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Friend or foe? Early life adversity to improve farmed animal welfare

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Early life experiences can have lasting impacts on an animal's development. Extensive research evidence aligns across both human and non-human rodent and primate laboratory animals showing negative impacts of early life adversity such as impairments in neurological and behavioural development. Farmed animals experience a range of adversities across their production lifetimes, often early in life, including species atypical social groupings, invasive husbandry procedures, and transport. Correspondingly, farmed animals also demonstrate a wide range of impairments such as stereotypic, injurious, and other abnormal behaviours. An individual, however, needs to experience adversity to be able to develop resilience and coping mechanisms that facilitate dealing with challenges later in life. Not all individuals will experience stress vulnerability following adversity, with some individuals instead developing stress resilience. This mini review collates evidence on the positive effects of early life adversity on improving adaptability in farmed species, both terrestrial and aquatic. While evidence across farmed animal species is currently much less than for humans, laboratory rodents or non-human primates, similar patterns emerge where mild adversity early in life, can improve the adaptability of the animal in the face of future stressors. Many views of optimised welfare posit that farmed animals should be housed in as natural environments as possible to limit many of the typical adversities they face. However, strategic mild exposure to early life adversity may facilitate improved animal welfare under intensive commercial farming conditions. Future research into this area could provide management tools to better predict and promote stress resilience over stress vulnerability.

KEYWORDS

enrichment, aquaculture, stress, resilience, livestock, domestic animals

1 Introduction

It is well established that what happens early in life can have long lasting impacts on how an animal develops, behaves, and performs later in life (Eyck et al., 2019; Veit and Browning, 2023). Early life developmental conditions can start to have impact as early as in ovo/*in utero*. For example, heat stress experienced during pregnancy in dairy cattle can reduce the growth and immunity of their offspring (Ghaffari, 2022). Or impacts can occur in critical periods after birth/hatching (Reh et al., 2020), through to reaching maturity such as demonstrated extensively in the emotional behavioural development of laboratory rodents (Callaghan et al., 2013; Schneider, 2013). Impacts may even occur via parental stock experiences as evidenced in breeding chickens that may be experiencing suboptimal environments and translate this experience through to their offspring (De Haas et al., 2021). If an individual has optimal conditions in which to develop and grow then there will be numerous physical and behavioural benefits to that individual across its lifetime (Bayne, 2018; Campbell et al., 2019; Zhang et al., 2022; Veissier et al., 2024). Conversely, early life stress, adversity, and trauma, can result in lasting negative consequences for an individual (Campbell and Roth, 2023; Dettmer and Chusyd, 2023).

When referring to 'early life conditions', this could encompass one or multiple factors that all contribute to the development of an organism. For example, this could include the social environment the animal is experiencing (e.g., pair versus single housing in calves: Bolt et al., 2017; maternal deprivation in piglets: Brückmann et al., 2020; Gimsa et al., 2022), their nutrition (e.g., malnutrition in sheep during gestation and post-weaning: Poore et al., 2014), the absence of desirable resources (e.g., perches for laying hen pullets: Gunnarsson et al., 2000) or degree of cognitive stimulation (e.g., rearing environmental complexity and cognitive task performance in piglets: Martin et al., 2015). If we look at what is characterised as adversity, Chelini et al. (2022), took three macro categories of human childhood adversities (household challenges, abuse, and neglect as defined in the renowned CDC-Kaiser ACE Study Felitti et al., 1998) and aligned them with corresponding categories in rodent studies. Limited bedding and nesting could fall under 'household challenges', resource scarcity would be 'abuse', and maternal separation was categorised as 'neglect' (Chelini et al., 2022). Based on this, farmed animals across different livestock and aquaculture industries are often routinely exposed to one or all of these adversities during early life with their restricted housing conditions, limited desirable resources, and frequent maternal deprivation. Evidence aligned across both human and non-human animal studies, shows early life adversity, of varying forms, can result in impairments in immune function, neurological development, and an increased risk for psychological and psychiatric disorders (De Bellis and Zisk, 2014; Cross et al., 2017; Danese and Lewis, 2017; Babicola et al., 2021; Dettmer and Chusyd, 2023; Lee and Jung, 2024). Unsurprisingly, farmed animals also demonstrate a wide range of behavioural and neurological impairments, such as stereotypic, injurious, and other abnormal behaviours and chronic health issues such as lameness and infectious pathogen susceptibility (Rodenburg and Koene, 2007; Palmer and O'Connell, 2015; Tatemoto et al., 2022). These impairments may result from their early life experiences as there is ever-growing evidence of optimised early developmental environments of farmed species alleviating negative behavioural and health impacts (e.g., poultry: Campbell et al., 2019; dairy calves: Costa et al., 2019). These long-term impacts in an organism following their early adverse experiences are facilitated by mechanistic changes in neurological, transcriptional and epigenetic pathways (reviewed in Basile et al., 2021; Burns et al., 2018; Short et al., 2020; Smith and Pollak, 2020).

