
Quantifying the impact of fast-growing rates on the welfare of broiler breeder females

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I. Background

For every farmed animal that makes its way to the supermarket shelf, there will be many other life fates [1] involved in the production chain, most of which consumers are often unaware of. Among them are individuals who do not make it into the slaughter age or who die during transportation. Another important group in this category is that of breeding animals, the parents, grandparents, and great grandparents of meat-producing animals. They are the subject of analysis here.

Recent surveys on the number of parent birds in the broiler industry are lacking, but their population can be estimated from the ratio of breeders to broilers² typically observed. For example, in 2013 the industry involved an estimated 417 million parent birds, responsible for the production of 58 billion broiler chickens [2] (a ratio of 1 breeder for every 140 broilers). Considering that in 2019 over 72 billion chickens were slaughtered for meat globally [3], this would amount to a population of about 517 million breeders. To put this number in perspective, this is almost twice the total number of cows slaughtered every year.

Although breeders are outnumbered by their progeny, they live 10-12 times longer (about 440 days) than a typical fast-growing (meat) broiler grown, during which they experience extremely challenging welfare conditions. It is easy to see why: meat chickens have been intensively selected for very high growth rates, supported by a very high feed intake. Although this has led to a high prevalence of musculoskeletal, cardiorespiratory and other metabolic disorders that accumulate over time, the chickens bred for their meat are slaughtered at a very young age (5-6 weeks), before these problems become severe enough to compromise the profitability of this business model. The situation is nonetheless different for their parents: while obviously sharing the same genetics for fast-growth and high feed conversion, breeders must live long enough to reach adulthood and reproduce. Yet, the

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² We refer from now on to broiler chickens slaughtered for their meat as simply broilers, and to the male and female birds that produce them as 'breeders'.

odds that a modern breeder becomes obese, severely ill or dies is very high over this longer lifespan. In experimental settings where breeders did not have their feed intake restricted, mortality rates were estimated at around 40% by 40-49 weeks of age [4].

Reproduction in the parent stock is also compromised, with low egg production and quality resulting from the strong negative correlation between muscle growth and reproductive efficiency [5]. This trade-off between selection for rapid growth and poor reproductive performance is the same that has made it more profitable for the poultry sector to develop different lines of chickens for ‘reproduction’ (egg-laying hens) and ‘growing’ (broiler chickens). Yet broiler breeders must combine both traits: a high breeding performance in individuals with the genetics for fast growth and high feed efficiency.

The traditional workaround chosen by the industry to improve the reproductive performance of breeders and increase their survival odds has been the adoption of severe levels of feed restriction to slow down growth and prevent obesity. To grasp the level of feed restriction required, consider that while broiler chicken weight has increased by over 400% in the last decades [6], the target weight of the parent stock to ensure optimal breeding has not changed. Therefore, increasingly higher levels of feed restriction were adopted over time, particularly for young pullets during the rearing period (Figure 1).

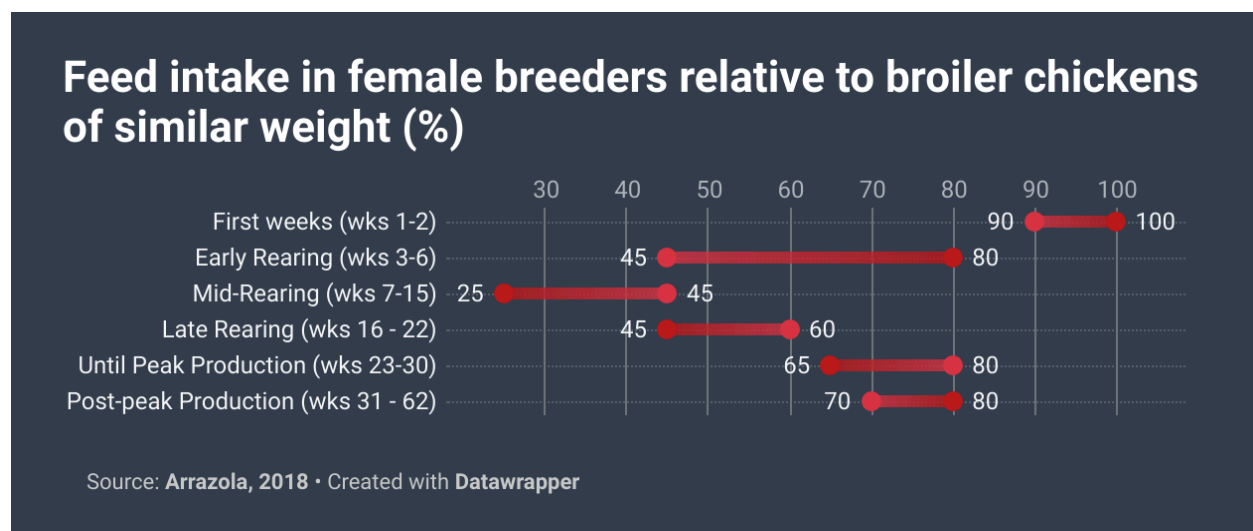


Figure 1. Estimated levels of feed restriction in fast-growing (Ross 308) broiler breeding females. Except for mid-rearing, percentages are estimated Arrazola (2018) [7] based on the recommended intake relative to (presumably unrestricted) consumption levels in broiler chickens of the same weight. Stricter levels are likely to be adopted in practice, however, during mid-rearing, as based on widely cited figures during this phase. Feed intake in this phase was adjusted to reflect this observation. Intake is mostly unrestricted during the first weeks of life to prevent developmental problems, then gradually reduced until reaching the highest restriction at mid-rearing. Feed provision is then increased to prepare pullets for production. Feed intake will keep gradually increasing until the peak of lay, at about 30 weeks, then being once again reduced to prevent fat deposition and a fast decrease in egg production afterward [8]. Feed restriction levels for males are not shown. In general, they are less severely restricted during rearing and more severely restricted during production to maintain fertility [8].

On the one hand, dietary restriction has reduced mortality and the prevalence of some health issues, including reproductive dysfunctions associated with heavier weights [5]. For example, although still higher than in egg-laying hens, mortality during laying in feed-restricted breeders has been estimated to range from 4-14% [9]. More recent data from commercial breeding farms in the United States estimates mortality to range from 10 to 16% [10]. Likewise, walking ability is improved under dietary restriction, and the pathogenic progression of pulmonary and cardiac disorders (still highly prevalent in breeders) is delayed [11].

However, chronic hunger is a major by-product of what has been mostly a band-aid solution to a commercial production need, with a cascade of multiple adverse effects on welfare (Figure 2). Prolonged hunger in parent birds has been shown to be associated with increased levels of aggression, injurious pecking, cannibalism, frustration, and higher levels of stress and immunosuppression [12–15]. Immunosuppression, in turn, increases the likelihood of welfare problems caused by infectious agents, including lameness, contact dermatitis (hock burns, breast blisters, and footpad dermatitis), and egg peritonitis, an extremely painful condition [16]. Because severe feed restriction also leads to excessive water intake and drinker-directed pecking, water provision may be also restricted to avoid spillage and preserve litter quality, potentially leading to extended periods of thirst [17,18].

Several strategies to alleviate the sensation of hunger and its welfare consequences have been studied. Among them are the addition of bulky fibers to the diet and the use of feeding schedules consisting of larger feed amounts on some days followed by one or more (non-consecutive) off-feed days [18,19]. The use of appetite suppressants has also been investigated. However, their effects on welfare have proved limited and controversial [20]. For example, rather than mitigating hunger, appetite suppressants have been associated with aversion to feed and gastric lesions in poultry [21]. Likewise, mixed welfare effects were observed both in qualitative feeding restriction strategies and skip-a-day feeding schedules, with positive effects on some welfare dimensions accompanied by adverse effects on others (reviewed in [18,22]).

