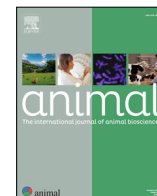




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Review: The roles of individuality and social life in shaping positive animal welfare in livestock species



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ABSTRACT

Positive animal welfare (PAW) emphasises “a good life” marked by the experience of predominantly positive affective states, and the development of competence and resilience according to species-specific and individual capabilities. Even though the concept of PAW has received increasing attention in past years, guidance for shaping future PAW-friendly farming systems is lacking. As highly social species, farmed animals have the potential to experience a rich social life that can influence their welfare. This has often been studied through the lens of negative interactions. However, to advance research on PAW, a focus shift on how affiliative interactions can contribute to and maintain positive group dynamics is needed. Affiliative interactions are mostly based on social preferences that are, in turn, dependent on the individuals involved and their contribution to group cohesion. Acknowledging the uniqueness of each individual in their perception, cognition and appraisal is a challenge for ensuring PAW not only at the individual level but also at the group level. In this narrative review, we argue that combining the study of individuality and social life will generate practical knowledge that can be used for promoting PAW. We first examine how individual differences in sensory and cognitive capabilities shape vertebrate animals’ appraisal of their environment and influence PAW. We then discuss key features of (intraspecific and interspecific) social life, such as affiliative interactions, social facilitation and socialisation, and their relevance for PAW. Finally, we explore how the interplay between individuality and social life can create conditions conducive to PAW. For this, we focus on the concepts of sociability and social competence as promising future research areas. Collectively, this review illustrates a complex framework emerging from the interplay between individuality and social life and paves the way for promoting PAW on farms and improving animal management.

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Implications

We offer a comprehensive overview of the evidence regarding how individuality, social life, and their interplay can influence positive animal welfare through experiencing positive affective states, and building competence and resilience. Our conceptual framework considers individuals (farmed animals) as part of a social

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system (farmed animal groups), with both providing opportunities to promote positive animal welfare on farms and improve herd management. Furthermore, we identify knowledge gaps and research needs for improving our understanding of how individuality and group dynamics contribute to positive animal welfare.

Introduction

In recent years, the field of animal welfare science has shifted its focus from minimising suffering to fostering environments where non-human animals (hereafter “animals”) can thrive, giving rise to the concept of positive animal welfare (PAW; Rault et al., 2020a; Turner, 2019; Lawrence et al., 2019). PAW has been defined by Rault et al. (2025) as “the animal flourishing through the experience of predominantly positive mental states and the development of resilience and competence”. In the context of farmed animals, implementing practices that support PAW is increasingly recognised as a route to achieve more ethical animal farming. However, to reach this step, one first needs to understand how PAW could be promoted in animals’ actual everyday lives.

Since most farmed animals are members of highly social species, improving their social environment offers considerable potential for them to experience PAW. However, little is known about how social group structure and organisation can contribute to the experience of positive affective states, resilience (i.e. the ability to resist and bounce back from challenges), and the acquisition of competence (i.e. building capacity to cope with challenges and make use of opportunities; Rault et al., 2025). In wild counterparts of domesticated species, group composition is shaped by factors such as philopatry, seasonal changes, and resource availability (Chen et al., 2022). These environmental influences drive physiological and behavioural changes in individuals (e.g. reproductive cycles, foraging and ranging behaviour) which, in turn, affect group dynamics via dispersion and immigration. In contrast, farmed animals typically have no opportunities to influence their group composition, restricting group dynamics and collective decision-making compared to their wild counterparts. Most farmed animals are kept in intensive housing systems, often characterised by single-sex groups, large group sizes, limited space, early weaning, and mixing with unfamiliar conspecifics of the same age category. Such management practices are not primarily designed for satisfying animals’ social needs and, hence, may not be conducive to building positive social relationships. Thus, the potential for a fulfilling social life contributing to PAW is likely to be constrained and remains largely unexplored.

Although social behaviour of farmed animals has been extensively studied, this research has mostly focused on negative interactions (e.g. aggression and injurious behaviour) due to their adverse impact on welfare and economic performance. In contrast, a considerable knowledge gap exists regarding the positive aspects of social life, such as social support, helping, social buffering, and affiliative relationships (Lee et al., 2022; Rault, 2012, 2019). Additionally, studies on social networks and collective behaviour highlight the complexity of group dynamics and emphasise the significance of specific individuals and their roles within a group, such as leadership or acting as “social glue” for group cohesion (e.g. Hirata et al., 2022; Sueur et al., 2018). As a consequence, some individuals can strongly influence the behaviour of the whole group. More importantly, these studies demonstrate that interactions between individuals are not random; rather, animals bond with, and show preferences for interacting with specific group members which, in turn, influences group dynamics. This indicates that the identity of individuals within a group is crucial in shaping its dynamics. Individuals interact uniquely and are perceived differently by their conspecifics depending on the nature of their

respective relationships, whether they involve a preferred partner, a sibling, an unfamiliar individual, or a competitor.

The possibility to identify individual features (i.e. the individuality) of an animal is offered within the framework of personality or coping styles, which refers to stable inter-individual differences in traits such as boldness, sociability, exploration, aggressiveness, and proactive-reactive tendencies (Réale et al., 2007). These inter-individual differences in behaviour may influence group dynamics and vice versa, yet their potential relevance in terms of promoting PAW remains unexplored. Although some effort has been made to describe individuality in farmed animals, such findings have rarely been applied to practical improvements in living conditions (Richter and Hintze, 2019). Nevertheless, individual differences in underlying cognitive and affective traits should be taken into account, as they shape the individual’s capacity to experience positive mental states (Rault et al., 2025), gain competence and build resilience. Understanding how these variations influence social interactions and impact individual vs group-level welfare could provide valuable insights for assessing and promoting PAW.

In contrast to the conventional separation between research on individuality and research on social life, the aim of this narrative review is to highlight how their combination promises to rethink animal welfare and promote PAW in farmed vertebrate species. To demonstrate the intertwining of individuality and social life, we take a “zoom-out” approach (see Video 1). First, we focus on individual animals and their variability along different spectra (sensation, cognition, affect) directly influencing the experience of positive affective states through feedback loops. This evidence addresses why individuals vary in appraising their social environment, adding complexity when individuals live together in groups. We then explore key features of social life and their implications for PAW. Building on this foundation, we propose future research directions for integrating individuality and social life as a promising way to promote PAW for farmed animals. Our examples mainly come from positive contexts (i.e. rewarding situations, affiliative interactions) thought to be associated with positive mental states (Rault et al., 2025), as research on the other main features of PAW, resilience and competence, is currently limited in this emerging field. Moreover, our examples are weighted towards mammalian farmed species, as non-mammalian taxa (e.g. birds, fish) are underrepresented in the PAW literature, although the points raised here may also apply to them. We also invoke knowledge about other species, including humans, when information about farmed species is lacking.

Individuality

In this section, we provide examples of how individual differences in sensory perception, cognitive abilities, appraisal, and affective style may influence PAW. We also consider how PAW may be affected by feedback once a behavioural or physiological outcome has been expressed, thereby influencing judgement bias. Connections between these concepts are summarised in Fig. 1, and key terms used in this section are defined in Table 1.

Individual differences in sensory perception

State of the art

Farmed vertebrates share the five most common sensory modalities with humans (smell, hearing, taste, vision, and touch) but their range and acuity differ between species. Farmed animals therefore likely perceive their surroundings in different ways than humans (Nielsen, 2018; Shettleworth, 2009). To enable them not only to survive but also to thrive (Rault et al., 2025), it is important to consider how they perceive their environment, not only as

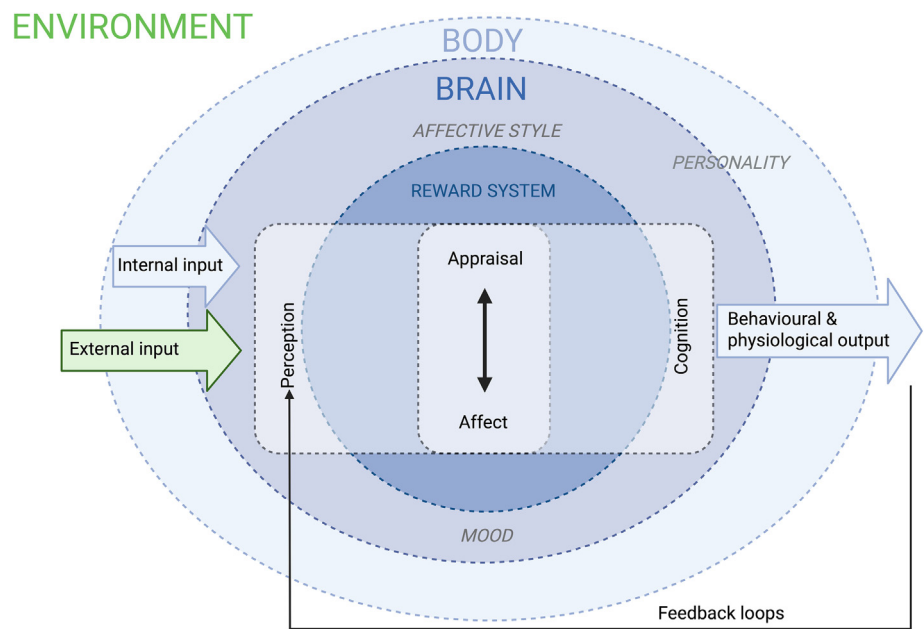


Fig. 1. Selected elements contributing to individual differences that can influence positive animal welfare in livestock species. Circles represent physical entities, with the body as the outer circle, which contains the brain (middle circle). The brain houses the reward system (inner circle), comprising multiple structures involved in reward processing, such as the nucleus accumbens and orbitofrontal cortex. Lines are dotted to represent the ongoing interactions between the environment, body, brain and reward system. Rectangles represent processes occurring within the brain: perception, cognition, appraisal and affect, which are influenced by external and internal stimuli (from outside, and inside the body, respectively). Overlapping rectangles illustrate the bidirectional interplay between appraisal and affect in interaction with perception and cognition within the reward system, which is reflected in the behavioural and neurophysiological output of the individual. Detected discrepancies between outcomes and expectancies (reward prediction errors) lead to reassessment of the situation via feedback loops. Affective styles emerge when consistent patterns in all aforementioned brain processes appear within an individual. Affective style contributes to the individual's overall personality, which is indicated by stable inter-individual differences in behavioural and physiological outputs.

