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Abstract

Provision of perches in enriched colony or cage-free hen housing facilitates birds' ability to express natural behaviors, thus enhancing animal welfare. Although considerable research has been conducted on poultry perches, further investigation is needed of perching behavior and preference of laying hens to perch exposure and perch types. This study aimed to assess preference of young laying hens for round vs. hexagon perches and to characterize temporal perching behaviors of the young hens brought to an enriched colony setting from a cage pullet-rearing environment. A total of 42 Lohmann white hens in six equal groups, 17 weeks of age at the onset of the experiment, were used in the study. Each group of hens was housed in a wire-mesh floor pen equipped with two 120 cm long perches (one round perch at 3.2 cm dia. and one hexagon perch at 3.1 cm circumscribed dia., placed 40 cm apart and 30 cm above the floor). Each group was monitored continuously for 9 weeks. Perching behaviors during the monitoring period, including perching time, perch visit, and perching bird number, were recorded and analyzed daily using an automated perching monitoring system. Results revealed that the laying hens showed no preference between the round and hexagon perches ($P = 0.59-0.98$). Young laying hens without prior perching experience showed increasing use of perches over time ($P < 0.01$). It took up to five to seven weeks of perch exposure for young hens to show consistent perching behaviors in the enriched colony setting. This study also found that laying hens spent about 10% of daytime on the perches and over 75% of hens perched at night after approaching consistent perching behaviors. In general, the results supplemented to the existing knowledge base for the quantitative behavior study on laying hens' temporal perch use.

Keywords

Perch utilization, Perch preference, Alternative housing, Behavior and welfare, Automated monitoring

Disciplines

Agriculture | Bioresource and Agricultural Engineering | Poultry or Avian Science

Comments

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1 Perch-Shape Preference and Perching Behaviors of Young Laying Hens

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9 Abstract

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11 natural behaviors, thus enhancing animal welfare. Although considerable research has been conducted on
12 poultry perches, further investigation is needed of perching behavior and preference of laying hens to
13 perch exposure and perch types. This study aimed to assess preference of young laying hens for round vs.
14 hexagon perches and to characterize temporal perching behaviors of the young hens brought to an
15 enriched colony setting from a cage pullet-rearing environment. A total of 42 Lohmann white hens in six
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28 **Keywords:** Perch utilization, Perch preference, Alternative housing, Behavior and welfare, Automated
29 monitoring.

30 **1. Introduction**

31 Laying hens are highly motivated to perch, thus provision of perches in hen housing can accommodate
32 hen's natural behavior needs, enhancing animal welfare (Olsson and Keeling, 2002; Cooper and
33 Albentosa, 2003; Weeks and Nicol, 2006). To improve laying hen welfare, the EU Directive banned
34 conventional cages from 2012 and set forth the minimum standards that perches must have no sharp edges
35 and perch space must be at least 15 cm per hen in alternative hen housing systems (Council Directive
36 1999/74/EC, 1999). Because of the EU's ban on conventional cages, enriched colony housing (**ECH**)
37 became a popular alternative hen housing system. In 2014, 58% of the laying hens in the EU were housed
38 in ECH systems (Windhorst, Personal Communication). Although laying hens are mostly housed in
39 conventional cages in the United States (approximately 85%) and many other major egg-producing
40 countries (e.g., China, Mexico, Japan, Indian, Brazil), ECH systems have been adopted by some egg
41 producers in these countries. In the ECH systems, the perch is one of the most essential enrichments for
42 the hens.

43 Many studies have investigated the effects of perch provision on production performance, health, and
44 well-being of laying hens over the past four decades (Struelens and Tuytens, 2009; Hester, 2014).
45 Benefits of providing perches to laying hens include stimulating leg muscle development and bone
46 mineral deposition (Enneking et al., 2012; Hester et al., 2013a), increasing volume and strength of certain
47 bones (Hughes et al., 1993; Appleby and Hughes, 1990; Barnett et al., 2009), reducing abdominal fat
48 deposition (Jiang et al., 2014), and reducing fearfulness and aggression (Donaldson and O'Connell,
49 2012). On the contrary, detrimental effects associated with perches include keel bone deformities, foot
50 disorders, and bone fractures (Appleby et al., 1993; Tauson and Abrahamsson, 1994; Donaldson et al.,
51 2012). Studies have also shown inconsistent results related to the impact of perches on feather condition
52 or mortality of laying hens. For example, Duncan et al. (1992), Glatz and Barnett (1996), and Wechsler

53 and Huber-Eicher (1998) reported beneficial impacts, whereas Tauson (1984), Moinard et al. (1998), and
54 Hester et al. (2013b) reported detrimental impacts. These inconsistent results, to a large extent, could be
55 attributed to differences in perch design, spatial arrangement of perches, or timing of birds' introduction
56 to perches in the studies (Struelens and Tuytens, 2009; Hester, 2014).

57 The EU Directive has required that perches must have no sharp edges (Council Directive 1999/74/EC,
58 1999). Pickel et al. (2011) found that peak force on the footpads of hens was greater when standing on the
59 perches with sharp edges (square perch) as compared to round perches. This finding provided certain
60 scientific evidence for the requirement of no sharp edges because the extra force on the footpads may lead
61 to severe foot disorders such as bumble foot and toe pad hyperkeratosis. Consequently, round perches are
62 most commonly used in alternative housing systems. However, the peak force on the keel bone of hens
63 was much greater when resting on round *vs.* square perches (Pickel et al., 2011), which could contribute
64 to development of more keel bone deformity. It should be noted that the pressure peaks on the keel bone
65 were approximately 5 times higher compared with the pressure peaks on a single footpad (Pickel et al.,
66 2011). In addition, round perches might be less adequate in terms of providing the stability necessary to
67 accommodate the hen's landing or long-term roosting. For instance, Duncan et al. (1992) found that hens'
68 feet slipped back and forth on round perches but not on square perches. Therefore, a hexagon perch,
69 combining the shape features and advantages of both square and round perches, might prove to be more
70 attractive to hens because of its potential to improve hens' ability to grasp the perch and reduce the
71 chance of peak pressure on the keel bone and footpads. A review of literature did not reveal research
72 information regarding hen's comparative use of round *vs.* hexagon perches.

73 Some studies showed that early access to perches had positive effects on musculoskeletal health of pullets
74 as well as subsequent long-term health of hens (Hester et al., 2013a; Yan et al., 2014; Habinski et al.,
75 2016). Similarly, research found that rearing pullets without early access to perches could impair the
76 spatial cognitive skills of hens (Gunnarsson et al., 2000), thus may be detrimental to their subsequent
77 perching ability and long-term welfare. However, raising pullets in conventional cages without perches is
78 the most typical management practice in current commercial ECH systems. Thus there is still a need to

79 further investigate and characterize perching behaviors of young laying hens (without perch exposure)
80 introduced to ECH systems.
81 The objectives of this study were a) to assess hens' preference for perch shape between round and
82 hexagon perches, and b) to quantify and characterize temporal perching behaviors of young laying hens
83 after transfer from pullet-rearing cages into an enriched colony setting. The results contribute to scientific
84 information on laying hen perch design and responses of novice birds to perch introduction.

85 **2. Materials and Methods**

86 The study was conducted in an environment-controlled animal research laboratory located at Iowa State
87 University, Ames, Iowa, USA. Before the onset of the experiment, the experimental protocol was
88 approved by the Iowa State University Institutional Animal Care and Use Committee (Log # 5-12-7364-
89 G).