Another approach, proposed as a more ethical solution to the welfare of parent birds [18], is the use of slower-growing genotypes, which can be raised without the need for feed restriction [23,24]. They include breeds such as the Ranger Classic, Ranger Gold and the Hubbard JA787, JA757 and JA987 [18]. Dwarf female lines, which also have reduced growth potential and weigh about two thirds the weight of a standard female breeder, may not require feed restriction either [5] (when feed restriction is used with dwarf lines, it is usually less strict, reducing the frequency of abnormal behaviours [25]).

In the absence of feed restriction, water restriction is also typically not needed [14,26]. The desired growth rate of the offspring will determine, however, whether males will need to be feed restricted. Slower-growing broilers can be produced from a slower-growing female breeder crossed either with a slower- or fast-growing male. In the latter case, the offspring will have only slightly slower growth [27]. While parent males from slower-growing genotypes may not require feed restriction, standard, fast-growing males do (e.g., the male parents of JA757 broilers, considered in welfare schemes such as the Better Chicken Commitment, are standard males that require feed restriction).

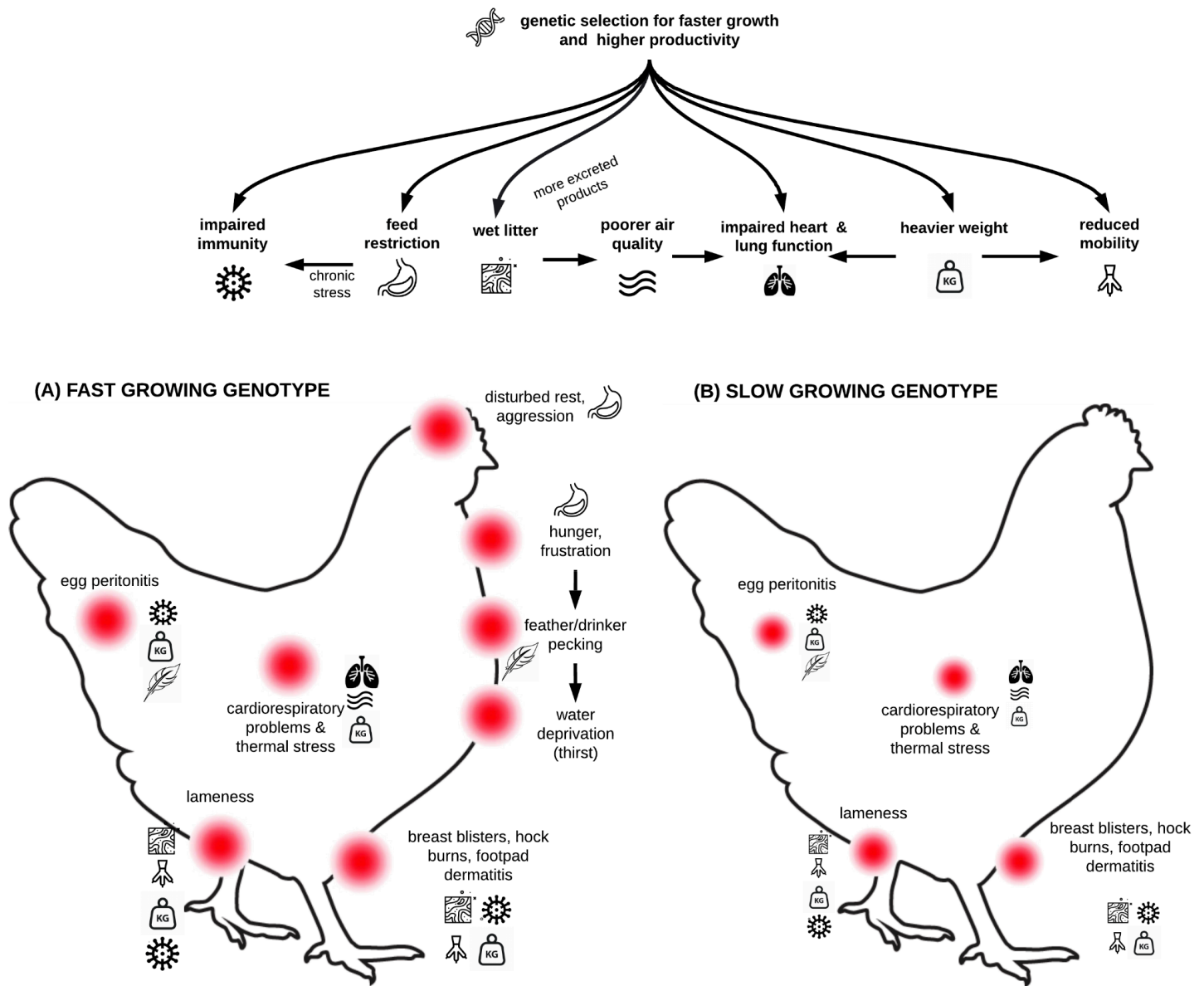


Figure 2. Direct and indirect welfare consequences of genetic selection for faster growth and increased productivity in female breeders. The list of hazards and consequences shown is not exhaustive of their multiple relationships. Feed restriction is both a direct cause of welfare challenges (hunger, frustration, aggression, lack of rest) and an indirect risk factor of multiple welfare problems (e.g through its negative effect on immunity, increased risk of feather pecking and water restriction). Welfare challenges shown within the chicken outlines (red circles) are accompanied by their main risk factors (represented by icons). (A) Main welfare challenges experienced by fast-growing broiler breeders; (B) Main welfare challenges experienced by slower-growing broiler breeders. Lower icon sizes represent a reduced risk, hence reduced prevalence of the challenge (circles of smaller size).

Given the cascade of negative welfare effects associated with selection for fast-growth (Figure 2), the use of slower-growing breeds is also expected to have other consequences for the welfare of breeders,

reducing the likelihood of the welfare challenges associated both with a genetics for rapid growth and with poor immune function, heavier weight, reduced mobility and impaired heart and lung function.

In this chapter, we investigate the extent to which a transition from fast-growing to slower-growing genotypes can affect the welfare of broiler breeders, using the [Cumulative Pain framework](#) to this end [28]. The analysis is focused predominantly on the welfare effects of hunger in female breeders as they greatly outnumber male breeders (at a ratio of approximately 100 hens to 8 roosters). We start by reviewing the conditions in which broiler breeders are raised, to then discuss the possible time in pain of different intensities (Box 1) endured by broiler breeders as a result of hunger.

II. The Life of Breeders

Although management differences may be present among farms and countries, broiler breeding is usually a standardized process consisting of processing at the hatchery (where sexing, vaccination and bodily mutilations take place), a rearing (growing) phase, a laying (production) phase, transport and slaughter. Here we focus on the growing and production stages, when potential differences in the welfare challenges experienced by fast- and slower-growing genotypes are more likely to be present. Thorough descriptions of housing and living conditions of broiler breeders are available in the management manuals of breeding companies [29] and several literature reviews [14,18,23,26], so they are only briefly summarized here.

After leaving the hatchery, day-old chicks are transported to a rearing farm, where they are typically kept in groups of 1,000 to 3,000 birds per pen for 18 to 22 weeks. Rearing farms are usually single-tier aviaries, with litter (e.g. wood-shavings, peat, straw) covering most or all the floor area. Pens may have raised platforms and perches. Although some farms may rear breeders in cages, this is not standard practice, hence will not be considered. Because males and females are provisioned with different feeding schedules, they are kept separately during rearing. Aviaries are well-lit (100 lux) for the first two days, during which approximately 23 hours of light are provided [29]. Daylength then decreases gradually, until reaching 12 hours (30 lux) on day 4 and 8 hours from week 2 onwards. At about 18 weeks of age, light intensity is slightly increased to bring hens into reproductive condition and 12 hours of light are provided [29]. Feed restriction levels typically used for female breeders are described in Figure 1. Feed is generally provided once per day, being consumed in as little as 15 minutes [23].

