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# Quantifying the burden of behavioral deprivation in broiler chickens

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## I. Background

In a natural environment, pain and pleasure are extremely adaptive: while the unpleasantness of pain steers the animal away from life-threatening stimuli and behaviors, pleasure motivates animals to seek activities and resources that will enhance their chances of survival and reproduction. Although in captivity food and shelter are provided by humans, an animal's highly adaptive drive to seek, choose and care for critical resources, and to nurture such abilities - as manifested through behaviors such as foraging, exploration, mate-seeking, play and social contact - does not suddenly vanish. For example, despite over 8,000 years of domestication [1], modern chickens still retain a similar behavioral repertoire as that of their wild ancestors, the red junglefowl [2]. Given the opportunity, they will still spend a substantial fraction of their behavioral time budget foraging and exploring the environment, as well as perching and dustbathing.

Still, in modern commercial broiler production the expression of many of these drives is greatly constrained as a by-product of environmental and genetic factors. For example, certain management practices, particularly the use of high stocking densities and a lack of environmental enrichment (e.g., perches, suitable litter) limit movement and/or the possibility to perform many of these motivated behaviors. Additionally, many of the selective pressures acting to maintain animals' physical fitness in a natural environment are relaxed in captivity, and replaced by strong artificial selection for human-desirable traits (e.g., fast growth, meat yield) that often correlate poorly with well-being. In broiler chickens, rapid growth and heavy body weights are associated with increased incidences of lameness and leg disorders [3–5], poor cardiorespiratory functioning due to disproportionately-sized lungs and hearts [6] and poorer immune system functioning [7]. Altogether, these conditions make it physiologically and physically challenging for broilers to express behaviors that involve locomotion.

Accordingly, modern fast-growing birds are generally very inactive, spending the vast majority of their days sitting, lying or resting. Inactivity also increases as they age [8–10]; a recent study by one of the authors (LCD) found that 6-week-old broilers spend about 80% of the day being inactive [11]. This may be due to a number of factors, including increasingly poor leg health and lameness, which is

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known to be painful [12], as well as the increased metabolic costs of activity at heavier body weights [13].

Thwarted behavioral needs may lead to frustration and fear, which can also manifest as aggression, abnormal behaviors (e.g., stereotypies such as pacing), displacement behaviors (e.g., excessive grooming) and physiological signs of stress [14]. In this Chapter, we assume that the frustration of motivated behaviors may trigger affective (emotional) experiences of a negative valence [15], which we refer to as ‘psychological pain’ [16]. This is in line with research showing that motivation and emotion operate in synchrony to coordinate behavior at all levels across both brief and lengthy time periods [17,18]. It is this affective component that amplifies motivation by bringing attention to unsatisfied needs, creating increased urgency and amplifying behavior [17,19]. In fact, some authors propose that emotions are the true motivators of behavior [20]. Work with non-human animal models also highlights a substantial overlap in neural systems underlying motivation and emotion (reviewed in [17]).

An alternative hypothesis would be that broilers’ motivation to perform specific behaviors may have been altered by artificial selection for productivity. Artificial selection for rapid growth has included selection for high feed efficiency, which may have indirectly favored low activity levels and the performance of less energetically costly behaviors (e.g., sitting) [21], thus favoring the diversion of energy for growth. Modern broilers could thus be genetically predisposed to low activity; in this case, the intensity of the motivation to forage, explore and perch would have been reduced [21,22]. This argument, however, does not consider the fact that, as in humans, animals that are more inactive may deposit more fat (which reduces feed efficiency; [23]), but may not necessarily synthesize more muscle (protein) mass, as intended by breeding goals towards the production of lean chicken meat [24].

In this Chapter we use the [Cumulative Pain Framework](#) to quantify the time commercial broiler chickens experience in negative affective states (psychological pain) as a result of the deprivation of behaviors they may still be motivated to perform: foraging/exploration, perching and dustbathing. As the reader will note, many are the knowledge gaps and uncertainties in this exercise. The endpoint, therefore, is not yet a definitive conclusion about how much psychological pain broiler chickens experience as a result of the deprivation of behaviors they are potentially motivated to perform, but rather a starting point for discussion and the development of a logical approach to address this question. Accordingly, if the reader wants to change any of the assumptions regarding the duration and intensity of the psychological pain depicted in any of the Pain-Tracks, 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 described in this Chapter will automatically update estimates of the times in pain. Here, we analyze two scenarios, as in the other Chapters of this book:

- (1) a conventional scenario represented by the use of fast-growing breeds (e.g., Aviagen Ross 308, 708, Cobb 500) reaching a slaughter weight of approximately 2.5 kg at 42 days (average daily weight gain of the EU and USA) and raised under typical intensive conditions, and
- (2) a reformed scenario with broilers raised under conditions proposed by the Better Chicken Commitment (BCC), namely: a lower stocking density ( $\leq 30$  kg/m<sup>2</sup>), the provision of perches and enrichment and the use of slower-growing strains. In the latter case, we restrict the analysis to strains of birds that reach the same slaughter weight (~2.5 kg) in approximately 56 days (a growth rate consistent with typical figures achieved by various breeds approved under the BCC such as JA 987, 787

and Ranger Gold). As explained in Chapter 1, this choice was governed by the availability of data on the incidence of important welfare challenges in slower-growing breeds.

## II. Foraging and Exploration

In chickens, foraging encompasses two distinct behaviors, often performed in an alternating sequence: ground pecking (rapid, downward movements of the beak towards the litter or other substrates) and ground scratching (backward kicks at the substrate using one leg) [2]. Junglefowl start to perform these behaviors within the first few days of life [2]. Even in captivity, red junglefowl have been shown to spend 60% and 34% of daylight hours ground pecking and ground scratching, respectively [25]; this suggests that, even when provided with accessible feed, junglefowl continue to engage in high levels of foraging behaviors.

In commercial broiler breeds, foraging is less commonly observed, with its occurrence depending on factors such as the genotype, age and management. The extent to which modern broilers experience negative affective states (e.g., frustration, boredom) as a result of the impossibility to perform these behaviors depends, however, on the extent to which they are still motivated, but unable, to do so. With the exception of ground pecking while sitting, foraging and exploration largely involve standing and walking. Due to their rapid growth and heavy body weights, fast-growing broilers may be physically limited in their ability to stand and walk. Moreover, the pain associated with lameness-causing conditions may further limit the ability to forage and explore.

Several lines of evidence indeed suggest that foraging motivation is likely preserved in broilers, but not realized owing to these physical constraints. First, fast-growing broilers with more severe gait impairments spend less time walking and tend to spend less time ground pecking while standing [10], with some evidence that the lower the prevalence of poor gait and leg deformities the longer the time spent exploring [26]. When treated with a non-steroidal anti-inflammatory drug, broilers with even mild gait impairments spend more time in locomotion [27], suggesting that pain associated with even low degrees of lameness can affect exploratory behavior.

Additionally, broilers outfitted with a suspension harness (designed to reduce the weight load on their legs) were shown to walk about 35% further than those not provided with the device [28]; this effect only emerged when the birds had reached 13 days of age, in line with the notion that walking is not limited by 'weight' exclusively in the first two weeks of life. Similarly, 6-week old fast-growing broilers equipped with weight-reducing devices walked for about three times longer periods than broilers with simple harnesses, whereas slower-growing broilers equipped with weight-increasing devices spent about three times less time walking than those with unweighted harnesses [29]. In another study, fast- and slower-growing broilers completed two runway tests each week from 3 to 12 weeks of age, in which they were feed deprived then walked a runway to reach a food reward; motivation (i.e., the duration of feed deprivation) affected completion amongst slower-growing broilers, whereas physical ability affected completion amongst fast-growing broilers [30]. These results suggest that even fast-growing strains are motivated to forage, but bearing a heavy weight is a key factor limiting their walking and exploratory behavior.