90 **2.1. Experimental Birds and Management**

91 A total of 42 Lohmann white laying hens in two successive batches (21 hens per batch) were used in the
92 study. The birds were reared in a commercial pullet-rearing cage house (six pullets per cage) until the
93 commencement of the experiment when they were at 17 weeks of age (**WOA**). All the birds had similar
94 physical conditions, including body weight (1200 - 1250 g), feather coverage (no damage/loss), feet and
95 keel bone conditions (no abnormal sign), and no prior perching experience at the onset of the experiment.
96 For each batch, the birds were randomly assigned to three groups, with seven birds per group.
97 Three identical enriched experimental pens (P1, P2, and P3) were used in the study. These experimental
98 pens (Fig. 1), each measuring $120 \times 120 \times 120$ cm (L×W×H), had a wire-mesh floor (2.5×2.5 cm wire-
99 mesh, 2057 cm²/bird space allowance), a $120 \times 30 \times 40$ cm elevated nest box (45 cm above floor, 514
100 cm²/bird), two $60 \times 15 \times 10$ cm rectangular feeders (installed outside of the left and right sidewalls), two
101 nipple drinkers (on the rear wall at 40 cm above floor), and two parallel 120 cm long metal perches (a 3.2
102 cm dia. round perch and a 3.1 cm circumscribed circle dia. hexagon perch, each giving a minimum of 17
103 cm perch space per bird). Both perches were installed on adjustable brackets, 30 cm above the floor and

104 40 cm away from each respective sidewall, with a horizontal space of 40 cm between the two perches.
105 The adjustable brackets allowed for quick relocation and placement of perches. The hexagon perches
106 were oriented to present a flat surface on the top (Fig. 2a). All resource allowances, including perch, floor,
107 feeder, nest, and nipple drinkers met or exceeded those in the legislation or recommendations for the
108 hens. The experimental room was equipped with mechanical ventilation and heating/cooling to maintain
109 the desired temperature of 21°C and relative humidity of 40-60% throughout the experiment.
110 The lighting scheme applied in the study followed the commercial management guidelines (Table 1),
111 including light, dim (dawn and dusk), and dark periods. Artificial light was the only light source
112 throughout the experiment, and light was provided with compact fluorescent lamps for the daytime (20
113 lux) and light-emitting diode lights for the dim period (1-2 lux). Light intensity was measured and
114 adjusted using a light meter (Model EA31, FLIR Systems Inc., Wilsonville, OR, USA¹), and lighting was
115 maintained at comparable levels at the same spot of the respective perch.
116 All birds underwent a 9-week test period (17-25 WOA). During this test period, the round and hexagon
117 perches were continuously provided, and the birds had free access to both. The locations of the two
118 perches were swapped once a week (at the end of each week) to avoid potential location effects (Table 2).
119 The nest box door was blocked to restrict hen access during the dark period, i.e., the door was closed and
120 reopened an hour before the onset of dusk and dawn periods, respectively. Feed (commercial corn and soy
121 diets) and water were available *ad-libitum* for the hens throughout the test. Feeders were replenished and
122 eggs were collected once a day at 17:00 h. The experimental pens were cleaned each week right after
123 relocation of the perches. Wood shavings were placed under the wire-mesh floor to absorb the manure
124 moisture and for easier cleaning.

125

126

¹ Mention of product or company name is for presentation clarity and does not imply endorsement by the authors or Iowa State University, nor exclusion of other suitable products.

127 **2.2. Automated Perching Monitoring System**

128 A real-time, sensor-based perching monitoring system was built by incorporating six pairs of load-cell
129 sensors (Model 642C, Revere Transducers Inc., Tustin, CA, USA) supporting six metal perches (two
130 perches per pen, Fig. 2a), coupled with a LabVIEW-based data acquisition system (version 7.1, National
131 Instrument Corporation, Austin, TX, USA). This monitoring system consisted of a compact FieldPoint
132 controller (NI cFP-2020, National Instrument Corporation) and two 8-channel thermocouple input
133 modules (NI cFP-TC-120, National Instrument Corporation), collecting data at 1 Hz sampling rate. Each
134 pair of load-cell sensors was fitted with the adjustable brackets and coupled to a metal perch, forming the
135 weighing perch (Fig. 2a). For each weighing perch, an equation was developed by establishing
136 relationship between a series of standard load weights (i.e., 0, 1500, 3000, 4500, 6000, and 9000 g) and
137 the corresponding analog voltage outputs (Fig. 2b). The data acquisition system automatically read analog
138 voltage outputs of the weighing perches and converted the electronic signals to load weight using the pre-
139 defined equations, thereby providing real-time measurement of load weight on the perches (Fig. 2c). The
140 load weight of perching birds on each perch was then converted to the number of perching birds on the
141 corresponding perch (Fig. 2d) by using a series of determined weight thresholds (Table 3). This
142 monitoring system was validated by comparing results with human observations and had been applied in
143 a previously published perch study (Liu and Xin, 2017). Using this system, perching behaviors of the
144 birds were continuously monitored throughout the test period, covering the first day to nine weeks of
145 perch exposure (**WPE**).

146 **2.3. Characterization of Temporal Perching Behaviors**

147 With the knowledge of the time-series (one sample per second) numbers of perching birds on each perch,
148 perching behaviors of birds were quantified daily using an automated VBA program in Excel (Microsoft
149 Office 2016, Redmond, WA, USA). Three primary perching behavior responses were determined,
150 including a) perching time (**PT**) – time spent perching, min/bird; b) perch visit (**PV**) – number of jumps
151 onto and off perch, number/bird; and c) perching birds number (**PBN**) – number of simultaneously

152 perching birds. From these three primary responses, three types of derived behavior parameters were
153 obtained, including 1) perching time ratio (**PTR**) – proportion of perching time for a given period (i.e.,
154 light, dim, dark period, or entire day), %; 2) perching frequency (**PF**) – perch visit per hour for a given
155 period (i.e., light, dim, dark period, or entire day), times/bird-h; and 3) perching bird proportion (**PBP**) –
156 proportion of simultaneously perching birds relative to the group total during the dark period, %. In this
157 study, birds were not individually identified; thus all behavior variables were presented as group averages.

158 **2.4. Statistical Analysis**

159 All statistical analyses of the perching behavior variables were performed using SAS Studio 3.5 (SAS
160 Institute, Inc., Cary, NC, USA). The group of hens was considered experimental unit, leading to six
161 replicates in the study. Proportion values of daily PT, daily PV, and dark-period PBN for the respective
162 perch were first analyzed to assess preference between round and hexagon perches. Then data of all the
163 behavior variables for both perch types were pooled to characterize temporal perching behaviors of the
164 young hens. All analyses were implemented with generalized linear mixed models using GLIMMIX
165 procedure. A Gaussian distribution was specified for the analyses of PF, whereas a beta distribution was
166 specified for all the proportion data. Evaluation of the perch preference was accomplished by testing the
167 null hypothesis that the proportion of daily PT, daily PV, or dark-period PBN on respective perch equaled
168 0.5. Data at 1 WPE were excluded from the analysis of perch preference due to the infrequent perch use
169 (acclimatization). In addition, Tukey-Kramer tests were used for pairwise comparisons among different
170 WPEs for all the behavior variables. Effects were considered significant at $P < 0.05$. Normality and
171 homogeneity of variance of data were examined by residual diagnostics. Unless otherwise specified, data
172 are presented as least squares means along with the standard error of the mean (**SE**).

