

# A risk assessment of health, production, and resource occupancy for 4 laying hen strains across the lay cycle in a commercial-style aviary system

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**ABSTRACT** Different strains of commercial laying hens have been molded by varying selection pressures, impacting their production, health, and behavior. Therefore, assumptions that all laying hen strains use the given resources within aviary systems similarly and maintain equal health and performance may be false. We investigated interactions among patterns of aviary resource use by 2 strains of white and 2 strains of brown laying hens (4 units per strain, 144 hens per unit) with daily egg production, location of egg laying, keel fractures, and footpad damage across the lay cycle. Hens' distribution among resources (litter, nest, wire floor, ledge, and perch) was recorded during light and dark periods at 28, 54, and 72 wk of age. Daily egg production and location were recorded, and 20% of hens per unit were randomly selected and assessed for keel bone damage, foot health, and plumage quality. Production and health risks associated with hens' resource use were assessed using multi-variable regression. During the day, more brown hens

occupied wire floors, while larger numbers of white hens were on perches and litter. More brown hens were on lower-tier wire floors in the dark, while more white hens occupied top tiers. Brown hens laid more eggs outside nests, showed lower incidence of keel fractures, and had better plumage quality than white hens. White hens had higher odds of keel fractures (4.2) than brown hens. Odds of keel fractures were 3.7 and 5.7 times higher at 54 and 72 wk than at 28 wk in all strains ( $P \leq 0.05$ ). Occupying the upper tier at night increased odds of keel fractures by 5.4 times. Occupying perches was associated with lower odds of foot lesions and poor plumage quality in all strains across the lay cycle ( $P \leq 0.05$ ). Finally, white hens were associated with lower odds of non-nest laying (0.76), whereas higher nest use by brown hens resulted in higher odds of non-nest egg laying (1.56) across the lay cycle ( $P \leq 0.05$ ). Distinct strain differences in resource use in an aviary were associated with different risks to hens' production, health, and welfare.

**Key words:** risk assessment, strain, laying hen, keel, egg

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## INTRODUCTION

Housing laying hens in noncage systems such as aviaries has considerably increased as the laying hen industry in North America is phasing out caged housing in an attempt to meet consumer and legislative demands for improved hen welfare. Aviary housing systems are specifically designed to allow hens to fulfill their natural behavioral needs to nest, perch, forage, explore, and

dust bathe by providing the birds with resources they have high motivation to use (as reviewed by Cooper and Albertosa [2003]). For instance, aviaries provide hens a greater opportunity to perform species-specific behaviors such as roost on elevated perches and platforms; dust bathe, scratch, and forage in a litter-covered floor area; jump and fly through vertical spaces across tiers; and lay into enclosed nests.

Providing such additional resources and spaces to fulfill these behaviors has resulted in complicated multiple, stacked aviary tiers connected through platforms and perches with feed, water, and nests distributed across that vertical space. Such complex configurations of aviary designs might impair even hen distribution throughout the available spaces, use of shared resources, and, in turn, hen health. For example, falls and collisions

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from tiers and perches in aviaries are a contributing factor to the high prevalence of keel bone fractures reported in commercial laying hens (Wilkins et al., 2011; Harlander-Matauschek et al., 2015; Stratmann et al., 2015). Moreover, flock synchrony might also impair hen distribution and use of shared resources within the complex design of aviaries (Webster and Hurnik, 1994; Duncan, 1998). Synchrony can arise from bird-based factors such as the hen's internal biological rhythm, which motivates them to perform certain behaviors at certain times of the day, such as prelay behavior and oviposition during the morning period. External factors such as social facilitation, when performance of a behavior by one hen encourages other hens to perform the same behavior, may also lead to synchrony. This flock synchrony might influence hens to use resources simultaneously, and when coupled together with the complexity of aviary designs, including distribution of resources across the multitier structure of aviaries, synchrony could potentially lead to overcrowding and subsequently aggression, frustration, and the economic concern of reduced productivity (Abrahamsson and Ragnar, 1995; Odén et al., 2002; Freire et al., 2003).

Adding to the complex aviary design and flock synchrony, interstrain variability of laying hens might also influence patterns of hen distribution and resource use in ways that subsequently impact their health and production. Several anecdotal reports from producers and scientists studying laying hen behavior suggest substantial differences exist among strains in their behavior and preferences, such as brown strains not using perches to the same degree that white strains do (Ali et al., 2016; Kozak et al., 2019). White Leghorns that were selected mainly for egg production were found to be less social and perform foraging behavior less intensively than a domesticated hen strain that was not selected for production traits (Schütz and Jensen, 2001). Klein et al. (2000) reported differences in foraging behavior between Lohmann-selected Leghorns and DeKalb chicks, while Braastad and Katle (1989) concluded that layer strains selected for high feed conversion efficiency were less active, showed less foraging behavior, and were less aggressive than birds selected for low feed conversion efficiency. Recent research that was conducted on the same flock as that of the present study reported distinct strain influences in the distribution pattern of laying hens throughout tiers (Ali et al., 2016), use of different resources during the light period (Ali et al., 2019b) and during nighttime (Ali et al., 2019a), and nest use (Villanueva et al., 2017). For instance, DeKalb White and Hy-Line W36 hens occupied litter areas in larger numbers than Hy-Line Brown and Bovans Brown hens during midday and evening, whereas more hens of both brown strains were found in nests than white hens during the morning (Ali et al., 2019b). During the night, white hens occupied the highest locations within aviaries more frequently than brown hens (Ali et al., 2019a).

Such differences in patterns of distribution and resource use by various layer strains within tiered aviaries might also influence their production and health

measures. For instance, particular strains of hens might aggregate near and inside nests in the morning to perform prelay behavior and oviposition; however, inadequate space for simultaneous access to nests by all hens may result in mislaid eggs (i.e., litter- or system-laid eggs) by individuals unable to access nests at this time (Villanueva et al., 2017). Similarly, hens preferentially roost on higher perches at night (Schrader and Müller, 2009; Brendler and Schrader, 2016; Campbell et al., 2016), simulating the roosting of ancestral jungle fowl high in trees to avoid predators (Wood-Gush and Duncan, 1976; Wood-Gush et al., 1978); thus, insufficient perching space might lead to overcrowding and occasional falls and subsequent keel bone damage (Stratmann et al., 2015). Moreover, not being able to perch might affect a hen's foot health (Hughes and Appleby, 1989; Knowles and Broom, 1990; Hughes et al., 1993) or plumage quality (Appleby and Hughes, 1995). Therefore, the main goal of this research was to investigate interactions between different patterns of resource use exhibited by different strains of laying hens (DeKalb White, Hy-Line W36, Bovans Brown, and Hy-Line Brown) when housed within the same aviary design with their production and health across the lay cycle. This study highlights the possible risks associated with housing laying hens in an aviary without considering the fit between their genetic predisposition and how resources are provided in the aviary. More frequent keel fractures were predicted to be associated with tendencies to use perches and roost in higher locations at night, and keel fractures were predicted to be more prevalent in white strains than in brown strains at 72 wk than at 28 wk. Risks of mislaying eggs were predicted to be associated with nest overcrowding and to be observed more in brown rather than in white strains.

## MATERIALS AND METHODS

### *Ethics*

All research protocols were approved by the Michigan State University Institutional Animal Care and Use Committee before the start of data collection.

### *General Description of Housing and System Management*

A total of 2,304 laying hens of 4 genetic strains ( $n = 576$  each: Hy-Line Brown [B1]; Bovans Brown [B2]; DeKalb White [W1]; and Hy-Line W36 [W2]) were used. The hens were part of a larger study, from which results have been published with regard to the distribution of the strains throughout the various tiers and substrates of the aviary, during light and dark periods at 28 wk of age (Ali et al., 2016, Ali et al., 2019a,b). The present study focused specifically on describing the possible influences of different patterns of resource use exhibited by these different strains of laying hens within multitier aviaries on their production and health measures across the entire lay cycle.