Management practices can also diminish (or enhance) foraging and exploration performance. For one, stocking density may affect these behaviors directly through reducing the amount of floor space available to perform them, or indirectly through the reduction in litter quality that accompanies

housing a larger number of birds. Overall, broilers kept at lower stocking densities have been shown to walk, ground peck and ground scratch more [31–34], suggesting that they are motivated to perform these behaviors when there is more space to do so. Additionally, providing broilers with oral enrichment elements (mealworms) has been also shown to affect foraging, leading to more litter pecking and scratching while the enrichment remains available [35].

## 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 behaviors 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.

Considering the criteria defining the pain intensity categories (Box 1), we hypothesize the intensity of the psychological pain experienced by broilers with respect to their inability to fulfill this motivation. On one hand, the previously-reviewed evidence suggests that even fast-growing broiler breeds are still motivated to forage and explore the environment. This is in line with the notion that the 'seeking system' — an ancient and powerful neural system that strongly compels organisms to move and forage with the goal of exploration, independently of external triggers, cues or incentives [36] — is preserved in modern breeds.

On the other hand, empirical evidence that modern broilers experience negative affective states as a result of behavioral deprivation is limited, with no measurable evidence of the negative impacts of behavioral deprivation on broiler welfare (e.g., aggression, the performance of abnormal behaviors, physiological indicators of stress). Additionally, although we consider the hypothesis that conventional strains have a lower motivation for locomotion as a result of selection for high feed efficiency unlikely (inactivity may lead to the deposit of more fat, lower feed efficiency [23], and lower deposition of protein mass [24]), existing evidence does not enable us to completely rule out this possibility. Therefore, we consider that there would be some probability (uncertainty range: 10-50%, mid-point: 30%) that foraging/exploration deprivation is not associated with any negative affective states in fast-growing strains.

The remaining probability (uncertainty range: 50-90%, point estimate: 70%) represents the possibility that fast-growing broilers experience frustration as a result of the inability to forage and explore their surroundings. However, we consider that this frustration is unlikely to be very intense, of a Disabling or Excruciating nature, since the inability to forage does not appear to affect the broilers' ability to perform important maintenance behaviors such as eating and drinking (see criteria in Box 1). Additionally, observation that foraging and exploration are largely reduced in broilers with severe gait impairments suggests that they may not be willing to exchange the opportunity to perform these behaviors with the physical pain that is required to perform them, similarly suggesting a lower (Hurtful or Annoying) intensity. By the same logic, however, some negative affect is suggested by the fact that moderately lame birds will forage and explore (though at a reduced frequency), indicating that they are willing to endure some physical pain occasionally (i.e., associated with standing and walking while lame) to perform these behaviors. Therefore, we tentatively and conservatively split the point estimate of 70% into a 20% probability to the Hurtful category (associated with evidence showing that moderately lame birds will still forage occasionally), and 50% probability to the Annoying category.

These hypotheses are outlined in Pain-Track 1. The likelihood that the psychological pain associated with the frustrated motivation to forage and explore is of a given intensity is represented as a percentage in the first four rows. In the bottom row, the Pain-Track depicts the estimated number of hours in pain **per day**, for each of the weeks of the production cycle. Pain-Track 1 starts at week 3, under the hypothesis that at young ages, body weight [28], limited space and poor litter quality are each unlikely to limit the ability to forage or move around.

**Pain-Track 1.** Hypothesis for the intensity and duration (hours, bottom row) of the psychological pain endured **per day** by commercial broilers as a result of the deprivation to forage and explore the environment in each week of the production cycle. **Scenario:** fast-growing breed under typical intensive conditions. Estimated prevalence of birds affected: 100%.

|                     | Week 3 | Week 4 | Week 5 | Week 6 |
|---------------------|--------|--------|--------|--------|
| <b>Excruciating</b> |        |        |        |        |
| <b>Disabling</b>    |        |        |        |        |
| <b>Hurtful</b>      | 20%    | 20%    | 20%    | 20%    |
| <b>Annoying</b>     | 50%    | 50%    | 50%    | 50%    |
| <b>Duration (h)</b> | 0-10.3 | 0-10.4 | 0-10.6 | 0-10.8 |

### Estimating Duration

We assume that the intensity of the psychological pain will not change with increasing age, but the duration of this pain will, given the increasing constraints on the physical ability to stand and walk, the increasing proportion of energy consumption (leaving less energy available for locomotor activity), the decline in room to forage and the decline in litter quality. Each day, the estimated duration of pain is determined as the difference between (1) the hypothetical desired duration of foraging/exploration and (2) the realized duration. The hypothetical values for the minimum desired daily duration of foraging/exploration are assumed to correspond to the amount of foraging performed at weeks 1 and 2, when foraging is less constrained by stocking density, litter quality and/or physical ailments, but may still be somewhat constrained by the lack of environmental complexity in an indoor environment, the lack of positive feedback from foraging, adequate substrates and the large fraction of energy allocated to growth. To this end, we use the mean from two behavioral studies with 1 to 2-week-old fast- and slower-growing birds, which showed that they spent about 15.5% [37] and 12.6% (fast-) and 13.5% (slower-growing) of their days foraging and walking [38] (these estimates assume that all walking is for the purposes of foraging or exploration). We take these findings as a reference to estimate the uncertainty interval containing typical time budgets: 10 to 20%. This range corresponds to 1.4 to 4 hours per day (considering that commercial birds are awake for 14-20 h/day; see Chapter 1) during which broilers would be foraging if they were as fit and had as much space as 1 to 2 week-old chicks under typical commercial (indoor) conditions.

The hypothetical values for the maximum desired duration of foraging/exploration is assumed to correspond to the time budget of the red jungle fowl [25] ‘minus’ the time commercial broilers allocate to distracting activities such as eating and drinking, during which frustration is assumed to be absent. Considering that eating and drinking together account for approximately 20% of the daytime budget of fast-growing commercial broilers in the first 6 weeks of life [37], and conservatively assuming that an additional 10% of the time budget may be allocated to other distracting activities (e.g., comfort behaviors, or simply a longer time dedicated to eating and drinking), this leads to a maximum desired duration of approximately 70% (or up to 11 hours per day if up to 16 active hours/day are considered in the case of junglefowl). When the minimum and maximum ranges are considered together, the hypothetical desired daily duration of foraging/exploration could thus range from **1.4 to 11 hours per day**. Such a wide range reflects the many uncertainties associated with this

estimate, as well as the expected variation in the commercial flocks in terms of management and physical conditions that make standing painful.