An individual, however, also needs to experience adversity or stressors to be able to develop resilience and coping mechanisms that facilitate dealing with stressful experiences and challenges later in life (Meehan and Mench, 2007; Monaghan and Haussmann, 2015; Dhabhar, 2018; Jessop, 2019). Phenotypic development in response to the surrounding environment is an evolutionarily advantageous strategy (Langenhof and Komdeur, 2018). For all animals, Langenhof and Komdeur (2018) hypothesised four factors that would determine an individual's successful adaptation to their environment; perceiving if there was a need for a response to a stimulus, evaluating what an effective response would be, the individual's ability to deliver that response, and bearing the cost of that response. Circumstances that facilitate adjustment to adversity during the developmental phase would improve an individual's ability to exhibit the correct (and least costly) responses to environmental triggers across their lifetime, as specific to the species and their behavioural ecology. In support of positive impacts of early life adversity, there is evidence across a range of animal taxa showing stressful experiences early in development, can result in more adaptive coping strategies later in life (e.g., mice: Bodden et al., 2015; Santarelli et al., 2017, rats: Oomen et al., 2010, fish: Fontana et al., 2021; Zare et al., 2024, monkeys: Parker et al., 2019). Given that there are both positive and negative impacts of early life adversity, there is also an extensive body of literature aimed at understanding what adverse early life experiences and/or what individual differences, such as personality traits, can lead to an outcome of improved biological functioning, versus long-term detriment (Parker and Maestripieri, 2011; Brenhouse and Bath, 2019; Hartmann and Schmidt, 2020). That is, what constitutes the tipping point between stress resilience, and stress vulnerability (Murthy and Gould, 2018; Kentner et al., 2019).

The background provided here alludes to the extent of the information around early life adversities, long-term impacts and mechanisms across many species. However, there is much less research on the positive impacts of early life adversity in farmed animal species (see Lucas et al., 2024 for a framework on early life experiences of pigs). This mini review is aimed at collating evidence on the positive effects of early life adversity on improving adaptability in farmed species, both terrestrial and aquatic. An understanding of the consequences of early adversity of varying degrees and forms as relevant to different species can contribute toward strategies for mitigating developmental risks of animals under our care, thus improving their welfare.

2 Positive effects of early life adversity

The literature to date in farmed animals on the impacts of early life adversity is not as abundant as that across laboratory rodents and primates. However, there are several studies across varying taxa detailing the improvements in adaptability resulting from stressors that highlight the potential for further research in this area. The studies detailed in this section are also summarised in Table 1. Looking at the evidence in birds, Japanese quail subjected to

TABLE 1 A summary of the negative, neutral, and positive effects of early life adversity on growth, behaviour, and stress reactivity across farmed species.