At around 20 weeks males and females are transferred to a laying unit (males are often transferred a few days earlier), where they are housed at a ratio of approximately 100 hens to 8 roosters. Group sizes are larger (3,000-8,000 birds), and natural mating is predominantly used. Given their different feeding schedule, males and females are fed separately. Laying houses will often have a slatted and a littered area. Other than nests for the hens, no other enrichment is typically provided. During production, lighting regimes usually consist of about 12 hours of light until peak production (at about 30 weeks of age) and 16 hours of light thereafter. The production period usually lasts about 40-45 weeks, adding up to a total of 60-65 weeks of life. This period may be longer for slower-growing genotypes, extending up to 70 weeks of life [30]. Hens are normally slaughtered at a body weight of 4 to 5 kg.

Box 1 Definition of Pain Intensity Categories

Annoying: experiences of pain perceived as aversive, but not intense enough to disrupt the animal's routine in a way that alters adaptive functioning or affects the behaviours that animals are motivated to perform. Similarly, Annoying pain should not deter individuals from enjoying pleasant experiences with no short-term function (e.g., play) and positive social interactions. Sufferers can ignore this sensation most of the time. Performance of cognitive tasks demanding attention are either not affected or only mildly affected. Physiological departures from expected baseline values are not expected to be present. Vocalizations and other overt expressions of pain should not be observed.

Hurtful: experiences in this category disrupt the ability of individuals to function optimally. Different from Annoying pain, the ability to draw attention away from the sensation of pain is reduced: awareness of pain is likely to be present most of the time, interspersed by brief periods during which pain can be ignored depending on the level of distraction provided by other activities. Individuals can still conduct routine activities that are important in the short-term (e.g. eating, foraging) and perform cognitively demanding tasks, but an impairment in their ability or motivation to do so is likely to be observed. Although animals may still engage in behaviors they are strongly motivated to perform (i.e., exploratory, comfort, sexual, and maintenance behaviors), their frequency or duration is likely to be reduced. Engagement in positive activities with no immediate benefits (e.g., play in piglets, dustbathing in chickens) is not expected. Reduced alertness and inattention to ongoing stimuli may be present. The effect of (effective) drugs (e.g., analgesics if pain is physical, psychotropic drugs in the case of psychological pain) in the alleviation of symptoms is expected.

Disabling: pain at this level takes priority over most bids for behavioral execution, and prevents all forms of enjoyment or positive welfare. Pain is continuously distressing. Individuals affected by harms in this category often change their activity levels drastically (the degree of disruption in the ability of an organism to function optimally should not be confused with the overt expression of pain behaviors, which is less likely in prey species). Inattention and unresponsiveness to milder forms of pain or other ongoing stimuli and surroundings is likely to be observed. Relief often requires higher drug dosages or more powerful drugs. The term Disabling refers to the disability caused by 'pain', not to any structural disability.

Excruciating: all conditions and events associated with extreme levels of pain that are not normally tolerated even if only for a few seconds. In humans, it would mark the threshold of pain under which many people choose to take their life rather than endure the pain. This is the case, for example, of scalding and severe burning events. Behavioral patterns associated with experiences in this category may include loud screaming, involuntary shaking, extreme muscle tension or extreme restlessness. Another criterion is the manifestation of behaviors that individuals would strongly refrain from displaying under normal circumstances, as they threaten body integrity (e.g. running into hazardous areas or exposing oneself to sources of danger, such as predators, as a result of pain or of attempts to alleviate it). The attribution of conditions to this level must therefore be done cautiously. Concealment of pain is not possible.

III. Chronic hunger

Food is one of the most basic of all survival needs. The motivation to seek food and eat is ubiquitous in the natural world, and one of the most powerful drivers of animal behavior [31]. Attending this drive will take precedence over most other motivations and bids for behavioral execution, as failure to do so can very quickly impair biological functioning. We refer to this motivation as 'hunger', an aversive (negatively valenced) state [15] that signals the need for food. Like with other forms of pain

[32], hunger signaling must be loud enough to drive attention away from other tasks and stimuli, imposing a new action priority to prevent survival from being compromised.

In the case of human populations, the aversive nature of the sensation that accompanies food deprivation has been long used as a method of punishment and torture. Prolonged food deprivation has been described as “*excruciating until the point of becoming an unbearable source of pain*”, with the obsession with food dominating all thoughts, to a life-threatening point where one would risk their life for a small piece of bread (reviewed in [33]). In a famous clinical study conducted in the 1940s, known as the Minnesota Semi-Starvation Experiment, participants had their dietary intake cut in half for a period of six months. The results showed that this level of food restriction - associated with an average weight loss of about 25% of body weight - resulted in severe emotional distress and depression, a constant preoccupation with food, a decline in concentration, comprehension and judgment capabilities, as well as a need for psychological treatment during recovery [34]. Even in the short term, partial food deprivation was associated with mood instability, irritability, difficulty concentrating, impaired cognitive function, greater risk-taking and an incapacity to assess danger properly [33].

As one would expect from an evolutionary perspective, the mechanisms regulating the motivation to seek food (appetitive behavior) and consume it (consummatory behavior) are extremely ancient in the history of life, and shared by many species. Indeed, various animal species, including chickens [35,36], have been used as models for the understanding of hunger, satiety and appetite regulation in humans. In young rats, for example, chronic caloric restriction has been shown to decrease turnover rates of brain serotonin (a neurotransmitter implicated in nearly every type of behavior, but best known for its effects on promoting well-being) and lead to symptoms of depression and anxiety [37].

In broiler breeders, chronic feed restriction has been similarly associated with multiple symptoms indicative of distress, including neurophysiological changes used typically as indicators of stress in avian species (reviewed in [18]). For example, in a study with Cobb female breeders [38], feed restriction significantly changed blood heterophil to lymphocyte ratios (HLR), plasma circulating corticosterone, ghrelin, serotonin, dopamine and brain heat shock protein levels, with a significant linear relationship between the severity of feed restriction (75, 60, 45, and 30% of ad libitum intake) and HLR, blood corticosterone and dopamine levels. In another study, chronically elevated corticosterone as a result of commercial feed restriction during rearing significantly reduced the production of new neurons in the hippocampus [39].

Although the relationship between some of these parameters and feed restriction may be attributed to the physiological changes and metabolic stress resulting from the reduced caloric intake, and not necessarily signal a negative affective state resulting from hunger [15,40], evidence is also robust of changes in various indicators of affect that accompany the severe levels of feed restriction imposed on breeders. For example, behavioral symptoms of frustration and distress are widely observed among feed-restricted birds, and consistent with the notion that attention is predominantly shifted away from other (less important) motivations and towards finding food. In general, the time spent in locomotor, foraging and pecking activities increases substantially along with the severity of feed restriction (reviewed in [18]), a finding often interpreted as a sign of continuous and unmet drive to search for food. Feed-restricted growing breeders also forgo important activities such as preening other comfort behaviors and resting (reviewed in [18]), further supporting the notion that the sensation of hunger cannot be easily ignored, with the search for food becoming a very important priority (compatible with the criteria defining the Hurtful and possibly Disabling categories, Box 1).

Other frequently observed abnormal behavioral patterns include pecking at nonfood objects (e.g., drinkers, aviary structures) and at other birds and overdrinking. Increased levels of aggression and abnormal sexual behaviour are also widespread [41]. Compensatory feed intake has also been shown to be linearly associated with the level of restriction [42].

