

Review

The importance of early life experiences for the development of behavioural disorders in domestic dogs

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Abstract

Behavioural disorders are a major reason for euthanasia and sheltering of pet dogs. The prevention and treatment of behavioural disorders requires a better understanding of the underlying causes. Early life experiences, such as maternal care, attachment and socialisation, have long lasting and serious consequences for the behavioural and physiological development of an individual. The complex interplay between these factors is likely to have consequences for the future dog-owner bond and the vulnerability to develop behavioural disorders. Here, we summarise the current literature on the interactions between maternal care, attachment formation, and the sensitive socialisation period and their potential consequences on adult dog behaviour. Based on the findings we highlight gaps in knowledge and provide suggestions for future research which are necessary to formulate recommendations for pet dog breeding and socialisation.

Keywords

maternal care, attachment, socialisation, behavioural development, behavioural disorders, dog breeding, HPA, adolescence.

1. Introduction

Aggression, anxiety and separation related behavioural disorders are commonly seen in pet dogs worldwide, with a high impact for the owner and

society (Voith, 2009). In the United States, Canada, Australia and Finland, about 70% of the dogs referred to a behavioural clinic are diagnosed with behavioural disorders related to aggression, while separation related behavioural disorders are seen in 9–19% of dogs and anxiety in 14–21% (Denenberg et al., 2005; Bamberger & Houpt, 2006; Tiira et al., 2016). These behavioural disorders have been demonstrated to be the main cause for sheltering in 11–34% of sheltered dogs and the main reason for 10–16% of euthanasia requests (Lambert et al., 2015). Note that we distinguish ‘problem behaviour’ (normal behaviour for the dog yet unwanted behaviour for the owner) and behavioural disorders (pathological behaviours excessive in frequency, duration and/or intensity and/or applied in the wrong context). These terms are used interchangeably in the literature, but here we focus on pathological behaviour, which substantially decreases an individual’s capacity to cope with its environment.

In The Netherlands, and probably in other western European countries as well, the demand for dog pups largely exceeds the capacity of national breeders to produce litters (Four Paws, 2013). About 150 000 new pups are obtained by owners in the Netherlands each year, of which only 40% are bred by Dutch breeders (Feiten en Cijfers, HAS Hogeschool & Faculteit Diergeneeskunde, 2015). This high demand has led to the establishment of both legal and illegal networks that import pups to western European countries, with low regard for adequate vaccinations, weaning age or socialisation programs (Van Uhm, 2010; Four Paws, 2013). Puppies sold through these networks are often bred in large puppy mills, where they stay in small cages and are weaned and transported at an early age (Van Uhm, 2010). During this age period social and non-social stimulation is essential for a normal behavioural development, enabling a young pup to adapt to a new environment and the regular challenges within, as will be discussed in this review. This stimulation, however, is difficult to realise in puppy mills and trading networks due to their magnitude and prevailing housing and transport conditions.

A recent review on the behaviour of dogs originating from commercial breeders, puppy farms and pet stores, highlights the increased incidence of behavioural disorders such as fear and aggression towards other dogs and humans in commercially bred dogs (McMillan, 2017). One study categorised breeders as “responsible” or “irresponsible” based on the outcome of 11 questions (e.g., number of available litters, age of pup at purchase, was

mother dog seen interacting with her pups) and found that the prevalence of aggression and separation related behavioural disorders is higher in dogs obtained from irresponsible breeders (Gray et al., 2016). The increased incidence of behavioural disorders in commercially bred dogs may be caused by a lack of appropriate stimulation during early life (Jagoe, 1994 in Serpell & Jagoe, 1995). Thus, in addition to other major factors influencing behaviour, such as genetics (Haupt, 2007) and responsible ownership (Jagoe & Serpell, 1996), the early life experiences of the pup play a major role in its further behavioural development (Wilsson, 2016). While research on domestic dogs is scarce, studies on primates and rodents corroborate the importance of the early life phase in shaping the individual phenotype (Harlow et al., 1971; Sanchez et al., 2001). Especially negative experiences or insufficient stimulation, as well as minimal maternal care and attachment, have been shown to increase the chance for the development of behavioural disorders. This review focusses on the domestic dog, while literature on other mammal species is incorporated as well, to highlight research areas potentially of interest.

In most mammal species, the attachment bond between infants and their mother is established before and during the so called sensitive period for socialisation in early postnatal life (Bowlby, 1958, 1982; Ainsworth, 1978; Carter, 1998). During this crucial period, interactions with the social environment shape the neuronal and behavioural profiles of an individual (Weaver, 2009; Roth & David Sweatt, 2011; Sachser et al., 2013). Although the central nervous system retains some level of plasticity in adult life, its capacity for adjustments based on experiences is substantially greater during the sensitive period for socialisation (Knudsen, 2004).

Scott & Fuller (1965) were the first to investigate the early sensitive period for socialisation in dogs. Since then this topic has attracted much attention, but experimental research is scarce partly due to ethical considerations which arose as soon as the impact and consequences of social deprivation for the experimental animals involved became clear. The majority of the existing literature on the importance of early life experiences in domestic dogs describes the human-dog relationship and compares human-dog attachment with human-infant attachment. The mother-pup bond and its interactions with the subsequent socialisation period, as well as its influence on the development of behaviour, has not been studied in much detail so far (but see Previde et al., 2009 and Mariti et al., 2014). In addition, studies on behavioural patterns of human-dog attachment bonds in connection to the

quality and/or quantity of mother dog-pup attachment are lacking. Especially the formation of the attachment bond of a pup with its mother during the sensitive period, in which future socio-emotional behaviour is shaped, should comprehensively receive more attention to gain better insight into the development of (abnormal) behaviour in dogs. This review aims at elucidating the complex interplay between the formation of the mother-pup attachment bond and early socialisation, as well as their importance for the development of behaviour and behavioural disorders, and the consequences for the human-dog bond. To stimulate future research we also highlight deficits in the current knowledge on these topics. Finally, the results of this review may provide critical arguments to help policy makers take further steps against commercial dog trade and puppy mills and to better inform future dog owners.

2. The first step: mother–pup relationship

In dogs, primarily the female cares for the young (Pal, 2005). In the following section, we will review evidence suggesting that dog pups develop a specific attachment style towards their mother, based on the quality and quantity of maternal care. We discuss parallels with attachment theory in the human literature and point out the gaps in knowledge on attachment formation in dogs. Finally, we review the physiological mechanisms involved in maternal care and attachment and the role of the mother-pup relationship in the development of behaviour, as well as the risk for potential behavioural disorders.

