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Group size and perching behaviour in young domestic fowl

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Abstract

To test the hypothesis that young domestic fowl perform less perch-related antipredator behaviour with increasing group size, White Leghorn pullets were reared in four replicate groups of 15, 30, 60 and 120 at a constant density of 5 birds/m². Each pen contained perches 20, 40 and 60 cm above the ground. Perch space per bird per perch level was the same for all groups. It was predicted that, with increasing group size, domestic fowl would (1) spend less time on perches (i.e. more time down on the floor); (2) be less vigilant while perching; (3) spend relatively more time preening down on the floor. As predicted, the proportion of 3- to 18-week-old birds roosting on perches during scans throughout the photoperiod decreased with increasing group size, from 41 ± 1.7% in groups of 15 birds to 33 ± 1.6% in groups of 120 birds. This effect was due to reduced use of the lower perches; use of the highest perches was high at all group sizes. The proportion of birds vigilant on the highest perches of those present on that perch level decreased with increasing group size. The proportion of birds engaged in the vulnerable activity of preening down on the floor increased with group size. The frequency of transitions between floor and perches was not affected by group size but birds received more disturbances from other birds when on the top perch level in the larger groups. Thus, the decline in vigilance on the top perch level with increasing group size was not due to reduced disturbance from other birds. In conclusion, despite domestication and protection from non-human predators, changes in the use of perches by young domestic fowl with increasing group size were consistent with the antipredator hypothesis. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Antipredator behaviour; Chickens; Housing; Perches; Roosting; Vigilance

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1. Introduction

The antipredator behaviour of the jungle fowl (*Gallus gallus*), ancestor of the domestic fowl (*Gallus gallus domesticus*), has been shaped by millions of years of selection pressure from predators in the wild. Domestication of this species appears to have commenced about 10,000 years ago (Crawford, 1990) but the birds were usually free-ranging and exposed to non-human predators until the 1940s when production methods became more intensive. Although, domestication has altered behaviour quantitatively, qualitatively, domestic fowl continue to exhibit the antipredator behaviour that evolved in their wild ancestors. For example, they roost in trees (Wood-Gush and Duncan, 1976; Wood-Gush et al., 1978), use discontinuous vertical cover, especially when performing vulnerable activities such as resting and preening (Newberry and Shackleton, 1997), move closer together when performing vulnerable activities (Keeling and Duncan, 1991), alarm call (Evans et al., 1993) and exhibit tonic immobility when restrained on their back (Gallup et al., 1971).

Jungle fowl and feral domestic hens move in isolation from other adults when brooding chicks and rely on vegetative cover and camouflage for protection from predators. Brood size varies from about 1 to 10 chicks and predation exacts a heavy toll. When the chicks are sufficiently developed to be able to perch up in trees, starting as early as 4–8 weeks of age, the hens typically congregate in stable groups of about 2–10 hens with their offspring, a dominant adult male and one or more subordinate males (Johnson, 1963; Collias and Collias, 1967; Nishida et al., 1992). Considerable variability has been observed in the age at which feral domestic fowl first start to perch in trees, and early perching behaviour appears to be associated with a “roosting call” from the hen that encourages her chicks to fly up into a tree to be brooded (Collias and Joos, 1953; McBride et al., 1969; Wood-Gush et al., 1978).

By contrast, female chicks (pullets) raised for commercial egg production are reared without adults, in groups varying from about 10 individuals to several thousand individuals depending on the housing system. Pullets must learn how to perch if they are destined to be housed in a non-cage layer house as adults. Otherwise, they may fail to use nest boxes located above floor level when introduced into the layer house (Brake, 1987; Appleby et al., 1988). During rearing, there are no hens to encourage pullets to perch and no opportunities for pullets to be brooded on the perches. Nevertheless, if exposed to perches by 4 weeks of age, they will perch readily as adults (Appleby and Duncan, 1989; Gunnarsson et al., 1999). The impact of group size on the development of perching behaviour in young domestic fowl reared under commercial conditions has not been systematically investigated.