Feed-restricted breeders also go to the extreme of exposing themselves to otherwise highly aversive stimuli (crossing a 4 meters long runway with water filled above their leg length) to gain access to a foraging opportunity (exploration of a shavings-filled litter area), even in the absence of actual food rewards [43]. As argued by the authors, this finding adds to evidence that commercial restriction levels result in chronic (continuous) hunger in broiler breeders, with high levels of foraging motivation indicating that food is not *'out of sight, out of mind'* [43]. This risk taking behavior suggests that the possibility of Disabling pain cannot be ruled out. Hungry broiler breeders are also impaired in their ability to learn [44], a finding also suggesting that the intensity of the experience is consistent with, at least, the Hurtful category of pain, which predicts some level of impairment in cognitive performance [28] (Box 1).

Although most studies on the effect of food restriction in breeders were conducted during the rearing period, when feed restriction levels are highest (Figure 1), evidence suggests that hunger is still present throughout production. In an experiment conducted with Ross 308 breeders aged 35-44 weeks [45], hens sitting firmly in a nest to lay an egg left it on nearly all occasions (80 out of 81) when feed was concurrently delivered, indicating that the motivation to feed was higher than the motivation to use a nest moments before laying an egg. Indeed, on a quarter of the occasions where the nest box was abandoned, no egg was laid. The literature is well established in showing that nests are a highly valued resource for laying hens, with the lack of a nest in the moments that preceded egg laying being one of the most severe sources of frustration in these birds [46,47]. In hens deprived of a nest, multiple behaviours symptomatic of frustration are observed, such as stereotyped pacing, increased aggression and displacement preening [48,49]. In general, hens will pay high costs for access to a nest site, including walking past dominant or unfamiliar birds in narrow corridors, squeezing through narrow gaps and pushing through weighted doors [12,46,49]. As the sitting phase approaches, the costs paid to access a nest become increasingly higher [50], and consistent with the 'Disabling' level of pain intensity [28,47] (Box 1). Therefore, the observation that broiler breeders in the sitting phase leave the nest box and may forgo the opportunity to lay an egg suggests that the feeling of hunger at this time is highly disruptive, and likewise consistent with the Disabling definition of pain intensity.

Other research findings also support the notion that the state of severe chronic hunger endured by broiler breeders can be very intense. In a well-designed experiment, the authors injected sodium urate (SU) crystals in the ankle of laying hens to induce a painful arthritic-like condition [51]. The procedure is a model of severe tonic pain that mimics naturally occurring gout. In humans, similar injection of SU into the knee joint induced pain 2 h later, and 4 hours later subjects were prostrated owing to extreme pain [52]. While a range of pain-coping behaviors were observed in those birds kept in a barren environment (e.g., one-legged standing, severe lameness, sitting, ruffled feathers, eyes semi-closed), complete analgesia (i.e. absence of all pain-coping behaviors) was shown in hens that received the injection just prior to egg laying [51]. These results suggest: (1) that nest search and oviposition are extreme priorities to laying hens, capturing so much of their attention to the point of suppressing a painful condition such as the induced gouty arthritis and (2) that gouty arthritis is more likely of a Hurtful nature (since Disabling pain cannot be ignored, by definition). Thus, the observations that feed-deprived broiler breeders forgo the opportunity to lay an egg to be able to eat

indicates that the negative affective state associated with chronic hunger would be at least as intense as the deprivation of a nest prior to oviposition.

The hypotheses for the intensity of the hunger sensation, proposed in Pain-Track 1, reflect the findings reviewed. To account for the possibility that the negative state associated with hunger is of a Disabling intensity during the ‘laying phase’, we assign a 20% likelihood to this category. This estimate is conservative given the behavioral observations reviewed, namely that the motivation to feed is higher than the motivation to use a nest moments before laying an egg (percentages may be alternatively interpreted as the proportion of time spent at each level of intensity over the course of a day). We also assume that higher levels of feed restriction are associated with a higher likelihood of more intense categories of pain intensity. For example, during mid-rearing, when feed restriction is highest, we assume that the likelihood of Disabling pain is higher (60%).

Although in the first couple of weeks chicks feed intake is unrestricted, we cannot completely rule out the possibility that some discomfort is present, given the likely impairment in the signalling of satiety in modern breeds of broilers as a result of selection for higher food intake and faster growth [53,54]. For example, compared to slower-growing strains, fast-growing birds have a lower expression of components of the appetite regulation pathways in the brain (basal hypothalamus), intestine, and exocrine organs [55]. Because satiety may not be achieved even under unrestricted feeding conditions, a 25% probability was attributed at this phase to the Annoying category.

The neurophysiological impairment of satiety may also imply that female breeders are less able to habituate to the lower levels of intake over time. Indeed, as discussed previously, evidence suggests that high levels of feeding motivation and distress are present during the production phase [45]. Still, we take a conservative approach and do not completely rule out the possibility that female breeders habituate to the sensation of hunger over time. To this end, we assign an increasingly higher likelihood that the sensation is only of an Annoying nature as the hen ages. Further research is critically needed to determine how feed restriction affects hunger in breeders over time, considering the entire production cycle. Estimates of duration in Pain-Track 1 are reviewed in the next section.

Pain-Track 1. Hypothesis for the intensity and duration of the pain endured per day by conventional female broiler breeders as a direct result of hunger over the rearing and production phases. The duration considers estimated conscious (awake) hours per day, and assumes no discomfort from hunger while the bird is asleep.

	Wks1-2	Wks 3-6	Wks 7-15	Wks 16-22	Wks 23-30	Wks 31-62	Hours in Pain
Excruciating	0%	0%	0%	0%	0%	0%	
Disabling	0%	40%	60%	40%	20%	20%	1960 [1830-2090]
Hurtful	0%	55%	40%	55%	70%	70%	4170 [3830-4500]
Annoying	10%	5%	0%	5%	10%	10%	523 [480-569]
Hours awake (day)	10 - 16	12-16	14-18	14-18	14 - 18	14-18	
Total Hours (all weeks)	140-224	280-448	882-1134	686-882	784-1008	3136-4032	

Estimated duration of the hunger sensation in a typical day

The evidence reviewed indicates that breeders are most likely to be continuously hungry [18,43,45]. This is likely to be the case even immediately after the consumption of the daily meal: generally, the small daily ration of food is consumed in a few minutes, after which birds are often observed 'spot' pecking empty feeders, walls, drinkers and other objects, a behavior interpreted as a strong indication of an unfulfilled and frustrated motivation to continue feeding [18]. Even pullets on a non-daily feeding schedule (skip-a-day feeding) show signs of unfulfilled feeding motivation after a meal (e.g., pecking at empty feeders, overdrinking and consuming litter), despite the larger feed allotment during on-feed days [7]. So although the intensity of hunger may vary to some extent with circadian rhythms and with the time since the last meal (a possibility embedded in the pain-track, as the distribution of proportions in each time segment can be interpreted as the variation in pain intensity over the course of a day), we assume that some sensation of hunger will be always present while the birds are fully conscious (awake).

To our knowledge, information on the extent to which birds experience pain, hunger and other negative affective states while sleeping is lacking. To err on the side of caution and avoid inflating the estimated times in pain due to hunger, we conservatively assume that no hunger or any frustration from the thwarted motivation to feed is felt when individuals are sleeping. Overall, sleep in birds is comparable to that in mammals, with both high-amplitude slow-wave and low-voltage fast-wave EEG sleep patterns present in chickens [56]. Chickens have, however, an additional phase of sleep that mammals lack: unihemispheric slow-wave sleep, during which one half of the brain rests while the other half is awake; this is why chickens can sleep with one eye open and the other closed, an adaptation that allows them to be concurrently alert for predators and asleep [57]. Because during this phase fully developed large amplitude slow waves characteristic of electrophysiological sleep may be present [58], we conservatively assume that no awareness of hunger is possible even at this time.