2.1. Maternal care

During the first two weeks of a dog pup's life (i.e., the neonatal period; Scott & Marston, 1950), its senses are not fully developed yet. Like most altricial species, a new born dog pup is blind and deaf, and cognition and motor skills are poor due to the immaturity of the brain (Fox, 1971a). In this virtually isolated state, pups are highly dependent on their mother for nourishment, warmth, and elimination, the latter of which is stimulated through anogenital licking by the mother (Rheingold, 1963; Wilsson, 2016). From three weeks of age pups signal distress upon brief separation from the mother in the form of whining and yelping, which decreases in intensity with age (Elliot & Scott, 1961). This initial phase of distress upon maternal separation is also seen

in monkeys and humans (Kaufman & Rosenblum, 1967), and is followed by a phase of despair and depression if separation is prolonged. Prolonged or permanent maternal separation at an early age has potentially detrimental consequences in dogs; disease and mortality related to separation stress occur more often in pups weaned at six weeks of age compared to pups weaned at twelve weeks (Slabbert & Rasa, 1993). In addition, early permanent maternal separation, a common occurrence in commercial breeding, may play a role in the development of behavioural disorders, as will be discussed further in this review.

In the rodent literature, the quality and amount of maternal care is typically quantified by measuring the time females spend licking/grooming their pups and arched back nursing (Liu et al., 1997). Maternal care in dogs predominantly comprises physical contact with the pups, licking the pups (including anogenital licking) and nursing, all of which occur frequently during the first weeks of a pup's life but then gradually decrease over time (Rheingold, 1963; Overall, 2013). Recently, different nursing postures have been described in dogs: vertical nursing (female standing or sitting), lateral nursing (female lying on side) and ventral nursing (female lying on her stomach) (Bray et al., 2017a). Since the accessibility of the teats vary per nursing posture, it is conceivable that different styles between females may differentially affect their pups, as has been suggested by another recent study with guide dogs of the same author: the nursing style of the mother dog appeared to influence the success rate of guide dog training in the pups, with ventral nursing being associated with failure and vertical nursing with success (Bray et al., 2017b). Ventral nursing requires less effort than vertical nursing, as it is easier for the pups to stay attached to the mother's nipple. The authors suggested that pups from mothers with a primarily ventral nursing style experience too few challenges in their early days and this deprives them of the opportunity to acquire a certain degree of independence, leading to an increased incidence of anxiety-related behaviours with a lower success rate in guide dog training as a consequence.

In rodents, the extent of maternal caregiving may vary among individuals, with profound consequences for the offspring's behavioural and physiological development. Suboptimal levels of maternal care in these species may lead to heightened stress responsiveness (Meaney et al., 1994; Champagne et al., 2003; Czerwinski et al., 2016) and decreased cognitive function (Liu et al., 2000). Also in dog pups the quality and quantity of maternal care shows

considerable variation among females (Rheingold, 1963; Czerwinski et al., 2014; Bray et al., 2017a), and appears to affect the behavioural development of dog pups (Foyer et al., 2016; Guardini et al., 2016; Bray et al., 2017b). In German Shepherds, mother-pup interactions such as physical contact, nursing, licking and sniffing or poking the pup with the nose were recorded. Pups that received a higher amount of maternal care scored higher in engagement with humans and inanimate objects at 18 months of age (Foyer et al., 2016). These findings are corroborated by several studies; a questionnaire-based study asked dog owners to grade the quality of maternal care, specified as spending time with and taking care of the pups, on a scale of 1 to 7. Lower scores, indicating an estimated poor quality of maternal care by the owner, were associated with more fearful behaviour in the adult dog (Tiira & Lohi, 2015). Likewise, a longer daily duration of maternal care (i.e. physical contact, licking, ano-genital licking and nursing) during the first three weeks postpartum was associated with more exploratory behaviour and less signs of stress, such as increased locomotion and vocalisations during isolation, in eight week old puppies (Guardini et al., 2016). Finally, pups separated from the mother at 30 to 40 days of age, that consequently receive a lower amount of maternal care compared to pups separated at 60 days of age, were more likely to develop a variety of behavioural problems as an adult, including fearfulness on walks, noise reactivity and excessive barking (Pierantoni et al., 2011).

Collectively, the described literature indicates that, also in dogs, elements of maternal care, such as nursing style and amount of nursing and licking, are an important predictor for the development of adult behaviour.

2.2. Mother–infant attachment

An attachment bond is an affectional bond seen in many mammal species, that is characterised by proximity seeking behaviour, a feeling of security in the presence of the attachment figure, and distress upon separation from this figure (Gubernick, 1981). The primary caregiver, usually the mother, responds to the infant's behaviour by providing care, comfort and protection (Bowlby, 1958), thereby increasing the infant's chances of survival.

In most mammals, the attachment bond with the primary caregiver is formed during the postnatal period (Carter, 1998). The process of attachment formation is likely an evolutionary adaptive and conserved process; young animals are born with a predisposed repertoire of species-specific attachment

behaviours that promote proximity to their caregiver (Ainsworth, 1978). The young often show a preference for a particular attachment figure above others or above strangers, seek and maintain proximity to that figure, and may show an acute stress response to brief separation from the attachment figure (Bowlby, 1973). Even in the absence of food supply, young animals have a strong preference to stay near their mother (Lorenz, 1935; Bowlby, 1958, 1982; Harlow & Zimmerman, 1959; Harlow & Harlow, 1965), which shows the importance of the bond once it has been established. The attachment bond with the mother reduces fear and the mother thus functions as a *secure base*, which encourages the young to explore its environment (Gubernick, 1981). Most research on the attachment bond has been done in humans. The developmental process of attachment in many non-human mammals, including dogs, may be similar to the process described in human children, but research is lacking.