Table 1
Glossary of terms related to individuality in livestock species.

Term	Definition
Affective style	Consistent inter-individual differences in emotional reactivity and emotional regulation (Davidson, 2004). See in Goursot et al. (2021) for suggestions on including additional concepts (personality, coping) into this definition. Affective styles are stable individual traits measured through behavioural and neurophysiological indicators (Goursot et al., 2021). Different from affective states.
Feedback loop	A positive (or negative) feedback loop between two variables, S and B (e.g., representing a state and a behaviour), is defined as a process in which a change in S induces a change in B, which in turn leads to a change in S in the same (or opposite) direction as the initial change (DeAngelis et al., 1986; Montalcini et al., 2025).
Personality	A correlated set of behavioural and physiological patterns that are consistent over time and situations within an individual (Gosling and John, 1999; Réale et al., 2007).

species but also as individuals. Indeed, each individual lives in its own *Umwelt*, or subjective environment, that shapes its perceptions of the world in ways that differ but overlap to varying degrees with those of others (Schroer, 2019). Sensory systems are constantly bombarded with stimuli from the surrounding environment. How this information is organised, interpreted, and experienced by the animal is referred to as perception (Spielman et al., 2014). Perception functions as both a bottom-up and a top-down process, where bottom-up refers to the processing of sensory input into perceptions and top-down refers to perceptions arising from cognition as influenced by knowledge and experience, which vary greatly among individuals (Rørvang et al., 2020; Barrett, 2017). In humans, the concept of sensory processing sensitivity is well established. This term refers to personality traits describing stable inter-individual differences in sensitivity to different environmental stimuli, as influenced by thresholds for detection, cognitive processing, and emotional reactivity (Greven et al., 2019; Greven et al., 2025; Dunn, 2001). These

differences influence how individuals perceive and respond to both social and non-social stimuli. Evidence for comparable inter-individual variation in sensory processing in animals is limited. Studies on dogs suggest the existence of “sensory processing sensitivity traits” (Braem, 2024; Murphy, 1998), which may influence how individuals perceive and respond to social signals (Greven et al., 2025). In cats, there is individual variation in responsiveness to combinations of insect-repelling iridoids in plants such as catnip and silver vine (Uenoyama et al., 2026). In cattle, a survey of handlers identified a possible connection between animal response to handling and sensory acuity (Estévez-Moreno et al., 2021). In pigs, large individual differences in olfactory investigation (sniffing) have been detected, which could reflect both individual preferences and differences in sensory processing (Rørvang et al., 2023), although attempts to predict the valence of individual pigs’ responses to different odours did not yield consistent findings (Grut et al., 2025). In a review on individuality in horses, Mills (1998) noted

that individuals differ in the extent to which their behaviour and performance are affected by environmental disturbances. However, such variation in responsiveness may reflect differences not only in sensory perception but also in other personality traits such as boldness and fearfulness. Larose et al. (2006) reported individual variation in laterality of eye use by horses when viewing different stimuli, which provides an indication of an individual's perception of specific situations as shaped by temperament, age, and previous experience. In a study of sensory processing sensitivity in horses, Lansade et al. (2008) detected four personality traits that were stable across context and time: tactile sensitivity, gustato-olfactory sensitivity, auditory sensitivity, and visual sensitivity. These results support the view that, like humans, individual horses react differently to specific sensory stimuli, making it likely that the same applies in other farmed species.

For a sensory modality to influence affective states, there must either be a direct pathway linking sensory detection with emotional processing, or a conditioned association must be formed between sensory stimuli and emotional responses through individual experience (Rouby et al., 2009). The sensory system having the most direct link to emotions is olfaction, among the first of the sensory systems to develop in vertebrate fetuses. Olfactory processing is strongly integrated with limbic brain circuits. The olfactory bulb projects directly to regions including the amygdala and hippocampus, linking olfaction with emotional processing as well as learning and memory (Herz, 2016; Wilson and Sullivan, 2011; Gottfried, 2010). This explains why odours can elicit negative and positive odour memories. Human well-being is greatly influenced by olfactory input (Oleszkiewicz et al., 2021; Hedblom et al., 2019) and the impact of odours on farmed animals' affective states could be even greater, especially in macrosmatic species. Odours can also acquire motivational significance. For example, pigs are attracted to truffles, which contain volatile compounds including 5 α -androst-16-en-3 α -ol that resemble boar pheromones (Claus et al., 1981). Such biologically relevant odour cues may trigger approach and rooting behaviour by engaging affective and motivational systems. However, it remains unclear whether these responses primarily reflect changes in affective state or learned associations with food rewards.

A clearer illustration of individual-specific sensory sensitivity is found in maternal olfactory recognition in sheep. Ewes learn quickly after birth to discriminate the unique odour profile of their own lamb from that of unrelated conspecifics, and this selective recognition underpins filial bonding and maternal care (Poindron et al., 2007; Nowak et al., 2011). Such exclusive olfactory preferences are closely associated with affective and physiological responses in the mother, including heightened maternal motivation and neuroendocrine changes around parturition (Dwyer, 2014). Human research indicates that olfactory stimuli can modulate emotional processing through limbic pathways (Ross and Mason, 2017), suggesting that future work should prioritise determining how odours influence affective states in animals. In general, emotional associations formed with visual, auditory, tactile and chemical stimuli may have a significant impact on welfare, with the emotional valence attached to specific sensory stimuli being influenced by inherited inclinations, but modified depending on the contexts in which each individual experiences them (Bombail, 2019).

There is some evidence that sensory enrichment through sequential exposure to a variety of novel odours enhances cognitive function in humans (Woo et al., 2023) and that exposure to specific odours promotes neurogenesis of specific sensory neuron subtypes in mice (Hossain et al., 2025). Such effects may enhance sensitivity to relevant odours and the ability to discriminate them from other odours, which could contribute to the development of

social and other competences and their maintenance as animals age.

Knowledge gaps

There is a need for investigations into the sensory preferences of farmed species so that the provided sensory environment is conducive to PAW. Such studies could expose individuals to different types, intensities and cocktails of sensory stimuli and measure their behavioural responses along a continuum ranging from strong exploration to strong avoidance. However, preference tests alone may not reveal whether animals perceive an environment as genuinely positive or simply less aversive than the alternatives. Combining such tests with motivation or consumer-demand paradigms, measuring how much individuals will work to access particular sensory environments, may help quantify the strength of these preferences. Studies should also examine longer-term effects of sensory environments on neural plasticity and resilience. For all sensory modalities, research is also needed to evaluate individual differences in sensory preferences, neurodiversity in sensory perception, and how these differences might be accommodated in husbandry systems.

Research focused on sensory enrichment through sequential exposure to attractive novel odours and other sensory stimuli (e.g., harmonious sounds, objects with different textures) may reveal competence-enhancing cognitive benefits in farmed animals, which may in turn promote positive affect. Placing such stimuli in unpredictable locations or making them available at unpredictable moments may encourage exploration and reduce welfare issues such as injurious behaviour, provided that individuals retain some control over their level of exposure. It is also of interest to assess how specific sensory cues associated with reward can be used to promote resilience in mildly stressful situations. Studies in animals suggest that odours or other sensory stimuli previously paired with positive outcomes may mitigate stress responses or facilitate coping, highlighting a promising avenue for welfare-oriented sensory enrichment (e.g., Bombail et al., 2019).

Individual differences in cognitive abilities

State of the art

In humans, the relationship between cognitive abilities or skills and positive affect is dynamic (e.g. Allerhand et al., 2014). Positive effect can facilitate memory (Teasdale and Fogarty, 1979), improve creative problem solving (Estrada et al., 1994) and lead to better work performance (Warr and Nielsen, 2018). The reverse is also possible, whereby cognitive abilities promote positive affect. For example, in a human cohort, Chmiel et al. (2012) observed a positive relationship between general cognitive ability (assessed by verbal ability, reasoning ability, visual-spatial ability and processing speed) at 12 years of age and the frequency of experiencing positive affect 40 years later, whereas this association was negative for experiencing negative affect. Gale et al. (2012) found similar effects, though these effects were attenuated when adjusting for potential confounders (e.g. the personality trait neuroticism). Such attenuating effects were also observed in elderly people, the most studied age group when linking cognitive abilities with subjective well-being. Yazdani and Siedlecki (2021), for example, found that variables such as self-rated health, emotional stability, and conscientiousness partially accounted for a detected relationship between cognitive performance and subjective well-being, the latter being conceptualised based on life satisfaction, positive effect, and negative effect. These studies highlight the importance of investigating individual differences underlying the association between cognitive abilities and positive well-being.