In brief, 16 aviary units (Natura 60; Big Dutchman, Holland, MI) were used to house the 4 different strains of laying hens. The 16 units were divided equally among 4 rooms, and laying hen strains were allocated so that all strains were present in each of the rooms (1 unit per strain per room  $\times$  4 strains  $\times$  4 rooms = 16 units in total). Each aviary unit consisted of a 3-tiered wire enclosure (each tier had an internal ceiling height of 61 cm for a total height of 240 cm from the floor to top of the tiered aviary structure) and a litter area with wood shavings (composed of a litter area underneath the tiered enclosure and an open litter area in front of the tiered enclosure). The floor of the top tier was 180 cm in height. Units were stocked at 144 hens per unit following United Egg Producers (2017) recommendations for cage-free egg layers. Hens were provided with a 5-cm feeder space and 88 cm<sup>2</sup> of nesting space. The nest ran the length of each unit in the upper tier, with one central partition creating 2 compartments of equal size. The colony nest was 52-cm wide, and each compartment was 122-cm long.

Each unit had 8 round metal perches extending the full length of the unit (244 cm) that allowed 89% of the hens to perch simultaneously (at 15 cm per hen). Each hen had 1,132 cm<sup>2</sup> of usable floor area consisting of 551 cm<sup>2</sup> per hen in the tiered enclosure (439 cm<sup>2</sup> on wire floors plus 112 cm<sup>2</sup> of solid metal ledge space) and 581 cm<sup>2</sup> per hen in the litter areas. Pin-metered (nipple) drinkers were provided at a rate of 1 per 9 hens. For further details on aviary design and available space per hen, see the study by Ali et al. (2016).

After the 25th week of age (when the target of  $\sim$ 90% of egg production was achieved), doors on the lower tier of the aviary enclosures opened each morning at 11:30. These doors allowed hens daily access to litter-covered floor areas after egg laying. The doors closed again at 01:00, approximately 5 h after all the lights were off. For a full description of the lighting program and other details on system management, please see the study by Ali et al. (2016).

### **Observations, Measurements, and Data Collection**

Observations were conducted over 3 consecutive days at each of the 3 periods relative to the level of production throughout the lay cycle. Peak lay observations were conducted when hens were 28 wk old (3 wk after first opening the aviary doors), whereas mid lay and end lay observations were conducted when hens were 54 and 72 wk old, respectively. These ages were selected before the start of the study, based on typical production levels for these strains. During each period, direct observations and video recording of hens' distribution across different resources within the tiers and litter areas were conducted during light and dark periods. A count of all hens in a unit took approximately 90 s during direct observations. During the light period (i.e., when the lights were on), a total of 3 observation sets per unit were conducted per day (3 sets  $\times$  3 D). Morning observations

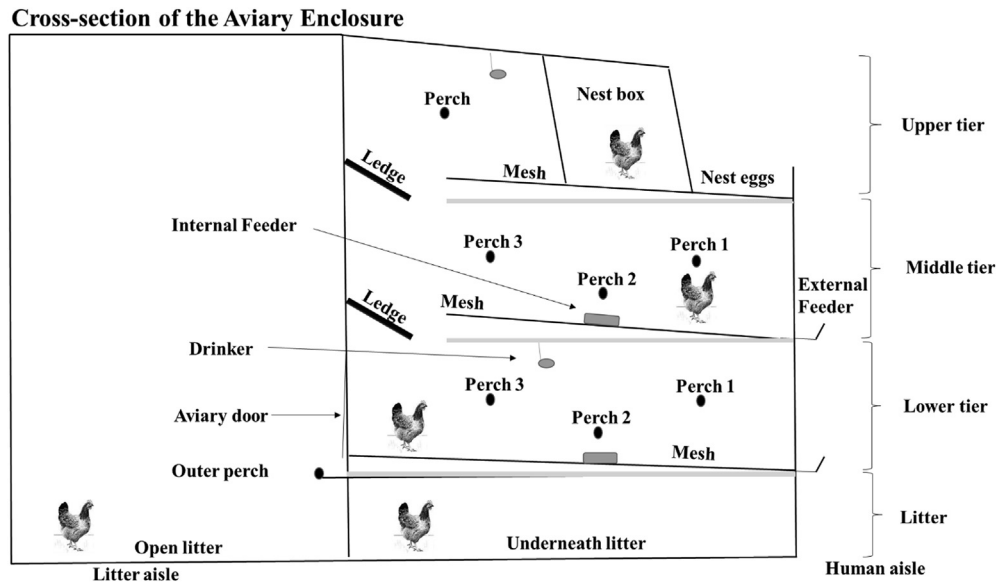
were conducted 15 min after the lights were on (morning: starting at 5:15), during the middle of the light period (midday: starting at 12:15), and 2 h before the lights were off (evening: starting at 18:00). The observations conducted during midday after the aviary doors opened at 11:30 began 30 min later than the exact midpoint of the light period to allow hens to distribute throughout the tiers and litter areas of the units.

For the dark period (i.e., when the lights were off), direct observations of hen occupancy of different tiers inside the tiered enclosures were conducted over 3 consecutive days at each of the 3 periods. Two sets of observations were performed; the first was 30 min after full darkness (dark PM: starting at 21:30), and the second observation was conducted 2 h before lights were on (dark AM: starting at 3:00). During each observation, 2 counts of hens were made for each of the 16 units, with the second count made approximately 1 h after the first count.

Across the 3 D of each period, the rooms were visited in a different randomized order. Before the start of data collection, 3 observers were trained for 3 D to establish synchrony within observer pairs and ensure a high level of interobserver reliability. All observations were performed by a pair of observers (composed of 2 of the 3 previously trained observers). One observer was located in the human access aisle, whereas the second observer observed from the litter aisle. This placed one observer on each side of the tiered enclosure to allow for simultaneous recording of the birds' distribution within a unit from both human and litter aisles (Figure 1). Counts of hens from the litter aisle were made when the observer was positioned at the end of the row or in the preceding unit to the one being observed.

During data collection, each observer counted the number of hens per location throughout the aviary unit, starting from the litter area or bottom tier, depending on whether hens had litter access, and then worked upward. During the light period, hens in the upper tier, including the perch and metal ledge, and nest were counted only by the observer in the litter aisle, as shown in Figure 1. A folding, 2-step stool was used to help the observer see into the nest. At night, when the nest was closed, the observer in the human aisle climbed on the enclosure to look down to count hens on the top tier, perch, and ledge. Feeders in the center of the 2 lowest tiers were used to divide the aviary in half to avoid double counting of hens on those levels. If the feed belt ran during data collection, observations were paused for 5 min to allow hens to settle down before attempting to count them. To mitigate effects of feeding activity on hen distribution, aviary units were observed in a random order each day, over 3 consecutive days at each age, and observed twice during each time of day. Thus, all units were equally likely to be observed during feeding, and by having multiple observations at each time of day and age, we were more likely to get a representative sample of the hens' use of each level and area of the aviary.

The observers used slow and calm movement to avoid disturbance to birds as they moved between units. At



**Figure 1.** An end view of the aviary unit showing human and litter aisles and locations of the litter area, solid metal ledges between the middle and upper tiers, wire floors, the colony nest, perches (black circles), drinkers (gray ovals), and external and internal feeders (gray boxes). Adapted from the study by Ali et al. (2016).

night, disturbance of hens was minimized by using green headlamps, which allowed observers to see hens in the darkened room without rousing them to movement (Ali et al., 2016; Campbell et al., 2016). During the observer training period, the hens also had the opportunity to acclimate to the presence of observers in the room performing the routine data collection.