To study attachment in human children, a well-known and frequently used tool is the Strange Situation Test (SST), designed by Mary Ainsworth (1978) and based on her joint work with John Bowlby (Bretherton, 1992). In the SST procedure, the infant's behaviour is recorded during eight different episodes in an unfamiliar setting (Ainsworth, 1978). During these episodes the behavioural responses upon separation and reunion with the attachment figure are recorded and compared to behaviour exhibited in the presence of a stranger. Based on the SST, four different attachment styles are described for human infants: secure, anxious-ambivalent, avoidant and disorganised (Ainsworth, 1978, Table 1). Attachment styles appear to be influenced by temperament in humans, where proneness to distress is associated with insecure attachment styles (Goldsmith & Alansky; 1987). Notably, attachment is not a one-way process, and the development of a particular attachment style also depends on the nurturing behaviour of the mother, i.e., maternal care (Ainsworth, 1978). A secure attachment style is associated with a higher sensitivity and responsiveness of the mother to the infant's attachment behaviours, whereas an insecure attachment style is associated with lower sensitivity and responsiveness (Ainsworth, 1978; Grossmann et al., 1985; Table 1). Modified versions of the SST have been successfully performed in dogs, however, mainly to investigate the human–dog attachment bond (Topál et al., 1998; Gácsi et al., 2001; Palestrini et al., 2005; Schöberl et al., 2016). Intriguingly, these studies describe similar behaviours of the dog towards the human attachment figure as are seen in the human child: dogs

Table 1.
Overview of the relationship between maternal caregiving and attachment style in human infants and adults, and similarities with attachment styles described in human–dog relationships.

Maternal caregiving in humans ^{1,2}	Attachment styles and behaviours as described in humans ^{2,3} and dogs ^{4,5,6}	
Sensitive, responsive ^{1,2}	Secure	
	Secure ^{2,4}	Proximity to caregiver ^{2,4,5,6} Distress during separation ^{2,5,6} Low interest in strangers ^{2,5,6}
Insensitive, unresponsive ^{1,2}	Insecure	
	Anxious-ambivalent ² or ambivalent ⁴	High distress during separation ^{2,4} Difficult to comfort upon reunion ^{2,4} Seek constant reassurance and proximity ²
	Avoidant ^{2,4}	No separation distress ² Ignore caregiver ^{2,4} Similar towards stranger ²
	Disorganised ^{3,4}	Disoriented behaviours ³ Confused ³ Approach-avoidance conflict on reunion ⁴

Note that the influence of maternal care on attachment styles in dogs has not yet been studied.

¹Grossmann et al. (1985).

²Ainsworth (1978).

³Main & Solomon (1990).

⁴Schöberl et al. (2016).

⁵Palestrini et al. (2005).

⁶Topál et al. (1998).

show distress upon separation from the owner, which cannot be alleviated by the presence of a stranger, and show proximity seeking behaviour upon reunion with the owner. In the study by Topál et al. (1998) 51 owner–dog pairs underwent an SST and behaviour of the dog in the presence of their owner or a stranger were recorded. Dogs exhibited significantly more play, physical contact and exploratory behaviour in the presence of their owner. In separation episodes where only the stranger was present, the dogs spent more time

near the door of the test room compared to episodes with the owner present. Contact seeking behaviour was seen more during reunion with the owner compared to the stranger entering the room. Cluster analysis revealed differences in attachment levels among the dogs, but specific attachment styles were not distinguished. In another study 17 adult dogs underwent an SST and showed higher activity levels and more play behaviour in the presence of the owner compared to a stranger, and spent most of their time oriented at the door of the test room upon separation from the owner (Palestrini et al., 2005). Yet another study has described similar attachment styles in dogs as have been found in humans, based on approaching behaviour, play, exploration and physical contact seen during separation and reunion with the owner during a SST (Solomon et al., 2014 in Schöberl et al., 2016; Table 1).

Only two studies so far have investigated the intraspecific attachment bond between adult dogs (Mariti et al., 2014) and mother-pup attachment bond (Previde et al., 2009). At the age of 45–55 days, dog pups of different breeds were either introduced to a novel environment or a stranger, or briefly separated from their mother. The pups showed a behavioural repertoire similar to that described in human children: seeking proximity to the mother, distress upon separation, and a secure base effect in the presence of the mother (Previde et al., 2009). These findings suggest parallels in the development and nature of attachment bonds in social animals, but more studies on the intraspecific attachment bond in dogs are needed in order to substantiate this assumption.

As described, attachment is not a one-way process. Since humans and dogs are both altricial species in which maternal caregiving plays a vital role, it is conceivable that, as in humans, attachment styles in dogs also develop under the influence of the quality and quantity of maternal care. However, information on the influence of maternal caregiving on attachment styles in dogs is lacking, while this aspect may also affect the dog-human attachment formation and, thus, urgently requires further investigation. Also the potential role of temperament on attachment styles in dogs, as is seen in humans, has yet to be elucidated. Subsequently, mother-pup attachment bonds could be compared to human–dog attachment bonds to validate extrapolations based on research on human mother–child attachment. This approach may provide insight in the development of attachment-related behavioural problems in the domestic dog.

2.3. Physiological mechanisms underlying maternal care and the attachment bond

The common patterns found in attachment and behaviour between humans and dogs may partly be explained by corresponding subcortical neural and neurochemical mechanisms underlying parenting behaviour and care (Rilling & Young, 2014). For example, the neuropeptide oxytocin plays an important role in promoting maternal caregiving and the formation of an attachment bond between mother and infant (Nelson & Panksepp, 1998; Rilling & Young, 2014; Bos, 2016). In humans, parents with high levels of oxytocin show more affection toward their children, facilitating a secure attachment style of the infant to the parent (Rilling & Young 2014). Recent research shows that oxytocin may play an important role in the dog-human bonding as well (Beetz et al., 2012; Handlin et al., 2012; Romero et al., 2014; Nagasawa et al., 2015) and interactions between dogs and humans can result in increased levels of oxytocin in both species (Beetz et al., 2012). The role of oxytocin in the formation and maintenance of the attachment bond between the mother and her offspring specifically in dogs remains unclear.