The realized duration of foraging and exploring is represented by the range of values from studies that report both the foraging and locomotion time budget for each week of age [8,37,38]: 9-15% at week 3 (1.3-3 hours/day); 8-13% at week 4 (1.1-2.6 hours/day); 5-11% at week 5 (0.7-2.4 hours/day) and 4-12% at week 6 (0.5-2.4 hours/day). However, these values likely represent the higher end of the time budget, as they derive from studies conducted under carefully-controlled conditions (e.g., lower density, enrichment, good husbandry, long dark periods, small groups), which to some extent 'shields' less resilient breeds (e.g., typical fast-growing strains) from welfare problems observed under more challenging commercial conditions, and which may constrain behavioral expression. Therefore, we extend the lower range values to increase the likelihood that it includes the time budgets under typical commercial settings (weeks 3, 4, 5 and 6, respectively: 0.65-3; 0.55-2.6; 0.35-2.4 and 0.25-2.4 hours/day). They are subtracted from the hypothetical desired daily duration of foraging/exploration calculated previously (1.4-11 hours/day) and the results shown in the bottom row of Pain-Track 1.

### *Better Chicken Commitment*

Under the Better Chicken Commitment, broilers are expected to have a greater ability to forage and explore. For one, at the same age, slower-growing breeds will be lighter, and thus likely to have more freedom of movement than fast-growing broilers. Additionally, at a lower stocking density, broilers are less likely to be limited by the amount of floor space available. Moreover, when broilers are provided with pecking substrates (e.g., maize roughage, mealworms, bales of peat or hay, pecking stones), either alone or in combination with elevated surfaces, they seem to be well used [38] and lead to an increased incidence of foraging and exploration behaviors [35,38-41] (although some authors found that the latter effect is short-lasting [35]). Importantly, better leg health (Chapter 2), disease resistance and cardiorespiratory function (Chapter 3) should facilitate behavioral expression in slower-growing birds compared to fast-growing strains.

Accordingly, the behavioral time budgets of fast- and slower-growing broilers differ, with the latter spending more time standing, perching, foraging, dustbathing, preening and in locomotion [8,9,11,26,37]. In studies that compared the behavioral time budget of fast-growing strains with that of slower-growing birds growing at approximately 43-48 g/day, from week 3 onwards, the time slower-growing birds spent in locomotion or foraging was approximately 2 to 3 times longer than that spent by conventional strains [8,11,38]. We use these estimates to determine the 'realized duration of foraging and exploring' in slower-growing breeds (see previous section) as corresponding to 2 to 3 times that calculated for faster-growing strains. This is likely a conservative assumption, since the carefully-controlled environments of these studies may have favored less-resilient fast-growing breeds, potentially making welfare differences between conventional and slower-growing breeds less pronounced than what may be typical of more challenging commercial conditions. Considering the lighter weight, better leg health and lower density experienced under the BCC scenario, we assume that foraging is unconstrained in the first three weeks of life (instead of two weeks, as assumed for fast-growing strains). The estimated intensity of the pain, when frustration is present, is assumed to be the same as that experienced by fast-growing birds (justified in the previous section).

Pain-Track 2. Hypothesis for the intensity and duration (hours, bottom row) of the psychological pain endured **per day** by commercial broilers as a result of the deprivation of the possibility to forage and explore the environment in each week of the production cycle. **Scenario:** Better Chicken Commitment. Estimated prevalence of birds affected: 100%.

|              | Week 4 | Week 5 | Week 6 | Week 7 | Week 8 |
|--------------|--------|--------|--------|--------|--------|
| Excruciating |        |        |        |        |        |
| Disabling    |        |        |        |        |        |
| Hurtful      | 20%    | 20%    | 20%    | 20%    | 20%    |
| Annoying     | 50%    | 50%    | 50%    | 50%    | 50%    |
| Duration (h) | 0-9.7  | 0-9.9  | 0-10.3 | 0-10.5 | 0-10.5 |

### III. Perching and Roosting in Elevated Areas

Free-living chickens often rest on elevated structures (e.g., tree branches, bushes) to physically distance themselves from ground predators and better monitor their surroundings [42]. The drive to seek elevated structures to perch and roost seems to have been retained in modern breeds of commercial chickens. For example, in young laying hens, perching frequency is higher in smaller groups, when individual predation risk is higher [43]. This drive to rest on an elevated surface appears to be stronger during the overnight hours. For instance, in one study of captive red junglefowl and commercial laying hens, all overnight resting occurred on the provided perches, with perching beginning around one hour prior to sunset [44], whereas another study found that 90% of hens perched within 10 minutes of the lights being turned off [45].

In commercial broiler breeds, evidence suggests that perching and roosting are also associated with a lower perceived threat of predation, in addition to reducing true threats of aggression. Compared to unenriched conditions, broilers raised with elevated surfaces are possibly less fearful, as evidenced by their shorter durations of tonic immobility [46]<sup>2</sup> (Box 2). They also demonstrate lower rates of aggressive behaviors [33] and lower heterophil/lymphocyte ratios, suggesting they may be less stressed, too [48]. Perching and roosting are also likely beneficial to welfare in other, indirect ways. For example, experimental evidence suggests that the provision of perches, platforms or straw bales may improve leg and foot health, as they have been linked to longer latencies to lie [49], a lower prevalence of tibial dyschondroplasia, improved walking ability [50] and a reduced incidence of foot pad dermatitis [51]. By acting as an additional surface to rest on, the provision of elevated structures also has the potential to indirectly increase the floor space available for the performance of other behaviors, such as foraging and exploration.

<sup>2</sup> Other studies have evaluated fear via flight distance or response to a novel object, but these indicators can be confounded by walking ability [47], so they may not be accurate measures of fear in broilers.

## Box 2. Tonic immobility

Tonic immobility is an involuntary reflexive reaction characterized by a reversible, but profound, motor inhibition believed to be a last line of defense in unavoidable attacks. From an evolutionary perspective, tonic immobility is believed to have evolved as a response to predator attacks after flight and fight responses have failed - a last resort in the face of inescapable danger. Accordingly, some studies [52,53] have shown that tonic immobility can increase prey survival, for example by increasing the likelihood that predators will drop or cache the individuals for consumption at a later time, providing them with further opportunities to flee. Tonic immobility is observed in a wide variety of vertebrate and invertebrate species, from ants and spiders to fish, rodents and even humans, such as victims of sexual assault [54]. In chickens, tonic immobility has been shown to be elicited by both fear-inducing and painful stimuli [55]; however, this strategy is counterproductive in commercial systems where individuals cannot escape, and are in fact making themselves available to attackers [56].

Although perches and raised platforms are not typically available in conventional broiler farms, when available, broilers will use them. Usage, however, is likely constrained by the physical conformation of modern breeds. Genetic selection for rapid muscle growth has led to increased breast muscle size in fast-growing broilers, which has shifted their center of gravity [57] and possibly affected their ability to balance on a perch. Indeed, slower-growing broilers have been shown to perch more than fast-growing broilers [8,9,37,58,59] at a similar age, possibly as a result of differences in body weight or conformation. Foot health issues (e.g., contact dermatitis, which is more prevalent in fast-growing broilers) may also affect broilers' ability to hold onto a perch, as may leg health problems [27]. Likewise, fast-growing broilers' perching and roosting behavior is also heavily influenced by the design of the elevated structure itself, with a preference for elevated platforms or grids to traditional bar-type perches [58,60] as resting and balancing on a round bar may be difficult for these birds. For instance, several studies have noted that broilers spend less than 15% of their time budgets perching on traditional wooden perches [8,9,26,59,61], and from 25 to 45% perching on flat perches [33,37].

In Pain-Track 3 we outline the hypothesis for the potential frustration associated with the inability of fast-growing birds raised under typical commercial conditions to perch or roost (the opportunity that elevated structures offer in terms of minimizing physical pain is discussed in other chapters). Given the adaptive antipredatory function of perching, as well as evidence to suggest that broilers raised without the opportunity to perch are more fearful [46,62], stressed [48] and aggressive [33], we tentatively hypothesize that the inability to perch or roost is aversive for broilers. This is also suggested by observations that broilers make use of elevated structures when they are available, indicating a retained motivation to perch and roost.