Given the relationship between cognitive abilities and positive affect in humans as well as the importance of considering individual differences in this context, one may ask what we know about these complex relationships in animals. Even though most research has not (yet) focused on the link between different cognitive abilities and PAW, several studies have investigated the bidirectional relationship between cognitive abilities and animal welfare (Franks, 2018). This research shows how cognitive aspects, such as cognitive enrichment, predictability and expectations as well as knowledge and information, can affect animal welfare and, in turn, shape cognitive capacities: “Across the animal kingdom, we find that the same environments that set animals up for improved welfare and coping skills later in life also tend to have beneficial effects on cognitive outcomes.” (Franks 2018; p. 10). Franks (2018) also highlights the relevance of understanding and considering individual differences in this context.

Cognitive enrichment (i.e. cognitive stimulation by providing opportunities for learning) is considered a promising way to promote PAW (e.g. Manteuffel et al., 2009; Meehan and Mench, 2007). For example, the “eureka” moment occurring when finding the solution to a problem has been associated with playful behaviour interpreted as indicating positive affect (dogs: McGowan et al., 2014; calves: Hagen and Broom, 2004). In pigs, individuals trained on an auditory discrimination paradigm to receive food had higher heart rate variability and showed more exploratory behaviour, and less fearful and agonistic behaviour, in challenging situations compared to control pigs fed conventionally (Zebunke et al., 2013). This result was found in otherwise relatively barren conditions, raising the question if cognitive enrichment has the same effect in more complex housing conditions. Moreover, the way animals react to and benefit from cognitive enrichment depends on the individual, rendering it difficult to apply a “one-size-fits-all” approach to cognitive enrichment (Richter and Hintze, 2019).

Investigations are also exploring the possibility of advancing PAW by promoting flow, a cornerstone of positive human psychology that describes absorption in an intrinsically rewarding activity (Clark, 2023; Hintze and Yee, 2023). It is important to consider that a flow-inducing task must align with the individual's current cognitive abilities; in humans, tasks that are too challenging may lead to frustration, whereas those that are too simple will not sustain interest (Csikszentmihalyi, 1990), and this concept can likely also be applied to animals (Hintze and Yee, 2023). Thus, tasks must be adjusted to individual abilities, with more challenging tasks offered if interest in solving easier ones wanes with increasing mastery. Nevertheless, flow may also be maintained by offering a choice of tasks with different solutions within the same level of difficulty. This is suggested by a study in which raccoons were offered a puzzle box with three different solutions at each of three different levels of difficulty, wherein only one solution offered a food reward (Griebeling et al., 2026). When the task providing the food reward was easy to solve, raccoons were more likely to persist in seeking solutions to the other ‘unrewarded’ tasks, whereas they were less likely to persist in seeking solutions to ‘unrewarded’ tasks if the food-rewarded task was difficult to solve.

Knowledge gaps

Empirical knowledge about individual differences in cognitive abilities and their relevance to PAW in farmed animals is scarce. Both directions of the relationship between the development of cognitive abilities and positive affect need to be investigated while at the same time considering individual differences. Practical applications of cognitive enrichment need to be adapted to farm conditions, as methods that function well in small groups may be

less effective in large groups. Computer automation of tasks adjusted to each individual offers promise for large-scale application on farms.

Individual differences in appraisal and affective styles

State of the art

Appraisal theory has been applied to the processes by which farmed animals form an appraisal of a situation or environmental stimulus and react to it (Veissier et al., 2009; Greiveldinger et al., 2007; Désiré et al., 2002). Initial appraisal usually occurs rapidly, without conscious awareness (Gendron and Feldman Barrett, 2009; Kappas, 2006; Arnold, 1960). This “automatic” view of appraisal was pioneering for the study of affective states (Gendron and Feldman Barrett, 2009; Kappas, 2006) and may have contributed to a componential view of emotions based on behavioural, physiological and cognitive outputs during an emotional reaction (Paul et al., 2005). Perceptual and cognitive mechanisms are crucial to the appraisal process (Scherer et al., 2001; Lazarus, 1993; Schachter and Singer, 1962). The individual's sensory modalities (see section “Individual differences in sensory perception”) shape the initial perception of external features of an environmental stimulus (e.g. colour, odour, texture and sound). During stimulus “checks” (Scherer et al., 2001; Lazarus, 1993; Schachter and Singer, 1962), the individual's cognitive abilities (see section “Individual differences in cognitive abilities”) contribute to recognising the novelty and valence associated with the stimulus based on previous experience and resulting expectations. These features are integrated with information about current and predicted internal states to determine the appraised salience of the stimulus (see section “Individual differences in feedback loops and judgement bias”). Based on these potential individual differences reflecting distinct perceptual and cognitive backgrounds, the same stimulus is likely to be appraised differently by different individuals. Thus, an appraisal framework (Fig. 1) provides a basis for interpreting individual affective responses (Yeo and Ong, 2024). Complementarily, the framework of affective styles, suggesting individual differences in emotional reactivity and regulation, is presented later in this section.

An important moderator in the appraisal process is the individual's capacity to cope with a situation or stimulus (Scherer et al., 2001; Lazarus, 1993; Schachter and Singer, 1962). Coping refers to how an individual reduces the potential impact of aversive or stressful stimuli through fight-or-flight sympathetic responses (Finkemeier et al., 2018; Korte et al., 2005). Thus, coping reflects individual differences in reacting to negative situations (Koolhaas et al., 1999), which correlate with distinct and objectively measurable individual physiological reactions varying from immune (Koolhaas, 2008) to serotonergic (Koolhaas et al., 2007) reactions. Such studies have mostly focused on rodents and humans, but links between behavioural and physiological coping responses have also been documented in farmed animals (e.g. pigs: Kanitz et al., 2019; Krause et al., 2017; Bolhuis et al., 2003; Atlantic salmon: Vindas et al., 2017; laying hens: Carvalho et al., 2018). From a PAW perspective, it is relevant to investigate how individuals with different coping styles may also differ in physiology, generating positive emotions and associated behavioural outcomes (Paul et al., 2005).

Meanwhile, personality research, referring to the investigation of stable inter-individual differences in behaviour across time and situation (Réale et al., 2007), has become central for investigating individual differences in animals. In contrast to coping, whereby animals are dichotomised into proactive and reactive coping styles, personality research allows for numerous personality traits (such as those equivalent to the human Big Five;

Gosling and John, 1999). Investigation of the number and labelling of these traits remains a challenge in farmed animals (Finkemeier et al. 2018), and studies examining the affective states underlying observed stable behavioural differences between individuals are limited (Goursot et al., 2021; but see Kremer et al., 2021; Lecorps et al., 2018; Asher et al., 2016). Personality assessments in non-human animals have tended to focus on negative test scenarios (e.g. novelty or startle tests for assessing boldness, social isolation tests for assessing sociability; reviewed by Woodrum Setser et al., 2023; O'Malley et al., 2019; Finkemeier et al., 2018; Murphy et al., 2014; Forkman et al., 2007), with a view towards identifying “problematic” individuals with vulnerability to stress, lower performance, depression, anxiety or unwanted behaviour (Goursot et al., 2021; Wang et al., 2020). However, there are some exceptions (Montalcini et al., 2023; Occhiuto et al., 2022). For example, individual differences in “positive” behavioural traits such as juvenile playfulness have been documented in dogs (Svartberg, 2005), rodents (Lampe et al., 2019; Richter et al., 2016; Svartberg, 2005) and chickens (Oscarsson et al., 2026), although playfulness is not necessarily closely linked to positive affect (Oscarsson et al., 2026). Individual patterns of play (in pigs: Zupan et al., 2019) and sex differences in tickling preferences (in rats: Gonzalez et al., 2026) could be further explored for between-individual differences in positive contexts.

Therefore, we encourage more PAW focus in personality research to identify individuals with a relatively high potential to show more frequent positive reactions, higher sensitivity to rewards, greater capacity for agency, or more balanced emotional regulation contributing to resilience and competence. Methodologically, shifting from reactivity tests to free-choice tests in personality research would be a promising first step in line with the concept of agency, central for PAW (for operationalisation ideas, see Woodrum Setser et al., 2023). For instance, it would be logical to use environments that offer opportunities for the performance of spontaneous play (in pigs: Brown et al., 2015; Zupan et al., 2019) for testing stable individual differences in playfulness. Such approaches might also identify individuals with greater influence in enhancing the welfare of others in social groups (e.g. through positive emotional contagion; see sections “Social life” and “The interplay between individuality and social life”).