During sensitive windows in early life neural structures mature (Knudsen, 2004), while environmental and social factors can profoundly affect this process (Sachser et al., 2013; Blakemore & Mills, 2014; Brydges, 2016). Interestingly, in new born rats, a stress hypo-responsive period (SHRP) has been described (Sapolsky & Meaney, 1986), during which adrenocorticotrophic hormone (ACTH) and glucocorticoid (GC) release in response to a stressor is strongly attenuated and modulated under the influence of maternal care (Rincón-Cortés & Sullivan, 2014). The SHRP coincides with the development of the nervous system, which is highly plastic and susceptible to external influences during the perinatal period. Given the potential negative impact of high levels of GC, the SHRP is thought to protect the developing brain (Sapolsky & Meaney, 1986; Rincón-Cortés & Sullivan, 2014). Some evidence for the presence of an SHRP was also found in dogs: brief maternal separation did not elicit a physiological stress response in pups of three or four weeks of age, but urinary cortisol did increase after maternal separation at five and six weeks of age, suggesting the SHRP lasts until four weeks of age in dogs (Nagasawa et al., 2014).

As described above, the variation in quantity and quality of maternal care between female dogs has important implications for the subsequent development of the pup (Foyer et al., 2016; Bray et al., 2017b), however, the

physiological mechanisms behind this relation have not yet been elucidated in this species. In rodents, maternal care influences stress responsivity in the young animal also beyond the SHRP, by programming the development of the hypothalamic-pituitary-adrenal (HPA) axis (Champagne et al., 2003; Rincón-Cortés & Sullivan, 2014), leading to heightened or reduced sensitivity to stressors later in life (e.g., Liu et al., 1997; Caldji et al., 1998; Capitanio et al., 2005; Champagne & Curley, 2005; Champagne et al., 2008; Sachser et al., 2013). High levels of maternal care in the form of licking/grooming and arched back nursing lead to lower stress responsiveness in adulthood, both physiologically and behaviourally (Liu et al., 1997). Conversely, offspring that received low maternal care show increased and prolonged ACTH and GC release after a stressful stimulus as an adult (Champagne et al., 2003; Lupien et al., 2009; Meaney et al., 2013). Prolonged elevations of GC, especially during maturation, may lead to a dysregulation of the HPA axis, and impaired neural development and cognitive function (De Kloet et al., 2005; Lupien et al., 2009; Rincón-Cortés & Sullivan, 2014; Brydges, 2016). Indeed, in rats the physiological changes produced by low levels of maternal care are accompanied by more fearful behaviour in novel situations as an adult (Caldji et al., 1998).

In short, maternal care influences the offspring's neuroendocrine and behavioural responses to stress, with effects lasting into adulthood (Rincón-Cortés & Sullivan, 2014). Low levels of maternal care lead to increased HPA axis activity, which may impair neural development and results in heightened stress responsivity in the adult animal and a higher risk of disease on the long term (De Kloet et al., 2005). It is conceivable that similar physiological mechanisms occur in dogs, and the potential cognitive and emotional deficits caused by poor quality of maternal care could pose a high risk for the development of behavioural disorders, such as fearfulness, in this species (Tiira & Lohi, 2015). However, solid research on this topic in dogs is necessary in order to firmly draw these conclusions.

3. Socialisation

Following the neonatal period and transitional period, where the mother-pup bond is of utmost importance, the first socialisation period begins. In this section, we discuss the different phases of the sensitive period for socialisation and its components, such as experiences with social and non-social stimuli,

and play behaviour. Appropriate stimulation during the sensitive period for socialisation results in a sociable dog with good adaptive capacity, that can build relationships with humans and conspecifics and is able to cope with novelty (Case, 2005). Inadequate and insufficient experiences on the other hand increase the risk of developing behavioural problems later in life. We also discuss the role of the mother dog during this sensitive period.

3.1. Early socialisation (3.5 to 12 weeks)

During the neonatal period, the pups' senses are not yet fully developed, making the young highly dependent on their mother. In the third week of life (i.e., the transitional period), the eyes and ears of the pup gradually open, they begin to walk and explore, and by the end of the third week pups are no longer dependent on their mother for elimination (Scott, 1958). This developmental stage marks the beginning of the early socialisation period, which is defined by both physiological and behavioural changes. A commonly accepted time frame for the early socialisation period in dogs is from 3.5 to approximately 12 weeks of age (Scott & Marston, 1950; Scott & Fuller, 1965; Table 2). However, defining the exact timing of this sensitive period in dogs is difficult due to breed-specific variation (Scott & Fuller, 1965). For example, Morrow et al. (2015) found that Cavalier King Charles spaniel pups had a significantly delayed onset of the early socialisation period compared to Yorkshire terrier pups and German shepherd pups. Therefore, not the timing but the processes acting during attachment and socialisation should be the main point of focus.

During the early socialisation period, a pup learns through experience to associate social and non-social stimuli with positive or negative emotions. These experiences allow the pup to build adaptive capacity in order to cope with and adapt to new situations. To avoid fear responses in the dog's future it is recommended to expose a pup during the early socialisation period to any social or non-social stimuli (e.g. objects, sounds, textures, locations and situations) that will likely be part of their adult environment (Battaglia, 2009; Howell et al., 2015). A retrospective study found that dogs raised in domestic environments (i.e., dogs that spent their sensitive period for socialisation at the stimulus-rich breeder's home) were less likely to develop fear and aggression towards unfamiliar people compared to dogs raised in non-domestic environments (Appleby et al., 2002). In a questionnaire study with companion dogs, more socialisation experiences between eight and

Table 2.
Overview of the timing of the sensitive periods and developmental transitions during early life in dogs (Scott & Marston, 1950; Scott, 1958; Scott & Fuller, 1965).

Neonatal (0–2 weeks)	Transitional (2–3 weeks)	Early socialisation		Late socialisation (12 weeks– 6 months)	Adolescence (6 months– 1 year)
		3–5 weeks	5–8 weeks	8–12 weeks	
Vision and hearing underdeveloped	Opening of eyes and ears	Brain maturation and myelination	Brain maturation and myelination	Myelinated nerves	Sexual maturation
Poor locomotory skills	Increased locomotor activity	Sensitive to novelty in environment SHRP	Sensitive to novelty in environment Weaning	Adult EEG waves	
Immature brain	Immature brain	Exploratory behaviour	Peak sensitivity to human contact	Reinforcement of socialisation	Sexual maturity
Care seeking behaviour	Care seeking behaviour	Play with mother littermates	Increasing fear of novelty Decreasing exploration Play with mother		
		Play with littermates	Play with littermates	Play with littermates	

SHRP = stress hypo-responsive period.

twelve weeks of age were associated with lower fearfulness in adult dogs (Tiira & Lohi, 2015). Thus, sufficient exposure to relevant stimuli during the early socialisation period appears to be associated with lower fearfulness and aggression in dogs.

