



Filial attachment in sheep: Similarities and differences between ewe-lamb and human-lamb relationships[☆]



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ABSTRACT

Animals develop relationships with intra- and interspecific partners, including humans. In some cases this can lead to strong emotional bonds indicating the existence of attachment. The sheep is well known to develop various forms of social attachment (mothers towards young, lambs towards siblings). The relationship they can develop with humans is much less understood. In this review, based on the attachment theory framework developed in human infants, we outline features and mechanisms that participate in the development and the expression of affiliative behaviours that lambs can develop with their mother or a human. Behavioural tests comparing responses towards a presumed attachment figure with those directed towards unfamiliar or familiar conspecifics demonstrate that lambs do search specifically the proximity of their mother or human caregiver. Differential emotional responses in the presence (calmness) or the absence of the partner (agitation) are also expressed. However, a relationship with a human takes place more easily when lambs are reared without their primary attachment figure, the mother. Human-lamb attachment is then facilitated by positive social contacts (gentling, hand-feeding) provided by a specific caregiver. In the case of attachment with the mother, suckling is the main reward. Although the existence of a sensitive period is still unclear, in both cases attachment develops more rapidly if positive interactions take place immediately after birth. Three neurochemical systems have profound impact on the expression of filial attachment in sheep: the gut peptide cholecystokinin, endogenous opioids, and oxytocin, all known to play a key role in prosocial behaviours in mammals. In addition, positive nutritive or non-nutritive interactions activate specific brain regions that are involved in the expression of social and emotional behaviours. In conclusion, lambs do develop intra- and interspecific attachment but not in a concomitant manner as the presence of the mother strongly reduces their motivation to interact with a human. Nonetheless, under artificial rearing conditions the human becomes a salient attachment figure.

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1. Introduction

Social behaviour is believed to exist because it is beneficial to those who engage in it, which means that these individuals are better off than they would be on their own. In mammals, social behaviour serves many purposes and

is exhibited in a wide variety of forms (Alcock, 2009). Even the so-called solitary species, which as adults interact socially only to mate, have a close behavioural interaction with their mothers when they are young (Eisenberg, 1983). Many mammals are more successful at finding food when they search as a group; this is especially true if food resources are clumped together in only certain places. Ungulates clearly gain protection from predators by living in social groups, since nearly all of them are vulnerable, at least when young (Veissier et al., 1998). Sociality thus provides several modes of defence not available to solitary individuals and members of a social group are probably better able to detect predators by depending on mutual vigilance.

The stability of the group relies on individual recognition that may even lead to some kind of affiliation between related or unrelated individuals (Rault, 2012). In some cases a strong bonding process may take place between two or more individuals. Social bonds are a subset of affiliative or positive behaviours, which are most simply characterised by approach rather than avoidance or withdrawal. The best described examples of social bonds include parent-offspring relationships in ruminants and primates (Broad et al., 2006; Maestripieri, 2001; Nowak et al., 2011a; Poindron et al., 2007) and adult heterosexual relationships in monogamous species (Wang and Aragona, 2004; Young and Wang, 2004). Such social bonds are associated with reproduction and social stability and are most readily interpreted in the context of their evolutionary and adaptive functions (Gubernick, 1981).

Mammals do not interact exclusively in an intra-specific context and a great complexity in relationships between various populations is found in nature. Those existing between members of different species are termed interspecific relationships and some may be beneficial (mutualism: Boucher and Douglas, 1985; Farine et al., 2012). Interspecific relationships are rather common in mammals (Stensland et al., 2003). They fall into two main categories: spontaneous and usually temporary associations, or induced and often long-lasting ones. The first category is seen in wild species, one of the most famous examples being found in species sharing the African savannah. An obvious advantage is a more efficient anti-predator strategy since some species may benefit from early detection of predators by identifying alert signals emitted by other species (Fichtel, 2004; Kitchen et al., 2010; Magrath et al., 2009). In parallel, predators can also form temporary interspecific hunting association and this increases their hunting success (Minta et al., 1992). In the second category, induced and long-lasting interspecific relationships are usually found amongst domesticated and farmed animals. By mixing species varying in fear behaviour, some may benefit from the protection of others that can be aggressive towards predators. Such characteristic has been used to protect vulnerable small ruminants by inducing mixed bonds between herds of cattle and flocks of sheep in order to reduce attacks on the latter by coyotes in North America (Anderson et al., 1992; Hulet et al., 1987), or by raising dogs with sheep to guard them against wolves in Europe (Rigg, 2001). In the web of induced interspecific relationships, the most common and probably best

known association is the one that involves animals and humans: it can be intense, vital and lifelong in some species (pets) or casual and temporary in others (farm species). Yet, our scientific knowledge of the mechanisms leading to the establishment and maintenance of these diverse interspecific relationships, and their nature, is far more limited than in the case of intraspecific relationships. Surprising this is even true for the case of the animal-human relationship.

Although animals are widely employed in human societies, it is only recently that the scientific community have acknowledged the relationship that frequently, perhaps inevitably, develops between “them” and “us”. Indeed, an increasing body of evidence suggests that it results in profound behavioural and physiological changes in the animal subject in both laboratory and field settings (Hemsworth and Boivin, 2011; Konok et al., 2011; Odendaal and Meintjes, 2003; Scott, 1992; Waiblinger et al., 2006; Waiblinger, 2009). Such effects are not confined to obvious cases involving primates and dogs, but appear in less expected species like farm animals. The relationship between humans and farm animals has been shown to have strong impacts on their welfare, ease of handling, and productivity. Farm animals that receive additional gentle human contact are less fearful of humans than those that receive minimal contact (Hemsworth and Boivin, 2011; Waiblinger et al., 2006; Waiblinger, 2009). They are also less agitated during loading and transport, during veterinary procedures, and spend more time near their stockperson. Thus, the affinity for the stockperson appears as a good indicator of positive animal-human relationships. While our understanding of the human aspects that influence these interactions in livestock production has improved considerably over the last decade or so, we still know very little about the way humans are perceived by animals or included in their social network.

Can they bond to us in the same way they bond to each other? We attempt to answer this question in the present review by taking the sheep as a model. Under farming conditions sheep interact both with conspecifics and humans, interactions with humans being more frequent under intensive livestock production systems or in more traditional pastoral shepherding. Amongst farm animals, it is the subject that has been studied the most extensively in the field of affiliative behaviours both for interspecific and intraspecific relations, especially at a young age when individuals develop strong bonds (Nowak, 2006; Nowak and Boivin, 2002; Nowak et al., 2011a). As the mechanisms of attachment to the mother have been well described from a behavioural and physiological point of view (Nowak et al., 2007), it will be used as a base to investigate whether the interactions that lambs have with humans may fall into the category of attachment behaviours. In a first step, we summarize the general attributes of the concept of attachment and the criteria used to measure it that have been developed from research on humans and extrapolated to sheep. Then, we illustrate this point by drawing together the behavioural, physiological and neurobiological mechanisms involved in the development and/or the expression of intra- and inter-specific bonding in the lamb. Finally, this paper also considers some of the main weaknesses in our

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