Greater individual variability is predicted when animals face positive stimuli (e.g. by expressing individual preferences, Rault et al., 2020a; Fraser and Duncan, 1998), whereas responses to negative or life-threatening stimuli are often constrained by their importance for survival, which may limit the number of adaptive responses. However, assessment of positive appraisal does not imply neglecting negative appraisal. Just as the presence of a motivation to approach cannot be interpreted without accounting for the absence of a motivation to avoid (McNaughton et al., 2016), both positive and negative appraisal are relevant to understanding individual differences in appraisal. For example, some individuals may react more intensively to positive stimuli while others react more intensively to negative stimuli (Davidson, 2004). The concept of affective styles, referring to individually consistent patterns in emotional reactivity and regulation (Davidson, 2004), could fit this idea.

Knowledge gaps

Affective styles directly depend on individual differences in brain physiology, and these already exist in human infants (Davidson and Fox, 1989). Yet, it is unclear how such differences emerge. One framework for describing individual differences in affective styles comes from the reinforcement theory of personality (McNaughton and Corr, 2019; Gray, 1970), which assesses how individuals differ in their balance between activity of the

Behavioural Inhibition System (BIS) and the Behavioural Activation System (BAS). BIS mediates approach-avoidance decisions, with higher BIS tendencies linked to negative affective styles, while BAS regulates behaviour leading to reward acquisition, with higher BAS tendencies linked to positive affective styles (McNaughton and Gray, 2024; Ford et al., 2014). Animal welfare research investigating stable BIS/BAS tendencies in pigs across time and situations shows promising results (Ferreira et al., 2025). Assessing repeatable individual responses to both negative and positive stimuli will add to a more nuanced understanding of PAW. In such studies, it is necessary to tease out changes in (short-term) affective states and (longer-term) moods that are context-dependent from affective styles inherent to the individual. This requires not only conducting repeated measures in different contexts to assess the stability of individual traits (for methodology, see Goold and Newberry, 2017), but also investigating state-trait interactions (e.g. Paul et al., 2005).

There is also a need to broaden personality assessments to incorporate positive traits, using both behavioural and physiological indicators to elucidate components of affective responses. There is, for instance, no concept aligned with PAW that refers to a mechanism parallel to stress coping (i.e. that focuses on individual differences in reactions or spontaneous behaviours related to amplifying the effects of positive stimuli and agency), that is measurable at both behavioural and physiological levels.

Individual differences in feedback loops and judgement bias

State of the art

Positive affective states may influence decisions when appraising new stimuli or situations, leading to a positive feedback loop (Fig. 1) that could reinforce individual differences in experiencing positive affective states. The accumulation of short-term positive emotional experiences is thought to generate positive mood, which affects the way an animal appraises their environment, increasing awareness of positive cues and reducing sensitivity to negative ones (Boissy and Erhard, 2014; Mendl et al., 2009). Thus, living in a complex environment conducive to a positive mood may increase anticipation of further positive outcomes. In these conditions, animals tend to exhibit a more optimistic appraisal of ambiguous stimuli and situations (i.e. positive judgement bias: Lagisz et al., 2020). An optimistic judgement bias may encourage exploration, leading to an increased potential for making further rewarding discoveries. These, in turn, produce additional positive emotional experiences, thereby further intensifying the positive mood (Mendl et al., 2010), especially if outcomes are perceived as being even better than expected (i.e. resulting in a positive reward prediction error: Lecorps and Weary, 2024).

In a meta-analysis by Lagisz et al. (2020), which synthesised effect sizes from judgement bias tests across animal species (primarily mammals), effects were more evident in males than females, which may reflect sex differences in the neurobiology of learning and memory (Jonasson, 2005) or in how stress modulates memory processes (Andreano and Cahill, 2009). This result suggests that the positive feedback loop between affective state and appraisal of new events could also be more pronounced in certain animals due to biological factors. The reinforcement of positive judgement biases in response to positive feedback may also be modulated by personality. For example, pigs with a reactive coping style exhibited higher optimism in a judgement bias test when housed in a more enriched environment compared to a less enriched environment, whereas housing conditions did not affect the response patterns of pigs with a proactive coping style (Asher et al., 2016).

While negative feedback loops between two variables typically promote their stability, positive feedback loops typically amplify their variation over time (DeAngelis et al., 1986; Sih et al., 2015). Therefore, positive feedback loops between animals' affective state and cognitive biases could maintain and reinforce initial individual differences in positive states (Montalcini et al., 2025). In the context of PAW, positive feedback between rewarding outcomes and affective states could, in principle, lead to an infinite “fanning out” of individual differences over time. However, this divergence is expected to stabilise as animals mature, especially in a monotonous farm environment, due to ceiling effects on learning opportunities, trade-offs with physical development processes, and other constraints, whereas excessively elevated positive affect could become maladaptive (e.g. by increasing risk-taking and exposure to predation).

Knowledge gaps

Studying individual differences in judgement biases and how they are influenced by experience would contribute to understanding individual differences in affective states. Research is needed to assess whether judgement biases are a sensitive measure at the positive end of the valence spectrum (i.e. when comparing responses to somewhat good versus very good environments or stimuli), and to what extent individuals of different species are sensitive to reward prediction errors. It is also relevant to investigate individual responses to different frequencies of positive and negative reward prediction errors (i.e. elation vs disappointment), and how they influence resilience to frustration and resistance to addictive habits (e.g. stereotyped behaviour).

Social life

Since farmed animals live in social groups for most of their lifetime, we now consider how social interactions can contribute to, and be shaped by, positive affective states (see Table 2 for terminology definitions). Social life is a central component of farmed animals' experience and can play a critical role in shaping PAW. Understanding the multifaceted nature of social life requires examining both individual-level processes and group-level dynamics (Fig. 2). In early life, socialisation lays the foundation for how animals navigate their social environment, influencing the development of affiliative and prosocial behaviours (Luo et al., 2025). These behaviours, in turn, support the formation of stable

affiliative relationships and enduring social bonds (Goumon et al., 2025; Brent et al., 2014). Through social transmission of information, individuals can benefit from the experiences of others, fostering competences (de Oliveira and Boivin, 2024). Together, these elements contribute to social cohesion, a group-level property that supports safety and predictability.

Early-life socialisation

State of the art

Sensitive periods (e.g. *in-utero*, early-life, at weaning) are periods during which an animal's experiences have a relatively effective or lasting impact on their perception and appraisal of their environment (Walasek et al., 2025; de Oliveira and Boivin, 2024; Bateson, 1979). Socialisation commences during an early sensitive period, during which young individuals become familiar with features of their social world and learn about the characteristics of individuals with whom they should, and should not, interact socially. For example, animals are more prone to include humans within their relational world if they have been exposed to them during their sensitive period for socialisation. Beyond reducing fear of humans, socialisation to humans facilitates positive human-animal relationships that contribute to PAW in farmed animals (Rault et al., 2020b). Interspecific socialisation is also relevant for farming systems that include multispecies herds that can benefit from each other's presence (Hübner et al., 2024).

Within species, lack of sufficient contact with conspecifics during the socialisation period impairs the development of affiliative species-specific social behaviour (e.g. puppies, Sacchettino et al., 2023). Socialisation promotes the establishment of relationships between individuals. For instance, later in life, pigs preferred pigs that they had socialised with as piglets over previously unfamiliar pigs (Petersen et al., 1989). Although there is conflicting literature on the impact of early socialisation of pigs with non-littermates, such experience has been reported to improve behavioural flexibility in reversal-learning tasks (Weller et al., 2019), and increase social confidence and reduce agonistic interactions after weaning (Mesarec et al., 2020; Camerlink et al., 2018; Hessel et al., 2006; D'Eath, 2005). Early socialisation of piglets with non-littermates also led to quicker formation of a stable hierarchy when later grouped with unfamiliar pigs (D'Eath, 2005) and reduced the stress concomitant with social interactions when grouped with strangers after weaning (Kutzer et al., 2009). A suggestion that socialisation

Table 2
Glossary of terms related to social life in livestock species.

Term	Definition
Affiliative behaviours	Non-aggressive and non-reproductive behaviours (Brent et al., 2014) that serve to initiate, advertise or reaffirm dyadic or group relationships or cohesiveness or, more generally, facilitate proximity between individuals.
Affiliative relationship	A social relationship involving non-random (i.e., preferential) affiliative associations and interactions (Goumon et al., 2025).
Behavioural synchronisation	A social mechanism by which individuals of a group or dyad coordinate their behaviour in time, expressing the same behaviour at the same time and at the same location (Duranton and Gaunet, 2016).
Prosocial behaviour	A social act from a donor to a recipient with a high likelihood that the act benefits the recipient, without necessarily precluding benefits to the donor (Rault, 2019). Prosocial behaviour includes comforting, care-giving, sharing, social demonstration and cooperation.
Social bond	A relationship involving frequent and non-random (i.e. preferential) mutual affiliative associations and interactions that are consistent across a biologically relevant time frame, and that contributes to stress modulation (Goumon et al., 2025).
Social cohesion	Describes the inter-individual distances between group members over time, wherein group members aggregate through shared activities, behavioural synchronisation, affiliative behaviours, and common goals (e.g. safety, resource acquisition, mating, offspring care).
Social facilitation	Social mechanism by which the frequency, intensity, initiation or motivation of behavioural responses already in an animal's repertoire (in contrast to social learning) increase when in the presence of a conspecific engaged in the same behaviour at the same time (Rørvang et al., 2018; Clayton, 1978).
Social learning	Social mechanism whereby the acquisition of information or a new behavioural skill is enhanced by observing, or interacting with, another individual referred to as the demonstrator (typically a conspecific; Rørvang et al., 2018; Box, 1984). The acquired knowledge or behaviour remains in the observer's repertoire when the demonstrator is not present.
Socialisation	Process of acquiring social rules and adopting behavioural patterns applicable to an individual's social environment (Petak, 2018).