Evidence to determine the magnitude of this aversiveness is however lacking or conflicting. Unlike research with laying hens, demand elasticity experiments, in which an animal's motivation to access a resource (e.g., a perch) is quantitatively measured via their willingness to pay for access, have not been conducted with broiler chickens. Similarly, it is currently unclear whether motivation increases after

periods of deprivation (e.g., if limited space prevents repeated perching or if social hierarchy prevents certain individuals from perching) or whether broilers who have never experienced perching or roosting (i.e., raised without perching structures) ‘miss’ the opportunity in the same manner as those who have experienced perching or roosting. Additionally, data for broilers’ overnight behavior — when perching and roosting motivation is expected to be strongest based on the behavior of chickens in the wild — is limited. Although the intensity of the aversiveness associated with the inability to perch is unlikely to reach the criteria defining the Disabling category of pain intensity (Box 1), as broilers still perform activities such as eating and drinking, evidence is therefore not available that enables us to determine whether the Hurtful or Annoying categories are more representative of the experience. Thus, we conservatively attribute in Pain-Track 3 the same likelihood for these categories. Because broilers raised under intensive conditions are generally not provided with environmental enrichment, including elevated structures for perching and roosting, we hypothesize that 100% of these birds are affected (100% prevalence).

Based on observations that both junglefowl and commercial laying hens begin to perch for the night about 1 hour prior to sunset (or prior to the lights being turned off) [44], that perching behavior peaks in broilers around dawn and dusk [38,58] and that perching overnight is more frequent than during the day [59], and without evidence to suggest otherwise, we tentatively assume that psychological pain associated with the inability to perch and roost will be most prominent: 1) when searching for a safe, elevated site, which we estimate to last approximately 30-60 minutes and 2) during dark hours (4-10 hours under typical lighting regimes; Chapter 1). Outside of these periods, we conservatively assume that the inability to perch is not a driver of feelings of frustration or fear. During the dark hours, we assume that psychological pain due to roosting deprivation is limited to the time when broilers are awake (not sleeping). Although research on commercial broilers’ overnight rest is limited, one study of young broilers noted less than 2 minutes of activity per hour during the dark period [63], while another noted that broilers spend approximately 85% of the dark period asleep or resting [64]. We thus hypothesize that broilers may experience mild distress due to the inability to roost during up to 15% of the dark period, corresponding to 0.6 to 1.5 hours per night.

Finally, in the absence of evidence to suggest otherwise, in Pain-Track 3, we assume that motivation to perch remains steady with age, and thus hypothesize that the intensity and duration of the pain associated with the inability to perch or roost would be similar over time, with motivation to perch starting as early as 1 week of age [59]. Although perching increases as broilers age, peaking at around 4 to 5 weeks of age [9,33,37,38,62,65] before rapidly declining [9,37], there is no evidence to suggest that motivation changes with age, particularly if it serves an antipredatory function. Instead, observed differences are likely linked with broiler weight and learning; it takes time to learn how to use the perches, as well as reaching a body size/height at which birds can easily maneuver onto the perches.

Pain-Track 3. Hypothesis for the intensity and duration of the psychological pain endured **per day** by broiler chickens as a result of deprivation of an elevated site for roosting from weeks 1-6. **Scenario:** fast-growing breed under typical intensive conditions. The estimated prevalence of birds affected is 100%.

|              | i.<br>Search for roosting site | ii.<br>Dark hours |
|--------------|--------------------------------|-------------------|
| Excruciating |                                |                   |
| Disabling    |                                |                   |
| Hurtful      | 50%                            | 50%               |
| Annoying     | 50%                            | 50%               |
| Duration (h) | 0.5-1                          | 0.6-1.5           |

### Better Chicken Commitment

Under the Better Chicken Commitment, broilers would be provided with at least 2 m of perch space per 1,000 birds; therefore, some birds would be capable of perching, assuming the structure is of a suitable design. In one study, at their heaviest weight, each slower-growing broiler used about 19 cm of perch space [66]; thus, a 2-m long perch space could only accommodate approximately 10 birds (1% of 1,000 birds) at one time. Naturally, more birds would be able to fit at a younger age; if we assume that, at their smallest, any given slower-growing bird occupies 10 cm of perch space, then up to 20 birds (2%) of every 1,000 birds could be accommodated across each 2 m of perch space. Altogether, we hypothesize that from 1 to 8 weeks of age, 98-99% of birds would be unable to perch or roost simply due to a lack of available perch space<sup>3</sup>, and thus would experience the frustration or fear associated with the deprivation of these behaviors.

Pain-Track 4 summarizes our hypothesis for the intensity and duration of the psychological pain endured per day by slower-growing broilers as a result of the deprivation of an elevated site for roosting. As with fast-growing birds, we assume that motivation to perch and roost will remain constant over time, as does the intensity and duration of the negative state potentially emerging from the inability to fulfill these motivations. Since slower-growing broilers perch for similar durations at 1 to 6 weeks and 6 to 12 weeks of age [37], we have also assumed that physical ability to perch will not decline with age, and thus neither will the duration or intensity of pain (hence the lack of columns for each age in Pain-Track 4).

<sup>3</sup> The rationale for the requirement of only 2 meter of perch space per 1,000 birds in the BCC is not clear, but may be related to the cost associated with the structures, and the managerial difficulties associated with them: they make catching more difficult (birds can hide under them) and are difficult to clean. It is also the author’s experience (LCD) that producers do not think broilers use these structures enough to warrant the additional costs and management challenges associated with their provision.

Pain-Track 4. Hypothesis for the intensity and duration of the psychological pain endured **per day** by fast-growing broiler chickens as a result of deprivation of an elevated site for roosting from weeks 1-8. **Scenario:** Better Chicken Commitment. The estimated prevalence of birds affected is **98-99%** (see text for justification).

|              | i.<br>Search for roosting site | ii.<br>Dark hours |
|--------------|--------------------------------|-------------------|
| Excruciating |                                |                   |
| Disabling    |                                |                   |
| Hurtful      | 50%                            | 50%               |
| Annoying     | 50%                            | 50%               |
| Duration (h) | 0.5-1                          | 0.6-1.5           |

## IV. Dustbathing

Dustbathing is common in poultry and other bird species, consisting of a sequence of coordinated movements. Initially, the bird squats in the substrate and uses the wings to throw dust through the feathers, next rising and shaking off the dust. Other elements include the raking of the substrate with the beak, ground scratching, wing shaking, and head and side rubbing [67]. Typically, chickens will dustbathe about once every other day, often for 20 to 35 minutes at a time, after which they stand up and shake the dust off their plumage [68]. From a functional perspective, dustbathing has been associated with the removal of surplus stale lipids from the feathers [68] (improving the insulation capacity of the feathers), dandruff and possibly ectoparasites [69].