Observations that were conducted while aviary doors were closed (i.e., morning and dark observations) were carried out by counting the number of birds within each location, as described previously. Observations that were conducted when aviary doors were open (midday and evening) also included data captured using a combination of video and direct observation of hens in the litter area. Ceiling-mounted high-resolution digital video cameras (VF450; Clinton Electronics, Loves Park, IL) were used to record hen distribution on the open litter area. Hens on the litter underneath the enclosure were counted by the observer in the human aisle, and their distribution was simultaneously recorded using a handheld video camera (VIXIA, HFM41; Canon, Ōita, Japan). To ensure accurate counts were made of hens underneath the enclosure (as this was difficult owing to the narrow opening available for observers to look through), live counts were later confirmed using the video footage.

Egg number and location (nest area, system, and floor) were recorded daily along with mortality on each day of behavioral observation. During each period, 20% of the hens per unit were also assessed for basic health and well-being parameters including keel fractures and deviations, footpad health, and plumage quality following a modified version of the Welfare Quality (WQ) scoring system (Welfare Quality, 2009). Welfare assessments were conducted during the dark period of the third day of each period. Hens were randomly selected from different locations (i.e., wire floors,

perches, and ledges) and different tiers of the aviary and temporarily kept in a spent hen transport cart (Alternative Design, Siloam Springs, AR). The hens were handled gently and individually scored for keel bone deformations (fractures and deviations), footpad condition, and plumage damage; the sampled hens per each unit were assessed for each measure (i.e., keel bone fractures) using a 2-point score (0 = no lesion or not affected, 1 = lesion or affected). Multiple assessors conducted the WQ evaluations. Before starting the WQ assessment in each room, 1 hen from that particular room was scored by all the assessors to ensure parity in scoring. Any disagreement among assessors was settled by discussion within the group before proceeding to data collection.

### Data Processing and Statistical Analyses

Before analysis, all hen count data obtained from direct observations and video recordings were collated and converted to the percentage of hens per tier/resource. Total daily egg production was calculated as a percentage for each unit by first dividing the total number of eggs laid in a day in that unit by the actual number of hens in that unit and multiplying by 100 (e.g., if 125 eggs were laid in a unit with 137 hens, then the daily production percentage would be 91.24%). The percentages of eggs laid each day in nests, litter, and the tiered enclosure in a unit were calculated based on the total number of eggs produced that day by hens in that unit (e.g., if 101 eggs were laid in nests of 125 total eggs, the percentage of nest-laid eggs for the unit would be 80.8%). For welfare measures, the number of affected hens across the 4 units per strain (i.e., hens with keel fracture, keel deviation, footpad injury, and damaged plumage) was transformed into percentages of affected hens of the sampled hens per each strain for each period

(e.g., if 21 hens showed keel bone fractures of the 29 hens assessed per unit, the percentage of affected hens for the unit would be 72.4%). For each of the 4 strains, there were 4 aviary unit replicates, and aviary unit was the experimental unit for all statistical tests. Each live observation set was composed of 2 counts of hen distribution within each unit for each of the 5 times of day (light period: morning, midday, and evening; dark period: dark PM and dark AM) across 3 time periods (peak lay, mid lay and end lay). There were 24 total observations for each strain during each individual time of day (e.g., for light: morning, midday, and evening); this was calculated as follows: 24 = 2 counts/unit per observation set \* 3 D of observation for each time period of data collection (peak lay, mid lay, and end lay) \* 4 units per strain.

Statistical analyses were performed using R software (version 3.3.1), package “stats” (R Core Team, 2013). Descriptive statistics were calculated using the psych package, and data are presented as mean  $\pm$  SEM;  $P \leq 0.05$  was considered significant. Generalized linear mixed models were developed with family set to “binomial” (because data were normal and met assumptions of equal variance), using the lme4 package (Bates et al., 2014), to describe the influence of laying hen strain in terms of resource use, tier occupancy within the aviaries, different times of day, different periods, and all possible interactions. Fixed effects in the models included strains of hen (B1, B2, W1, W2), times of day (morning, midday, and evening), periods (peak lay, mid lay, and end lay), and their interactions, whereas response variables included different tiers (bottom, middle, and top tier) and resources (wire floor, perch, ledge, nest, and litter).

Following the same design, generalized linear mixed models were developed to describe the influence of laying hen strains on egg production, physical measures of welfare, across different periods, and all possible interactions. Fixed effects in the models included strains of hen (B1, B2, W1, W2), periods, and their interactions, whereas response variables included egg production (eggs laid by hens [%] and location of eggs [nest, enclosure, and litter]) and health measures (keel fractures and deviation, footpad and plumage damage). Aviary unit and day of observation were included as random effects for all models, and  $P \leq 0.05$  was considered significant. Statistically significant effects were further analyzed using Tukey’s honestly significant difference multiple comparison procedure using the “multcomp” package (Hothorn et al., 2008).

To explore production and health risks associated with hens’ resource use across strains, multivariable, mixed-effects beta regression models using the “betareg” package (Hallgren et al., 2014) were deployed to analyze the data. Mixed-effects beta regression modeling fitted the bounded nature of proportions in our data set and could properly adjust to account for random factors and nonindependent observations.

Four different regression models were generated to identify possible risks in keel fractures, footpad and plumage

damage, and incidence of non-nest-laid eggs associated with hens’ strains, stage of production, distribution across tiers, and resource use within aviaries across light and dark periods. Both strains of brown hens (B1 and B2) and of white hens (W1 and W2) were typically similar to each other in their patterns of occupancy of the various substrates and tiers in the aviary enclosure, egg production and location, and prevalence of health issues. Therefore, observations of resource use, egg production, and health parameters of both brown strains B1 and B2 and both white strains W1 and W2 were combined and used for calculations of regression coefficients and odd ratios. For each model, possible predictor variables were included, and a subset of these variables was selected using backward stepwise elimination, retaining variables with  $P \leq 0.05$  only. The Akaike information criterion was used to determine the most appropriate model that completely fit our data set (i.e., backward elimination was conducted until the lowest Akaike information criterion was achieved, while  $P$ -values were  $\leq 0.05$ ). Aviary unit and day of observation were included as random effects for all the models. Finally, coefficient estimates were transformed and presented as odd ratios (OR).

Finally, following Landis and Koch (1977), interobserver reliability was calculated using Cohen’s kappa agreement coefficient (K), using the “Cohen.Kappa” function in the psych package of R. Interobserver reliability was measured when trainees were observing the same area of the same aviary simultaneously. Interobserver agreement was very high (kappa = 0.96 [ $P < 0.001$ ], CI = [0.90, 0.99]). Moreover, to examine the degree of hens’ movement from the top tier to the middle or bottom tiers between dark PM and dark AM periods, kappa coefficients of agreement ( $K$  coefficients) were calculated. For each strain at each period (peak lay, mid lay, and end lay), the difference between the 2 dark PM observations and the 2 dark AM observations for the top tier within the unit was used to calculate the  $K$  coefficient (Ali et al., 2016).

## RESULTS

### Daytime Resource Occupancy

Interactions between strain and observational period during the light periods were found for wire floor ( $Z = 9.86$ ;  $P = 0.023$ ), perch ( $Z = 6.85$ ;  $P = 0.031$ ), and litter ( $Z = 5.25$ ;  $P = 0.039$ ; Table 1) occupancy. Specifically, more brown hens (B1 and B2) than white hens (W1 and W1) were observed on the wire floors of all tier levels across different observational periods (peak lay:  $P = 0.011$ , mid lay:  $P = 0.023$ , and end lay:  $P = 0.029$ ). Contrarily, more white hens occupied perches across different observational periods (peak lay:  $P = 0.021$ , mid lay:  $P = 0.031$ , and end lay:  $P = 0.025$ ). White hens (W1 and W2) also occupied the litter area in larger numbers than brown hens (B1 and B2) during peak lay ( $P = 0.020$ ) and mid lay ( $P = 0.024$ ) periods, whereas such differences were not significant during the end lay period. Nest occupancy

**Table 1.** Distribution of hens on different resources in an aviary during the light period across different stages of the lay cycle.