In the wild, living in a larger group can increase the probability that a predator will be detected early, allowing all group members time to escape (Elgar, 1989; Lima and Dill, 1990). Living in a larger group can also reduce the probability of being caught by a predator due to a dilution effect (Hamilton, 1971) and a confusion effect (Landeau and Terborgh, 1986). Thus, vigilance tends to decline with increasing group size (Elgar, 1989; Lima and Dill, 1990). The potential benefit of reduced predation risk when living in a large group must be weighed against the potential cost of increased intra-group competition for resources. These opposing pressures influence observed group sizes and antipredator

behaviour under natural conditions (Pulliam and Caraco, 1984). In species that forage on the ground and use trees for protection from predators, the relative time spent on the ground and at different heights in trees has been interpreted as a compromise between avoiding predation and foraging successfully under competition pressure (Robinson, 1981; Stanford, 1995).

Although pullets reared for commercial egg production are protected from predators in indoor housing, Keeling (1997) found that laying hens performed escape behaviour sooner in response to an approaching ground predator model if they were standing on a very low perch than if they were standing on an elevated perch. This result suggests that they had a greater sense of security when perching above the floor. If so, they may also experience a greater sense of security when living in a larger group and, thus, spend more time down on the floor. Alternatively, larger group sizes may be associated with greater fear resulting in increased use of perches. Bilčík *et al.* (1998) found that the duration of tonic immobility was elevated in hens housed in larger groups.

The objective of this investigation was to determine the impact of group size and age on the perching behaviour of young domestic fowl kept under indoor housing conditions with equal resource availability across group sizes. We assumed that, in indoor housing conditions, use of perches for vulnerable activities such as resting and preening represents an antipredator response derived from the use of tree branches for these activities by jungle fowl. We also assumed that the proximate mechanism motivating domestic fowl to use perches is that they feel safer on perches than on the ground. We hypothesised that use of perches and related antipredator behaviour would decline with increasing group size. Specifically, we predicted that, with increasing group size, domestic fowl would (1) spend less time up on perches (*i.e.* more time down on the floor); (2) be less vigilant while perching; (3) spend relatively more time preening down on the floor.

2. Methods

2.1. *Animals, housing and husbandry*

We obtained female chicks of a White Leghorn strain, with intact beaks, from a local commercial hatchery. We reared them from 1 day to 18 weeks of age in floor pens in four replicate groups of 15, 30, 60 and 120 birds. The 16 pens were arranged in randomised blocks within a poultry house. The pen walls were constructed of plywood to a height of 1.5 m to provide a visual barrier, with chicken wire above for ventilation. The size of the pens was adjusted between group sizes to give a constant stocking density of 5 birds/m² in all pens. Each pen contained four round hanging feeders, one in each corner, with the available trough space adjusted to provide 4 cm of feeding space per bird. Pens were also supplied with three hanging water lines, centred along three of the pen walls, providing one water nipple per five birds. The floor of each pen was covered with a 5 cm deep layer of wood shavings.

The perch units comprised three, horizontal, parallel 3 cm wide by 3 cm deep soft-wood rails with bevelled edges, supported by vertical legs. The three rails were arranged in a stair-step design, 20, 40 and 60 cm above the ground, respectively, with a horizontal

distance of 20 cm between each rail. The rails were held together at each end by a sloping rail set at a 45° angle that was too steep for the birds to perch on. The length of the rails was varied according to group size (0.25, 0.5, 1.0 and 2.0 m for groups of 15, 30, 60 and 120 birds, respectively) to provide a constant amount of perch space per bird in all groups. From 3 to 12 weeks of age, there were two perch units in each pen, providing a total of 10 cm of perching space per bird. At 12 weeks of age, two additional perch units were added to each pen, increasing the perching space to 20 cm per bird. Each perch unit was centred along one side of the pen, with the lowest rail towards the pen centre.

Food (standard commercial pullet dietary regimen) and water were provided *ad libitum*. The photoperiod was 23 h during the first week, gradually lowered to 8.5 h by 3 weeks of age, and raised to 10.5 h from 12 to 18 weeks of age. The mean light intensity was 5 lx at floor level and 11 lx at the highest perch level. The room was heated by hot water pipes. The temperature was 33°C during the first week, and gradually lowered until the birds were 12 weeks old, after which it was maintained at about 18°C.