173 **3. Results**

174 **3.1. Preference of Laying Hens between Round and Hexagon Perches**

175 The laying hens showed no preference for round vs. hexagon perches based on daily perching time (PT),
176 daily perch visit (PV), and dark-period perching bird number (PBN). Specifically, the hens showed a

177 daily PT of $50.1 \pm 4.3\%$ for the round perch and $49.9 \pm 4.3\%$ for the hexagon perch ($P = 0.98$), daily PV
178 of $49.7 \pm 1.0\%$ (round) and $50.3 \pm 1.0\%$ (hexagon) ($P = 0.74$), and dark-period PBN of $47.7 \pm 4.1\%$
179 (round) and $52.3 \pm 4.1\%$ (hexagon) ($P = 0.59$). Because the birds showed no preference for perch shape,
180 the response variables were pooled in the presentation and analysis of diurnal and temporal perching
181 behaviors in the following sections.

182 **3.2. Diurnal and Temporal Perching Behavior of Laying Hens**

183 3.2.1. Diurnal Perching Pattern

184 A representative diurnal perching pattern of laying hens at 9 WPE (25 WOA) is illustrated in Figure 3.
185 Six out of the seven hens perched simultaneously during the dark period, with all perching hens
186 continuously roosting on perches throughout the dark period (23:15 h - 6:45 h, Fig. 3a). In contrast, only
187 one, two, or three hens (occasionally, four or five hens) perched simultaneously during the light period,
188 with hens jumping on and off the perches frequently throughout the light period (7:00 h - 23:00 h, Fig.
189 3a). During the transition of light to dark period (started at 23:00 h until total dark at 23:15 h), hens
190 jumped on and off the perches frequently (Fig. 3b). Immediately following lights off, hens' activity
191 ceased. During the transition of dark to light period (started at 6:45 h until full light at 7:00 h), hens got
192 off the perches in the early part (first 2-3 min) (Fig. 3c).

193 3.2.2. Temporal Perching Time Ratio and Perch Frequency

194 Perching time ratio (PTR) and Perching frequency (PF) of laying hens at 1-9 WPE for each period are
195 shown in Table 4. PTR for all the periods increased over time during the 9-week period of perch exposure
196 ($P < 0.01$). PF for all the periods also increased over time ($P < 0.01$), with the exception that the PF during
197 the dark period was consistently low ($P = 0.75$). In general, it took about 6-7 WPE for the young hens to
198 show consistent perching behaviors (i.e., no significant difference in perching behavior from any of the
199 following WPEs). Specifically, PTR for the dark period approached stabilization at 6 WPE ($P = 0.74$ -
200 1.00), and PTR for the light period approached stabilization at 7 WPE ($P = 0.53$ -1.00), whereas the rest
201 variables approached stabilization at 2-3 WPE.

202 3.2.3. Temporal Proportion of Hens Perching during the Dark Period
203 Perching bird proportion (PBP) of laying hens during the dark period at 1-9 WPE is shown in Figure 4.
204 Dark-period PBP increased over time during the 9-week period of perch exposure ($P < 0.01$).
205 Specifically, from 1 to 9 WPE, dark-period PBP averaged $34.8 \pm 7.4\%$, $49.7 \pm 4.8\%$, $58.2 \pm 4.7\%$, $67.4 \pm$
206 2.3% , $69.9 \pm 1.9\%$, $73.3 \pm 1.5\%$, $75.6 \pm 1.5\%$, $76.0 \pm 1.6\%$, and $78.7 \pm 1.9\%$, respectively. Dark-period
207 PBP approached stabilization at 5 WPE ($P = 0.06-0.89$).

208 **4. Discussion**

209 According to our literature review, this study is the first effort to assess preference between round and
210 hexagon perches and to continuously monitor and characterize temporal perching behaviors of young
211 laying hens (17-25 WOA) after transfer to enriched colony housing from a cage-rearing pullet house (no
212 perches). By taking advantage of the automated sensor-based perching monitoring system, perch
213 utilization by the hens was continuously recorded at 1-9 WPE. The young hens without prior perching
214 experience were found to use the perches increasingly with WPE. It took them up to 5-7 weeks to get
215 used to or maximize the use of the perches. These hens did not show preference between the round perch
216 and the hexagon perch.

217 **4.1. Perch-Shape Preference of Laying Hens**

218 Limited published studies existed regarding perching behavior and preference of laying hens subjected to
219 different shapes of perches (Struelens and Tuytens, 2009); and no information was found about
220 behavioral responses of hens to hexagon perch in the literature. In the current study, laying hens showed
221 no preference between the round and hexagon perches with regards to perching time, perch visit, and the
222 number of perching birds on the respective perch. This outcome coincides with the finding of an earlier
223 study by Lambe and Scott (1998) who reported that hens showed no difference in time spent on round *vs.*
224 rectangular perches or single *vs.* double wooden perches. Likewise, an earlier study found that hens
225 showed no perch size preference (1.5, 3.0, 4.5, 6.0, 7.5, 9.0, or 10.5 cm perch width) as judged by the
226 perch use at night (Struelens et al., 2009). In contrast, several earlier studies found certain perch features

227 being preferred by laying hens. For instance, Struelens et al. (2008) found hens like to roost on high
228 perches at night when given the opportunity to do so. Appleby et al. (1992) found that a perch with a
229 slightly rough surface was preferred by hens. Studies have found detrimental impacts of using perches,
230 including keel bone deformities, foot disorders and bone fractures (Appleby et al., 1993; Tauson and
231 Abrahamsson, 1994; Donaldson et al., 2012). To overcome these detriments, Scholz et al. (2014) and
232 Stratmann et al. (2015) investigated soft-surface perches that were shown to provide the most stable
233 footing on perching and reduce the risk of perch-related keel bone injury. The benefit of the soft-surface
234 perches arose from the compressible materials absorbing kinetic energy during collisions and increasing
235 the spread of pressure on the keel bone during perching. Future research may focus on improving the
236 perch surface materials as opposed to perch shape.

237 **4.2. Diurnal and Temporal Perching Behavior of Laying Hens**

238 The diurnal perching patterns of laying hens observed in the current study agreed well with observations
239 in earlier studies. The times when birds went up to perches in the evening and came down from perches in
240 the morning were associated with the changes in light intensity (Yeates, 1963; Lambe and Scott, 1998;
241 Olsson and Keeling, 2000; Struelens et al., 2008). These cited studies found that much more movement of
242 the hens on and off perches during the light period as compared to the dark period and hens frequently
243 became very active, jumping on and off perches as dark period approached. In addition, more than 90% of
244 the hens were on perch within 10 min. In comparison, little information was reported regarding when and
245 how birds got off the perch upon lights-on in the morning. In the current study, the majority of the hens
246 were observed to get off the perches at the beginning of the dawn-transition period, which could be
247 attributed to the intrinsic motivation of feeding and drinking of the birds after a relatively long period of
248 resting/sleeping in the dark period.