Socialisation periods or similar sensitive periods are seen in many mammal and bird species, including rodents and humans (Scott, 1962). In wolves it is suggested that a sensitive period for interspecific socialisation to humans is also present, but it is much shorter than in dogs, ending around three weeks of age (Klinghammer & Goodmann, 1987). It is thought that the more flexible sensitive period in dogs is a result of domestication, as it allows dogs more time to form strong social bonds with humans during this developmental period (Udell et al., 2010).

Although animals keep learning about their environment throughout their life, they are substantially more sensitive to environmental stimuli during the sensitive period for socialisation (Knudsen, 2004). This increased sensitivity to environmental stimuli is caused by underlying physiological changes. In the first two weeks of a pup's life the central nervous system is still immature. Brain activity during awake and sleeping states cannot be distinguished using electroencephalography (EEG; Fox, 1971a) and auditory or visual stimuli do not evoke reactions in the pup (Scott, 1958). As the pup's visual and auditory senses start developing from three weeks of age and motor skills are rapidly improving (Pal, 2008), the nervous system also develops at a rapid pace. Between three and five weeks of age, the somatomotor, visual and auditory cortex show increased dendrite length and number, and myelination (Fox, 1971a). Changes in the EEG responsiveness now become evident and at eight weeks of age, the EEG of pups shows adult-like patterns (Fox, 1971a). These physiological changes are accompanied by an increase in approaching and exploratory behaviour, and altogether indicate an increased sensitivity of the pup to both social and non-social stimuli (Scott & Fuller, 1965; Fox & Stelzner, 1966; Battaglia, 2009). At the beginning of the early socialisation period the central nervous system has reached a level of maturity that allows conditioning and associative learning (Scott, 1958), and as the pup interacts with its environment and learns about relevant stimuli, the connections between neural synapses become stronger and neural circuits more stable (Coppinger & Coppinger, 2001; Knudsen, 2004). Between three and five weeks of age, a drop in heart rate can be detected in pups, followed by an increase in heart rate that peaks at 7–8 weeks (Scott & Fuller, 1965; Lindsay,

2013). Simultaneous with this increase in sympathetic activity, the maturation of the central nervous system, and the ending of the SHRP, pups show another change in behaviour. From 5 weeks of age (with some notable breed differences in onset; Morrow et al., 2015), dogs gradually become more fearful of novel unfamiliar stimuli (Freedman et al., 1961; Woolpy & Ginsburg, 1967), recovery after a fear response becomes increasingly delayed (Scott & Fuller, 1965), and desensitisation to a new stimulus will take increasingly more time and effort. This neophobia increases until it inhibits exploration tendencies by the end of the early socialisation period, around 12 weeks of age (Table 2). In order to avoid fear responses to stimuli and consequent negative associations or trauma during this time, the exposure and intensity of stimuli should be tightly controlled and increased gradually (Overall, 2013; Rooney et al., 2016). Exposure of pups to various stimuli on video images as early as three to five weeks of age has been shown to reduce fear responses at 7–8 weeks of age (Pluijmakers et al., 2010). Gradual exposure results in a moderately challenging environment for the pup, which has been shown to promote resilience (Macri & Würbel, 2006). Resilient dogs are better able to cope with new challenges in the future.

3.1.1. Intraspecific socialisation and play

The sensory and cognitive development at three weeks of age allows for the formation of social relationships (Scott & Marston, 1950; Scott, 1962). The primary social relationships are formed with the mother and littermates. Through these relationships the pup learns to identify itself with its own species, a process termed filial imprinting (Bolhuis 1991; Dehasse, 1994). The process of imprinting has first been comprehensively described in geese by Konrad Lorenz (1935). It is seen in many bird and mammal species, and is defined as “the acquisition of a preference for a familiar object” (McCabe, 2013). During a sensitive time period a young animal acquires a preference for the mother or caregiver, as this is, from a functional perspective of surviving, the most relevant ‘object’ in their environment.

In humans, the primary social relationships are also formed during the early socialisation period, with one major difference compared to dogs. In dogs, the neonatal period is followed by a transitional period in which the pup rapidly matures, and consequently a pup enters the early socialisation period in a relatively physically mature state. Since the pups are not fully dependent on their mother at this time, the mother dog frequently leaves the nest for brief periods of time, and as a consequence the strongest primary

social relationships in dogs are formed with the littermates (Scott, 1963). This promotes the characteristic pack forming in most canids. By contrast, in humans the neonatal period is directly followed by a sensitive period for socialisation, thus before the transitional period of maturation. Consequently, the human infant is highly dependent on its caregiver — usually the mother — during the early socialisation period, and the strongest social relationship is formed with this person (Scott, 1963).

Fox & Stelzner (1967) demonstrated the importance of social contact with conspecifics during the early socialisation period for the appropriate social development in dogs. Seventeen pups were reared under three different conditions: hand-reared from birth to 3.5 weeks of age and then isolated until 12 weeks (II-group), reared by the mother and then isolated from 3.5 to 12 weeks (CI-group), or reared by the mother and isolated from 8 to 12 weeks (CCI-group). At 12 weeks these pups underwent a series of behaviour tests. Pups of the II-group showed the largest deficits in social development, whereas the pups of the CCI-group behaved as expected of a dog, with no apparent deficits. Pups of the CI-group showed a mixture of the behaviours, with some showing deficits in social behaviour and others appearing normal. The variation within this group could possibly be explained by individual differences between pups and/or small group size (Scott & Fuller, 1965). The results, however, not only emphasise the importance of social contact during the early socialisation period, but also provide evidence for the role of the mother dog in social development. When pups are between 5 and 7 weeks of age the mother gradually starts to wean her pups by walking away, growling, baring her teeth, or biting softly (Rheingold, 1963; Wilsson, 1984), introducing the pups to dominant and submissive social interactions. Also through other social interactions apart from weaning, the mother dog will discipline her pups, providing them with important information on social behaviour (Case, 2005). Therefore, for a proper social development it is crucial for pups to stay with their mother at least until natural weaning has occurred, which is usually when the pups are around 7–9 weeks old (Wilsson, 1984; Case, 2005), but may differ among breeds.