Stage	Substrate	B1	B2	W1	W2
Peak lay	Wire floor	45.96 ± 8.69 <sup>a</sup>	43.64 ± 7.36 <sup>a</sup>	22.31 ± 2.23 <sup>b</sup>	26.96 ± 3.96 <sup>b</sup>
	Perch	8.84 ± 1.25 <sup>a</sup>	9.43 ± 1.02 <sup>a</sup>	18.20 ± 2.32 <sup>b</sup>	17.93 ± 2.03 <sup>b</sup>
	Ledge	3.90 ± 0.63	3.02 ± 0.36	5.51 ± 0.89	5.97 ± 0.75
	Nest	16.01 ± 1.96 <sup>a</sup>	15.54 ± 1.89 <sup>a</sup>	9.85 ± 0.96 <sup>b</sup>	10.81 ± 1.02 <sup>b</sup>
Mid lay	Litter	25.29 ± 4.35 <sup>a</sup>	28.37 ± 3.32 <sup>a</sup>	44.14 ± 7.96 <sup>b</sup>	38.33 ± 3.96 <sup>b</sup>
	Wire floor	39.33 ± 5.30 <sup>a</sup>	44.28 ± 6.89 <sup>a</sup>	18.63 ± 1.89 <sup>b</sup>	17.96 ± 1.96 <sup>b</sup>
	Perch	6.57 ± 0.85 <sup>a</sup>	5.69 ± 0.77 <sup>a</sup>	14.16 ± 2.63 <sup>b</sup>	10.99 ± 0.96 <sup>b</sup>
	Ledge	6.00 ± 0.75	6.70 ± 1.56	7.11 ± 0.99	6.93 ± 0.89
End lay	Nest	12.07 ± 3.23 <sup>a</sup>	11.38 ± 2.02 <sup>a</sup>	7.90 ± 1.10 <sup>b</sup>	8.60 ± 1.03 <sup>b</sup>
	Litter	36.03 ± 6.96 <sup>a</sup>	31.96 ± 3.63 <sup>a</sup>	52.20 ± 9.36 <sup>b</sup>	55.53 ± 9.69 <sup>b</sup>
	Wire floor	29.83 ± 2.89 <sup>a</sup>	33.20 ± 5.96 <sup>a</sup>	21.29 ± 2.63 <sup>b</sup>	15.69 ± 1.25
	Perch	5.12 ± 0.45 <sup>a</sup>	4.57 ± 0.81 <sup>a</sup>	11.35 ± 1.25 <sup>b</sup>	10.74 ± 0.98 <sup>b</sup>
	Ledge	7.35 ± 1.20	7.03 ± 0.89	8.24 ± 0.93	7.52 ± 1.03
	Nest	8.47 ± 0.85	7.52 ± 0.66	7.75 ± 0.45	7.03 ± 1.06
	Litter	49.23 ± 8.219	47.69 ± 6.96	51.36 ± 7.96	59.03 ± 9.63

<sup>a,b</sup>Different superscripts indicate differences ( $P < 0.05$ ) among different strains for that substrate.

All parameters are expressed as the mean percentage of hens ± SEM of the 4 strains (B1 = Hy-Line Brown, B2 = Bovans Brown, W1 = DeKalb White, and W2 = Hy-Line W36) occupying wire floor, perch, ledge, nest, and litter space during the light period, throughout the aviary, and across different stages of the lay cycle.

was always higher for brown hens than for white hens in the peak lay ( $P = 0.031$ ) and mid lay ( $P = 0.038$ ) periods but not in the end lay period, whereas no differences were detected in ledge occupancy by different strains across different observational periods, as shown in [Table 1](#).

### Nighttime Resource Occupancy and Movement

Generally, more brown hens (B1 and B2) occupied the wire floor ( $Z = 10.23$ ;  $P = 0.001$ ) than white hens

**Table 2.** Distribution of hens on different resources in an aviary during the dark period and across different stages of the lay cycle.

Stage	Substrate	B1	B2	W1	W2
Peak lay	Wire floor				
	Bottom tier	34.03 ± 3.63 <sup>a</sup>	33.63 ± 4.63 <sup>a</sup>	2.08 ± 0.36 <sup>b</sup>	2.78 ± 0.23 <sup>b</sup>
	Middle tier	24.31 ± 3.02 <sup>a</sup>	22.92 ± 4.32 <sup>a</sup>	8.33 ± 1.03 <sup>b</sup>	5.56 ± 0.96 <sup>b</sup>
	Top tier	12.50 ± 2.63 <sup>a</sup>	13.89 ± 1.96 <sup>a</sup>	30.56 ± 3.96 <sup>b</sup>	34.03 ± 4.23 <sup>b</sup>
	Perch				
	Bottom tier	6.94 ± 2.23	8.33 ± 1.23	5.56 ± 0.96	2.08 ± 0.23
	Middle tier	6.25 ± 1.36	5.56 ± 1.23	9.03 ± 0.96	10.42 ± 1.36
	Top tier	3.47 ± 0.96 <sup>a</sup>	4.17 ± 0.66 <sup>a</sup>	12.50 ± 1.03 <sup>b</sup>	11.81 ± 1.32 <sup>b</sup>
	Ledge				
	Middle tier	6.94 ± 1.02 <sup>a</sup>	5.55 ± 0.96 <sup>a</sup>	14.58 ± 1.36 <sup>b</sup>	15.37 ± 1.96 <sup>b</sup>
	Top tier	5.55 ± 0.85 <sup>a</sup>	6.25 ± 1.03 <sup>a</sup>	17.36 ± 2.63 <sup>b</sup>	18.07 ± 2.96 <sup>b</sup>
	Mid lay	Wire floor			
Bottom tier		29.58 ± 3.96 <sup>a</sup>	30.77 ± 3.66 <sup>a</sup>	4.22 ± 0.96 <sup>b</sup>	5.67 ± 0.96 <sup>b</sup>
Middle tier		20.42 ± 2.23 <sup>a</sup>	22.38 ± 3.36 <sup>a</sup>	11.97 ± 1.25 <sup>b</sup>	13.47 ± 1.58 <sup>b</sup>
Top tier		15.49 ± 2.36 <sup>a</sup>	14.69 ± 1.36 <sup>a</sup>	27.46 ± 3.69 <sup>b</sup>	24.82 ± 1.69 <sup>b</sup>
Perch					
Bottom tier		5.63 ± 1.36	6.29 ± 0.69	4.92 ± 0.98	4.25 ± 0.89
Middle tier		7.04 ± 0.99	5.59 ± 0.85	11.26 ± 1.25	10.63 ± 1.59
Top tier		4.23 ± 0.89 <sup>a</sup>	4.20 ± 0.52 <sup>a</sup>	11.27 ± 1.36 <sup>b</sup>	12.06 ± 1.99 <sup>b</sup>
Ledge					
Middle tier		8.45 ± 1.02 <sup>a</sup>	7.69 ± 1.36 <sup>a</sup>	13.38 ± 1.96 <sup>b</sup>	14.18 ± 2.09 <sup>b</sup>
Top tier		9.15 ± 1.63 <sup>a</sup>	8.39 ± 1.99 <sup>a</sup>	15.49 ± 2.96 <sup>b</sup>	14.89 ± 1.96 <sup>b</sup>
End lay		Wire floor			
	Bottom tier	31.38 ± 3.96 <sup>a</sup>	36.49 ± 3.96 <sup>a</sup>	7.91 ± 1.23 <sup>b</sup>	7.19 ± 0.96 <sup>b</sup>
	Middle tier	24.08 ± 2.85	21.89 ± 1.63	25.89 ± 3.96	20.14 ± 6.63
	Top tier	9.48 ± 1.36 <sup>a</sup>	8.75 ± 1.39 <sup>a</sup>	18.70 ± 2.09 <sup>b</sup>	21.58 ± 2.63 <sup>b</sup>
	Perch				
	Bottom tier	6.56 ± 0.96	7.29 ± 1.63	5.75 ± 0.99	5.03 ± 0.77
	Middle tier	8.75 ± 0.63	8.02 ± 1.36	12.94 ± 1.23	10.79 ± 1.36
	Top tier	5.10 ± 0.85 <sup>a</sup>	4.37 ± 0.23 <sup>a</sup>	10.07 ± 1.02 <sup>b</sup>	10.79 ± 1.03 <sup>b</sup>
	Ledge				
	Middle tier	10.22 ± 1.02	7.30 ± 1.36	7.19 ± 0.91	9.35 ± 0.55
	Top tier	4.38 ± 0.22 <sup>a</sup>	5.84 ± 0.37 <sup>a</sup>	11.51 ± 1.36 <sup>b</sup>	15.10 ± 1.23 <sup>b</sup>