249 Laying hens are highly motivated to perch at night (Weeks and Nicol, 2006). Studies have shown that
250 perching-experienced birds in cages/pens roosted on perches to a very high degree (80-100%) after dark
251 when perch space was sufficient (Tauson, 1984; Appleby et al., 1993; Tauson and Abrahamsson, 1994;

252 Wall and Tauson, 2007; Pickel et al., 2010). In the current study, on average 78.7% of the hens perched
253 during the dark period at 9 WPE, which was consistent with the findings from the cited studies. Although
254 the novice young hens (without prior perching experience) increased perching at night in the current
255 study, some birds always remained on the floor during the dark period. This result paralleled the findings
256 of several earlier studies. A large variation in time spent perching among individual birds at night (dark
257 period) has been reported (Lambe and Scott, 1998) and some individual birds did not use the perches at
258 all (Appleby and Hughes, 1990; Appleby et al., 1992; Lambe and Scott, 1998). Moreover, Appleby et al.
259 (1992) found that the birds roosted on the floor tended to be the same individuals. The perch monitoring
260 system utilized in the current study was not designed or intended to determine or discern perching
261 behavior of individual birds. The birds roosting on the floor at night in the current study and the cited
262 studies might have been attributed to the dominance hierarchy among group-housed hens. Dominance
263 hierarchy influences spatial distribution of birds on perches (Lill, 1968), and the subdominant birds may
264 not be allowed to use perch at night. Floor-roosting may also be associated with the antipredator behavior
265 of chickens (Hu et al., 2016). Hu et al. (2016) found that the degree of vigilance behavior of hens has
266 decreased during domestication, which might have contributed to the reduced proportion of hens perching
267 at night. However, this is not always the case. Laying hens in commercial aviary were found to prefer
268 roosting in the highest enclosure levels, leading to crowing on upper perches and ledges while perch space
269 remained available on lower levels (Brendler and Schrader, 2016; Campbell et al., 2016).

270 Perch utilization during the light period observed in this study (10% of the light period at 9 WPE) was
271 much lower than that reported in earlier studies (ranging between 25-50%). Tauson (1984) reported hens
272 perching 25-50% of the daytime, while others reported hens spending about 25% of the daytime on
273 perches (Appleby et al., 1992; Valkonen et al., 2009). Yet, some studies reported that hens spent about
274 32-38% of the daytime on perches (Newberry et al., 2001; Barnett et al., 2009). More studies reported that
275 hens spent about 47-51% of the daytime on perches (Appleby & Hughes, 1990; Struelens et al., 2009).

276 For all these cited studies, the results were derived from manual observations, i.e., live observation or off-
277 site observation of recorded videos, which covered limited parts of the light period (daytime) at certain

278 ages (e.g., a couple of hours a day at each age). As a result, these results might not be inclusive enough to
279 represent the actual daily usage, especially considering variations observed in perching behavior through
280 the light period. When comparing the results in the current study with our earlier study that investigated
281 perching behavior of hens as affected by horizontal space between parallel perches using the same
282 automated perching monitoring system (Liu and Xin, 2017), hens in the current study spent much lower
283 proportion of the daytime on perches (i.e., 10% vs. 21%) but had much higher perching frequency (8.0 vs.
284 1.9 times/bird-h). It should be noted that there were three distinct differences between the earlier study
285 and the current study that may have influenced the perch utilization. First, hens in the earlier study were
286 chosen from a commercial aviary house and were experienced in using perches, whereas pullets used in
287 the current study came from pullet-rearing cages and had no prior perching experience. Second, birds in
288 the earlier study were older (68 WOA), whereas birds in the current study were much younger (17-25
289 WOA) that were presumably more energetic. Third, stocking density was higher in the earlier study than
290 in the current study (11 hens/m² vs. 5 hens/m²).

291 In terms of the temporal perching behavior, the results of the current study agreed well with the findings
292 of earlier studies. In general, perch use increased significantly with WPE within the first 1-2 weeks after
293 the birds were introduced to perches. Hens tended to use the perch consistently throughout the subsequent
294 WPE. Newberry et al. (2001) found that daytime perch utilization varied with bird age, with the total
295 proportion of birds perching increasing from 27.5% in the youngest birds (3-6 WOA) to 47.4% when the
296 birds were at 12-15 WOA. Faure and Jones (1982a) found that White Leghorn birds without perching
297 experience took two days to get used to using perch when the perch was first introduced at 17 WOA. In
298 addition, Duncan et al. (1992) found that overall time spent in daytime perching was relatively consistent
299 over the laying cycle. In contrast, Faure and Jones (1982b) found when providing perches to 15-week old
300 pullets, repeated perch exposure increased the time spent on perches in daytime by the perching birds but
301 did not affect the non-perching birds. However, individual variance of perch use was not determined in
302 the current study. Therefore, we were unable to tell perching or lack thereof by individual birds nor could
303 we determine perching variance among the individual birds.

304 **5. Conclusion**

305 This study revealed that Lohmann white laying hens showed no preference between the round and
306 hexagon perches during a 9-week perch exposure after transfer into an enriched colony setting. Young
307 laying hens without prior perching experience showed increasing use of perches over time and it took
308 them up to five to seven weeks of perch exposure to show consistent perching behaviors in the enriched
309 colony setting. This study also found that laying hens spent about 10% of daytime on the perches and
310 over 75% of hens perched at night after they approached consistent perching behaviors.

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319 **References**

- 320 Appleby, M.C., 1995. Perch length in cages for medium hybrid laying hens. *Br. Poult. Sci.* 36, 23–31.
321 doi:10.1080/00071669508417749
- 322 Appleby, M.C., Hughes, B.O., 1990. Cages modified with perches and nests for the improvement of bird
323 welfare. *Worlds. Poult. Sci. J.* 46, 38–40. doi:10.1079/WPS19900007
- 324 Appleby, M.C., Smith, S.F., Hughes, B.O., 1993. Nesting, dust bathing and perching by laying hens in
325 cages: Effects of design on behaviour and welfare. *Br. Poult. Sci.* 34, 835–847.
326 doi:10.1080/00071669308417644
- 327 Appleby, M.C., Smith, S.F., Hughes, B.O., 1992. Individual perching behaviour of laying hens and its
328 effects in cages. *Br. Poult. Sci.* 33, 227–238. doi:10.1080/00071669208417462