2.2. Behaviour observations

We made two rounds of behavioural observations of the birds in each pen by direct observation from the aisle in front of each pen during each of five, 3-week age periods between 3 and 18 weeks. During each observation round, half of the pens were observed in the morning, and the other half in the afternoon. The order of observing pens and the time of day was balanced in a Latin square design. Observations were made by four observers familiar to the birds. To minimise disturbance, one observer sat quietly in front of each pen during each observation round, with only her head and shoulders protruding above the solid pen wall. Between observations, we made frequent checks for inter-observer concordance to ensure consistency of behaviour recording.

We made six sets of instantaneous scans of each pen during each observation round. Each set of scans comprised the following, performed in rapid succession. First, we recorded the total number of birds on each perch level (i.e. at 20, 40 and 60 cm above the floor) and on “other” locations such as on the top edge of the feeders or on the wire strung above the water lines (that was intended to deter perching on the water lines). Then we recorded the number of birds that were vigilant (i.e. eyes open, head up alert or looking around) at each perch level. Finally, we recorded the number of birds that were preening (i.e. manipulating their feathers with their beak) at each perch level and on the floor. Subsequent sets of scans were made at 30 min intervals.

We made a 5 min focal sample of each of 12 individually identified birds in each pen during each observation round. These birds had been randomly selected at 3 weeks of age and marked with aniline dye, followed by application of large numbered wing tags at 12 weeks. The order of observing the focal birds was randomised for each age period. During the focal samples, we used a computer to record behaviour in real time. We recorded all transitions in location between the floor and the perches by the focal bird. We also recorded all disturbances at each perch level and on the floor in which the focal bird, while lying or preening, stood for at least 1 s, fell off a perch or moved away immediately after being bumped into or jostled by another bird.

2.3. Statistical analysis

Data averaged for each pen over scan or focal bird and time of day were analysed using the general linear model (GLM) procedure of the SAS Institute (1989). We used a split plot design with group size (3 d.f.) and block (3 d.f.) in the main plot, tested against their interaction (9 d.f.), and age period (4 d.f.) and the interaction of group size with age period (12 d.f.) in the sub-plot, tested against the residual error (48 d.f.). We transformed the data to arcsines or logarithms as needed to meet assumptions of normality and homogeneity. We performed a repeated measures GLM on any variables showing significant sphericity.

3. Results

3.1. Perching behaviour

The overall mean proportion of birds perching during our daytime observations was $38.0 \pm 1.92\%$. There was a significant decline in the total proportion of birds observed perching with increasing group size, from $41.3 \pm 1.74\%$ in groups of 15 birds to $33.4 \pm 1.62\%$ in groups of 120 birds ($F_{3,9} = 8.63$, $P = 0.005$; Fig. 1). This group size effect was consistent over all age periods ($F_{12,48} = 1.77$, $P = 0.081$) and resulted from lower use of the middle perches ($F_{3,9} = 12.99$, $P = 0.001$) and lowest perches ($F_{3,9} = 23.44$, $P < 0.001$) by birds in larger groups (Fig. 1). Use of “other” perching locations was low and variable across group size ($F_{3,9} = 7.78$, $P = 0.007$). The birds used the upper perches at a high rate in all group sizes ($F_{3,9} = 0.97$, $P = 0.45$; Fig. 1).