Knowledge on the time broiler breeders spend sleeping (as opposed to simply resting) is also scarce. In one study with laying hens, the authors found that the percentage of sleep in a dark period of 10 hours was 83.8%, or slightly over 8 hours [58], as measured by electrophysiological recordings from electrodes implanted in the brain of the chickens. It is thus likely that hens are not continuously asleep during the entire period of darkness. Indeed, active behaviours such as preening during the night have been shown to be common, indicating that when the dark cycle is long birds may spend part of this time awake. Similarly, it is also unlikely that birds will be fully awake for all the time when lights are on. For example, broilers exposed to long cycles of light (20-23 hours per day) spend most of their time lying, and have been shown to doze or sleep for at least a quarter of this time [59]. The duration ranges shown in Pain-Track 1 therefore consider a wide range of hypotheses for the time birds spend fully awake per day, with minimum and maximum sleeping times of 6 and 10 hours, respectively. Since young chicks may sleep for longer periods, we assume minimum and maximum sleeping times of 8 and 14 hours, respectively, in the first two weeks, and 8 and 12 hours, respectively, during early rearing. Given the uncertainty regarding these values, we assume a uniform distribution of probabilities for this range of duration (all hypotheses are assumed to be equally likely).

Hunger in slower-growing breeder genotypes

Research has shown that, different from fast-growing strains, slower-growing genotypes can be fed *ad libitum* diets [4,18,25,60]. Thus, hunger would not be a welfare challenge for these birds. Additionally, slower-growing birds have a higher expression of components of the appetite regulation pathways in the hypothalamus, intestine, and exocrine organs [55]. More importantly, different from conventional breeds, empirical observation has pointed to the absence of indicators of feeding frustration in slower-growing breeders not exposed to feed restriction. For example, breeders of slower-growing genotypes take several hours of the day to consume their feed [23]. Slower-growing breeders also take a higher proportion of their daily time budget resting, which has been suggested to indicate satiety [25].

Nonetheless, a mild level of feed restriction may still be required for intermediate growing strains during rearing [7,61,62]. Therefore, we assume that mild feed restriction (70% of *ad lib* consumption) could still be practiced with slower-growing strains during the rearing period. This assumption is also aimed at accounting for the fact that, even if not required, feed restriction may be still practiced by producers as a cost reduction strategy.

Feed intake at 70% of *ad lib* consumption represents a similar level of feed restriction as that practiced with fast-growing birds during the laying phase (weeks 31-62). Therefore, we assume a similar distribution of pain intensity as that assumed for fast-growing breeders during weeks 31-62 (Pain-Track 2). Still, slower growing breeders are known to show fewer signs of hunger (lower glucose/fatty acids ratio) than fast-growing strains under similar levels of feed restriction [42]. Recent research with conventional and slower-growing breeders confirms these outcomes, showing that slower growing broiler breeders experience lower feeding motivation under *ad libitum* feeding conditions, and fewer signs of chronic stress when feed restricted [61]. Therefore, we assume a 10% lower likelihood of Disabling pain.

Pain-Track 2. Hypothesis for the intensity and duration of the pain endured per day by slower-growing female breeders as a direct result of hunger over the rearing phase. The duration considers estimated conscious (awake) hours per day, and assumes no discomfort from hunger while the bird is asleep.

	Weeks 7-22	Hours in Pain
Excruating	0%	
Disabling	10%	179 [157-201]
Hurtful	80%	1432 [1252-1612]
Annoying	10%	179 [157-201]
Hours awake (day)	14-18	
Total Hours (all weeks)	1564-2016	

IV. Other welfare challenges endured by breeders

So far we focused on the welfare effects of feed restriction in parent birds, specifically the chronic hunger experienced by female breeders exposed to this practice. Still, breeders also endure multiple additional welfare harms, as summarized in Figure 2. Unfortunately, research on their welfare is extremely scarce, with very few reports on the commercial prevalence and severity of many of the challenges affecting these birds (e.g. lameness, contact dermatitis, cardiopulmonary conditions, reproductive disorders). For example, to our knowledge, there is no published data on the prevalence of leg disorders in broiler breeders kept in commercial conditions. Similarly, data is also lacking on the extent to which cardiopulmonary conditions affect commercial flocks. Importantly, the extent to which these welfare harms affect slower-growing breeders, as compared with fast-growing birds that are feed-restricted, is yet unknown.

In this section we therefore examine the possible impact of a condition for which some data from commercial operations is available: egg peritonitis syndrome (EGS). EGS is a common and very painful reproductive disorder affecting breeding birds, and the leading cause of mortality in laying and broiler hens. Surprisingly, it is a condition that has been mostly kept out of the research scope in the animal welfare sciences (according to one author, producers who experience it “only talk about it to close associates” [63]), despite its major estimated effects on welfare [16]. The data is, however, restricted to conventional broiler breeder strains, with no available data to determine the extent to which slower-growing breeding birds are affected by EGS. Therefore, we do not use estimates on the impact of EGS in the welfare comparison between fast- and slower-growing breeds. Instead, this exercise is aimed at providing a better estimate of the overall burden of pain endured by conventional female breeders over their lives.

Egg Peritonitis Syndrome

As a result of selection for high prolificity and early sexual maturity, reproductive disorders are highly prevalent in commercial poultry breeds. In a previous study, we showed that egg peritonitis syndrome (EGS, a painful and often fatal reproductive condition) is the main production disease and leading cause of mortality in egg-laying hens [16]. EGS is a disease characterized by the inflammation of the oviduct and abdominal cavity, often triggered by the presence of yolk (Figure 3). Yolk material by itself induces only a mild inflammatory response and may be reabsorbed, but because it is an excellent growth medium, secondary infections by bacteria such as *E. coli* often occur [64]. Infection can also spread to other organs, causing pancreatitis, hepatitis, splenitis, nephritis or even multi-organ failure and death. In chronic cases, the yolk form clumps in the abdominal cavity, leading to a life of discomfort [16].



Figure 3. Illustration of egg yolk peritonitis syndrome (EGPS), a common, painful and potentially fatal inflammation of the oviduct (dark pink in the illustration) and/or abdominal cavity (not shown), often triggered by the presence of yolk as a result of partially or fully formed eggs reaching the abdominal cavity or by the retention or rupture of eggs in the oviduct. The accumulation of leaked yolk can lead to fibrinous deposition (amorphous yellowish mass in the illustration) in the visceral cavity. The "penguin-like" stance adopted by the hen is typical in individuals afflicted by this condition, and is believed to be an attempt to relieve some of the intense visceral pain. Illustration: Olga Kurkina.

Despite the somewhat lower reproductive potential of broiler breeder females compared to egg laying hens, multiple risk factors make them particularly prone to egg peritonitis syndrome. First, chronic stress - a major issue in breeder hens due to chronic hunger and aggression, as reviewed here - has been described as one of the most important causes for internal laying (a risk factor for egg peritonitis) [65]. Body weight is also a risk factor for egg peritonitis; despite feed restriction to slow down growth, broiler breeder hens are still much heavier than egg laying hens, being slaughtered with 4-5 Kg at 60-65 weeks, compared to a slaughter weight of 2-2.5 Kg in hens of the same age.