329 Barnett, J.L., Tauson, R., Downing, J. a, Janardhana, V., Lowenthal, J.W., Butler, K.L., Cronin, G.M.,
330 2009. The effects of a perch, dust bath, and nest box, either alone or in combination as used in
331 furnished cages, on the welfare of laying hens. *Poult. Sci.* 88, 456–470. doi:10.3382/ps.2008-00168
332 Brendler, C., Schrader, L., 2016. Perch use by laying hens in aviary systems. *Appl. Anim. Behav. Sci.*
333 182, 9–14. doi:10.1016/j.applanim.2016.06.002
334 Campbell, D.L.M., Makagon, M.M., Swanson, J.C., Siegford, J.M., 2016. Perch use by laying hens in a
335 commercial aviary. *Poult. Sci.* 95, 1736–1742. doi:10.3382/ps/pew111
336 Cooper, J.J., Albentosa, M.J., 2003. Behavioural priorities of laying hens. *Avian Poult. Biol. Rev.* 14,
337 127–149. doi:10.3184/147020603783637508
338 Council Directive 1999/74/EC, 1999. Laying down minimum standards for the protection of laying hens.
339 *Off. J. Eur. communities* 53–57.
340 Donaldson, C.J., Ball, M.E.E., O’Connell, N.E., 2012. Aerial perches and free-range laying hens: The
341 effect of access to aerial perches and of individual bird parameters on keel bone injuries in
342 commercial free-range laying hens. *Poult. Sci.* 91, 304–315. doi:10.3382/ps.2011-01774
343 Donaldson, C.J., O’Connell, N.E., 2012. The influence of access to aerial perches on fearfulness, social
344 behaviour and production parameters in free-range laying hens. *Appl. Anim. Behav. Sci.* 142, 51–
345 60. doi:10.1016/j.applanim.2012.08.003
346 Duncan, E.T., Appleby, M.C., Hughes, B.O., 1992. Effect of perches in laying cages on welfare and
347 production of hens. *Br. Poult. Sci.* 33, 25–35. doi:10.1080/00071669208417441
348 Enneking, S. a., Cheng, H.W., Jefferson-Moore, K.Y., Einstein, M.E., Rubin, D. a., Hester, P.Y., 2012.
349 Early access to perches in caged White Leghorn pullets. *Poult. Sci.* 91, 2114–2120.
350 doi:10.3382/ps.2012-02328
351 Faure, J.M., Jones, R.B., 1982a. Effects of age, access and time of day on perching behaviour in the
352 domestic fowl. *Appl. Anim. Ethol.* 8, 357–364. doi:10.1016/0304-3762(82)90068-2
353 Faure, J.M., Jones, R.B., 1982b. Effects of sex, strain and type of perch on perching behaviour in the
354 domestic fowl. *Appl. Anim. Ethol.* 8, 281–293. doi:10.1016/0304-3762(82)90211-5

355 Glatz, P.C., Barnett, J.L., 1996. Effect of perches and solid sides on production, plumage and foot
356 condition of laying hens housed in conventional cages in a naturally ventilated shed. *Aust. J. Exp.*
357 *Agric.* 36, 269–275.

358 Gunnarsson, S., Yngvesson, J., Keeling, L.J., Forkman, B., 2000. Rearing without early access to perches
359 impairs the spatial skills of laying hens. *Appl. Anim. Behav. Sci.* 67, 217–228. doi:10.1016/S0168-
360 1591(99)00125-2

361 Habinski, A.M., Caston, L.J., Casey-Trott, T.M., Hunniford, M.E., Widowski, T.M., 2016. Development
362 of perching behavior in 3 strains of pullets reared in furnished cages. *Poult. Sci.* pew377.
363 doi:10.3382/ps/pew377

364 Hester, P.Y., 2014. The effect of perches installed in cages on laying hens. *Worlds. Poult. Sci. J.* 70, 247–
365 264. doi:10.1017/S0043933914000270

366 Hester, P.Y., Enneking, S.A., Haley, B.K., Cheng, H.W., Einstein, M.E., Rubin, D.A., 2013a. The effect
367 of perch availability during pullet rearing and egg laying on musculoskeletal health of caged White
368 Leghorn hens. *Poult. Sci.* 92, 1972–1980. doi:10.3382/ps.2013-03008

369 Hester, P.Y., Enneking, S.A., Jefferson-Moore, K.Y., Einstein, M.E., Cheng, H.W., Rubin, D.A., 2013b.
370 The effect of perches in cages during pullet rearing and egg laying on hen performance, foot health,
371 and plumage. *Poult. Sci.* 92, 310–320. doi:10.3382/ps.2012-02744

372 Hu, J.Y., Hester, P.Y., Makagon, M.M., Vezzoli, G., Gates, R.S., Xiong, Y.J., Cheng, H.W., 2016.
373 Cooled perch effects on performance and well-being traits in caged White Leghorn hens. *Poult. Sci.*
374 pew248. doi:10.3382/ps/pew248

375 Hughes, B.O., Wilson, S., Appleby, M.C., Smith, S.F., 1993. Comparison of bone volume and strength as
376 measures of skeletal integrity in caged laying hens with access to perches. *Res. Vet. Sci.* 54, 202–
377 206. doi:10.1016/0034-5288(93)90057-M

378 Jiang, S., Hester, P.Y., Hu, J.Y., Yan, F.F., Dennis, R.L., Cheng, H.W., 2014. Effect of perches on liver
379 health of hens. *Poult. Sci.* 93, 1618–1622. doi:10.3382/ps.2013-03659

380 Lambe, N.R., Scott, G.B., 1998. Perching behaviour and preferences for different perch designs among

381 laying hens. *Anim. Welf.* 7, 203–216.

382 Lill, A., 1968. Spatial organisation in small flocks of domestic fowl. *Behaviour* 32, 258–290.

383 doi:10.1163/156853968X00225

384 Liu, K., Xin, H., 2017. Effects of horizontal distance between perches on perching behaviors of Lohmann

385 Hens. *Appl. Anim. Behav. Sci.* 194, 54–61. doi:10.1016/j.applanim.2017.05.001

386 Moinard, C., Morisse, J.P., Faure, J.M., 1998. Effect of cage area, cage height and perches on feather

387 condition, bone breakage and mortality of laying hens. *Br. Poult. Sci.* 39, 198–202.

388 doi:10.1080/00071669889123

389 Newberry, R.C., Estevez, I., Keeling, L.J., 2001. Group size and perching behaviour in young domestic

390 fowl. *Appl. Anim. Behav. Sci.* 73, 117–129. doi:10.1016/S0168-1591(01)00135-6

391 Olsson, I.A.S., Keeling, L.J., 2002. The push-door for measuring motivation in hens : laying hens are

392 motivated to perch at night. *Anim. Welf.* 11, 11–19.

393 Olsson, I.A.S., Keeling, L.J., 2000. Night-time roosting in laying hens and the effect of thwarting access

394 to perches. *Appl. Anim. Behav. Sci.* 68, 243–256. doi:10.1016/S0168-1591(00)00097-6

395 Pickel, T., Schrader, L., Scholz, B., 2011. Pressure load on keel bone and foot pads in perching laying

396 hens in relation to perch design. *Poult. Sci.* 90, 715–724. doi:10.3382/ps.2010-01025

397 Scholz, B., Kjaer, J.B., Schrader, L., 2014. Analysis of landing behaviour of three layer lines on different

398 perch designs. *Br. Poult. Sci.* 55, 419–426. doi:10.1080/00071668.2014.933175

399 Stratmann, A., Fröhlich, E.K.F., Harlander-Matauschek, A., Schrader, L., Toscano, M.J., Würbel, H.,

400 Gebhardt-Henrich, S.G., 2015. Soft perches in an aviary system reduce incidence of keel bone

401 damage in laying hens. *PLoS One* 10, e0122568. doi:10.1371/journal.pone.0122568

402 Struelens, E., Tuytens, F.A.M., 2009. Effects of perch design on behaviour and health of laying hens.

403 *Anim. Welf.* 18, 533–538.