<sup>a,b</sup>Different superscripts indicate differences ( $P < 0.05$ ) among different strains for that substrate.

All parameters are expressed as the mean percentage of hens ± SEM of the 4 strains (B1 = Hy-Line Brown, B2 = Bovans Brown, W1 = DeKalb White, and W2 = Hy-Line W36) occupying the wire floor, perch, and ledge litter space during the dark period, throughout the aviary.

**Table 3.** Amount of hen movement from the top tier in the dark period observation in different stages of the lay cycle as indicated by kappa coefficient (K).

Stage	B1	B2	W1	W2
Peak lay	0.89	0.92	0.65	0.71
Mid lay	0.84	0.79	0.56	0.52
End lay	0.69	0.72	0.39	0.45

Results are expressed as K coefficients (degree of agreement), with higher values indicating higher agreement among percentage of hens and, therefore, less movement of hens from the top tier within an aviary unit (B1 = Hy-Line Brown, B2 = Bovans Brown, W1 = DeKalb White, and W2 = Hy-Line W36).

(W1 and W2), whereas the latter occupied perches ( $Z = 8.96$ ;  $P = 0.011$ ) and ledges ( $Z = 7.52$ ;  $P = 0.019$ ) in larger numbers during the dark period across different stages of the lay cycle (Table 2). Specifically, brown hens (B1 and B2) occupied wire floors of the bottom and middle tiers in greater numbers than white hens across different stages of the lay cycle (peak lay:  $P = 0.014$ , mid lay:  $P = 0.020$ , and end lay:  $P = 0.0285$ ), whereas more white hens occupied top-tier wire floors across the lay cycle ( $Z = 12.52$ ;  $P = 0.001$ ). Similarly, white hens consistently occupied top-tier perches in larger numbers than brown hens across the lay cycle (peak lay:  $P = 0.001$ , mid lay:  $P = 0.013$ , and end lay:  $P = 0.023$ ). In addition, more white hens (W1 and W2) occupied ledges of the middle and top tier than brown hens during the peak and mid lay periods ( $P = 0.021, 0.026$ ) as well as the top tiers during the end lay period ( $P = 0.034$ ; Table 2). A considerable degree of tier-to-tier movement between dark PM and dark AM periods was recorded, with white hens consistently showing more tier-to-tier movement (lower K values) than brown hens across different stages of the lay cycle (Table 3).

### Egg Production and Location

An interaction was also observed between hen strains, egg production, and location for egg laying across different stages of the lay cycle (Table 4;  $Z = 2.52, 5.36$ ;  $P = 0.021, 0.002$ ). Both strains of brown hens laid more eggs throughout the tiered enclosure than W1 and W2 hens during the peak lay period ( $P = 0.031$ ), whereas W1 and W2 hens laid a higher percentage of their eggs inside the nests than B1 and B2 hens across the lay cycle (peak lay:  $P = 0.010$ , mid lay:  $P = 0.023$ , and end lay:  $P = 0.039$ ). B1 and B2 hens laid a higher percentage of their eggs in the litter than the W1 and W2 hens across the lay cycle (peak lay:  $P = 0.012$ , mid lay:  $P = 0.019$ , and end lay:  $P = 0.021$ ). Finally, average daily egg production differed by strains as hens of both white strains laid more eggs than the hens of both brown strains (peak lay:  $P = 0.024$ , mid lay:  $P = 0.031$ ; Table 4).

### Health Measures

An interaction was observed between hen strains and different stages of the lay cycle in the prevalence of keel

fractures ( $Z = 9.36$ ;  $P = 0.001$ ), keel deviations ( $Z = 6.36$ ;  $P = 0.025$ ), footpad quality ( $Z = 12.85$ ;  $P = 0.001$ ), and plumage damage ( $Z = 6.96$ ;  $P = 0.009$ ), as shown in Table 5. Explicitly, higher percentages of keel fractures and deviations were recorded in W1 and W2 hens than in B1 and B2 hens across the lay cycle (keel fractures: peak lay:  $P = 0.031$ , mid lay:  $P = 0.035$ , and end lay:  $P = 0.029$ ), and differences in keel deviations were significant during the mid lay period ( $P = 0.036$ ). Contrarily, B1 and B2 hens showed a higher prevalence of footpad lesions than the white strains across the lay cycle (peak lay:  $P = 0.001$ , mid lay:  $P = 0.004$ , and end lay:  $P = 0.021$ ). B1 and B2 hens also showed a higher prevalence of plumage damage than white hens particularly during the mid and end lay periods ( $P = 0.024, P = 0.009$ ), as shown in Table 5.

### Risk Assessment: Resource Occupancy, Egg Production, and Health Measures

The results of the multivariable mixed-effects beta regression models are presented in Table 6. Strains of laying hens, stages of the lay cycle, usage of different substrates (i.e., perches, litter, ledges, nests), and tiers (bottom, middle and top), during either the light or dark period, and tier-to-tier movement during the dark period were associated with the incidence of keel fracture ( $Z = 8.96$ ; CI = 0.5–2.36;  $P < 0.001$ ), footpad quality ( $Z = -8.63$ ; CI = 0.13–1.37;  $P < 0.001$ ), plumage damage ( $Z = -7.96$ ; CI = 0.03–3.42;  $P < 0.001$ ), and non-nest laying ( $Z = -6.96$ ; CI = 0.73–1.25;  $P < 0.001$ ) in aviaries.

In this aviary system and under the reported management practices, white hens (W1 and W2) had increased odds of experiencing keel fractures (OR = 4.21) compared with brown hens (B1 and B2). Hens of all 4 strains were more prone to keel fractures during the mid lay (OR = 3.69) and end lay (OR = 5.63) periods than during the peak lay period; however, hens of white strains (OR = 7.63) were more susceptible to keel fracture than hens of brown strains (OR = 4.25; Table 6) during the end lay period. Using the top tier more frequently for roosting during the dark period was associated with 5 times higher odds of experiencing a keel fracture, and roosting on the upper-tier perch specifically was associated with an increase in the odds of keel bone fractures (OR = 2.66). Moreover, roosting on ledges was associated with increasing the odds of keel fractures (OR = 2.21), particularly roosting on the top-tier ledge (OR = 3.23; Table 6). Finally, the white strains showed the highest tier-to-tier movement during the dark period, which was associated with increasing the odds (OR = 7.23) of keel fracture more than brown hens.

