood, 1983). This inability to discriminate may also facilitate the communal nursing of others' pups. On the other hand, under asynchronous breeding, when it may be easier for females to recognize their littermates' young, infanticide can occur. Under this condition infanticide can increase the perpetrator's reproductive success by diverting the victim's care behaviour towards its own pups as long as the victimized female continues to care for the pups in the communal nest. Victims may continue caring because physiological constraints might prevent the immediate shutdown of care behaviour, e.g. milk production (Sayler & Salmon, 1971). Therefore, infanticide might be an important manipulative tactic that makes possible the prolonged exploitation of caring effort of other females.

We investigated caring behaviour and infanticide as two opposite facets of communal breeding and their consequences on reproductive success in triplets of unrelated female mice. Specifically, we studied (1) how the level of infanticide and asynchrony influence the time spent caring for the offspring, and how breeding asynchrony affects (2) the occurrence of infanticide and (3) reproductive success. Our hypotheses were as follows. First, for infanticide to be an effective tactic to exploit others' efforts, a female should maintain some level of care even after becoming a victim of infanticide. Furthermore, because effective exploitation requires that females do not discriminate between caring for their own and alien pups this level of care should not depend on the level of asynchrony of litters. Second, increasing asynchrony between litters in the same nest results in increasing frequency of infanticide because female mice can discriminate between their own and others' pups better as the age difference between pups increases. Nevertheless, as the difference between the pups' ages increases, the time available for exploitation decreases. Therefore, we expect an inverted U-shaped relation between asynchrony and level of infanticide. Third, as a consequence, a U-shaped relation between asynchrony and reproductive success (i.e. number of weaned pups) is expected. To understand better the temporal dynamics of infanticide in our results we developed a simple dynamic model of infanticide.

METHODS

Animals and Observation Design

The study was carried out in the local zoological garden (Nagyerdő Kultúrpark, Debrecen, Hungary) between 24 April and 16 December 2009. We used outbred laboratory mice derived from inbred strains (C57BL/6J, BALB/c, DBA/1J) randomly mated with each other for several generations before the observations. The original stocks were obtained from the Charles River Laboratory (Sulzfeld, Germany). Pups were weaned at 21–25 days of age, and then housed in same-sex crèches established in glass terraria (80 × 40 cm and 40 cm high). Each crèche contained a maximum of 30 individuals. Environmental enrichment was provided in the form of 15–20 sanitary paper tubes and two or three small cardboard boxes. Animals were kept in a controlled room maintained at approximately 60–70% humidity at 22 (±2) °C under a 12:12 h light:dark cycle (light on at 0800 hours). They had ad libitum access to food (Altromin 1310 standard mouse diet, vegetables and dry dog food) and water in their home crèches.

From the weaned same-sex groups three females and a male were randomly selected to form a breeding unit. Seventeen breeding units were set up and housed thereafter in terraria (40 × 20 cm and 25 cm high) in the same room as the weaned individuals. Three plastic nestboxes (6.5 × 9.5 cm and 9.5 cm high) with paper towels as nest-building material were provided, and the bottom of the terraria was covered with wood chips. The tail of each female was covered with Porcimark spray (Kruuse, Langeskov, Denmark) in three colours, red, blue and green, to allow individual identification of mice in each observation unit. Units with females of advanced pregnancy were checked every day to identify the day of deliveries. Each female was weighed and pups were counted either at weekly cleanings, or on days when any of the females in the unit gave birth or weaned pups were removed from the unit. However, because we expected that most of the infanticide would occur within a few days of delivery, an extra check of pups was done 3.1 ± 1.9 (mean ± SD, $N = 142$) days after delivery to get a more accurate estimate for the timing of infanticide. We could determine the identity of females that had given birth by the sudden drop in their body mass. If two (or three) females gave birth on the same day in the same unit (23 of 142 litters) we assigned one-half (or one-third) of the newborn pups to each of these females as an estimate of its litter size. Otherwise, we were able to

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