



Daughters are more strongly attached to their mother than sons: a possible mechanism for early social segregation



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Social factors hypotheses predict that social segregation between male and female adult ungulates is due to social preferences among same-sex peers and avoidance of the opposite sex, rather than aggregation due to body size dimorphism and differential needs of the sexes. It is suggested that if such social preference/avoidance exists its roots should be early in life. While juvenile ungulate males show social preference for same-sex and same-age peers a few weeks after birth, no studies have confirmed such a phenomenon in juvenile females. In this study we investigated another possible mechanism that would result in an early social preference for same-sex conspecifics among juvenile females: we hypothesized that offspring–mother attachment is stronger for daughters than for sons. Attachment was measured in lambs, *Ovis aries*, using three characteristics defined initially in children: proximity seeking, distress following separation and exploration in the mother's presence. Lambs were tested at 3 weeks of age in two experimental situations in which they could interact with the mother, a familiar ewe or an unfamiliar ewe. (1) During a choice test between the mother and the familiar ewe, daughters maintained closer proximity with the mother than sons did. During the test without the mother (a familiar versus an unfamiliar ewe) daughters were more distressed than sons were. (2) In an isolation–reunion–separation test, reunion with the mother increased exploratory behaviour more in daughters than in sons. Overall, our results reveal that daughters displayed stronger attachment behaviours and could be more strongly attached to their mother than sons are. Such early preference may be a key factor leading to social preference among females and social segregation between the sexes.

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Sexual segregation is widespread among polygynous ungulates with adult males and females living in sex-separated groups outside the mating season (review: Main, Weckerly, & Bleich, 1996; Ruckstuhl & Neuhaus, 2000, 2002, 2005). During this period, adult females associate with their offspring forming philopatric groups (red deer, *Cervus elaphus*: Clutton-Brock, Guinness, & Albon, 1982; bighorn sheep, *Ovis canadensis*: Festa-Bianchet, 1991; Geist, 1971; social antelopes: Jarman, 1974; white-tailed deer, *Odocoileus virginianus*: Mathews & Porter, 1993) whereas males form all-male

groups of variable size and live outside their natal home range (domestic sheep, *Ovis aries*: Arnold, Wallace, & Rea, 1981; Michelena et al., 2005; American bison, *Bison bison*: Lott, 1991; grey kangaroos, *Macropus fuliginosus*: MacFarlane & Coulson, 2009; Mediterranean mouflon, *Ovis gmelini*: Cransac, Gerard, Maublanc & Pépin, 1998; isard, *Rupicapra pyrenaica*: Richard-Hansen, 1993; impala, *Aepyceros melampus*: Murray, 1981). This sexual segregation may be explained by the differential use of habitat by adult males and females according to their differential energy requirement due to body size dimorphism and differences in their reproductive strategy. The sexual dimorphism–body size hypothesis predicts that in a heterogeneous home range, composed of habitats that vary in forage quality and predation risks, small females would prefer small quantities of high-quality forage in contrast to larger

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males preferring abundant low-quality forage. According to the reproductive strategy, females with offspring would be also more inclined to choose a habitat with low predation risk than males in order to favour the survival of young and the mother's fitness (Main et al., 1996). More recently, some researchers have proposed that allometric and life history differences between the sexes due to dimorphism in body size (gastrocentric model hypothesis, Barboza & Bowyer, 2000) and predation risk (reproductive strategy) explain sexual segregation by the fact that males choose habitat to maximize energy gain in preparation for the breeding season and females select habitats with a combination of resources that contribute to offspring survival (Bowyer, 2004; Main, 2008; Mooring et al., 2005). While sexual segregation may be explained by a different use of habitat, this is not systematically the case since it has been shown that males and females remain socially segregated within a homogeneous habitat (Bon & Campan, 1996; Bon, Rideau, Villaret, & Joachim, 2001; Conradt, 1999). Conradt (1999, 2005) proposed that the sexes can be segregated either by social affinity (social segregation) or by habitat use (habitat segregation), both leading to variation in spatial segregation scale between same-sex groups (spatial segregation).

Many mechanisms have been proposed to explain social segregation including the avoidance of oddity effect, sex differences in activity budgets, forage selection within a habitat and social factors (MacFarlane & Coulson, 2009) such as preferential association between same-sex individuals and avoidance of the opposite sex. The activity budget and social factors hypotheses have frequently been used to explain sociosexual segregation (Michelena et al., 2004, 2005; Pérez-Barbería, Robertson, & Gordon, 2005; Ruckstuhl & Neuhaus, 2002). The activity budget hypothesis (Conradt, 1998; Ruckstuhl, 1998) predicts that segregation is caused by asynchrony between the sexes due to dimorphism in their body size and differences in time spent foraging and moving compared to lying down and ruminating (Ruckstuhl, 1998). Synchronizing activity budgets and staying in mixed-sex groups could be costly if an optimal activity budget and associated optimal foraging strategies are not pursued (Conradt, 1998; Ruckstuhl, 1998) leading to the formation of same-sex groups. Whereas the activity budget hypothesis has received wide support, its role in spatial segregation now tends to be controversial (Bowyer & Kie, 2004; Mooring et al., 2005) because activity budgets are seen by some to be a result of animal grouping (Mooring & Rominger, 2004). In regard to the social factors hypotheses, four mechanisms leading to sociosexual segregation have been proposed.