Citation	Species, Sex	Treatment and Age	Negative effect	Neutral effect	Positive effect
Calandreau et al., 2011*	Japanese quail (*Coturnix japonica*) (females)	Unpredictable stressors across 8 days at 2 weeks of age (noise, handling, restraint) compared to controls (no stressors applied).	Lower body weight.	Tonic immobility duration did not differ. Plasma corticosterone concentrations did not differ. Novel object test did not differ. Hole-in-the wall test did not differ.	Improved behavioural flexibility during spatial reversal learning.
Zimmer et al., 2013	Japanese quail (*Coturnix japonica*) (males and females)	Simulated maternal programming through egg-injected corticosterone and post-hatch random food deprivation.		Post-hatch food restriction did not affect corticosterone decreases during capture-handling-restraint. Neither adversity treatment affected neophobia responses.	Simulated maternal programming improved corticosterone decreases during capture-handling-restraint. Simulated maternal programming increased novel environment exploration. Both adversity treatments reduced the latency to eat in a novel environment.
Goerlich et al., 2012*	Domestic chickens (*Gallus gallus*) (males and females)	Intermittent social isolation, handling, temperature change, feed/water deprivation for 3 weeks at 4-26 days of age (in parent birds with parent birds and offspring tested).	Higher acute plasma corticosterone restraint stress response in parents.	Tonic immobility duration did not differ in offspring. Open field movement did not differ in offspring. Social reinstatement did not differ in offspring.	More correct choices during associative learning with an aversive stimulus (sex differences present) in the parents, more birds made a choice during associative learning in the offspring (sex differences present). Male offspring showed lower plasma corticosterone responses to restraint stress. Higher body weight in parental females. Higher body weight in treatment male offspring.
Nätt et al., 2009*	Domestic chickens (*Gallus gallus domesticus*), (males and females)	Unpredictable lighting schedule from day 26 onwards for parents (all offspring raised on predictable lighting).		No effect of treatment in a food dominance test in parent birds. No effect of treatment on body weight in parent birds.	Parent birds exposed to unpredictable lighting pecked more freely available vs hidden food in a foraging test. An increase in growth rate of (female) parent birds. Offspring of unpredictable lighting parents weighed more, grew quicker, had increased survival. Offspring of unpredictable lighting chose high energy food, chose freely available vs hidden food, and pecked more in a food dominance test (some sex differences present).
Salvatierra et al., 2009	Domestic chicks (*Gallus gallus domesticus*), (males and females)	Acute novelty exposure and acute novelty plus social isolation on day 1.		Novelty exposure + social isolation had no impact on open field and tonic immobility tests compared to controls.	Shorter latency to walk in open field test in novelty-exposed chicks. Shorter tonic immobility duration in the novelty-exposed chicks. Lower plasma corticosterone concentrations after the behavioural tests in the novelty-exposed chicks.
Vindas et al., 2016*	Atlantic salmon (*Salmo salar*) (presumed males and females)	Unpredictable stressors (noise, temperature change, handling, light, hypoxia) across 23 days from 11 months of age.	Lower body weight, body condition, and specific growth rate following the treatment but not at later sampling points.		Better specific growth rate at 6 and 10 weeks following treatment.
Takahashi and Masuda, 2018	Red sea bream (*Pagrus major*) juveniles	Daily net chasing for 3 weeks.		No difference in standard length (minus the tail fin). No difference in total body length, tail fin length.	Shorter latency to emerge from a start area. Greater avoidance of a novel threat. Shorter latency to forage in a new environment. Greater survival in a predator test.