404 Struelens, E., Tuytens, F.A.M., Ampe, B., Ödberg, F., Sonck, B., Duchateau, L., 2009. Perch width

405 preferences of laying hens. *Br. Poult. Sci.* 50, 418–423. doi:10.1080/00071660903110885

406 Struelens, E., Tuytens, F.A.M., Duchateau, L., Leroy, T., Cox, M., Vranken, E., Buyse, J., Zoons, J.,

407 Berckmans, D., Ödberg, F., Sonck, B., 2008. Perching behaviour and perch height preference of
408 laying hens in furnished cages varying in height. *Br. Poult. Sci.* 49, 381–389.
409 doi:10.1080/00071660802158332

410 Tauson, R., 1984. Effects of a perch in conventional cages for laying hens. *Acta Agric. Scand.* 34, 193–
411 209. doi:10.1080/00015128409435389

412 Tauson, R., Abrahamsson, P., 1994. Foot and skeletal disorders in laying hens: effects of perch design,
413 hybrid, housing system and stocking density. *Acta Agric. Scand. Sect. A - Anim. Sci.* 44, 110–119.
414 doi:10.1080/09064709409410189

415 Valkonen, E., Rinne, R., Valaja, J., 2009. Effects of perch on feed consumption and behaviour of caged
416 laying hens. *Agric. Food Sci.* 18, 257–267.

417 Wall, H., Tauson, R., 2007. Perch arrangements in small-group furnished cages for laying hens. *J. Appl.*
418 *Poult. Res.* 16, 322–330. doi:10.1093/japr/16.3.322

419 Wechsler, B., Huber-Eicher, B., 1998. The effect of foraging material and perch height on feather pecking
420 and feather damage in laying hens. *Appl. Anim. Behav. Sci.* 58, 131–141. doi:10.1016/S0168-
421 1591(97)00137-8

422 Weeks, C.A., Nicol, C.J., 2006. Behavioural needs, priorities and preferences of laying hens. *Worlds.*
423 *Poult. Sci. J.* 62, 296–307. doi:10.1079/WPS200598

424 Yan, F.F., Hester, P.Y., Cheng, H.W., 2014. The effect of perch access during pullet rearing and egg
425 laying on physiological measures of stress in White Leghorns at 71 weeks of age. *Poult. Sci.* 93,
426 1318–1326. doi:10.3382/ps.2013-03572

427 Yeates, N.T.M., 1963. The activity pattern in poultry in relation to photoperiod. *Anim. Behav.* 11, 287–
428 289. doi:10.1016/S0003-3472(63)80112-8

429

Table Captions

Table 1. Light schedule for laying hens used in the study

Table 2. Perch arrangements in the study

Table 3. Determination of number of birds on each weighing perch based on the threshold values

Table 4. Perching time ratio and perching frequency for light, dim, dark periods and the entire day during a 9-week perch exposure of laying hens

Figure Captions

Figure 1. A schematic representation of the experimental pens. (a) side view, (b) top view.

Figure 2. An automated perching monitoring system. (a) weighing perches, (b) an example of linear response of loadcell scale output to load weight on the weighing perch, (c) load weight of perching hens on each perch, (d) number of perching birds on each perch.

Figure 3. Diurnal perching pattern of hens at nine weeks of perch exposure: (a) diurnal pattern, (b) during dusk transition period, and (c) during dawn transition period.

Figure 4. Proportion of birds perching during the dark period. Data are presented as least squares means \pm SE. Values with different superscripts are significantly different at $P < 0.05$.

Table 1. Light schedule for laying hens used in the study

WOA ^[1]	WPE ^[2]	Dawn (1-2 lux)	Light (20 lux)	Dusk (1-2 lux)	Dark (0 lux)	Light hour (h/day)
17	1	08:45-09:00	09:00-21:00	21:00-21:15	21:15-08:45	12
18	2	08:15-08:30	08:30-21:30	21:30-21:45	21:45-08:15	13
19	3	07:45-08:00	08:00-22:00	22:00-22:15	22:15-07:45	14
20	4	07:30-07:45	07:45-22:15	22:15-22:30	22:30-07:30	14.5
21	5	07:15-07:30	07:30-22:30	22:30-22:45	22:45-07:15	15
22	6	07:15-07:30	07:30-22:45	22:45-23:00	23:00-07:15	15.25
23	7	07:00-07:15	07:15-22:45	22:45-23:00	23:00-07:00	15.5
24	8	07:00-07:15	07:15-23:00	23:00-23:15	23:15-07:00	15.75
25	9	06:45-07:00	07:00-23:00	23:00-23:15	23:15-06:45	16

^[1] WOA = weeks of age

^[2] WPE = week(s) of perch exposure

Table 2. Perch arrangements in the study

WOA ^[1]	WPE ^[2]	Batch 1						Batch 2					
		P1 ^[3]		P2		P3		P1		P2		P3	
		L ^[4]	R	L	R	L	R	L	R	L	R	L	R
17	1	C ^[5]	H	H	C	H	C	H	C	C	H	C	H
18	2	C	H	H	C	H	C	H	C	C	H	C	H
19	3	H	C	C	H	C	H	C	H	H	C	H	C
20	4	H	C	C	H	H	C	C	H	H	C	C	H
21	5	C	H	H	C	C	H	H	C	C	H	H	C
22	6	C	H	C	H	H	C	H	C	H	C	C	H
23	7	H	C	C	H	H	C	C	H	H	C	C	H
24	8	C	H	H	C	C	H	H	C	C	H	H	C
25	9	H	C	H	C	C	H	C	H	C	H	H	C

^[1] WOA = weeks of age

^[2] WPE = week(s) of perch exposure

^[3] P1, P2, and P3: testing pen 1, 2, and 3, respectively

^[4] L, R: left and right side of the testing pen, respectively

^[5] C, H: circular (round) and hexagon perch, respectively

Table 3. Determination of number of birds on each weighing perch based on the threshold values

PBN ^[1]	Threshold values for load weight ^[4] (g)	
	Period 1 ^[2]	Period 2 ^[3]
1	1000 - 1550	1150 - 1750
2	2200 - 2900	2500 - 3300
3	3400 - 4300	3850 - 4850
4	4600 - 5600	5200 - 6400
5	5800 - 6950	6500 - 7900
6	7050 - 8250	7950 - 9400
7	8250 - 9600	9400 - 11000

^[1] PBN = perching bird number, i.e., number of simultaneously perching birds.

^[2] Birds at 17-19 weeks of age (WOA) with body weight ranging from 1200 g to 1350 g.

^[3] Birds at 20-25 WOA with body weight ranging from 1350 g to 1550 g.

^[4] Threshold values for determining the number of simultaneously perching birds on each weighing perch. For example, if the measurement from the weighing perch shows a load weight of 1300 g, then there is one bird perching on the weighing perch.

Table 4. Perching time ratio and perching frequency for light, dim, dark periods and the entire day during a 9-week perch exposure of laying hens ^[1]