Generally, white hens (W1 and W2) in this system were less prone to footpad damage (OR = 0.33) than brown hens; however, hens of all 4 strains were more susceptible to footpad damage during the end lay period (OR = 3.23), but particularly brown hens (OR = 4.13; Table 6). In addition, more occupancy of litter areas

**Table 4.** Total egg production and location of eggs laid by 4 strains of laying hens in an aviary system across different stages of the lay cycle.

Stage	Strain	Eggs laid daily per hen (%) <sup>1</sup>	Location of eggs (as % of total laid) <sup>2</sup>		
			Nests	Enclosure	Litter
Peak lay	B1	90.25 ± 0.14 <sup>a</sup>	87.91 ± 0.84 <sup>a</sup>	5.13 ± 0.25 <sup>a</sup>	6.96 ± 0.18 <sup>a</sup>
	B2	90.85 ± 0.15 <sup>a</sup>	88.96 ± 0.80 <sup>a</sup>	5.16 ± 0.25 <sup>a</sup>	5.88 ± 0.21 <sup>a</sup>
	W1	92.52 ± 0.16 <sup>b</sup>	93.69 ± 0.74 <sup>b</sup>	1.85 ± 0.20 <sup>b</sup>	4.46 ± 0.16 <sup>b</sup>
	W2	92.68 ± 0.18 <sup>b</sup>	93.26 ± 0.36 <sup>b</sup>	2.16 ± 0.16 <sup>b</sup>	4.58 ± 0.14 <sup>b</sup>
Mid lay	B1	81.23 ± 0.25 <sup>a</sup>	92.85 ± 0.53 <sup>a</sup>	2.03 ± 0.86	5.12 ± 0.16 <sup>a</sup>
	B2	80.85 ± 0.19 <sup>a</sup>	93.23 ± 0.61 <sup>a</sup>	2.32 ± 0.89	4.45 ± 0.19 <sup>a</sup>
	W1	85.10 ± 0.36 <sup>b</sup>	96.69 ± 0.53 <sup>b</sup>	1.25 ± 0.56	2.06 ± 0.20 <sup>b</sup>
	W2	84.26 ± 0.42 <sup>b</sup>	95.69 ± 0.39 <sup>b</sup>	1.56 ± 0.49	2.84 ± 0.13 <sup>b</sup>
End lay	B1	69.36 ± 1.02	94.36 ± 0.68 <sup>a</sup>	1.02 ± 0.41	4.65 ± 0.11 <sup>a</sup>
	B2	70.85 ± 1.36	93.81 ± 0.75 <sup>a</sup>	1.23 ± 0.36	4.96 ± 0.13 <sup>a</sup>
	W1	74.96 ± 1.58	98.66 ± 0.68 <sup>b</sup>	0.36 ± 0.16	0.98 ± 0.16 <sup>b</sup>
	W2	75.56 ± 1.96	98.78 ± 0.56 <sup>b</sup>	0.53 ± 0.14	0.69 ± 0.15 <sup>b</sup>

All parameters are presented as means ± SEM for the aviary units of each strain (B1 = Hy-Line Brown, B2 = Bovans Brown, W1 = DeKalb White, and W2 = Hy-Line W36). Different superscripts indicate differences ( $P < 0.05$ ) among different strains for that parameter.

<sup>1</sup>Eggs laid daily are expressed as a percentage per hen calculated by using the actual number of hens in each unit.

<sup>2</sup>Location of eggs laid each day is expressed as a percentage of the total eggs laid that day (100%) in each unit.

by hens during the light periods and more hens roosting on perches during the dark period were associated with lower odds of footpad damage (OR = 0.53, 0.72). Finally, higher occupancy of the wire floor during the dark period was associated with increasing the odds of footpad damage (OR = 3.56).

Decreased odds of showing plumage damage were found for white hens (OR = 0.78), whereas hens of all 4 strains were more prone to plumage damage during the end lay period (OR = 2.69; Table 6) than during the peak lay period. During the end lay period, brown hens were more susceptible (OR = 2.72) to plumage damage than white hens. Occupying the wire floor in larger numbers (OR = 1.96), particularly during the dark period (OR = 2.58), was associated with increased odds of plumage damage. On the other hand, higher occupancy of litter areas during the light periods (OR = 0.69) and of perches for roosting at night (OR = 0.63) was more associated with reduced incidence of plumage damage.

White hens tended to lay more in the colony nests than brown hens; therefore, white hens were associated with decreased odds of non-nest laying in this system (OR = 0.76). However, during the end lay period, the odds of non-nest laying were reduced across all strains (OR = 0.45). Surprisingly, occupying nests in larger numbers during the light period was associated with higher odds of non-nest laying (OR = 1.56; Table 6), and occupying litter in larger numbers during the same period was also associated with a higher incidence of non-nest laying (OR = 1.25).

## DISCUSSION

Comparative analyses of hens' distribution across tiers and occupancy of various substrates (Tables 1–3), egg production and location (Table 4), and prevalence of keel fractures and deviations, footpad and plumage damage (Table 5) among 4 strains of laying hens in the aviary system revealed almost no differences between strains of

**Table 5.** Prevalence of keel deformation as well as footpad and plumage damage in 4 strains of laying hens and across different stages of the lay cycle.

Stage	Strain	Keel fracture	Keel deviation	Footpad damage	Plumage damage
Peak lay	B1	22.45 ± 1.02 <sup>a</sup>	4.53 ± 0.69	22.36 ± 1.23 <sup>a</sup>	7.40 ± 1.02
	B2	20.23 ± 1.32 <sup>a</sup>	7.03 ± 0.58	23.36 ± 2.36 <sup>a</sup>	9.32 ± 1.03
	W1	30.79 ± 2.23 <sup>b</sup>	7.21 ± 0.25	8.40 ± 0.98 <sup>b</sup>	10.02 ± 0.86
	W2	38.25 ± 2.75 <sup>b</sup>	7.19 ± 0.75	9.80 ± 0.86 <sup>b</sup>	12.30 ± 2.36
Mid lay	B1	43.32 ± 3.63 <sup>a</sup>	55.36 ± 3.69 <sup>a</sup>	32.60 ± 3.36 <sup>a</sup>	34.60 ± 3.63 <sup>a</sup>
	B2	39.36 ± 2.36 <sup>a</sup>	61.23 ± 2.56 <sup>a</sup>	35.36 ± 2.22 <sup>a</sup>	32.66 ± 1.36 <sup>a</sup>
	W1	62.20 ± 4.25 <sup>b</sup>	80.40 ± 5.63 <sup>b</sup>	11.80 ± 1.39 <sup>b</sup>	17.01 ± 2.36 <sup>b</sup>
	W2	59.40 ± 3.63 <sup>b</sup>	84.25 ± 7.36 <sup>b</sup>	9.60 ± 0.125 <sup>b</sup>	16.80 ± 4.63 <sup>b</sup>
End lay	B1	72.40 ± 4.69 <sup>a</sup>	65.36 ± 6.36	89.90 ± 5.63 <sup>a</sup>	90.33 ± 6.96 <sup>a</sup>
	B2	65.36 ± 6.96 <sup>a</sup>	75.20 ± 4.85	92.36 ± 6.96 <sup>a</sup>	96.63 ± 8.96 <sup>a</sup>
	W1	89.80 ± 5.45 <sup>b</sup>	60.60 ± 4.69	24.40 ± 2.36 <sup>b</sup>	20.03 ± 2.36 <sup>b</sup>
	W2	90.33 ± 4.58 <sup>b</sup>	74.20 ± 7.52	33.20 ± 4.63 <sup>b</sup>	35.16 ± 5.99 <sup>b</sup>

<sup>a,b</sup>Different superscripts indicate differences ( $P < 0.05$ ) among different strains for that parameter.