In laying hens, dustbathing seems to be a motivated behavior, with hens demonstrating observable indicators of frustration when prevented from performing it. For example, the removal of dustbathing materials has been shown to elicit gavel-calls [70] (a general signal of a frustrated internal state in chickens) and increase exploratory behavior [71], suggesting that layers ‘miss’ the possibility of dustbathing. Also, birds kept in wire cages exhibit a higher number of stereotypic pecks than caged birds with access to sand [72]. Importantly, hens have been found to be more motivated to dustbathe after a period of deprivation: the longer the deprivation, the higher the amount of dustbathing behavior when the opportunity arises [72–74]. The increase in motivation after deprivation suggests some influence of internal factors in controlling the motivation to dustbathe [68]. As proposed by Petherick & Rushen [68], restricting a behavior will be detrimental to welfare *‘if the motivation arises mainly from internal factors, if motivation remains high when the behavior cannot be performed and if motivation is reduced by performing the behavior rather than achieving the consequences’*.

Still, the frequency of dustbathing is low among broilers kept under typical commercial conditions, with some reports of dustbathing associated with a daily time budget of as little as <1% [64,75]. Such a low frequency may reflect, to some extent, the reduced physical capacity of fast-growing broiler strains owing to leg disorders, cardiopulmonary deficiencies and the diversion of energy towards growth as opposed to a low motivation to dustbathe. For example, lame birds spend less time dustbathing and more time sitting [10,76], but when provided with a non-steroidal anti-inflammatory drug (carprofen) they are more likely to dustbathe than those injected with saline, suggesting an inherent motivation to dustbathe that is hindered by pain [27]. Likewise, broiler chickens have also been shown to compensate for a period of deprivation by more dustbathing [76]. In fact, even lame birds (with tibial dyschondroplasia) have been shown to dustbathe after a period of deprivation [76].

Although some authors have suggested that increased dustbathing following deprivation could be the result of a build-up of feather lipids, the same effect of deprivation was found in both intact and uropygial gland extirpated layer birds, indicating that factors other than lipid level increase dustbathing motivation [68].

Low levels of dustbathing in broilers may also reflect a lack of a suitable substrate. Under commercial conditions, litter tends to become very wet and compact across the production cycle, limiting its attractiveness for dustbathing [77,78]. Some types of bedding material also have limited attractiveness. In general, sand and dust are preferred, with a much lower frequency of dustbathing behavior on other substrates [78,79]. Finally, by limiting movement, high stocking densities will also limit the performance of several behaviors, including dustbathing. Indeed, in studies where birds were housed at a lower stocking density and litter quality was maintained over time, the percentage of dustbathing observed was higher than in other studies, peaking at 3.6% [37].

Notwithstanding, failure of some studies to find evidence of a motivation to dustbathe [80–83] has led some authors to suggest that dustbathing could be a lesser priority than other behaviors [84,85], representing a pleasurable activity that birds engage in when given the opportunity [86]. In light of the conflicting evidence on whether deprivation of proper dustbathing opportunities has a negative impact on welfare, we tentatively split the likelihood that deprivation of dustbathing is associated with a negative welfare impact equally (i.e., we assume the highest possible degree of uncertainty) into the hypotheses that (1) the welfare of fast-growing broilers is not negatively impacted in any way (50%) and (2) there is some frustration associated with deprivation (Pain-Track 5). In the latter case, we attribute the intensity of the deprivation mostly to the Annoying category. Still, given observations that dustbathing increases with time since the last performance, hence the possibility that the putative need to dustbathe builds up over time, we consider a low (10-20%, mid-point: 15%) likelihood that intensity increases to a Hurtful level. These probabilities can also be interpreted as the temporal distribution of frustration levels in the intensity categories, with 35% of the time spent at the Annoying level, 15% at the Hurtful level, and 50% of the interval with no distress. These are the same probabilities attributed to the effect of dustbathing deprivation in laying hens [87].

In terms of duration, we assume that frustration would be present during the hours typically associated with the performance of the behavior in laying hens and the junglefowl, namely in the middle of the day and afternoon (from approximately 11:00 to 16:00) [68,88,89]. This is a conservative assumption that restricts the possible time spent in frustration to a five-hour interval. Should there be no effect of time of the day on the motivation to dustbathe in broilers [27], this interval may be longer. To account for the high level of uncertainty associated with these assumptions, to this five-hour interval we add the possibility of a 50% shorter or 50% longer duration (hence ranging from 2.5 to 7.5 hours). As before, we assume that motivation to dustbathe remains steady with age [37], but similarly to the case of foraging, we assume that dustbathing is not constrained in any way in the first two weeks of life, when litter quality is better and movement is less likely to be constrained by lameness and other ailments. It is worth noticing that Pain-Track 5 addresses the negative affective states directly emerging as a result of the deprivation of dustbathing, and does not consider other potentially negative (indirect) effects of the possibility to perform it, such as increased fearfulness [79,90].

Pain-Track 5. Hypothesis for the intensity and duration of the psychological pain endured **per day** by fast-growing broiler chickens as a result of dustbathing deprivation. The estimated prevalence of birds affected is 100%.

i.

|              |                                           |
|--------------|-------------------------------------------|
|              | Deprivation of<br>Dustbathing (weeks 3-6) |
| Excruciating |                                           |
| Disabling    |                                           |
| Hurtful      | 15%                                       |
| Annoying     | 35%                                       |
| Duration (h) | 2.5 - 7.5                                 |

### *Better Chicken Commitment*

Under the Better Chicken Commitment, the increased space available (provided by the lower stocking density and the provision of raised platforms and perches) and its effects on litter quality (likely to become less wet and compact) should increase the opportunities for dustbathing. Likewise, a higher level of activity and behavioral expression is expected given the lower prevalence of leg disorders (Chapter 2) and other ailments associated with faster growth (Chapter 3). Yet, given the high level of heterogeneity in management, and the possibility that the substrates available may not be the most appropriate for dustbathing (e.g., wood shavings), we assume that **10-60%** of the birds raised under the BCC will not be able to dustbathe when motivated to do so.

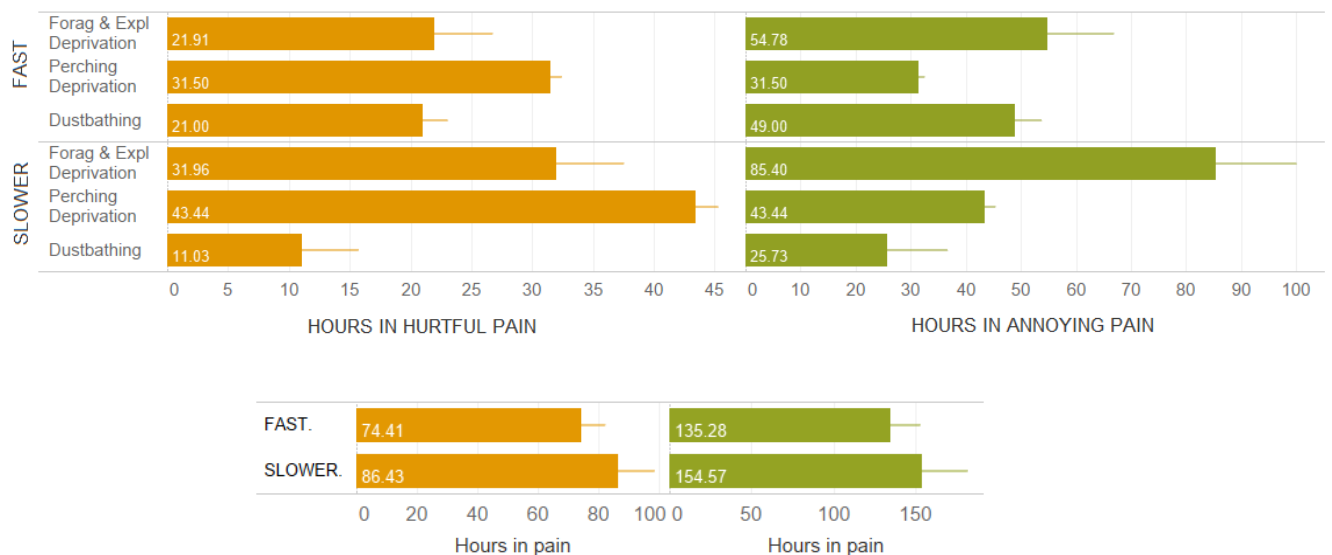
Pain-Track 6. Hypothesis for the intensity and duration of the psychological pain endured **per day** by fast-growing broiler chickens as a result of dustbathing deprivation. The estimated prevalence of birds affected ranges between 20 and 60% (see text for justification).