WPE ^[2]	PTR ^[3] (%)				PF ^[4] (number/bird-h)			
	light	dim	dark	daily	light	dim	dark	daily
1	2.8 ± 0.7 ^c	6.3 ± 1.8 ^b	26.2 ± 6.9 ^d	14.6 ± 3.2 ^b	4.9 ± 0.5 ^b	10.5 ± 2.0 ^b	0.1 ± 0.0	2.6 ± 0.3 ^c
2	5.8 ± 1.9 ^{bc}	12.5 ± 3.1 ^{ab}	39.4 ± 6.7 ^d	23.7 ± 3.8 ^{ab}	6.8 ± 0.5 ^{ab}	15.4 ± 1.0 ^{ab}	0.2 ± 0.0	3.8 ± 0.3 ^{bc}
3	5.8 ± 0.9 ^{bc}	12.3 ± 2.3 ^{ab}	50.6 ± 4.5 ^{cd}	25.5 ± 2.7 ^{ab}	7.6 ± 0.6 ^a	16.8 ± 1.6 ^{ab}	0.1 ± 0.0	4.5 ± 0.4 ^{ab}
4	5.4 ± 0.4 ^{bc}	15.0 ± 1.4 ^{ab}	62.1 ± 2.1 ^{bc}	27.6 ± 1.4 ^a	8.3 ± 0.3 ^a	18.9 ± 0.8 ^a	0.2 ± 0.0	5.3 ± 0.2 ^a
5	6.4 ± 0.4 ^b	16.5 ± 1.2 ^a	65.0 ± 1.6 ^{bc}	28.1 ± 0.8 ^a	8.4 ± 0.4 ^a	18.3 ± 1.0 ^a	0.1 ± 0.0	5.5 ± 0.2 ^a
6	6.3 ± 0.4 ^b	19.9 ± 2.4 ^a	70.4 ± 1.7 ^{ab}	29.0 ± 0.8 ^a	8.4 ± 0.4 ^a	17.7 ± 0.8 ^a	0.1 ± 0.0	5.6 ± 0.2 ^a
7	7.3 ± 0.7 ^{ab}	18.1 ± 2.1 ^a	72.8 ± 1.5 ^a	29.5 ± 0.8 ^a	8.6 ± 0.5 ^a	20.5 ± 1.4 ^a	0.1 ± 0.0	5.9 ± 0.4 ^a
8	9.4 ± 0.7 ^a	19.9 ± 2.0 ^a	73.3 ± 1.6 ^a	30.3 ± 0.8 ^a	8.4 ± 0.3 ^a	20.4 ± 0.8 ^a	0.1 ± 0.0	5.9 ± 0.2 ^a
9	9.7 ± 1.1 ^a	19.8 ± 1.3 ^a	75.5 ± 1.6 ^a	30.7 ± 1.3 ^a	8.0 ± 0.5 ^a	22.2 ± 0.9 ^a	0.2 ± 0.0	5.7 ± 0.4 ^a

^[1] Data are least squares means ± SE. Within each column, values with different superscripts are significantly different at P < 0.05.

^[2] WPE = weeks of perch exposure.

^[3] PTR = perching time ratio – proportion of perching time for a given period, %.

^[4] PF = perching frequency – perch visit per hour for a given period, number/bird-h.

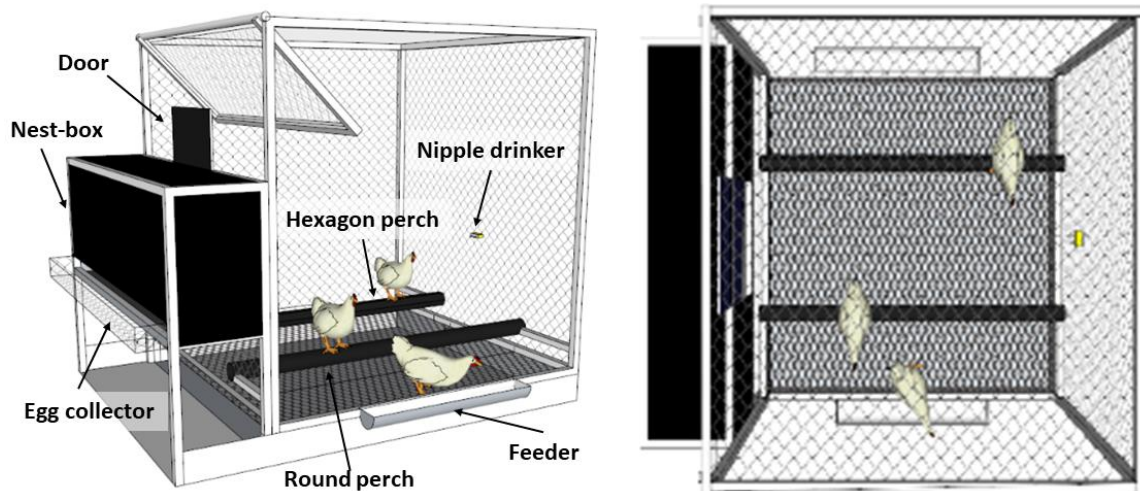


Figure 1: A schematic representation of the experimental pens. (a) side view, (b) top view.

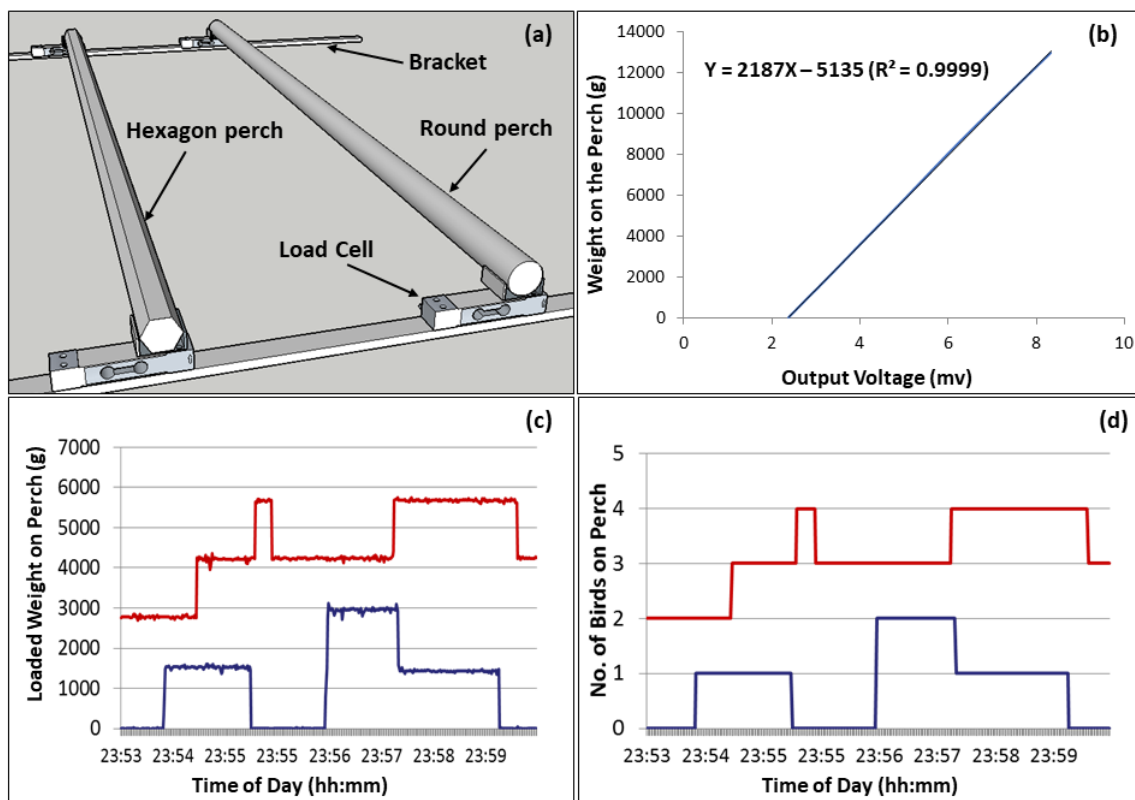
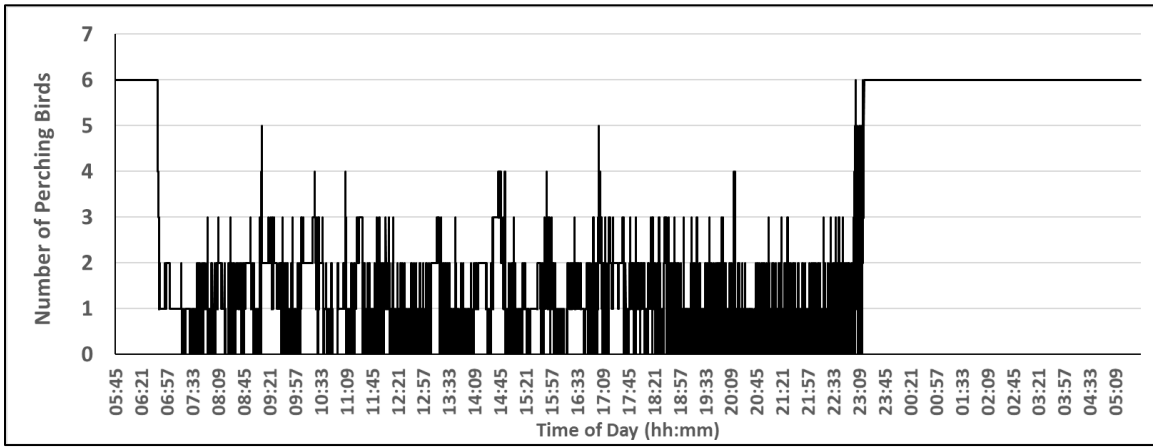
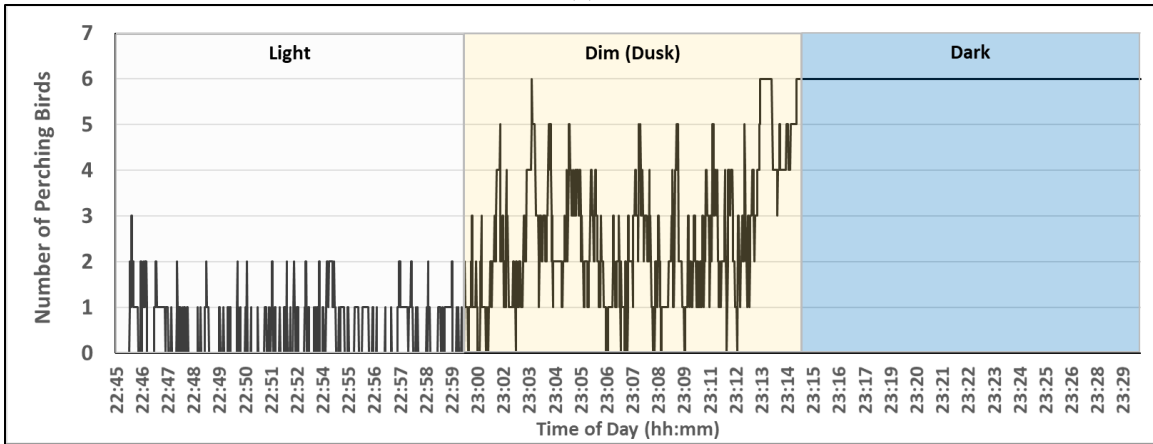