Accordingly, about two-thirds of primary breeder farms (67%) in the US reported having a slight, moderate or severe problem with *E. coli* peritonitis in a survey conducted in 2012 [10]. Peritonitis has been also reported as the main cause of mortality in broiler breeder females during all stages of the production cycle in Brazil [65]. In a Danish flock, egg peritonitis was the cause of 26% of deaths in young breeder birds (20-29 weeks), progressing throughout production to 41% in the oldest birds (≥ 50 weeks) [66]³. Considering the estimate of 10-16% cumulative (total) mortality in breeder flocks in the

³ No data on the prevalence of egg peritonitis is available for slower-growing breeder birds.

United States [10], this translates into approximately 2.5 to 6.5% of all fast-growing female breeders dying from egg peritonitis. As expected, this percentage is higher than that estimated for laying hens, from 0.3 to 2.4% depending on the housing system [67] (consistent with the observation that cumulative mortality is also lower in laying hens, about 3-8% at 70 weeks [67]). Considering a previously estimated case-fatality ratio of approximately 3 to 6 cases of non-fatal (chronic) peritonitis for every death from peritonitis [16], this would translate into approximately 7 - 39% of all fast-growing female breeders experiencing an episode of chronic peritonitis during their lives.

Table 1. Total estimated time in pain endured by female broiler breeders affected by the chronic (non-fatal) and acute (fatal) manifestations of egg peritonitis syndrome. A thorough justification of the values is available in [16]. In (B) estimates are weighted by the estimated prevalence of EGS in the breeder population, representing the expected time endured in pain by the “average” member of a broiler breeding flock (Box 2).

(A) Time in pain (h) endured by affected breeder females

	Chronic Peritonitis	Acute (septic) peritonitis (fatal)
Excruciating		2.25 [1.5-3.0]
Disabling	89.6 [54.42-128.8]	131.50 [64.08-198.9]
Hurtful	1120 [635.4-1605.0]	398.45 [163.3-633.7]
Annoying	2090 [879.9-3.300]	74.30 [39.24-109.4]

(B) Time in pain (h) by the “average” flock member (estimates weighted by prevalence)

	Chronic Peritonitis	Acute (septic) peritonitis (fatal)
Excruciating		6.8 min [3.8-9.8]
Disabling	21 [8-33]	6.6 [2.6-10.6]
Hurtful	258 [99-416]	19.9 [6.6-33.4]
Annoying	481 [124-837]	3.7 [1.6-5.8]
Prevalence	7-39%	2.5-7.5%

Box 2 Time in Pain endured by the Average Population Member

Although pain inherently concerns individuals, we operationally accept that the collective welfare of the members of a population can also be determined. Measuring cumulative pain at the population level is also necessary to account for the heterogeneity in the exposure of population members to different challenges. For example, while lameness is experienced by a large fraction of broiler chickens (Chapter 2), events such as fatal cases of ascites are only experienced by a few individuals.

Therefore, measurement efforts must consider the prevalence of each welfare challenge, so that pain is determined for the average member of the population (which may not necessarily correspond to any real organism). At the population level, the time spent at each level of pain intensity as a result of each challenge is determined by multiplying it by its prevalence. For example, if a condition causes 10 hours of Disabling pain and 70% of the population are affected, then the average member of this population could be said to experience 7 hours of Disabling pain due to the condition. Measurements at the population level enable comparing the impact of different practices and conditions across demographics, geographies and time.

In a previous study [16], we estimated the time in pain endured by laying hens affected by chronic and acute (fatal) manifestations of EGS. Since the production cycle of female broiler breeders and age of peak production is very similar to that assumed for laying hens (60-70 weeks, with peak production at around 38-30 weeks), there is in principle no reason to assume that the onset of EGS and its progression would be different between these two groups. Therefore, we assume that the time in pain endured by female broiler breeders affected by the fatal and non-fatal forms of EGS will be similar to that experienced by affected laying hens (Table 1A). A thorough justification of the values is available in the laying hen study [16]. In Table 1B, the time in pain endured by individuals affected by the condition is weighted by the estimated prevalence of birds in a flock that will be affected. The resulting values represented the expected time in pain endured by the “average” breeder in a flock.

V. The Burden of Pain in Broiler Breeder Females

In this section we present and discuss the estimates of the burden of pain (as measured by hours spent at each level of pain intensity) endured by fast-growing broiler breeder females as a result of chronic hunger. In Figure 4 the expected time in pain endured by each female breeder is shown. The figure also shows the possible time in pain averted “per broiler (meat) chicken” should fast-growing strains be replaced by slower-growing breeds, as in such case the parent stock does not require feed restriction. Only hours spent awake (14-18/day) are considered (e.g., if hunger were estimated to be felt continuously for 2 days, this would translate into 28-36 hours of hunger). The results consider the uncertainty regarding intensity of pain and duration of the sensation, as depicted in Pain-Track 1. However, if the reader wants to change any of the assumptions, an interactive web application can be used for this purpose, available at <https://pain-track.org/broilers>. In the web application, changes in any of the parameters will update the estimates on the time in pain endured.