i.

|              |                                           |
|--------------|-------------------------------------------|
|              | Deprivation of<br>Dustbathing (weeks 3-8) |
| Excruciating |                                           |
| Disabling    |                                           |
| Hurtful      | 15%                                       |
| Annoying     | 35%                                       |
| Duration (h) | 2.5-7.5                                   |

## V. The Burden of Pain from Behavioral Deprivation

Figure 1 shows the estimated time endured at each level of pain intensity by an “average” fast- and slower-growing broiler chicken (see Box 3 for a definition) as a result of the deprivation of foraging/exploration, perching/roosting and dustbathing. In this case, the times in pain at each intensity level endured by birds are weighted by the estimated proportion of birds affected. In all cases, estimated times are based on the pain-tracks justified previously. The estimates consider the uncertainty regarding intensity of pain and duration of each time segment in the pain-tracks, propagated through the model. 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>.



**Figure 1.** Total time endured at each level of pain intensity (hours) by an “average” broiler chicken as a result of behavioral deprivation. Error bars represent 95% uncertainty intervals.

Overall, differences between fast- and slower-growing birds (ADG: ~45-46 g/day) in the estimated time in pain due to the potential frustration emerging from behavioral deprivation are small. The small differences in the time spent in pain between fast- and slower-growing birds emerge mostly from differences in their lifespan. As shown in the Figure, the impact of the deprivation of the opportunities to forage and explore, perch and dustbathe is restricted to lower levels of intensity given (1) the observation that the ability to function, in terms of performing important maintenance behaviors such as eating and drinking, is not substantially disrupted and (2) the current lack of measurable negative impacts of their deprivation on broiler welfare. Evidence on the extent to which deprivation of these behavioral opportunities has a negative impact on welfare is therefore critically needed. We hope the many data gaps discussed in this Chapter are helpful in motivating further research.

### **Box 3 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 is 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.

## VI. Research Gaps and Opportunities

1. The strength of broilers' motivation to forage, perch and dustbathe must be better established, both for fast- and slower-growing broiler breeds. Operant and preference testing (e.g., demand elasticity experiments - which reveal the 'price' an animal is willing to pay to access a resource or opportunity - or choice tests), along with the study of behavioral or physiological changes following deprivation of access to resources (e.g., elevated surfaces, dusty substrate) would allow for a better understanding of broilers' motivation to perform motivated behaviors and the welfare impact of their deprivation.
2. Data on the overnight behavior of broilers is limited, a period when perching and roosting motivation may be the greatest. Therefore, the welfare impact of the inability to roost as well as the effects of rest disruption remain largely unknown.

## VII. References

1. Lawal RA, Martin SH, Vanmechelen K, Vereijken A, Silva P, Al-Atiyat RM, et al. The wild species genome ancestry of domestic chickens. *BMC Biol.* 2020;18: 13.
2. Kruijt JP. Ontogeny of Social Behaviour in Burmese Red Junglefowl (*Gallus Gallus Spadiceus*) Bonnaterrre. *Behaviour Supplement.* 1964; 1–201.
3. Wilhelmsson S, Yngvesson J, Jönsson L, Gunnarsson S, Wallenbeck A. Welfare Quality® assessment of a fast-growing and a slower-growing broiler hybrid, reared until 10 weeks and fed a low-protein, high-protein or mussel-meal diet. *Livest Sci.* 2019;219: 71–79.
4. Kestin SC, Gordon S, Su G. Relationships in broiler chickens between lameness, Liveweight, Growth Rate and Age. *Vet Rec.* 2001;148: 195–198.
5. Shim MY, Karnuah AB, Anthony NB, Pesti GM, Aggrey SE. Genetics, the effects of broiler chicken growth rate on valgus, varus, and tibial dyschondroplasia. *Poult Sci.* 2012;91: 62–65.
6. Collins KE, Kiepper BH, Ritz CW, McLendon BL, Wilson JL. Growth, livability, feed consumption, and carcass composition of the Athens Canadian Random Bred 1955 meat-type chicken versus the 2012 high-yielding Cobb 500 broiler. *Poult Sci.* 2014;93: 2953–2962.
7. Cheema MA, Qureshi MA, Havenstein GB. A comparison of the immune response of a 2001 commercial broiler with a 1957 randombred broiler strain when fed representative 1957 and 2001 broiler diets. *Poult Sci.* 2003;82: 1519–1529.
8. Dixon LM. Slow and steady wins the race: The behaviour and welfare of commercial faster growing broiler breeds compared to a commercial slower growing breed. *PLoS One.* 2020;15: e0231006.
9. Wallenbeck A, Wilhelmsson S, Jönsson L, Gunnarsson S, Yngvesson J. Behaviour in one fast-growing and one slower-growing broiler (*Gallus gallus domesticus*) hybrid fed a high- or low-protein diet during a 10-week rearing period. *Acta Agriculturae Scandinavica A: Animal Sciences.* 2016;66: 168–176.
10. Weeks CA, Danbury TD, Davies HC, Hunt P, Kestin SC. The behaviour of broiler chickens and its modification by lameness. *Appl Anim Behav Sci.* 2000;67: 111–125.
11. Dawson LC, Widowski TM, Liu Z, Edwards AM, Torrey S. In pursuit of a better broiler: a comparison of the inactivity, behavior, and enrichment use of fast- and slower growing broiler chickens. *Poult Sci.* 2021;100: 101451.
12. McGeown D, Danbury TC, Waterman-Pearson AE, Kestin SC. Effect of carprofen on lameness in broiler chickens. *Vet Rec.* 1999;144: 668–671.
13. Tickle PG, Hutchinson JR, Codd JR. Energy allocation and behaviour in the growing broiler chicken. *Sci Rep.* 2018;8: 1–13.
14. G. J. Mason CCB. Behavioural Restriction. In: M.C. Appleby, J.A. Mench, I.A.S. Olsson, B.O. Hughes, editor. *Animal Welfare.* CAB International; 2011. pp. 98–119.
15. Papini MR, Penagos-Corzo JC, Pérez-Acosta AM. Avian Emotions: Comparative Perspectives on Fear and Frustration. *Front Psychol.* 2018;9: 2707.
16. Alonso WJ, Schuck-Paim C. The Comparative Measurement of Animal Welfare: the Cumulative Pain Framework. In: Schuck-Paim C, Alonso WJ, editors. *Quantifying Pain in Laying Hens.* Independently published. <https://tinyurl.com/bookhens>; 2021.
17. Cromwell HC, Abe N, Barrett KC, Caldwell-Harris C, Gendolla GHE, Koncz R, et al. Mapping the interconnected