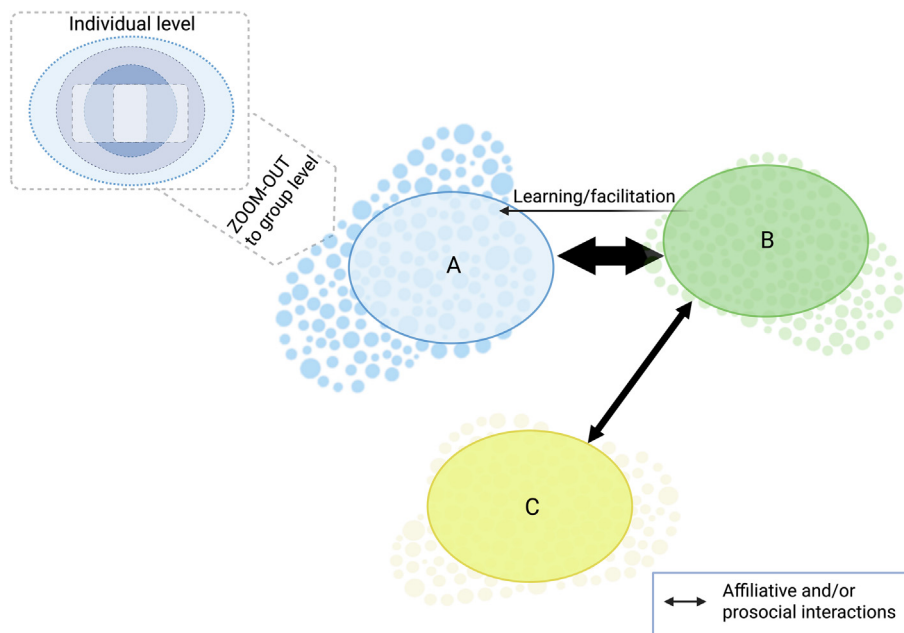


Fig. 2. Three individuals from a given livestock species A (zoomed out from Fig. 1), B and C, interacting in a social group, and varying in social relationships and socialisation background. Bi-directional arrows show affiliative and prosocial interactions, with the strength of the relationship represented by width of the arrow. The bonded individuals A and B have a particularly strong relationship. A benefits from learning from B. Dot clouds depict the impact of each individual's social background on its current social style, whereby a larger number of opaque dots reflects greater early life socialisation.

is a positive experience was reported by [Morgan et al. \(2014\)](#), who noted that socialised pigs were more “content” than control pigs, based on Qualitative Behaviour Analysis, a method whereby trained observers score the behavioural expressions of animals.

Knowledge gaps

Research on the socialisation of farmed animals has mainly focused on reducing aggression and promoting health and productivity. There is a need for PAW-focused studies to evaluate the impact of socialisation with a broad range of individuals (i.e. varying in age, sex, genetic background) on the development of social, sexual, and maternal competences, resilience following social conflict, and ability to experience predominantly positive affective states during social interactions ([de Oliveira and Boivin, 2024](#); [Scott, 1992](#)). To establish the existence and timing of any sensitive period for socialisation in different farmed species, studies should also elucidate whether socialisation experience must occur within a specific age period and, if so, how long outcomes last after completion of a socialisation programme.

Affiliative and prosocial behaviours

State of the art

Affiliative and prosocial behaviours are foundational positive social behaviours in group-living individuals, serving to develop, maintain and strengthen social relationships ([Brent et al., 2014](#)). Affiliative and prosocial behaviours differ in that affiliative behaviours are involved in creating and maintaining social bonds, whereas prosocial behaviours involve a cost for the performer and a benefit for the recipient. Affiliative interactions often include proximity-seeking, allogrooming and social play, while prosocial behaviours can take the form of food-provisioning, cooperation and protection. Hence, both contribute to improving the welfare of individuals.

As PAW requires that animals should experience mostly positive rather than negative emotions ([Rault et al., 2025](#)), it is logical to consider all the emotions relating to the performance of an affiliative or prosocial behaviour, and attempt to assess the balance between the negative and positive emotions experienced. This is because, firstly, affiliative and prosocial behaviours can occur in negative contexts: distressed states can precede positive affective states emerging from receiving affiliative and prosocial behaviours, such as when needy individuals seek attention from caregivers ([Iacobucci et al., 2015](#); [Weary et al., 1996](#)). Secondly, affiliative and prosocial behaviours may involve a mix of positive and negative emotions for the performer: on the one hand, if empathy leads to comforting and/or helping a distressed conspecific, alleviating the recipient's stress may be self-rewarding to the consoler ([de Waal and Preston, 2017](#)). On the other hand, the consoler may experience a negative affective state through emotional contagion (e.g. [Masilkova et al., 2021](#)).

Individuals receiving affiliative behaviours are thought to experience positive affective states ([Mellor, 2015](#)), such as calmness and openness to social engagement, through reduced sympathoadrenal activity and enhanced parasympathetic-vagal activity ([Uvnäs-Moberg, 1998](#)). For instance, licking has been reported to have a calming effect in cattle receiving it, including reduced heart rate, and assuming a relaxed posture with ears hanging and neck stretched ([Laister et al., 2011](#); [Schmied et al., 2008](#)). More generally, allogrooming in mammals (or allopreening in birds) refers to behaviours such as scratching, stroking, licking and nibbling the integument of another individual. It plays a crucial role in the formation and maintenance of social relationships and social cohesion ([Mendonça et al., 2021](#); [Rault, 2019](#); [Morrison, 2016](#)), and can reduce social tension in competitive situations (cattle: [Val-Laillet et al., 2009](#)), promote social exploration and individual recognition in an affiliative context (pigs: [Goumon et al., 2020](#); [Camerlink et al., 2014](#); [Camerlink and Turner, 2013](#)), and increase

optimism (capuchin monkeys: [Schino et al., 2016](#)). These benefits are not restricted to intraspecific interactions. Indeed, stroking and other gentle tactile contact given by humans can also have calming effects (pigs: [Villain et al., 2020a, 2020b, 2023](#); cattle: [Lange et al., 2020](#); horses: [Feh and de Mazières, 1993](#)), promote exploration (pigs: [Zupan et al., 2016](#); sheep: [Caroprese et al., 2006](#); [Napolitano et al., 2005](#)) and increase optimism (pigs: [Brajon et al., 2015](#)). However, animals may express distress if such actions are not performed by a familiar caretaker (pigs: [Tallet et al., 2014](#)). Biochemically, affiliative touch contributes to the release of dopamine, serotonin, opioids and oxytocin or its analogues (mice: [Elias and Abdus-Saboor, 2022](#); mammals: [Jablonski, 2021](#); horses: [VanDierendonck and Spruijt, 2012](#)), which may underlie the rewarding, anxiolytic, and analgesic effects of gentle tactile interactions (but see critiques on using oxytocin as an indicator of positive interactions in farmed animals: [Lürzel et al., 2020](#); [Guesdon et al., 2016](#); [Coulon et al., 2013](#)).

Beyond allogrooming, animals can engage in other positive social behaviours associated with increased optimism, such as synchronous swimming in bottlenose dolphins ([Clegg et al., 2017](#)) and playful handling (tickling) by humans in rats ([Rygula et al., 2012](#)). Play or “social joy” has been suggested to be one of the primary emotional systems associated with a positive affective state ([Panksepp, 2005](#)). Furthermore, play may contribute to PAW because of its immediate rewarding effect from having fun ([Mellor, 2015](#); [Špinka et al., 2001](#)). The positive emotional contagion of playful behaviour can be mediated by rapid behavioural mimicry of play signals in some cases (e.g. dogs: [Palagi et al., 2015](#)), although not others (e.g. cattle: [Gröbächer et al., 2020](#); keas: [Schwing et al., 2017](#)). Social play allows the acquisition of skills that may prepare individuals to respond quickly and efficiently to unexpected and physically or emotionally challenging situations ([Špinka et al., 2001](#)), hence promoting the development of competence and resilience. For instance, social play in rats has been associated with improved emotional regulation, impulse control, cognitive function, and social reciprocity ([Pellis et al., 2014, 2023](#)). Social play may contribute to social cohesion by reducing social tension (e.g. lemurs: [Antonacci et al., 2010](#)) and may generally promote tolerance, cooperation, and fairness ([Palagi et al., 2016](#)).

Increased levels of affiliative behaviours have been observed between individuals that have recently engaged in a conflict (e.g. pigs: [Norscia et al., 2021, 2024](#); horses: [Cozzi et al., 2010](#)). When directed by a winner towards a defeated individual, this so-called reconciliation behaviour seems to ameliorate the negative emotions (e.g. anxiety) of the latter (pigs: [Cordoni et al., 2023](#); sheep: [Papadaki et al., 2022](#); goats: [Schino, 1998](#)). Affiliative behaviour may also be performed by bystanders in the social group, alleviating their anxiety (pigs: [Norscia et al., 2021, 2024](#)). However, the affective states of the winner are less clear.