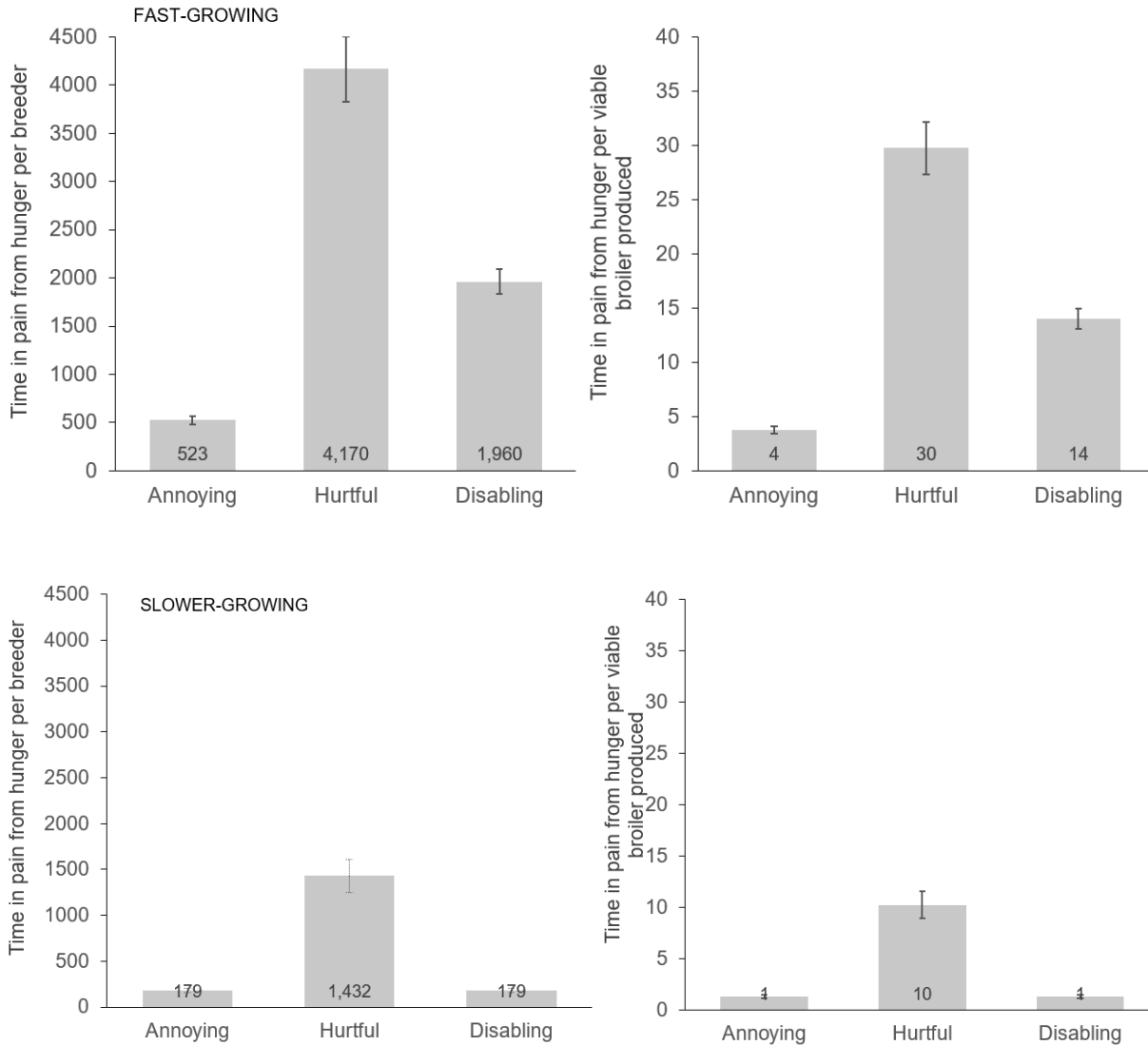


Figure 4. Estimated time endured in pain from chronic hunger by each broiler breeder female (left). In the panel on the right, estimates are divided by the number of eggs produced by each female (120-140), representing the number of viable broilers produced. Top panels: fast-growing breeders. Bottom panels: slower-growing breeders.

Overall, each fast-growing female breeder (Fig.4, left top) is expected to experience an average of nearly 2,000 hours of Disabling pain, and over 4,000 hours of Hurtful pain as a result of chronic hunger. These times correspond to a substantial fraction of the laying cycle (of approximately 5,000 hours, considering an average cycle of 56 weeks, the onset of lay at 20 weeks, and 14-18 active hours per day).

Such a burden makes chronic hunger in fast-growing broiler breeders the greatest source of physical pain that any chicken will endure over their life. Given the shorter life of broiler chickens, this is considerably less time in physical pain endured by their mothers. In fact, the average time in pain endured by the average broiler chicken as a result of all the multiple ailments analysed in this book

(Chapter 7) is also shorter than the time in pain endured by the average broiler breeder as a result of hunger alone. Naturally, there are many more broiler chickens (approximately 120-140 times more) than broiler breeders, so the impact of interventions to reduce hunger in the parent stock has a more limited effect when it is calculated in relation to each broiler (meat) chicken produced (Figure 4, right panel).

Broiler breeder females are laying birds with a lifetime similar to egg laying hens. Yet, the time in distress they experience as a result of chronic hunger alone is also substantially higher than the time in pain that egg laying hens experience as a result of any of the challenges they face over their life. For example, keel fractures are the greatest source of physical pain that laying hens endure during their lives. As estimated previously [68], fractured layers spend approximately 159 hours in Disabling pain and 2,248 hours in Hurtful pain as a result of an average of three keel fractures over their lives. Except for the mildest form of pain (Annoying), chronic hunger in fast-growing breeders thus appears to impose a substantially higher burden of pain than keel fractures on affected individuals - particularly of the more severe (Disabling) type of pain. This is expected, since broiler breeders are feed deprived since rearing, whereas the onset of keel fractures in laying hens occurs later in life, during production. Additionally, not every single laying hen suffers a fracture over her life, whereas all broiler breeding females are feed deprived. Finally, the pain from a fracture has its highest intensity (Disabling) restricted to the period immediately following bone and tissue rupture, then subsiding gradually to less intense levels as the healing process takes place. Conversely, as reviewed, there is strong evidence to suggest that broiler breeders do not habituate to the sensation of hunger, and that satiety is not achieved even immediately after eating the small daily rations provided.

The burden of 'Disabling' pain resulting from a lifetime of chronic hunger is also greater than that estimated for the average egg laying hen housed in different types of indoor systems (Figure 5) - including conventional cages - even though multiple harms are taken into account in the case of layers (behavioral deprivation, keel bone fractures, injurious pecking, depopulation, transport and egg-peritonitis). Should there be data to estimate the impact of these harms for broiler breeders too, the differences should be even greater. For example, while both broiler breeders and laying hens are exposed to injurious pecking, breeding can also endure high levels of aggression from males, which has not been analysed here. Given their heavier weight, it is also likely that broiler breeders have a higher incidence of lameness than laying hens, as well as a higher incidence of other diseases and welfare challenges associated with heavy weight (e.g. heat stress).

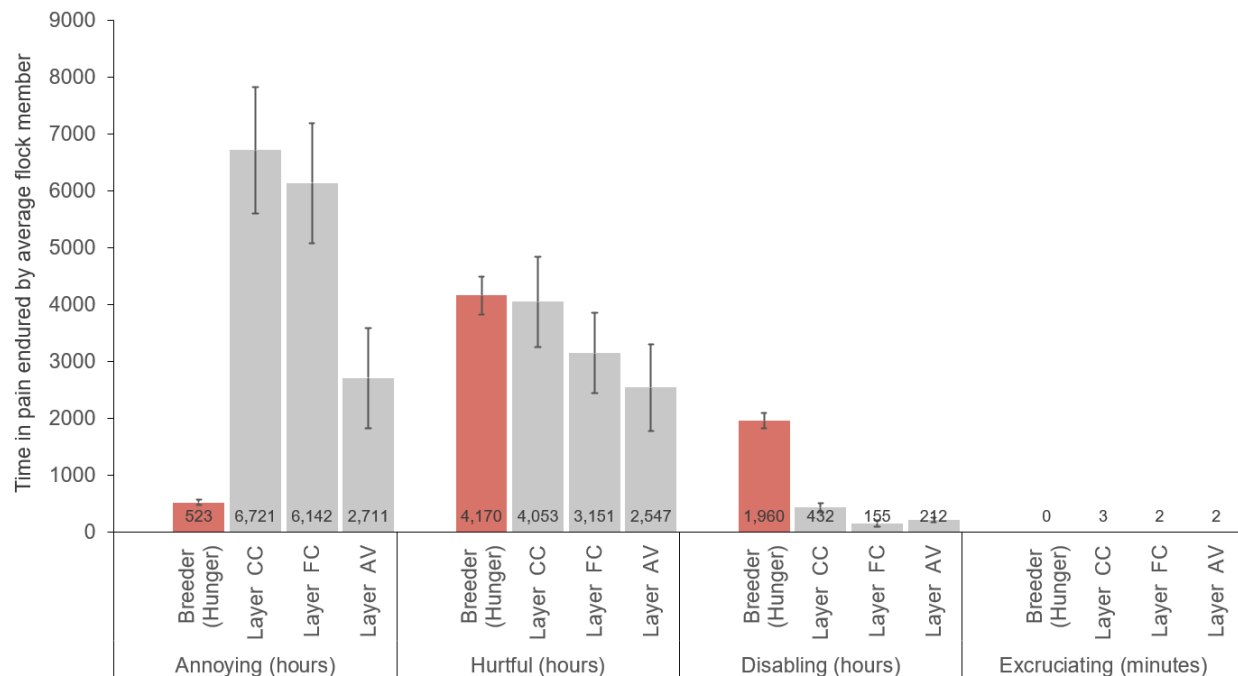


Figure 5. Estimated time endured in pain from chronic hunger by a fast-growing broiler breeder female (red bars) and by the average member of a flock of laying hens (grey bars) housed in different systems (CC: conventional cages, FC: furnished cages, AV: indoor aviaries). Estimates of the time in pain endured by layers is from Schuck-Paim and Alonso [69], and include the pain from behavioral deprivation, keel bone fractures, injurious pecking, depopulation, transport and egg-peritonitis.