- neural systems underlying motivation and emotion: A key step toward understanding the human affectome. *Neurosci Biobehav Rev.* 2020;113: 204–226.
18. Morewedge CK, Buechel EC. Motivated underpinnings of the impact bias in affective forecasts. *Emotion.* 2013;13: 1023–1029.
  19. Panksepp J. Cross-species affective neuroscience decoding of the primal affective experiences of humans and related animals. *PLoS One.* 2011;6: e21236.
  20. Tomkins S. *Affect, Imagery, Consciousness. Vol. III. The Negative Affects: Anger and Fear.* New York: Springer; 1991.
  21. Bizeray D, Leterrier C, Constantin P, Picard M, Faure JM. Early locomotor behaviour in genetic stocks of chickens with different growth rates. *Appl Anim Behav Sci.* 2000;68: 231–242.
  22. EFSA Panel on Animal Health and Welfare. Scientific Opinion on the influence of genetic parameters on the welfare and the resistance to stress of commercial broilers: Genetic selection of broilers. *EFSA j.* 2010;8: 1666.
  23. Pym RAE, Solvyns AJ. Selection for food conversion in broilers: Body composition of birds selected for increased body-weight gain, food consumption and food conversion ratio. *Br Poult Sci.* 1979;20: 87–97.
  24. Chambers JR, Gavora JS, Fortin A. Genetic changes in meat-type chickens in the last twenty years. *Can J Anim Sci.* 1981;61: 555–563.
  25. Dawkins MS. Time budgets in red junglefowl as a baseline for the assessment of welfare in domestic fowl. *Appl Anim Behav Sci.* 1989;24: 77–80.
  26. Abeyesinghe SM, Chancellor NM, Moore DH, Chang Y-M, Pearce J, Demmers T, et al. Associations between behaviour and health outcomes in conventional and slow-growing breeds of broiler chicken. *Animal.* 2021; 100261.
  27. Riber AB, Herskin MS, Foldager L, Berenjian A, Sandercock DA, Murrell J, et al. Are changes in behavior of fast-growing broilers with slight gait impairment (GS0-2) related to pain? *Poult Sci.* 2021;100: 100948.
  28. Rutten M, Leterrier C, Constantin P, Reiter K, Bessei W. Bone development and activity in chickens in response to reduced weight-load on legs. *Anim Res.* 2002;51: 327–336.
  29. Djukic-Stojcic M, Bessei W. The effect of weight load on the legs of broilers behaviour. *Biotechnology in Animal Husbandry.* 2011;27: 1667–1671.
  30. Bokkers EAM, Koene P. Motivation and ability to walk for a food reward in fast- and slow-growing broilers to 12 weeks of age. *Behav Processes.* 2004;67: 121–130.
  31. Hall AL. The effect of stocking density on the welfare and behaviour of broiler chickens reared commercially. *Anim Welf.* 2001;10: 23–40.
  32. Thomas DG, Son J-H, Ravindran V, Thomas DV. The Effect of Stocking Density on the Behaviour of Broiler Chickens. *Korean Journal of Poultry Science.* 2011;38: 1–4.
  33. Ventura BA, Siewerdt F, Estevez I. Access to barrier perches improves behavior repertoire in broilers. *PLoS One.* 2012;7: 1–8.
  34. Sanotra GS, Lund JD, Vestergaard KS. Influence of light-dark schedules and stocking density on behaviour, risk of leg problems and occurrence of chronic fear in broilers. *Br Poult Sci.* 2002;43: 344–354.
  35. Pichova K, Nordgreen J, Leterrier C, Kostal L, Moe RO. The effects of food-related environmental complexity on litter directed behaviour, fear and exploration of novel stimuli in young broiler chickens. *Appl Anim Behav Sci.* 2016;174: 83–89.

36. Panksepp J. *Affective Neuroscience: The Foundations of Human and Animal Emotions*. Oxford University Press, USA; 2004.
37. Bokkers EAM, Koene P. Behaviour of fast- and slow growing broilers to 12 weeks of age and the physical consequences. *Appl Anim Behav Sci*. 2003;81: 59–72.
38. Bergmann S, Schwarzer A, Wilutzky K, Louton H, Bachmeier J, Schmidt P, et al. Behavior as welfare indicator for the rearing of broilers in an enriched husbandry environment—A field study. *J Vet Behav*. 2017;19: 90–101.
39. De Jong IC, Gunnink H. Effects of a commercial broiler enrichment programme with or without natural light on behaviour and other welfare indicators. *Animal*. 2019;13: 384–391.
40. Bach MH, Tahamtani FM, Pedersen IJ, Riber AB. Effects of environmental complexity on behaviour in fast-growing broiler chickens. *Appl Anim Behav Sci*. 2019;219: 104840.
41. Vasdal G, Vas J, Newberry RC, Moe RO. Effects of environmental enrichment on activity and lameness in commercial broiler production. *J Appl Anim Welf Sci*. 2019;22: 197–205.
42. Duncan IJH, Savory CJ, Wood-Gush DGM. Observations on the reproductive behaviour of domestic fowl in the wild. *Applied Animal Ethology*. 1978;4: 29–42.
43. Newberry RC, Estevez I, Keeling LJ. Group size and perching behaviour in young domestic fowl. *Appl Anim Behav Sci*. 2001;73: 117–129.
44. Blokhuis HJ. Rest in poultry. *Appl Anim Behav Sci*. 1984;12: 289–303.
45. Olsson IA, Keeling LJ. Night-time roosting in laying hens and the effect of thwarting access to perches. *Appl Anim Behav Sci*. 2000;68: 243–256.
46. Tahamtani FM, Pedersen IJ, Toinon C, Riber AB. Effects of environmental complexity on fearfulness and learning ability in fast growing broiler chickens. *Applied Animal Behaviour Science*. 2018. pp. 49–56. doi:10.1016/j.applanim.2018.04.005
47. Vasdal G, Moe RO, De Jong IC, Granquist EG. The relationship between measures of fear of humans and lameness in broiler chicken flocks. *Animal*. 2018;12: 334–339.
48. Ohara A, Oyakawa C, Yoshihara Y, Ninomiya S, Sato S. Effect of Environmental Enrichment on the Behavior and Welfare of Japanese Broilers at a Commercial Farm. *J Poult Sci*. 2015;52: 323–330.
49. Bailie CL, Ball MEE, O'Connell NE. Influence of the provision of natural light and straw bales on activity levels and leg health in commercial broiler chickens. *Animal*. 2013;7: 618–626.
50. Kaukonen E, Norring M, Valros A. Perches & elevated platforms in commercial broiler farms: use and effect on walking ability, incidence of tibial dyschondroplasia & bone mineral content. *Animal*. 2017;11: 864–871.
51. Tahamtani FM, Pedersen IJ, Riber AB. Effects of environmental complexity on welfare indicators of fast-growing broiler chickens. *Poult Sci*. 2020;99: 21–29.
52. Thompson RKR, Foltin RW, Boylan RJ, Sweet A, Graves CA, Lowitz CE. Tonic immobility in Japanese quail can reduce the probability of sustained attack by cats. *Anim Learn Behav*. 1981;9: 145–149.
53. Sargeant AB, Eberhardt LE. Death Feigning by Ducks in Response to Predation by Red Foxes (*Vulpes fulva*). *Am Midl Nat*. 1975;94: 108–119.
54. Volchan E, Souza GG, Franklin CM, Norte CE, Rocha-Rego V, Oliveira JM, et al. Is there tonic immobility in humans? Biological evidence from victims of traumatic stress. *Biol Psychol*. 2011;88: 13–19.
55. Gentle MJ, Hill FL. Oral lesions in the chicken: behavioural responses following nociceptive stimulation. *Physiol Behav*. 1987;40: 781–783.