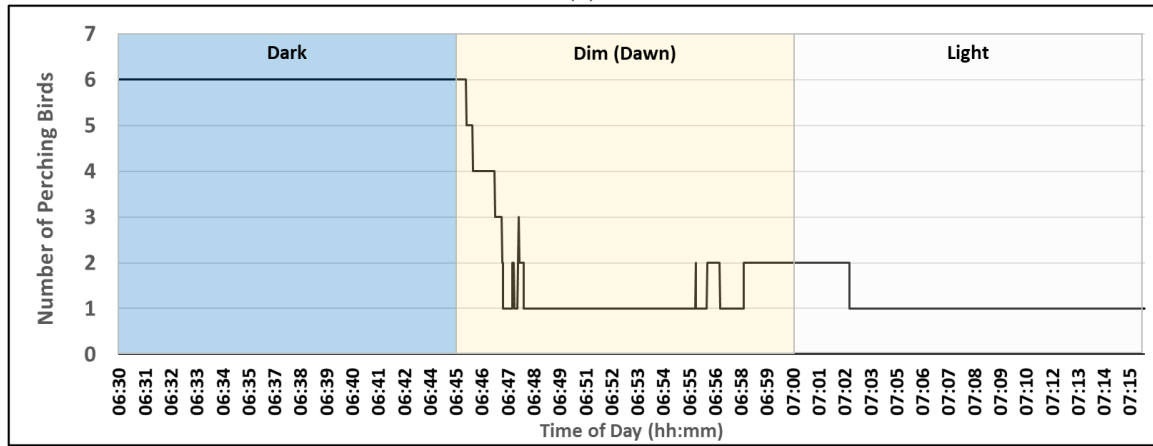
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(a)



(b)



(c)

Figure 3. Diurnal perching pattern of hens at nine weeks of perch exposure: (a) diurnal pattern, (b) during dusk transition period, and (c) during dawn transition period.

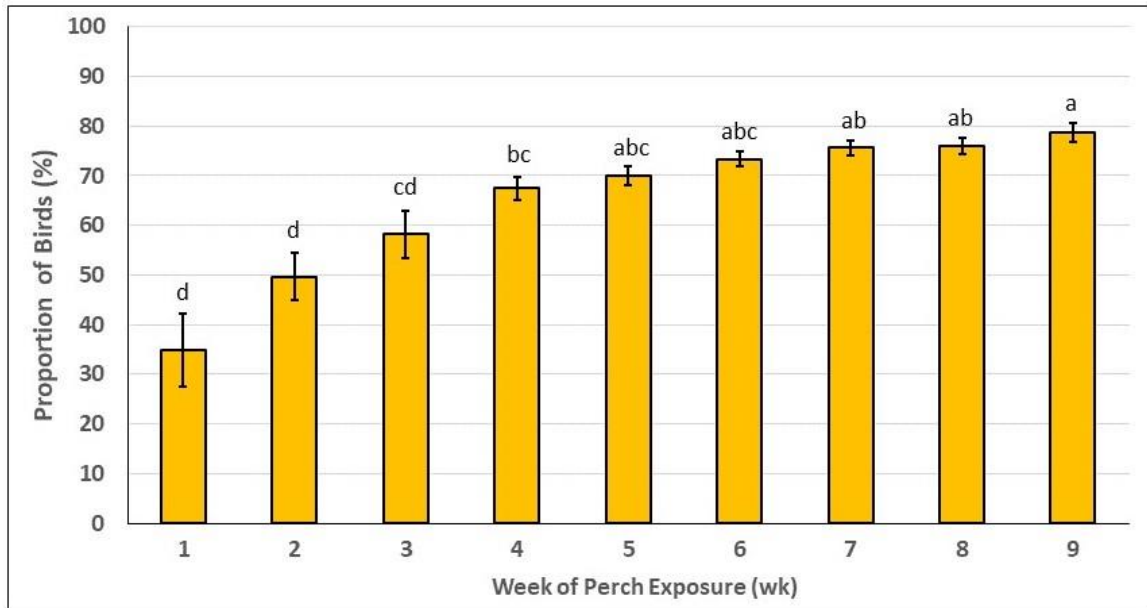


Figure 4. Proportion of birds perching during the dark period. Data are presented as least squares means \pm SE. Values with different superscripts are significantly different at $P < 0.05$.