Around the time pups acquire their social behavioural repertoire through interactions with their mother, interactions with littermates also contribute to the social, cognitive and physiological development of the pups. Intraspecific communication is largely established during play-fights among littermates, in which the pups alternately bite each other and learn to associate specific

vocalisations with pain (Dehasse, 1994; Case, 2005). Through these play-fights, pups learn how to interpret and display signals, such as agonistic, dominant, submissive and appeasement behaviours, as has been observed in a group of free-ranging dogs (Pal, 2008). In addition, the play-fights help improve the pups' motor skills. In a study on a group of free-ranging domestic dogs, play behaviour was first seen when pups were three weeks of age and the occurrence of play behaviour gradually declined after eight to nine weeks of age (Pal, 2008). Although the function of play in dogs is still a point of discussion, the most supported theory indeed involves motor skill and social development (Sommerville et al., 2017).

In rats, the inability to perform play behaviours during a sensitive period in early life has been shown to reduce social activity (Hol et al., 1999). Rats housed in isolation at four weeks of age, deprived of the opportunity to play, displayed decreased social activity in adulthood. Similarly, the provision of specific play enrichments in 6–7-week-old dog pups elicited more play opportunities, resulting in less fear and anxiety at the age of 1.5 years compared to a control group with less opportunities for play in the period of 6 to 7 weeks (van Eijk et al., 2006, unpublished).

Restriction of contact with conspecifics as a pup during the eight weeks following their first experience in public has been shown to be strongly associated with the occurrence of aggressive behaviour (i.e., growling, snapping, biting, or lunging at an unfamiliar dog) between one and three years of age (Wormald et al., 2016). Surprisingly, in the same study, commencing public social exposure at eight weeks of age was associated with higher odds of aggressive behaviour as an adult compared to starting public exposure at 18 weeks. A potential explanation may be that pups starting social exposure at eight weeks of age had a higher chance to have negative or traumatic experiences (intense exposure causing a fear response). Therefore, social interactions with unfamiliar conspecifics in the early weeks of life may better be restricted to a safe and controlled domestic environment.

3.1.2. *Interspecific socialisation*

As pups form social relationships with their littermates (i.e., intraspecific bond) they also become receptive to contact and social relationships with humans (i.e., interspecific bond) (Scott, 1958). The importance of early human contact for the successful formation of dog-human bonds later in life has been illustrated by Freedman et al. (1961). Freedman and colleagues divided 34 Cocker spaniel and Beagle pups into groups which were socialised

to humans at different ages (2, 3, 5, 7, or 9 weeks) or were not socialised at all (control). At 15 weeks of age all dogs were subjected to three behaviour tests and their performance in the tests was documented. In the handling test, the attraction of a pup to the handler was scored. Pups socialised at 2 weeks and control pups scored significantly lower than pups socialised at 5, 7, or 9 weeks. The leash-control test was designed to test resistance to training walking on a leash. Again the pups socialised to humans at 5, 7 and 9 weeks scored significantly higher than the other groups. In the reactivity test behavioural and physiological (heart rate, depth of respiration and muscle tension) responses to aversive stimuli were scored. Pups socialised to humans at 7 weeks scored significantly better than the controls. Overall, this group performed best in all three tests, whereas the control group scored lowest in all tests. Additionally, the control pups were extremely fearful and avoidant towards humans. Despite the small number of pups per group, which renders the results susceptible to the influence of individual differences, this study suggests that pups should be exposed and introduced to humans at an early age, during the sensitive early socialisation period (Battaglia, 2009), and ideally between five and eight weeks of age (Scott, 1963; Overall, 2013).

In summary, similar to the perinatal period, the experiences gained during the early socialisation period are likely to have long-term effects on a behavioural and physiological level, and contribute to the dog's (social) behaviour as an adult (Scott, 1962).

3.2. Late socialisation (12 weeks to 6 months)

The early or first socialisation period is followed by the late or second socialisation phase (Table 2), also called juvenile period in the literature. The late socialisation phase extends to approximately six months of age, when sexual maturity is reached (Scott, 1958; Case, 2005; Wilsson, 2016). Although considered less sensitive than the early socialisation period, the importance of the juvenile and succeeding adolescence period for further behavioural development has recently been discussed in rodents (Sachser et al., 2011; Brydges, 2016). Juveniles require extensive stimulation during these phases to reinforce their socialised state. This has been demonstrated by a study with a group of future guide dogs (Pfaffenberger & Scott, 1959), which were socialised to humans at the end of the early socialisation period, between 8 and 12 weeks. When the pups reached the age of 12 weeks, roughly half of them were quickly rehomed while the other half remained in the kennels with

conspecifics for 2–11 weeks. The dogs that remained in the kennels received no further reinforcement of socialisation to humans and the results of the study showed that these dogs were more likely to fail as guide dogs, largely due to fear and nervous behaviour. Also, a study on wolves emphasises the complementary function of experiences during the early and late socialisation phase. Young wolves that were socialised to humans until three months of age, but received no further reinforcement until 6 months of age, became fearful of humans and the positive effects achieved during early socialisation seemed to have disappeared. Wolf cubs that were reared and reinforced with human contact until 6 months of age, thus during both the early and late socialisation period, remained fearless of humans even without reinforcement during a subsequent period of over a year (Woolpy & Ginsburg, 1967). In line with these findings, dogs exposed to busy urban environments during the late socialisation period (between three and six months of age) are less likely to develop behavioural disorders in the form of avoidance behaviour and aggression towards unfamiliar people later in life (Appleby et al., 2002). These studies demonstrate the importance of the juvenile and adolescent period, as the behavioural profile of an individual as it was shaped early in life may be confirmed or adjusted during these periods, depending on the degree to which the current environment matches the rearing environment (Sachser et al., 2013; Groothuis & Taborsky, 2015).

4. Synthesis: plasticity and interactions

The reviewed literature so far confirms that the behaviour of an adult dog is determined to a large extent by the quality of maternal care, its attachment style to its mother, and the variety of both social and non-social stimuli provided during the early and late socialisation period. Insufficient or inadequate stimulation during these periods may increase the risk of developing behavioural disorders as an adult. Although the sensitive periods and mother-pup relationship have been presented separately in this review, they interact with each other in a complex manner, and in addition, these interactions are also influenced by genetic variation (Scott & Fuller, 1965). Given the complex interplay of genes and environment, the question can be raised: how reversible or irreversible are the consequences of early life experiences?