Special attention has recently been given to the stress buffering effect of prosocial behaviours, which are usually evaluated in negative contexts (e.g. comforting after distress, social support or helping during stressful situations), and are thought to help maintain social cohesion and improve welfare in social species. For discussion on the relevance of social buffering to PAW, see [Box 1](#). Comforting ([Lim and Hong, 2023](#)) is often expressed through allogrooming directed towards individuals in distress, providing them with relief from their distressed state (cattle: [de Freslon et al., 2020](#); horses: [Fletcher et al., 2023](#); [Shimada and Suzuki, 2020](#); [VanDierendonck and Spruijt, 2012](#)). However, the presence of conspecifics (chickens: [Guzman and Marin, 2008](#); [Marin et al., 2001](#); cattle: [Færevik et al., 2006](#); [Takeda et al., 2003](#)) or humans (sheep: [Guesdon et al., 2016](#); [Coulon et al., 2013](#); cattle: [Schmied et al., 2010](#); [Lensink et al., 2000](#)), with or without physical interac-

tion, also acts as social support by lowering the response to stressors (e.g. invasive procedures, social isolation).

Box 1

Social buffering: a blurred boundary between mitigating poor welfare and fostering positive animal welfare in livestock species.

Social buffering occurs “when the presence of one individual attenuates another’s stress response during a stressful event and/or helps the subject to recover more quickly after a stressful event” ([Ricci-Bonot et al., 2021](#)). It is hence traditionally associated with the mitigation of negative affective states and thus with the alleviation of poor welfare. However, social buffering may also create an environment conducive to positive animal welfare. By alleviating negative affective states, it may contribute to fostering experiences of consequent positive feelings such as safety and security (e.g. [Boissy and Dumont, 2002](#)), which may lead to positive affective states and resilience in human ([Syropoulos, 2020](#); [Wouters-Soomers et al., 2022](#)) and non-human animals ([Beery and Kaufer, 2015](#); [Denommé and Mason, 2022](#)). We therefore decided to include examples of stress buffering among the benefits of social life associated with positive animal welfare.

Interestingly, the pattern of reciprocating prosocial behaviours in a social group depends on species characteristics (e.g. [Schweinfurth and Call, 2019](#)). Furthermore, in rats, the performance of prosocial behaviour seems to depend on the giver’s bond with the receiver ([Lu et al., 2018](#)). In pigs, spontaneous helping of a trapped group mate appears to be modulated by the amount of distress signalling by the receiver (i.e. the trapped pig, [Moscovice et al., 2023](#)). These examples demonstrate that characteristics of the giver and receiver (e.g. previous social experience, emotional reactivity; see [Fig. 2](#)), as well as their relationship (see the knowledge gaps of section “Affiliative and prosocial behaviours”), modulate the performance of these behaviours.

Knowledge gaps

Most of the studies looking at positive social interactions (prosocial and affiliative behaviours) have been conducted on stable social groups, which is often not the case in livestock farming. Therefore, there is much potential to investigate these behaviours through the lens of PAW, in farmed species. Additionally, we encourage more focus on the identities of the individuals engaging in these behaviours, depicted in [Fig. 2](#).

The effects of intra-species affiliative behaviours have been extensively studied from the receiver standpoint while the benefits of performing those behaviours, or the effects of both parties being equally involved in the behaviour (e.g. symmetrical interaction), are not well documented in farmed species. In contrast, humans have been shown to benefit from appeasing effects while stroking an animal ([Barker and Wolen, 2008](#)). Furthermore, a small body of evidence suggests that positive affect stimulates social play in animals, but it is unclear to what extent play represents positive states rather than a reduction of negative affect ([Ahloy-Dallaire et al., 2018](#)). The potential benefits that human-animal interactions could have for farmed animals, besides the reduction of fear and stress and increased relaxation states during gentling, are still poorly understood. For instance, the effects of affiliative behaviours on social and non-social cognition and, hence, social competence have received little study.

In general, prosocial behaviours have been little studied in farmed animals. Postconflict affiliations (reconciliation between opponents; consolation or appeasement from a third party) and

third-party interventions (i.e. an individual interrupting an ongoing interaction between two other individuals) have been seldom studied in pigs (Norscia et al., 2021, 2024; Cordoni et al., 2023), goats (Schino, 1998) and sheep (Papadaki et al., 2022). Third-party interventions might be a means to maintain peace in a social group by limiting conflicts and the associated stress and anxiety, but also benefit the fitness of the intervener (e.g. faster ascension in the hierarchy: Papadaki et al., 2022). Furthermore, they have been mainly studied in agonistic contexts, although they can also occur in affiliative contexts (Schneider and Krueger, 2012).

Prosocial behaviours involve a mix of positive emotions (empathy and satisfaction of the donor, relief and gratitude of the recipient), which are not fully understood in humans and for which evidence is lacking in animals. Indeed, existing accounts of helping in animals are often described in terms of cognitive capacity or fitness costs and benefits (Schweinfurth et al., 2017), with no mention of the possible emotional aspect of helping others. Similarly, indirect reciprocity, whereby an individual helps those previously observed to help others (i.e. having a reputation of helping), has been shown in humans (e.g. Bateson et al., 2006) but strong evidence is lacking in farmed animals, though it has been shown in tufted capuchin monkeys (Schino et al., 2021). Further research could investigate whether indirect reciprocity is related to social competence and how this could promote PAW.

There is a sparsity of knowledge about prosocial behaviour directed by humans to farmed animals and vice versa. Dogs approach a human crying rather than a human talking (Custance and Mayer, 2012), which could be a sign of prosocial behaviour towards the human. The benefits of animal-assisted therapy for human receivers are often clear, but research is warranted to understand whether the animals are consciously helping humans in need, or if the behaviour/interactions are due to training.

Finally, the question remains whether prosocial behaviours act only to relieve negative feelings or if they can enhance positive feelings when performed in a positive context (e.g. cooperation). Social cooperation could be a promising aspect for promoting competence, although preliminary investigations show that animals may not fully understand the need of a partner (e.g. 'joint-log-lift' in pigs: McGettrick et al., 2025; Koglmüller et al., 2021).

Affiliative relationships and social bonds

State of the art

In a production setting, animals are not given much choice when it comes to forming a social group, which is typically decided upon and managed by farmers. They may, nevertheless, have opportunities to express avoidance or preference for a given individual or subgroup within their social environment. Farmed animals have been shown to have preferred partners in the form of affiliative relationships or social bonds (see Table 2). While affiliative relationships in farmed animals are well documented, evidence for intraspecific social bonds has been observed primarily between parents and offspring (i.e. parental bonds towards offspring and filial bonds of offspring towards parents: Newberry and Swanson, 2008). Evidence for bonds between sexually mature adults (pair bonds: Bales et al., 2021) or between conspecifics outside the parental or sexual context (peer bonds: Goumon et al., 2025) is more limited. Interspecific bonds also exist between some farmed animals and familiar humans (Nowak and Boivin, 2015). Overall, research on social bonds has hardly addressed PAW but has, rather, focused on the mitigation of negative impacts of social separation.

Affiliative interactions with preferred partners may provide important welfare benefits to an individual. As described in the section "Affiliative and prosocial behaviours" (state of the art), affiliative interactions are closely associated with reward systems,

which may be the driving force for the formation and maintenance of affiliative relationships and bonds. The importance of neurotransmitters and hormones such as dopamine, opioids and oxytocin, each playing roles in shaping the rewarding nature of social interactions, has been demonstrated in the context of social bonds in non-farmed animal species (Blumenthal and Young, 2023; Lee and Beery, 2021; Hostetler et al., 2017; Trezza et al., 2011; Ross et al., 2009; Aragona et al., 2003; Keverne et al., 1989). While multiple mechanisms may be involved in the development of inter-individual bonds, attachment at an early age is thought to be the most important in underpinning an individuals' life-long attachment relationships (Cassidy et al., 2013). Attachment processes mediate the strong motivation that exists among newborn and young animals to experience the comfort, security and feeding benefits of maternal care. A reciprocal motivation drives most parturient and lactating females to nurture and protect their own young. Key emotional and behavioural regulatory processes emerge during separation-and-reunion paradigms with a familiar caregiver. In these situations, the individual shows proximity seeking, feels calmer in the caregiver's presence, and expresses a preference for the caregiver – as seen, for example, in sheep interacting with their mothers or with humans (Nowak and Boivin, 2015).

The presence of a preferred partner, especially in the early stages of life, can have a significant impact on the acquisition of competences beneficial for social development and integration. The attachment mechanism contributes to later functioning through the building of an internal working model (Cassidy et al., 2013). In cattle, heifers kept with their dam and other cows during the first 3 months seem to have durably stronger sociality (e.g. when integrated into a new group) compared to calves reared in peer groups (Buchli et al., 2017; Wagner et al., 2012). The presence or absence of an adult attachment figure at an early age can also slightly, but durably, influence the later maternal competences of the young. For example, calves fostered by a cow did not reject their calves after calving but licked them and suckled them for longer than cows reared in isolation for the first 12 weeks of age (Le Neindre, 1989). Competences may also be acquired through social learning from preferred partners, such as an offspring's mother. This can reduce fear reactions in foals (Christensen et al., 2020; Christensen, 2016) and improve the flexibility of learning and coping abilities (Meagher et al., 2015; Stěhulová et al., 2008).