All parameters are presented as means ± SEM of percentage of hens of the 4 strains (B1 = Hy-Line Brown, B2 = Bovans Brown, W1 = DeKalb White, and W2 = Hy-Line W36) with keel deformation, footpad and plumage damage, calculated as the percentage of affected hens within a 20% randomly selected sample of hens per each aviary unit.



**Table 6.** Results of multivariable mixed-effects beta regression models used to investigate the effect of different patterns of resource use exhibited by hens of the 4 strains in a multitier aviary system on the prevalence of keel fractures, footpad and plumage damage, and incidence of non-nest laying across the peak, mid, and end lay periods.

Parameter	Odds ratio	Z (df = 48)	95% CI	P-value
<b>Keel fracture fixed effects</b>				
Intercept	1.09	8.96	0.50– 2.36	<0.001
Strain: W1–W2	4.21	3.36	2.50– 7.10	0.003
Stage: mid lay	3.69	3.36	1.37– 9.97	0.021
Stage: end lay	5.63	4.23	1.97–16.44	0.011
Strain × stage				
W1–W2 × end lay	7.63	5.63	2.37–24.53	0.001
B1–B2 × end lay	4.25	2.36	1.48–12.18	0.023
Resource × period				
Top tier × dark	5.36	3.32	1.57–18.17	0.012
Top-tier perch × dark	2.66	3.99	1.58– 4.48	0.026
Ledges × dark period	2.21	2.23	1.30– 3.74	0.031
Top-tier ledge × dark	3.23	2.85	2.84– 3.67	0.028
Resource × strain × period				
Top-tier movement × W1–W2 × dark	7.23	5.36	5.24– 9.97	0.006
<b>Foot lesions fixed effects</b>				
Intercept	0.66	–8.63	0.31– 1.37	<0.001
Strain: W1–W2	0.32	–4.36	0.05– 1.99	0.021
Stage: end lay	3.23	5.63	1.44– 7.24	0.012
Strain × stage				
B1–B2 × end lay	4.13	5.96	1.22–13.87	0.023
Resource × period				
Litter × light	0.53	–4.25	0.19– 1.43	0.016
Perch × dark	0.72	–6.96	0.22– 2.33	0.021
Wire floor × dark	3.56	4.69	0.16–78.25	0.003
<b>Plumage damage fixed effects</b>				
Intercept	0.36	–7.96	0.03– 3.42	<0.001
Strain: W1–W2	0.78	–3.36	0.42– 1.43	0.002
Stage: end lay	2.69	4.63	1.01– 7.09	0.032
Strain × stage				
Strain: B1–B2 × stage: end lay	2.72	4.52	0.68–10.59	0.036
Resource × period				
Wire floor × light	1.96	3.36	0.72– 5.1	0.003
Litter × light	0.69	–5.9	0.27– 1.75	0.002
Perch × dark	0.63	–4.63	0.19– 2.01	0.011
Wire floor × dark	2.58	4.98	0.55–14.73	0.016
<b>Non-nest–laid eggs fixed effects</b>				
Intercept	0.96	–6.96	0.73– 1.25	<0.001
Strain: W1–W2	0.76	–2.60	0.28– 1.99	0.001
Stage: end lay	0.45	–4.6	0.13– 1.47	0.021
Resource × strain × period				
Nest use × B1–B2 × light	1.56	2.96	0.47– 5.12	0.016

Abbreviations: B1, Hy-Line Brown; B2, Bovans Brown; W1, DeKalb White; W2, Hy-Line W36.

the same color across the lay cycle. The 2 white strain (W1 and W2) hens were similar to each other, except for a single case when the 2 white strains of hens differed in their use of the wire floor during the day at the end lay period (Table 1) while the 2 brown strains (B1 and B2) were similar to each other. However, differences in patterns of distribution and resource use were present between white and brown hens across the lay cycle and were associated with the variability of their health and production parameters. As all birds were raised in the same manner, difference in rearing environments is not a likely explanation for the differences observed in adult hens.

### Resource Occupancy Across the Lay Cycle

Distinct differences were detected between brown and white hens in their daytime pattern of resource occupancy during the peak lay period, and to some extent,

these were preserved across the mid and end lay periods. Specifically, more brown hens were observed on wire floors than white ones, whereas the latter occupied perches and litter areas in greater numbers across the lay cycle. Differences between brown and white strains in wire floor, litter, and perch occupancy may be attributed to some innate dissimilarities in preferences to using either graspable perches or flat surfaces during the day. Similar findings were reported by Faure and Jones (1982), with white Leghorn hens observed using perches of different types and heights more frequently than brown Leghorn hens during the day. White hens may also have used perches for undisturbed resting (Brendler and Schrader, 2016), whereas brown hens distributed themselves more evenly through the system. Hens use perches to enhance their perception of safety (Newberry et al., 2001); therefore, the lower daytime perch use exhibited by brown hens may be due to being less fearful than white hens (Fraisse and Cockrem, 2006;

De Haas et al., 2014). On the other hand, white hens occupied litter areas in greater numbers than brown hens, which seems to suggest they were not fearful of accessing the litter area. White hens may have a stronger instinct to roost or simply be more physically capable of readily accessing higher levels in the aviary. Brown birds, with a lower wing-to-body ratio, heavier body weights, and larger body sizes, may find it more difficult to move around levels in tiered aviary systems.

Brown hens may also have preferences for maintaining interbird distances appropriate for behaviors they are performing (Keeling, 1994). If brown hens were performing more dust bathing on the open litter areas, fewer hens might be expected in this area as these behaviors require more space than standing, sitting, or preening (Mench and Blatchford, 2014). A follow-up study of these hens found that brown hens of these strains maintained greater distance between themselves and conspecifics on the litter while dust bathing than the white hens, which also showed higher levels of simultaneous dust bathing activity (Grebey et al., 2020). However, the motivation behind the white and brown hens' differential occupancy of the perches and litter area is purely speculative at this point.

More brown hens were counted in nests during the light period in the peak lay period, which is consistent with findings of our previous study on the same flock at 36 wk of age (Villanueva et al., 2017). In the present study, differences in daytime nest occupancy were found to extend to mid lay when hens were 54 wk old. Such differences in nest occupancy between brown and white hens may reflect differences in their circadian drive to lay eggs in the morning (Yeates, 1963; Vestergaard, 1982; Channing et al., 2001) as it appears this drive is more robust in the brown strains we studied. Another explanation for such differences might be genotypic variation in strains' typical oviposition time (Tůmová et al., 2007; Tůmová and Gous, 2012). However, differences between brown and white hens in nest occupancy during the light period faded by the end lay period as levels of egg laying decreased, and the hens' need to use nests was subsequently reduced.

When the nighttime occupancy of different resources of these hens was examined, more white than brown hens were observed on top-tier wire floors, perches, and ledges across all periods, and more brown than white hens were observed on bottom-tier wire floors. Such differences in roosting patterns between brown and white hens were maintained across the middle and end stages of the lay cycle to a large extent. The white hens' pattern of roosting at height vs. preferring a particular type of substrate may be attributed to their tendency to prioritize roosting at height above the type of substrate on which they roost (Schrader and Müller, 2009). On the other hand, the dispersed roosting pattern across tiers exhibited by brown hens, regardless of the height of the roosting location, might be explained by a drive to maintain a greater interbird distance. Previous studies in litter-based systems found that ISA Brown hens tended to disperse across the space provided to them

(Channing et al., 2001; Odén et al., 2002), which may explain the large number of brown hens observed on wire floors and lower regions of the aviary at night in the present study. Recording hen movement across tiers through comparing hen roosting locations between dark PM and AM observations revealed a higher movement frequency from the top tier by white hens during the peak lay period, and the incidence of such movements increased during the mid and end lay periods.