(Continued)

TABLE 1 Continued

Citation	Species, Sex	Treatment and Age	Negative effect	Neutral effect	Positive effect
Luo et al., 2022	Domestic pigs (*Sus scrofa domesticus*) (females)	Repeated social mixing across 2 weeks from 4 weeks of age (pigs were also housed in barren or enriched conditions).		No effect on blood glucose and lactate after a behavioural frustration challenge in repeated mixed/single-mixed pigs. No effect on hair cortisol concentrations.	Lower plasma cortisol and serum lactate following a health challenge in barren-housed pigs exposed to repeated social remixing compared with barren-housed single-mixed pigs. Increased growth in the repeated social remixing pigs relative to single-mixed pigs following the health and behavioural challenges. Higher antibody titers in the enriched-remixed pigs relative to the enriched single-mixed and barren remixed pigs.
Rutherford et al., 2009	Domestic pig (*Sus scrofa*) (females)	Social mixing stress during pregnancy.		No effect of maternal mixing stress on piglet weight, litter size, or ponderal index.	Greater behavioural indicators of pain in tail-docked piglets from stressed mothers suggesting an adaptive heightened response to injury.
Boissy et al., 2001	Domestic cattle (*Bos taurus*) (males)	Repeated weekly social re-pairing from 8 to 22 weeks of age.			Regrouped calves were startled more often in a water spray test, took longer to feed in an umbrella test, paid more attention to a dog threat, and were more agitated during a restraint test. I.e., stress treatment calves showed greater behavioural reactivity to novelty.

*These studies also included mechanistic neurological measurements which have not been included in the summarised results of adversity impacts.

unpredictable stressors across 8 days including handling, noise, and restraint, showed a reduction in body weight across the stressor period relative to individuals not undergoing the stressors (Calandreau et al., 2011). However, in reversal learning of a spatial memory task, the stressed birds outperformed the controls suggesting this sub-chronic period of stressor application improved the behavioural flexibility of the birds (Calandreau et al., 2011). In a separate experiment with quails, Zimmer et al. (2013) simulated maternal stress programming through corticosterone egg injections and post-hatch adversity via random food deprivation. When the birds reached adulthood, there were long-term effects of both the pre- and post-hatch adversity treatments. Relative to controls, these birds showed reduced corticosterone reactivity to capture-handling-restraint, improved exploration of and increased willingness to feed in a novel environment (Zimmer et al., 2013). Using the same types of measures, a subsequent study showed these positive impacts of early adversity were transgenerational showing mothers were able to pass along their ‘stress-coping phenotype’ (Zimmer et al., 2017).

In chickens, effects of stressors were shown in both parent chicks and later in their offspring demonstrating there are also transgenerational impacts of stressors in this species. Birds that had undergone an intermittent social isolation/handling/food and water deprivation stressor across 3 weeks showed better performance in an associative learning test using an aversive (bitter taste) stimulus and offspring showed a lower plasma corticosterone response to a restraint stress (Goerlich et al., 2012). There were differences in the significance of impacts between males and females, but results suggest an early stressor can improve coping ability (Goerlich et al., 2012). Further evidence for developmental environment impacts in chickens, including transgenerational transfer comes from a study that raised birds in an environment with unpredictable lighting, equating to unpredictable food supply (Nätt et al., 2009). The offspring of these parents showed adaptive foraging strategies and performed better compared with offspring of parent birds raised on standard predictable lighting (Nätt et al., 2009). Similarly, Salvatierra et al. (2009) found that acute exposure to a novel environment at one day of age in individually housed chicks, was able to reduce corticosterone responses and measures of fear two weeks later. However, if the chicks were exposed to the novel environment as well as social isolation (pair-housed chicks) they did not show a reduction in fear and stress measures relative to chicks that had not experienced the novel environment stressor, nor been social isolated. This suggests that the social isolation stressor ameliorated the positive effects of the novelty stressor but did not compound as these birds responded similarly to control chicks (Salvatierra et al., 2009).