56. Gentle MJ. Pain issues in poultry. *Appl Anim Behav Sci.* 2011;135: 252–258.
57. Corr SA, Gentle MJ, McCorquodale CC, Bennett D. The effect of morphology on walking ability in the modern broiler: a gait analysis study. *Anim Welf.* 2003;12: 159–171.
58. Malchow J, Berk J, Puppe B, Schrader L. Perches or grids? What do rearing chickens differing in growth performance prefer for roosting? *Poult Sci.* 2019;98: 29–38.
59. Yngvesson J, Wedin M, Gunnarsson S, Jönsson L, Blokhuis H, Wallenbeck A. Let me sleep! Welfare of broilers (*Gallus gallus domesticus*) with disrupted resting behaviour. *Acta Agriculturae Scandinavica A: Animal Sciences.* 2018;67: 123–133.
60. Bailie CL, Baxter M, O'Connell NE. Exploring perch provision options for commercial broiler chickens. *Appl Anim Behav Sci.* 2018;200: 114–122.
61. Pettit-Riley R, Estevez I. Effects of density on perching behavior of broiler chickens. *Appl Anim Behav Sci.* 2001;71: 127–140.
62. Baxter M, Richmond A, Lavery U, O'Connell NE. Investigating optimal levels of platform perch provision for windowed broiler housing. *Appl Anim Behav Sci.* 2020;225: 104967.
63. Malleau AE, Duncan IJH, Widowski TM, Atkinson JL. The importance of rest in young domestic fowl. *Applied Animal Behaviour Science.* 2007. pp. 52–69. doi:10.1016/j.applanim.2006.06.017
64. Alvino GM, Archer GS, Mench JA. Behavioural time budgets of broiler chickens reared in varying light intensities. *Appl Anim Behav Sci.* 2009;118: 54–61.
65. Bailie CL, O'Connell NE. The influence of providing perches and string on activity levels, fearfulness and leg health in commercial broiler chickens. *Animal.* 2015;9: 660–668.
66. Nielsen BL. Breast blisters in groups of slow-growing broilers in relation to strain and the availability and use of perches. *Br Poult Sci.* 2004;45: 306–315.
67. van Liere DW. The Significance of Fowls' Bathing in Dust. *Anim Welf.* 1992;1: 187–202.
68. Olsson IAS, Keeling LJ. Why in earth? Dustbathing behaviour in jungle and domestic fowl reviewed from a Tinbergian and animal welfare perspective. *Appl Anim Behav Sci.* 2005;93: 259–282.
69. Martin CD, Mullens BA. Housing and dustbathing effects on northern fowl mites (*Ornithonyssus sylviarum*) and chicken body lice (*Menacanthus stramineus*) on hens. *Med Vet Entomol.* 2012;26: 323–333.
70. Zimmerman PH, Koene P, van Hooff JA. Thwarting of behaviour in different contexts and the gakeel-call in the laying hen. *Appl Anim Behav Sci.* 2000;69: 255–264.
71. Nicol CJ, Guilford T. Exploratory activity as a measure of motivation in deprived hens. *Anim Behav.* 1991;41: 333–341.
72. Vestergaard KS, Skadhauge E, Lawson LG. The stress of not being able to perform dustbathing in laying hens. *Physiol Behav.* 1997;62: 413–419.
73. Vestergaard K. The Regulation of Dustbathing and Other Behaviour Patterns in the Laying Hen: A Lorenzian Approach. In: Moss R, editor. *The Laying Hen and its Environment: A Seminar in the EEC Programme of Coordination of Research on Animal Welfare, organised by R Moss and V Fischbach, and held at Luxembourg, March 11–13, 1980.* Dordrecht: Springer Netherlands; 1980. pp. 101–120.
74. Vestergaard K. Dust-bathing in the domestic fowl - diurnal rhythm and dust deprivation. *Applied Animal Ethology.* 1982;8: 487–495.
75. Arnould C, Faure JM. Use of pen space and activity of broiler chickens reared at two different densities. *Appl*

Anim Behav Sci. 2004;87: 155–170.

76. Vestergaard KS, Sanotra GS. Relationships between leg disorders and changes in the behaviour of broiler chickens. *Vet Rec.* 1999;144: 205–210.
77. Baxter M, Bailie CL, O'Connell NE. An evaluation of potential dustbathing substrates for commercial broiler chickens. *Animal.* 2018;12: 1933–1941.
78. Shields SJ, Garner JP, Mench JA. Dustbathing by broiler chickens: A comparison of preference for four different substrates. *Appl Anim Behav Sci.* 2004;87: 69–82.
79. Baxter M, Bailie CL, O'Connell NE. Play behaviour, fear responses and activity levels in commercial broiler chickens provided with preferred environmental enrichments. *Animal.* 2018;13: 171–179.
80. Faure JM. Rearing conditions and needs for space and litter in laying hens. *Appl Anim Behav Sci.* 1991;31: 111–117.
81. Lagadic H, Faure J-M. Preferences of domestic hens for cage size and floor types as measured by operant conditioning. *Appl Anim Behav Sci.* 1987;19: 147–155.
82. de Jong IC, Wolthuis-Fillerup M, van Reenen CG. Laywel: welfare implications of changes in production systems for laying hens. Deliverable 4.3 Report on substrate needs and preferences. 2007. Available: <https://www.laywel.eu>
83. Orság J, Brouček J, Mačuhová L, Knížatová M, Flak P, Hanus A. Behaviour of hens deprived of dustbathing. 2011 [cited 24 Sep 2020]. Available: <https://www.semanticscholar.org/paper/db9b590634958c813620e411bb5e1c4f502e9d17>
84. Keeling LJ. Inter-bird distances and behavioural priorities in laying hens: the effect of spatial restriction. *Appl Anim Behav Sci.* 1994;39: 131–140.
85. Weeks CA, Nicol CJ. Behavioural needs, priorities and preferences of laying hens. *Worlds Poult Sci J.* 2006;62. Available: <http://agris.fao.org/agris-search/search.do?recordID=US201301090432>
86. Widowski TM, Duncan IJ. Working for a dustbath: are hens increasing pleasure rather than reducing suffering? *Appl Anim Behav Sci.* 2000;68: 39–53.
87. Schuck-Paim C, Alonso WJ. The Burden of Psychological Pain in Laying Hens: Behavioral Deprivation. In: Schuck-Paim C, Alonso WJ, editors. *Quantifying Pain in Laying Hens*. Independently published. <https://tinyurl.com/bookhens>; 2021.
88. Vestergaard K. Dust-bathing in the domestic fowl – diurnal rhythm and dust deprivation. *Applied Animal Ethology.* 1982. pp. 487–495. doi:10.1016/0304-3762(82)90061-x
89. Hogan JA, van Boxel F. Causal factors controlling dustbathing in Burmese red junglefowl: some results and a model. *Anim Behav.* 1993;46: 627–635.
90. Vestergaard KS, Kruijt JP, Hogan JA. Feather pecking and chronic fear in groups of red junglefowl: their relations to dustbathing, rearing environment and social status. *Anim Behav.* 1993;45: 1127–1140.