Affiliative relationships have the potential to facilitate collective movement (Jacobs et al., 2011) and cooperative behaviours (Leimar and Bshary, 2024). In farmed animals, cows were observed to be more prone to follow a group when they had seen a preferred group member joining the movement (Sueur et al., 2018). In pigs, individuals that most successfully completed a cooperation task appeared to form preferential dyadic associations to solve the task, suggesting that pigs may learn to associate with more proficient partners, or function best when together with preferred peers (Rault et al., 2021).

The presence of a preferred partner in an affiliative context may also amplify the benefits provided by prosocial behaviours and hence contribute to resilience. There is a large body of evidence relating to maternal social buffering of offspring stress, especially in laboratory animals (Sullivan and Perry, 2015) and pair or peer bonded animals (e.g. primates: Wittig et al., 2016; Young et al., 2014; Hennessy et al., 1995). In lambs, the presence of an adult was found to reduce distress behaviour, such as locomotory activity and vocalisations emitted in social isolation, but this reduction was the strongest in the presence of the mother (Gaudin et al., 2015). The same pattern was observed with a familiar human caregiver compared to an unknown one (Boivin et al., 1997). McLennan (2013) measured reduced behavioural (i.e. walking, pacing, vocalisations) and heart rate responses to separation when cows were

in the presence of a preferred partner compared to a familiar individual. On the other hand, Camerlink et al. (2023) reported that the strength of the relationship with a groupmate prior to weaning had no effect on cortisol levels, skin lesions or injuries at weaning in pigs.

Knowledge gaps

Research on the impact of affiliative social relationships on positive affective states, competence and resilience is overall rather limited in farmed animals. Research on social bonds has predominantly focused on the adverse impacts of early weaning on the welfare of mothers and offspring (Newberry and Swanson, 2008). While human-animal bonds have been extensively studied (Mellor et al., 2020; Rault et al., 2020b), research on peer bonds has received less attention despite potential implications for welfare (Goumon et al., 2025). Research on pair bonds between sexually mature adults has also been limited, mainly because true pair bonding is uncommon in livestock species. Indeed, pair bonds are more typical of certain bird species, such as geese and ducks, although their expression in commercial production systems is often limited. Yet, there is evidence that sexual activity among non-human mammals and birds is pleasurable and is engaged in by both sexes independently of its ultimate procreative purpose (Balcombe, 2009). Sexual activity and any emotional satisfaction (i.e. positive affective states) resulting from it are, in turn, likely to contribute to bonding and bond affirmation between adults of some species (Fisher et al., 2006). Overall, we encourage research into the value of grouping individuals based on their social preferences rather than the production stage for promoting PAW, and determining whether such potential animal-centered systems could be practicable for farmers.

An attachment figure can serve as a secure base, facilitating exploration and security and buffering the impact of stressful events (Payne et al., 2016; Cassidy, 2008), whereas this regulatory function is reduced or absent in insecure attachment (Woodhouse et al., 2020). While attachment theory is most applicable to systems with stable caregiver-offspring relationships (e.g., beef cattle, small ruminants, horses), it is less directly transferable to intensive systems where such bonds are limited (e.g. in poultry production). Nevertheless, underlying processes such as social buffering, emotional regulation, and the formation of social bonds may still contribute to positive affective states and resilience. Thus, further research is needed to determine how the quality of these relationships influences PAW in different farming contexts.

Social transmission of information and synchronisation

State of the art

Living in a social group allows opportunities for gaining knowledge and skills via social transmission mechanisms, including social learning and social facilitation. These processes contribute to the development of behavioural competence. For instance, social learning allows animals to more efficiently locate and exploit resources such as food (lambs: Veissier and Stefanova, 1993; heifers: Costa et al., 2016), and to engage with enrichment opportunities, including the manipulation of novel objects (pigs: Veit et al., 2017). Animals that can navigate their environment more effectively through accelerated acquisition of knowledge and skills are also more likely to accumulate rewarding, goal-directed experiences, which are central to PAW. Moreover, engaging with conspecifics can facilitate the expression of play behaviour through mechanisms such as social contagion. Play is often recognised as promoting positive affective states (e.g. Steinerová et al., 2024; but see Oscarsson et al., 2026) and as supporting the development of emotional and motor competence (Špinka et al., 2001; Trezza

et al., 2010), which may be facilitated by interactions with other individuals.

In the form of collective activities such as resting, grooming or movements, behavioural synchronisation contributes to enhancing perceived safety, and can reduce individual vigilance, thereby increasing the effectiveness of anti-predatory strategies (Duranton and Gaunet, 2016; Sakai et al., 2010; Dwyer, 2004). By allowing individuals to relax more fully, it may allow them to focus on rewarding experiences such as exploration and play rather than vigilance. It may also contribute to increased social cohesion and social affiliation (e.g. sheep: Michelena et al., 2008).

Knowledge gaps

Several knowledge gaps remain regarding the roles of social transmission of information and behavioural synchronisation in promoting PAW. First, while animals benefit from acquiring new skills, the mental states accompanying and resulting from such learning experiences remain unclear. Understanding whether these social mechanisms elicit states such as satisfaction, confidence, and social reassurance would clarify their impact on PAW beyond cognitive benefits. Similarly, although species are capable of cross-species social information use—for example, using human gaze or gestures to locate food—it is not known whether successfully interpreting human cues generates increased trust. Furthermore, research on behavioural synchronicity has primarily focused on its functional benefits, such as safety and reduced vigilance, while the affective outcomes of synchronisation (e.g. relaxation, positive engagement in play and exploration) are largely inferred rather than empirically demonstrated. Finally, the context-dependence of these processes remains poorly understood: it is unclear how factors such as group stability, familiarity, and social status moderate the welfare impacts of social transmission of information and synchronicity.

The interplay between individuality and social life

Because individuals differ in sensory perception, cognitive abilities and affective styles (section “Individuality”), as well as in early-life socialisation, other social experiences and resulting social preferences (section “Social life”), individuals can contribute to social life in distinct ways. This means that individuals may differ in the way they perceive and benefit from the same social opportunity. Individuality and social dynamics may interact in complex, bidirectional ways to shape welfare outcomes, with social environments influencing how individuals develop and express traits and individual behaviours shaping group-level dynamics. Fostering an integrated view of these processes shows high potential to better account for farmed animal individual and social needs, hence promoting PAW in their everyday lives.

Because many knowledge gaps have already been highlighted in the previous sections, here we focus on two promising examples for future research which illustrate the interplay between individuality and social life. The first concerns how individual characteristics (e.g. extraversion, agreeableness) may impact the welfare of the group, while the second considers how individual features may influence social structure at the dyadic and group levels.

Sociability, agreeableness and extraversion

Personality studies usually focus on individual features that are relevant to well-being at the individual level. However, some personality traits reflect social attributes that are highly relevant to group dynamics. Typically described social traits of non-human individuals are aggressiveness and sociability (Réale et al., 2007).

Aggressiveness refers to an individual's agonistic reaction towards conspecifics (Réale et al., 2007) and is supposedly opposite to the construct of human agreeableness (Finkemeier et al., 2018). Sociability refers to an individual's reaction to the presence or absence of conspecifics (excluding aggressive behaviour; Réale et al., 2007) and is supposedly equivalent to the construct of human extraversion (Finkemeier et al., 2018; Gosling and John, 1999).

Firstly, we consider it timely to shift the focus from the investigation of aggressiveness towards agreeableness. Indeed, agreeableness is relevant to PAW as, in humans, highly agreeable individuals show prosocial tendencies and high motivation to maintain positive relations with others (Graziano and Tobin, 2016; Wilmot and Ones, 2022). Research in children, for instance, shows that dyadic conflicts between highly agreeable individuals lead to more harmonious and constructive outcomes (Jensen-Campbell et al., 2003). Such studies could be inspiring for future research regarding group management in farmed animals.

With regards to extraversion, in humans, this trait describes people who are sociable, talkative, and assertive (McCabe and Fleeson, 2012). More extraverted people are more sensitive to rewards (McNaughton and Gray, 2024; Ford et al., 2014), hence experiencing positive affect more intensively (Smillie et al., 2015). This, in turn, has a positive impact on their social environment through their social contribution (Sun et al., 2017). In animals, although the assumed equivalent construct sociability is relatively well documented (Gosling and John, 1999), there is currently no way to measure extraversion in a human-equivalent manner (Ferreira et al., 2025). This could be because most animal personality research questions do not focus on internal states (as extraversion would require), as they are more difficult to grasp. In non-verbalising species, the most sociable individuals are typically defined as the ones seeking the presence of conspecifics the most. However, this trait is likely to be multidimensional as, for example, sociability towards unfamiliar conspecifics does not nec-

essarily reflect sociability within a group of familiar conspecifics (Ambruosi et al., 2024).