The higher incidence of nighttime movement by white hens is undoubtedly related to the larger number of hens that tended to roost on top-tier resources, than brown hens that tended to disperse across tiers. Crowding of the top-tier resources by white hens during the dark period might lead hens to either voluntarily switch to another roosting location or to fall involuntarily from their original location (Ali et al., 2019a). However, further investigation is required to distinguish what causes tier-to-tier movements in the dark period.

### ***Interaction Between Resource Occupancy, Production, and Health Across the Lay Cycle***

A high prevalence of keel fractures was recorded across the 4 strains of hens in the present study, particularly toward the end of the lay cycle. Similar reports of a high prevalence of keel damage in noncage systems have been identified in several studies (Sherwin et al., 2010; Käppeli et al., 2011; Tarlton et al., 2013; Petrik et al., 2015). In the present study, a higher incidence of keel fractures was associated with hens of both white strains than with hens of the brown strains, and a possible explanation might be the white hens' pattern of resource occupancy during the dark period. Such an explanation is further supported through the interactions we identified between occupancy of specific resources and incidence of keel damage. For instance, roosting on the perch and ledge of the top tier was strongly associated with a higher incidence of keel fractures, and white hens roosted on the top tier in larger numbers than brown hens. Furthermore, top-tier movement during the dark period was strongly associated with a higher incidence of keel fractures in white hens. Thus, the higher incidence of keel fractures in white hens may be attributed to a higher likelihood of falls from higher areas in the aviary. A similar association between keel fractures and resource use was reported by Stratmann et al. (2015), who suggested that installing ramps could potentially reduce keel bone damage. Several reports have confirmed the strong association between keel damage and collisions with housing structures and the pressure load on keel bones due to prolonged perching (Scholz et al., 2008; Sandilands et al., 2009; Pickel et al., 2010; Toscano et al., 2013). It is also possible that the incidence of keel fracture associated with both white strains could be attributed to a genetic predisposition (Heerkens et al., 2016; Eusemann et al., 2018). Candelotto et al. (2017) reported a strong

propensity for genetic regulation of fracture susceptibility, with clear differences in the frequency of experimental fractures across crossbred and pure lines. They further concluded that given the control of environmental differences in their experimental design, such differences were exclusively related to a genetic predisposition.

As expected, the risk of keel fractures increased in all strains during the mid lay and end lay periods compared with the peak lay period, with a higher risk in white over brown hens. Progressive bone resorption due to high calcium demands of egg laying and subsequent osteoporosis is a rational explanation for a high prevalence of keel fractures during the later stages of the production cycle (Whitehead, 2004; Regmi et al., 2016). However, the lower body weights and subsequently lower breast muscle coverage in the white hens, along with their preference for roosting on higher locations, even during the late stage of the lay cycle, might exacerbate differences in keel bone fractures among strains. Fleming et al. (2004) also related a high prevalence of keel fractures in modern white hybrid hen strains to a low amount of breast muscle, which leaves the keel bone relatively unprotected and vulnerable to fractures. Moreover, Gregory and Devine (1999) reported an association between the emaciation and subsequent reduction in breast muscle mass that happens to laying hens later in production to a subsequent higher incidence of keel bone fractures. This association could explain the higher incidence of keel fractures in white vs. brown hens and particularly during the late stages of the lay cycle.

Variable prevalences of footpad lesions in noncage systems have repeatedly been reported from different housing designs and across different stages of production (Simonsen et al., 1980; Abrahamsson and Tauson, 1995; Gunnarsson et al., 1995). In the present study, white hens were associated with less risk of footpad lesions, which can be explained by their pattern of resource use. For instance, white hens were recorded to be more frequently occupying the litter area during the day and roosting on perches during the night. A possible explanation could be that using litter and perches is associated with relieving pressure on the footpad and reducing risk of injury as a result of being in contact with the metal surfaces of wire floors. These findings are consistent with previous reports by Weitzenbürger et al. (2006) and Abrahamsson and Tauson (1997), who concluded that prolonged standing and walking on wired floors made hens more prone to footpad lesions. Similarly, Appleby et al. (1992) reported greater footpad damage in caged hens without perches than in those with perches; the more time the hens spent perching, the less the footpad damage. By the end of the lay cycle, increased risks of footpad lesions were found for hens of all strains, which match the findings reported by Blatchford et al. (2016) and Regmi et al. (2018) of increased foot lesions in aviary-housed hens as the hens' age progressed. However, these risks increased more for brown hens, wherein their pattern of resource use (i.e., occupying wire floor in greater numbers than

perches and the litter area) might be responsible for aggravating the incidence of foot lesions during the late stages of the production cycle.

Although white hens were observed occupying perches and litter areas in greater numbers than brown hens, brown strains were more susceptible than white hens to inferior plumage quality, particularly during the end lay period. Hens on litter exhibit foraging and dust bathing, which are associated with less feather pecking (Vestergaard, 1994; Johnsen et al., 1998) and the removal of lipids and ectoparasites, resulting in healthier plumage (Van Liere, 1992; Sandilands, 2001). Similarly, higher occupancy of perches was associated with better plumage quality, which could possibly be due to the fact that perching hens soil hens on wire floors, as perches in the present study were located above the wire floors.

Overall, white hens laid more eggs in nests than brown hens across the lay cycle, while the latter tended to lay in the litter and enclosure more frequently than white hens. This is consistent with the findings of Singh et al. (2009) who reported a higher incidence of floor laying in Lohmann brown than in Lohmann white hens and findings from this same flock at 36 wk of age (Villanueva et al., 2017). As the nests in the present study were located in the top tier, it is possible that the heavier brown hens found movement upward to the nests more difficult than white hens (Moinard et al., 2004).

Given that hens typically lay most of their eggs in the morning, not having enough space for hens to nest synchronously could be expected to result in either adaptation by hens to either lay eggs in nests at other times of the day or to lay eggs in other areas of the system. Villanueva et al. (2017) reported that brown hens adapted by laying more eggs outside the nest but maintained a strong circadian rhythm of morning egg laying, whereas white hens extended their occupancy of and egg laying in nests through the early afternoon and laid a higher percentage of their eggs in nests. Use of nests by white hens could have drawn more birds to continue using nests, which is in agreement with the findings of Tahamtani et al. (2018), who described hens' preference for laying in crowded nests. The incidence of floor laying for all strains of hens decreased during the mid and end lay periods, paralleling the overall reduction in egg production approaching the end lay period.

## CONCLUSION

Distinct differences in terms of distribution and resource occupancy between brown and white hen strains within aviaries were associated with different risks to hens' production and health. White hens' tendency to occupy perches and litter during the day, roost on the top tier at night, and exhibit more movement during the night put them at more risk of keel damage but less risk of footpad lesions and plumage damage than brown hens. On the other hand, more hens of brown strains occupied wire floors, which was associated with a higher incidence of footpad lesions and lower plumage

quality but less keel damage. Such knowledge is helpful for determining how to account for variability between strains and highlights the possible consequences of mismatching between a particular strain's needs and how resources are provided within a given aviary style. Although our specific conclusions can only be applied to the 4 strains and aviary style examined in the present study, our findings coupled with those of others suggest that white hens need more space for roosting at height in aviaries or simultaneous access to litter, whereas brown hens may need larger nest space allowances or nests provided at lower levels in aviaries. Calculations to estimate space needs of brown hens may also need to factor in preferences for distribution or more interbird space. Mismatches between aviary design and hen requirements could have consequences that are a threat to the welfare and productivity of laying hens in aviaries and counteract the intended benefits of transitioning hens to cage-free housing.

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