Benefits of developmental stress have also been seen in fish species. Vindas et al. (2016) exposed Atlantic salmon to unpredictable stressors across a 3-week period and demonstrated that relative to controls, these fish showed improved growth rates 6 and 10 weeks after experiencing the stressor, even though their growth was negatively impacted immediately following the stressful treatment (Vindas et al., 2016). As part of typical husbandry processes, these fish had undergone a 6-week smoltification and a transfer to seawater for 4 weeks. The improved growth during these periods suggested the stress treatment improved their adaptability to the new conditions (Vindas et al., 2016). In red sea bream juveniles raised in aquaculture hatcheries for stock enhancement release, short-term daily net chasing across three weeks resulted in changes in adaptability as measured through various behavioural tests (Takahashi and Masuda, 2018). The fish that had been exposed to net chasing were quicker to emerge from a starting area indicating greater boldness, they foraged quicker after being transferred to a new environment, showed quicker avoidance/escape from a novel threat and had greater survival after predator exposure, relative to control fish (Takahashi and Masuda, 2018).

Improvement as a result of early stress has also been demonstrated in pigs that were housed in enriched or barren conditions, then subjected to a single or repeated stressful mixing events after weaning (Luo et al., 2022). Contrary to predictions that the repeated mixing may place too high an allostatic load on the pigs, there were some physiological stress-related measures that showed this mixing had benefits including better growth in these pigs relative to single-mixed pigs (Luo et al., 2022). Similar to transgenerational impacts illustrated in chickens and quails, social mixing to cause stress in sows during pregnancy was able to cause greater pain-related behaviours in their tail-docked piglets (Rutherford et al., 2009). The authors interpreted this result as an evolutionarily beneficial strategy to be more attuned to adversity in the environment, particularly when at risk of bodily harm (Rutherford et al., 2009). Aligned with this result, calves that were stressed via repeated social regrouping showed greater behavioural reactivity across a series of behavioural tests suggesting these calves were more attuned to novelty in their environment (Boissy et al., 2001). The authors interpreted this as allowing greater adaptation to environmental change (Boissy et al., 2001).

3 Chronic mild enrichment stress

Another angle to the positive effects of early life adversity is looking at the benefits of chronic mild stress, that may be imposed by environmental changes intended to benefit the animal. Specifically, environmental enrichment, typically through increased environmental complexity, is deemed a positive intervention. However, the presence of enrichment can increase the novelty the animals are exposed to, increase their activity levels, and potentially the social interactions they engage in. All of these may place mild chronic stress on the animal (Veissier et al., 2024). The stress-inoculation hypothesis, drawing on research from laboratory rodents, proposes a framework that posits environmentally enriched lab rodents are under a state of chronic mild stress, where they develop resilience to stress as a result of this early mild exposure (Crofton et al., 2015). Similar application of enrichment to specifically test stress inoculation has been applied in laying hens through exposure to novelty and change in their rearing environments. Experiencing periodic change during the rearing period of chicks and pullets, may reduce later responses to stress-inducing situations. In a study by Campbell et al. (2018), novelty was provided for laying hen chicks during their first 3 weeks of life in the form of novel objects, sound playbacks, flashing lights, and visual wall displays. The birds were transferred to a free-range system before sexual maturity and then tested for their responses to two induced stressors at 38-42 weeks of age. When daily range access was prevented completely, and then the available range area was reduced, the non-enriched birds showed a greater albumen corticosterone response to these imposed stressors relative to the enriched birds (Campbell et al., 2018). In another study with laying hen chicks, Skånberg et al. (2023) compared static environments with a single choice of perch or litter type to multiple changes in the perch and litter types during the first 3 weeks of life. Reduced freezing by the treatment birds in a novel environment test suggests the exposure to the environment changes reduced fear responses in a typically stress-inducing situation (Skånberg et al., 2023).