(1) The male social affinity hypothesis (also referred to as the social preference hypothesis: Ruckstuhl & Neuhaus, 2000; the social affinity hypothesis: Bon et al., 2001; and the social factors hypothesis: Pérez-Barbería et al., 2005) suggests a principal role of male social affinity in sociosexual segregation. It predicts that male preference for same-sex peers may cause the formation of male-only groups in which the males develop fighting skills efficiently and establish a dominant hierarchy (Bon et al., 2001).

(2) The male avoidance of females hypothesis (Prins, 1989) proposes that segregation is due to males of all size classes avoiding females to reduce rates of male–male aggressive interactions, and increase time for other activities such as foraging.

(3) The female social affinity hypothesis (included in the social affinity hypothesis: Bon et al., 2001; and social factors hypothesis: Pérez-Barbería et al., 2005) assumes that affinity among females leads to the formation of female-only groups in which females can more efficiently develop skills associated with the rearing of offspring.

(4) The female avoidance of males hypothesis proposes that females avoid males of all size classes, male–male aggression or agonistic acts impeding cohesion among females (Bon & Campan,

1996; Cransac et al., 1998; Weckerly, McFarland, Ricca, & Meyer, 2004; Weckerly, Ricca, & Meyer, 2001).

Some researchers claim that these social preferences and avoidances observed in adult ungulates have their roots in infancy, develop and intensify during the ontogeny of social behaviours (Bon & Campan, 1996; Bon, Deneubourg, Gerard, & Michelena, 2005) particularly because spatial segregation between single-sex groups increases gradually with age (ungulates: Bon & Campan, 1996; Alpine ibex, *Capra ibex*: Bon et al., 2001; African buffalo, *Syncerus caffer*: Sinclair, 1977). In accordance with the male social affinity hypothesis, young male ungulates, even juveniles still dependent upon the mother's milk and protection, show preferred associations with same-sex and same-age peers within the adult female group (Mediterranean mouflon: Guilhem, Bideau, Gerard, Maublanc, & Pepin, 2006; American bison: Rothstein & Griswold, 1991; impala: Murray, 1981; chital deer, *Axis axis*: Schaller, 1967; bighorn sheep: Geist, 1968; Grant's gazelle, *Nanger granti*: Walther, 1972; pronghorn, *Antilocapra americana*: Kitchen, 1974; African buffalo: Korte, 2008) interacting among themselves with more agonistic and pseudosexual behaviours than juvenile females (reviews on ungulates: Lent, 1974; Pérez-Barbería & Yearsley, 2010; domestic sheep: Guilhem, Bideau, Gerard, & Maublanc, 2000; Sachs & Harris, 1978; American bison: Rothstein & Griswold, 1991; bighorn sheep: Hass & Jenni, 1993). In contrast, neither avoidance of males by young females nor preferred associations among juvenile females have ever been demonstrated (Mediterranean mouflon: Guilhem et al., 2006; Le Pendu, Briedermann, Gerard, & Maublanc, 1995; Siberian ibex, *Capra sibirica*: Byers, 1980). In this study we investigated another possible mechanism that would result in an early preferred interaction with same-sex conspecifics in females through a stronger offspring–mother attachment in daughters than in sons.

The ontogeny of social behaviour in ungulates begins soon after birth with the establishment of an attachment bond with the mother (for review: Lent, 1974). Attachment is defined by three criteria which were initially used in human infants (Ainsworth & Bell, 1970; Holmes, 1993): proximity seeking (attraction), distress and appeasement during separation–reunion with the attachment figure, and finally the use of the attachment figure as a secure base, increasing exploration by the young. In sheep, the mother–young relationship has been particularly well studied and attachment to the mother seems to develop within a few days after parturition (Nowak, Keller, & Lévy, 2011); however, no study has ever investigated the secure base of the mother and its impact on exploratory behaviour of the lamb, leaving the characterization of filial attachment incomplete. Proximity seeking with the mother from 24 h of age has been observed under natural (Shillito-Walser, Walters, & Ellison, 1984) and laboratory conditions such as in two-choice tests opposing mothers and unfamiliar ewes (Nowak et al., 1997a, 1997b; Nowak, Poindron, Le Neindre, & Putu, 1987). When separated from the mother, lambs display distress reactions (uttering high-pitched bleats, increased locomotor activity) and increased adrenal response (Moberg, Anderson, & Underwood, 1980; Moberg & Wood, 1981). There have been some reports that the mother–young relationship varies according to the sex of the lamb. For example, between 24 h and 1 week of age, studies showed that daughters were more distressed than sons by a separation from the mother (domestic sheep: Coutinho-Netto et al., 2003; Hernandez, Matthews, Oliver, Bloomfield, & Harding, 2009). Other studies observed that female lambs (3–7 weeks of age) maintain closer proximity with their mother than males (Mediterranean mouflon: Guilhem et al., 2006; domestic sheep: Walser & Williams, 1986) and reached their mother faster in two-choice tests (Nowak, 1990). Under natural conditions a stronger proximity with the mother is sometimes reported based on

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