Extraversion is more than sociability because, in humans, it includes additional facets, such as friendliness, assertiveness, excitement seeking, enthusiasm and expressiveness (Wilt and Revelle, 2016). Although not yet objectively measurable in animals, these facets could be highly relevant to the capacity to experience positive affective states (i.e. reward sensitivity, see BAS tendencies in section "Individuality") and well-being (Depue and Collins, 1999). As demonstrated in humans, extraversion (including all its facets) also has the potential to increase well-being at the group level (Sun et al., 2017; Smillie et al., 2015). For example, while feed-back loops operate at the individual level (see section "Individuality"), they may also operate at the group level. Thus, in farmed species, it could be interesting to investigate whether more sociable individuals express a higher ratio of positive to negative affective states than less sociable individuals. A first step would be to evaluate individual differences in social reward sensitivity (Stijovic et al., 2024), as suggested by Ferreira et al. (2025). Extending this idea, more sociable individuals may be more prone to PAW when permitted social interactions, yet more likely to experience negative affective states when such interactions are restricted, compared with their less sociable counterparts.

Fig. 3 illustrates a possible scenario: the most central group members in a social network may promote positive experiences for the whole group (as hypothesised for extraverted individuals), whereas the least connected individuals (i.e. at the periphery) may need fewer positive social experiences to reach a level of positive affective states similar to their more central counterparts. However, these individuals may also benefit from enhanced experiences in non-social dimensions. For example, perhaps certain relatively less sociable individuals would benefit from more sophisticated cognitive enrichments than the highly sociable individuals.

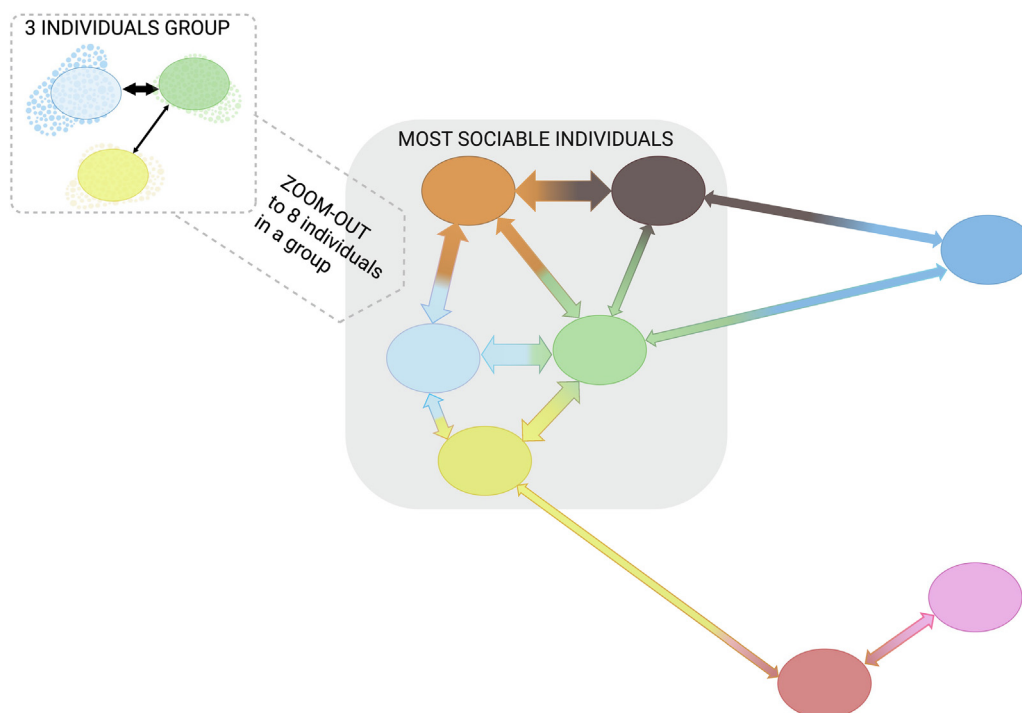


Fig. 3. Zoomed out view of Fig. 2, showing three interacting individuals from a given livestock species as members of a larger social group (e.g. a herd) with a complex social network. Each interaction is represented by a bidirectional arrow and the relative contribution of each individual is summarised by the location along the arrow where the two contributions blend: if the interaction is reciprocal, this blending occurs in the middle. The width of the arrows represents the strength of the interactions. The most sociable individuals, showing the most frequent and strongest interactions, are encompassed within the grey rectangle.

Social competence, social structure and individuality

The composition of social groups in terms of individual characteristics can influence group-level social dynamics. Homophily in personality traits, whereby individuals preferentially interact and associate with others exhibiting similar personality traits, has been shown to be an important factor contributing to variability in social relationships in different taxa of non-humans animals (e.g. social tension, vigilance, and dominance in water buffalo: [Bhattacharjee et al., 2024](#); exploratory behaviour in great tits: [Aplin et al., 2013](#), and zebra finches: [Schuett et al., 2011](#); sociability in bonobos: [Verspeek et al., 2019](#)). In a farming context, the expression of homophily could be enhanced by offering individuals more agency in selecting their group composition. While current intensive farm management strategies do not typically enable animals to choose which conspecifics they are grouped with, it could be interesting to investigate the grouping of animals according to their social preferences (e.g. homophily vs heterophily).

Beyond preference-based assortment, heterogeneous social exposure within groups may also play a key role in shaping social competence. Individuals interacting with a broader spectrum of behavioural phenotypes or different personalities may become more socially competent, for example, in terms of behavioural flexibility, conflict-resolution skills, and ability to develop and maintain affiliative relationships, ultimately promoting PAW. This is of particular relevance given that current production systems typically emphasise phenotypic homogeneity. Research on coping styles provides inspiration: for example, [Ruis et al. \(2002\)](#) showed that pairs composed of a dominant reactive gilt and a submissive proactive gilt exhibited lower stress levels than other combinations. The authors suggested that the dominant reactive individual may have mitigated aggression from the more proactive partner, illustrating how complementary traits (i.e. dominance and coping style) can shape interaction outcomes. Multiple individual traits (e.g. aggressiveness, exploratory tendencies, submissive behaviour) have been shown to influence affiliative network connections (e.g. flamingos: [McCully and Rose, 2023](#); great tits: [Firth et al., 2018](#)). Individual characteristics (e.g. age, dominance rank, social centrality) may also shape functional roles within groups such as leadership (i.e. initiation of spontaneous group movements), as observed in bison ([Ramos et al., 2018](#)), highland cattle ([Sueur et al., 2018](#)), and beef cattle ([Šárová et al., 2010](#)).

Extending the effects of group composition and heterogeneous social exposure, individual variation in affiliative behavioural tendencies (e.g. joiners vs initiators of play in pigs; [Zupan et al., 2019](#)) and responsiveness to conspecifics (e.g. play contagion in ravens; [Osvath and Sima, 2014](#)) may provide a further, closely linked layer through which social dynamics are structured. These differences are likely to contribute to variation in social integration and network position, and may interact with group composition (e.g. homophily or heterophily) and prior social experience to shape patterns of social embedding within groups. So far, research on mechanisms linking variation in affiliative behaviour and responsiveness to conspecifics to social dynamics remains very limited in farmed animals.

Despite growing evidence across taxa, to our knowledge, there is no research in farmed animals linking individuality and social structure from a PAW perspective. We therefore recommend future research to investigate the impact of incorporating different combinations of individual characteristics and traits into social groups of farmed animals, given that transferred or removed individuals may influence the dynamics of affiliative interactions and relationships (cattle: [Sosa et al., 2019](#)) and hence PAW.

Conclusion

Recognising farmed animals as unique individuals embedded within complex social systems opens new pathways for designing and implementing management practices that promote PAW at the individual and group level. While individuality and social life are both relevant in promoting PAW, evidence directly linking their interplay to positive welfare outcomes in farmed species remains limited. We propose that future research on PAW should move beyond studying individuality and social life separately. Admittedly, this framework (see [Video 1](#)) could be easier to implement on farms in some species, like dairy cows, for which individual data are routinely collected, than in others, such as chickens living in large flocks. Nevertheless, this type of research could be applied across a wider range of species as emerging technologies make it increasingly feasible to identify and track individuals even within large groups (e.g. laying hens: [Montalcini et al., 2023](#); [Rufener et al. 2018](#)). Integrated approaches are needed to examine how individual variation shapes social behaviour, how social contexts modulate individual predispositions, and how these bidirectional influences collectively shape PAW. Specifically, research could prioritise: (i) developing robust methods to assess individuality and social relationships across species in positive contexts, (ii) conducting longitudinal studies to identify developmental windows in which social experiences interact with individual predispositions, (iii) investigating how group structure, social network position, and personality heterogeneity contribute to PAW, and (iv) focusing on feedback processes by which individuals influence, and are influenced by, their social environment. For conciseness, we omitted discussion of other determinants (e.g. genetic factors) that could further affect individual predispositions to experience PAW. Nevertheless, addressing these factors will also be essential for designing welfare-enhancing environments that recognise animals both as members of social groups and as individuals with distinct capacities to experience PAW and promote it in others.

Supplementary material

Supplementary Material for this article (<https://doi.org/10.1016/j.animal.2026.101878>) can be found at the foot of the online page, in the Appendix section.

Ethics approval

Not applicable.

Data and model availability statement

No data were deposited in an official repository. Information can be made available by the authors upon request.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors did not use any AI and AI-assisted technologies, except for grammatical correction by non-native English speakers.

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Declaration of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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