Conversely, there are some livestock studies, aligning with rodent research (Crofton et al., 2015), demonstrating enrichment actually results in increased anxiety compared with non-enriched animals. For example, Dickson et al. (2024), provided enrichment objects (ball, chew rope, brush) during the weaning period of beef cattle with the intention of mitigating the stress that is experienced during this developmental phase of maternal separation, yarding, and social regrouping. However, in tests of attention bias, the enriched animals displayed measures that were interpreted as greater anxiety thus contradicting the original hypothesis (Dickson et al., 2024). Similarly, pigs tested in an attention bias test showed greater indicators of a negative state if they had been in enriched (substrate, toys) home pen housing versus impoverished home pens, contrasting with experimental predictions (Luo et al., 2019). A study by Backus et al. (2017) that also provided pigs with substrates and varying novel objects in their home pens as well as daily positive human contact and treats found measures that indicated, contrary to predictions, increased anxiety during novel object and human interaction tests. In a laying hen rearing enrichment trial, different novel objects were provided throughout 16 weeks of rearing compared with no enrichments or static perching structures (Bari et al., 2020). The implementation of a range area reduction stressor at 44 weeks of age resulted in an increase in albumen corticosterone in both the non-enriched and novel object treatment groups compared to a decrease in the hens that were exposed to the static perching structures (Bari et al., 2020). Thus, even with what could be considered chronic, mild early life adversity, there may be a tipping point between stress resilience and stress adaptability. Understanding what makes an individual resilient or vulnerable after adverse experiences and the mechanisms leading to this, is an extensive field of research in humans and laboratory species with great scope to widen to more farmed species.

4 Discussion and conclusions

Farmed animals experience a range of stressors across their production lifetimes, including, for example, species atypical social groupings or social transitions, invasive husbandry procedures, transport, and changes in housing environments. These processes can occur during both the early development stages and later when the animals reach maturity. For optimal animal welfare, individual animals need to be able to cope with and adapt to these adverse experiences to avoid long-term detriment. There are decades worth of literature on humans and non-human taxa (typically rodents, primates) around early life adversities that cause behavioural, neurological, and physiological consequences as well as the physiological, epigenetic, and neurological mechanisms that may be facilitating these impacts. However, not all individuals will experience detriment following adversity, instead adversity may lead to increased resilience. While the quantum of evidence across farmed animal species is comparatively less, we see similar patterns emerging. Some adversity early in life can improve the adaptability of the animal in the face of future stressors.

Moving forward, there is scope to better understand what adversities can promote adaptation in an individual so that we may apply interventions that could strategically improve how farmed species perform under the constraints of the commercial context. It has been proposed that the vulnerability or resilience of an individual could be determined by 'three-hits' (Daskalakis et al., 2013). An individual is going to be influenced by their (hit-1): genetic predisposition, (hit-2): early-life environment, and (hit-3): later-life environment. Furthermore, the exact features of the adversity, such as the type of stressor, its duration, the sensory modality it is experienced through, and the precise timing of exposure are all going to impact the short and longer-term outcome (Parker and Maestripieri, 2011). However, it is generally accepted that mild to moderate adversities have the potential to improve adaptability, whereas severe adversities will be detrimental (Parker and Maestripieri, 2011; Daskalakis et al., 2013). The outcomes are also likely to be impacted by the natural biology and ecological relevance of the adversity to the animal. For example, in squirrel monkeys, implementing maternal separation at an age when the young monkeys would naturally be temporarily separated from their mothers, leads to stress resilience. Comparatively, maternal separation in primates at young ages that would not be biologically relevant leads to stress vulnerability (Parker and Maestripieri, 2011). Many processes that farmed animals are subjected to fall outside the scope of what may be naturally expected for the species, which could contribute toward the extent of behavioural, neurological, and health impairments that are often seen. It may be possible to utilise 'natural' adversities for a particular species to strategically prepare the animal for future stressors. Or to expose the animals to adversities that will enable them to adapt to what is expected to impact them later in life, such as environmental change, or social regrouping. Many views of optimised welfare posit that farmed animals should be housed in as natural environments as possible to limit many of the typical adversities they face. However, strategic mild exposure to early life adversity may facilitate improved animal welfare under intensive commercial farming conditions. Future research into this area could provide management tools to better predict and promote stress resilience over stress vulnerability.

Author contributions

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Conflict of interest

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