The central nervous system remains plastic in adult life, keeping the capacity to modify neural connections based on the interactions with its environment (Kolb et al., 2008), although this capacity for adjustments is sub-

stantially smaller than during the sensitive period for socialisation (Knudsen, 2004). Some studies suggest that behaviour can be altered by experiences even later in life. For example, in rats that underwent early maternal separation, the increased neuroendocrine and behavioural stress responsivity could be attenuated by social enrichment after weaning, although the physiological changes in the hypothalamus caused by the early separation could not be reversed (Francis et al., 2002). In monkeys, social contact after 7 months of age in previously socially deprived animals appeared to have positive effects. Mothers that had had some social contact with conspecifics during their development, albeit late in development, appeared more likely to acquire an adequate maternal care style compared to mothers that had been completely socially deprived as an infant (Harlow et al., 1966). However, due to small sample sizes and large individual variation these results remain suggestive.

Whereas some evidence exists for plasticity in behavioural development in rodents (Champagne & Curley, 2005), literature on this matter in dogs remains scarce and is largely anecdotal and based on small sample sizes. In their influential book *Genetics and the Social Behavior of the Dog*, Scott & Fuller (1965) anecdotally describe the case of one mixed breed dog that was raised by humans, isolated from other dogs, and was introduced to her littermates for the first time at the age of nine weeks. Initially the dog appeared fearful, but the littermates showed “playful aggressiveness” and the dog reacted to this. A few days later the effects of poor socialisation in the first weeks of life were no longer apparent. Although the most sensitive window for filial imprinting had passed in this nine week old pup, the early socialisation period extends to twelve weeks, and it has even been suggested that sensitive periods may be prolonged under suboptimal circumstances lacking stimulation (Knudsen, 2004). Scott & Fuller (1965) further describe a group of Beagles that were kept in complete isolation from birth until 16 weeks of age, and thereafter were introduced to unfamiliar conspecifics for the first time. The isolated individuals were repeatedly attacked by the other dogs and seemed unable to develop social relationships. When researchers held play sessions with the isolated dogs, mimicking play-fights, they did manage to elicit play behaviour and after a few days the isolated dogs would respond to the researchers as properly socialised individuals would (Fuller, 1961; in Scott & Fuller, 1965). Besides the possibility of some plasticity in the social behaviour, this study also underlines the importance of play during the sensitive period for socialisation.

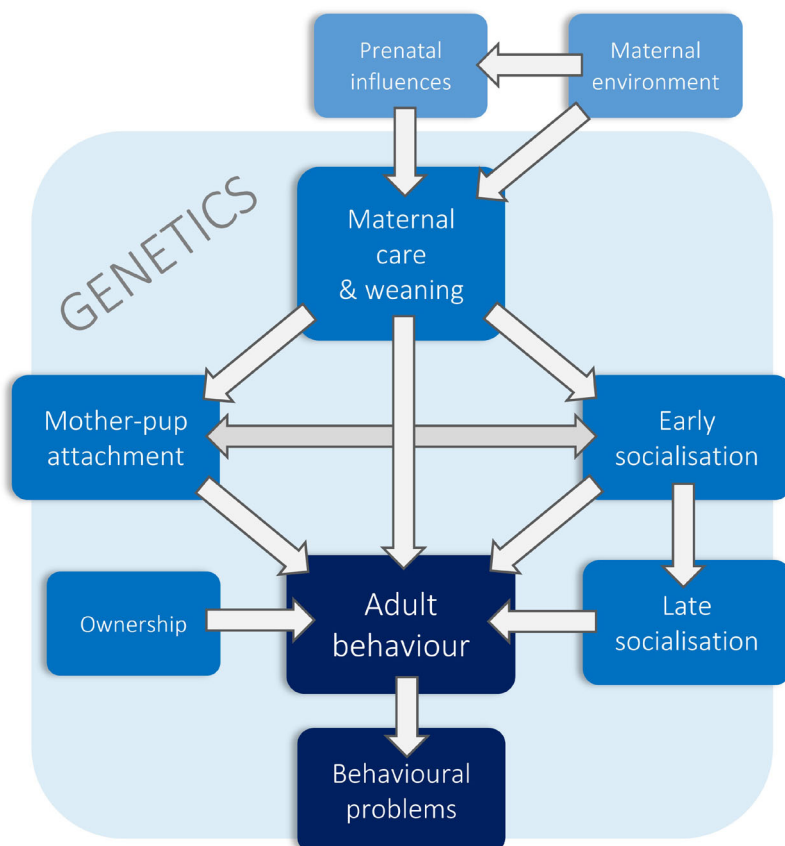


Figure 1. Graphical model of factors contributing to an adult dogs' behavioural profile.

In the previous sections we have emphasised the importance of both the early and late socialisation period for a proper behavioural development in dogs. It is clear that interactions between the early and late socialisation period influence the behaviour of these dogs. A poor start in life may be partly compensated by enrichment and proper stimulation later in life, whereas an optimal early environment may be counteracted by later poor experiences. Unfortunately, we cannot derive from the few available anecdotal examples whether counteracting effects of experiences in the late socialisation phase persist throughout adult life. Here, we assume that the adult behavioural profile — including the vulnerability to develop behavioural disorders — is the cumulative sum of experiences during the sensitive periods of early development (Battaglia, 2009; Figure 1). Nevertheless, behavioural profiles may

remain flexible to a certain degree even into adulthood, thus behavioural disorders may remain treatable and/or reversible given appropriate training and interventions.

5. Implications

In this review we have summarised and analysed the existing literature on mother-pup attachment and maternal care, early and late socialisation, interactions between these essential components in the early development, and their influence on the development of behaviour and behavioural disorders in domestic dogs. In the following, we list some applied implications of this scientific knowledge for dog breeders and other relevant parties. As we identified major gaps in knowledge on this topic in dogs, we also suggest opportunities for future research.