In light of these findings, we estimated the time in pain averted ‘per individual bird’ by interventions aimed at eliminating chronic hunger in broiler breeder females (use of slower growing strains that do not require feed restriction), compared to the transition of egg laying hens from conventional cages to indoor cage-free (aviary) systems (Figure 6). Except for Annoying pain, the time in pain averted per breeder with the use of slower growing strains is substantially greater than the time in pain averted for every laying hen raised in an aviary instead of a conventional cage (Figure 6). This makes chronic hunger the single most important source of concentrated pain (in individuals) in chickens. Naturally, since the global population of caged laying hens (about 6.5 billion) is much larger than the broiler breeder population (0.5 billion), the potential reduction in the total time in pain for the entire population of laying hens is still larger.

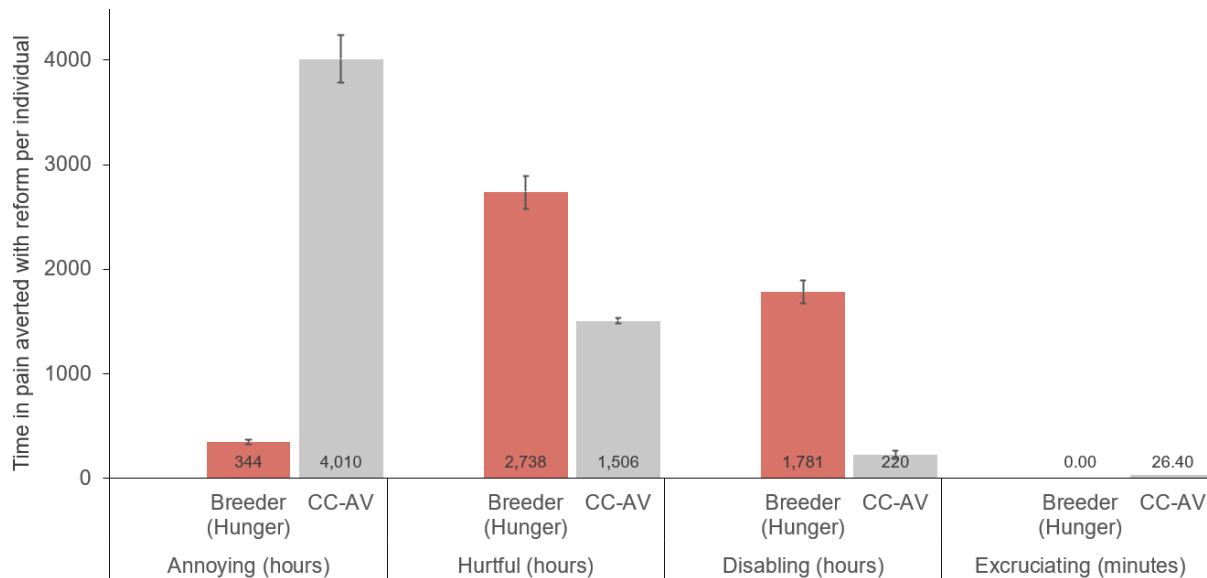


Figure 6. Estimated time in pain due to hunger averted by the replacement of fast-growing by slower-growing breeds (red bars) and by a transition from conventional cages (CC) to indoor aviary systems (AV) (grey bars).

It is worth noting that the estimated time in pain averted with the use of slower-growing strains of breeding females is the “minimum” time in pain averted by this intervention, as the estimates are based mostly only on the effect of mitigating chronic hunger. In addition to hunger, breeders are likely to experience various other negative effects of feeding restriction (Figure 2), including thirst, aggression and higher levels of feather pecking and skin lesions [61]. Unfortunately, data is not available that enables estimating the time in pain these challenges may cause. For example, to our knowledge, there are currently no published reports on the prevalence, frequency and duration of water deprivation in breeders, or on the frequency and severity of aggression suffered by female breeders over the production cycle.

Where the consequences of feed restriction are diffuse, data is also lacking that enables comparing the welfare of birds feed-restricted or not. Chronic hunger is a major stressor. Elevated baseline levels of plasma corticosterone have been widely reported in feed-restricted breeders (reviewed in [18,23,70]), increasing linearly in proportion with the level of feed restriction [38]. Likewise, conventional broiler breeders have been shown to have higher number of fault bars in their plumage (feather malformations due to chronic stressful events during feather growth), presumably due to their chronic feed restriction [61,71].

Chronic hunger also leads to restlessness and a reduced resting time, as feed-deprived birds keep searching for possible food sources: in general, the greater the level of feed restriction, the higher the activity levels and the lower the time resting [18,23]. Rest deprivation has been linked to impaired immunity in broilers and other species [72–74]. In addition to impairing immune function, the hormonal changes associated with chronic stress have been also shown to facilitate pathogen invasion by affecting the normal intestinal microbiota and epithelial structure of the host, increasing the likelihood of pathogen adhesion [75]. The negative effects of chronic exposure to stress on immune

function are widely documented in human and non-human animals, including chickens [76–79]. Chronic stress has a suppressive effect on the immune system, activating the release of corticotropin-releasing hormone (CRH) by the hypothalamus (a brain region that links the nervous and endocrine systems). Through a cascade of effects, CRH promotes the release of cortisol, a stress hormone known particularly for its anti-inflammatory and immunosuppressive action. Higher levels of cortisol are associated with a lower number of lymphocytes in blood, and a reduced production of cytokines and antibodies [76,80]. Animals exposed to stressors have also shown alterations in natural killer cell cytotoxicity (cells that kill aberrant cells, such as virally infected cells) and response to vaccination [81]. Accordingly, infectious diseases have been reported as the major cause of mortality in conventional breeder flocks [66].

The estimates are also conservative in that they do not consider the potential benefits achieved by the use of slower-growing genotypes in the mitigation of hunger in the grandparent stock, or in male breeders (approximately 1 male to every 12 females). Importantly, higher stress levels in female breeders due to hunger can also have long-term consequences for the welfare of their offspring (meat chickens) through epigenetic (transgenerational) effects [82,83], extending the adverse effects of feeding restriction to billions of meat chickens every year. For example, prenatal exposure of chickens to stress has been associated with changes in gene expression in the hypothalamus (a brain area associated with stress regulation) [84] and with higher levels of fear [85]. In other words, maternal stress levels, if reduced, can also reduce stress in the progeny [12]. Additionally, chickens born from hens exposed to higher levels of feed deprivation have also shown poorer immune responses [83]. Naturally, a heightened susceptibility to infectious diseases translates into additional time in pain, as well as a higher likelihood of exposure to septicemia, the main cause of carcass condemnations in broilers and a condition associated with Excruciating levels of pain [16].

In summary, although substantial, the estimated time in pain due to hunger that could be averted with the use of slower-growing breeder birds is very conservative. If other challenges were considered, the benefits of the substitution of genotypes would be possibly higher. It is worth mentioning the case of broiler breeders that are raised in cages. While our results indicate that broiler breeder females raised in aviaries endure a much greater burden of pain than meat chickens or even laying hens confined in conventional cages, the situation is possibly much worse for broiler breeders confined in cages. In this case, breeders have a substantially higher likelihood of developing severe emotional distress (e.g., learned helplessness), given the absence of any form of agency in this housing environment and the impossibility to search for food [86,87]. It is also possible that the sensation of hunger is experienced with a greater salience, since no distractions are available in the barren caged conditions [88] (research suggests that in barren environments the salience of pain is higher relative to that experienced in more complex environments, where multiple and competing incentives are available [32]).

VI. Research Gaps

- Further research on the extent to which chronic hunger is aversive in broiler breeders would be beneficial (e.g. demand elasticity or 'willingness to pay' tests). Studies on this and other welfare challenges do not require exposing birds to any additional aversive experience, as they could be conducted with flocks already exposed to typical conditions (e.g. feed restriction) in commercial operations.

VII. Acknowledgments

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