As discussed in this review, there is now a growing body of evidence that negative or traumatic experiences and/or lack of stimuli in the early development of dog pups may have negative long-term consequences on health and behaviour (Table 3). Pups weaned at six weeks of age show higher morbidity and mortality rates than pups weaned at twelve weeks (Slabbert & Rasa, 1993), and removal from the litter prior to eight weeks of age may cause severe distress (Serpell & Jagoe, 1995) and heighten the risk of behavioural disorders (Pierantoni et al., 2011). Rehoming pups at a later age, however, may also facilitate the development of behavioural disorders. According to a recent survey study, pups that were rehomed between 13 and 16 weeks of age showed a higher prevalence of growling, snapping and avoidance behaviour towards unfamiliar humans after one year of age, compared to pups rehomed between six and eight weeks of age (Jokinen et al., 2017). Therefore, the ideal moment to rehome dog pups may be a balance between biological needs such as a sufficient period of maternal care, and appropriate socialisation to the future environment. It should be noted that pups spend a large part of the sensitive period for socialisation at their breeder, who therefore has the prominent responsibility in the early socialisation process. Breeders should be strongly advised to provide their pups with a sufficient stimulating and variable environment, including social interactions with other dogs and humans, while taking care not to overstimulate the pups (Battaglia, 2009; Howell et al., 2015). A survey study with 48 Belgian dog breeders showed that environmental enrichment with non-social stimuli was provided by only

Table 3.

Overview of reviewed literature in dogs that provides evidence for the influence of maternal care and the early and late socialisation period on the development of behaviour and behavioural disorders.

Aggression	
Early and late socialisation	
Appleby et al. (2002)	A stimulus-rich environment during the early and late socialisation period is associated with a lower risk of developing aggression towards strangers
Gazzano et al. (2008)	Expert advice on raising a pup reduces the risk of developing behavioural disorders
Gray et al. (2016)	Pups from irresponsible breeders have a higher risk of developing aggression
Wormald et al. (2016)	Restriction of contact with conspecifics is associated with aggressive behaviour as an adult
	Starting public social exposure at 8 weeks is associated with higher odds of aggressive behaviour as an adult compared to starting public exposure at 18 weeks
Jokinen et al. (2017)	Rehoming pups at 13 to 16 weeks of age is associated with a higher prevalence of aggressive behaviour than rehoming at 6 to 8 weeks of age
McMillan (2017)	Pups from commercial breeders show more aggression towards dogs and humans
Fear and anxiety	
Maternal care	
Pierantoni et al. (2011)	Weaning at 30 to 40 days has a higher risk of developing fearful behaviour than weaning at 60 days
Tiira & Lohi (2015)	Poor maternal care quality is associated with more fearful behaviour in the adult dog
Bray et al. (2017b)	A ventral nursing style with easy nipple access is associated with more anxiety
Early socialisation	
Freedman et al. (1961)	Isolation from humans until 14 weeks of age leads to more fearfulness and avoidance towards humans
Appleby et al. (2002)	A stimulus-rich environment during the early socialisation period is associated with a lower risk of developing fear towards strangers
Van Eijk et al. (2006) (unpublished)	Play enrichment in 6–7-week-old pups results in less fear and anxiety as an adult
Pluijmakers et al. (2010)	Exposure to various stimuli on video images reduces fear responses in seven to 8-week-old pups

Table 3.

(Continued.)

Tiira & Lohi (2015)	More socialisation experiences between 8 and 12 weeks of age reduces the risk of developing fear
McMillan (2017)	Pups from commercial breeders show more aggression towards dogs and humans
Late socialisation	
Pfaffenberger & Scott (1959)	Lack of reinforcement of socialisation to humans after the early socialisation period increases the risk of developing fear and nervous behaviour
Woolpy & Ginburg (1967)	In wolves, lack of reinforcement of socialisation to humans after 12 weeks of age leads to the development of fear towards humans
Separation related behaviour	
Early socialisation	
Gray et al. (2016)	Pups from irresponsible breeders have a higher risk of developing separation related behavioural problems
Vaterlaws-Whiteside & Hartmann (2017)	A socialisation program tailored to the pup's behavioural and physiological development of a pup reduces the risk of separation related behaviour

a small percentage of the investigated breeders (De Meester et al., 2005). Breeders with less than ten litters appeared to stimulate their pups with inanimate stimuli more than breeders with more than ten litters, although this was still insufficient. In particular exposure to a large variety of unfamiliar locations was seldom provided and is recommended by the authors. A survey with dog owners revealed that almost one-third of dog pups in the United States and Canada are insufficiently exposed to other dogs and humans during the sensitive period for socialisation (Cutler et al., 2017). Recently, a socialisation program was developed tailored to the behavioural and physiological development of a pup during the first six weeks of its life. The program led to reduced separation related behaviour and general anxiety in dogs at the age of eight months, and is therefore recommended for pet dog breeders (Vaterlaws-Whiteside & Hartmann, 2017).

In The Netherlands, breeders are obligated by law to socialise dogs to humans and conspecifics during the sensitive period for socialisation (Article 3.22, Wet Dieren, Besluit houders van dieren). However, imported dogs are not protected by Dutch law, but by the law of their country of origin. The largest puppy trade network in western Europe imports pups from Hungary

and Slovakia (Van Uhm, 2010; Four Paws, 2013). In the Act of Animal Protection in Hungary no guidelines regarding dog breeding or socialisation are mentioned (Zoltán, 2011) and Slovakia has no specific law protecting dog rights (Global Animal Law Project). Alarmingly, the pup's essential behavioural needs and requirements during the socialisation period are often not taken into consideration in puppy farms (Van Uhm, 2010; Four Paws, 2013).

Apart from breeders, veterinarians have an important responsibility in ensuring the appropriate care of breeding dogs (Voith, 2009), as they are usually the first to examine the mother and her just born pups (Howell et al., 2015). Pups raised by owners who received expert advice, e.g., from veterinary behaviourists, are less likely to develop behavioural disorders later in life (Gazzano et al., 2008). Expert advice on dog behaviour and behavioural development therefore appears to be effective in reducing the prevalence of behavioural disorders in the pet dog population, and should be given to owners in a pro-active manner. Ideally, this advice is based on sound scientific findings, however, alarmingly little has been scientifically investigated regarding the early social development of dogs and the mother-pup attachment bond in particular. Lacking in-depth knowledge on dog attachment formation hampers the development of socialisation protocols and adequate advice to breeders and potential dog owners, with serious consequences for the welfare of dogs. Experts in this field univocally agree that more research on this topic is needed, given its relevance for animal welfare and society. Therefore, we have highlighted gaps in knowledge and proposed future research avenues to further investigate what shapes a dog pup during its early life and how to ensure good adaptive capacity and the fulfilment of essential needs.

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