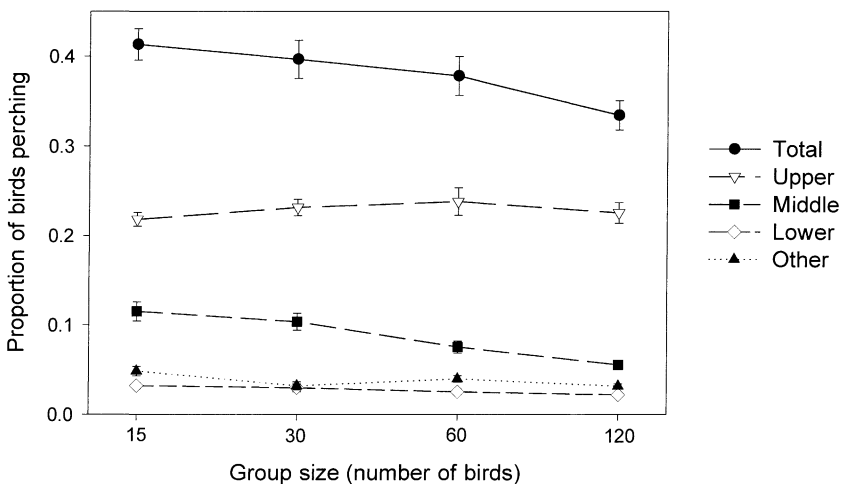


Fig. 1. Effect of group size on the total proportion of birds perching of those in the pen, proportion of those in the pen at each perch height (upper, 60 cm; middle, 40 cm; lower, 20 cm) and proportion on “other” perching locations such as on the water lines and feeders (mean \pm S.E.). Group size affected the total proportion and the proportions on the middle, lower and “other” perches ($P < 0.01$).

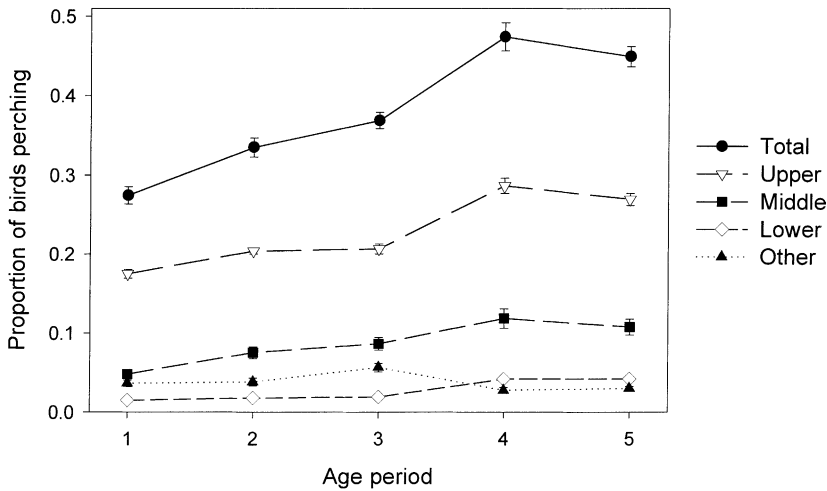


Fig. 2. Effect of age period ((1) 3–6 weeks; (2) 6–9 weeks; (3) 9–12 weeks; (4) 12–15 weeks; (5) 15–18 weeks) on the total proportion of birds perching of those in the pen, proportion of those in the pen at each perch height (upper, 60 cm; middle, 40 cm; lower, 20 cm) and proportion on “other” perching locations such as on the water lines and feeders (mean \pm S.E.). Perch space was doubled prior to age period four. Age affected all of the variables ($P < 0.001$).

Use of all perch locations varied with age ($F_{4,48} \geq 10.56$, $P < 0.001$), with the total proportion of birds perching increasing from $27.5 \pm 1.10\%$ in the youngest birds (3–6 weeks old) to $47.4 \pm 1.77\%$ when the birds were 12–15 weeks old (Fig. 2). There was a relatively large increase in perching after 12 weeks of age coinciding with the introduction of two additional perch units. In the preceding age period, use of “other” perching locations was relatively high.

Because we built longer perches for larger groups to maintain a constant perch space allocation per bird, the maximum number of birds that could perch together on a single perch at the each perch level varied between group sizes. The maximum number observed perching on each perch at the preferred top level was 3, 5, 10 and 18 in groups of 15, 30, 60 and 120 birds, respectively, in the youngest birds (3–6 weeks of age) and 1, 3, 7 and 13, respectively, in the oldest birds (15–18 weeks of age).

3.2. Vigilance

The proportion of the birds that were vigilant of those present on each perch level declined with increasing group size only on the highest perches ($F_{3,9} = 4.79$, $P = 0.029$; Fig. 3). The proportion of birds on the middle and lowest perches that were vigilant was relatively high and increased with increasing group size (middle perches, $F_{3,9} = 2.23$, $P = 0.15$; lowest perches, $F_{3,9} = 17.83$, $P < 0.001$; Fig. 3). These opposing trends at different perch levels cancelled each other out when considering the total number vigilant of those on the perch units ($F_{3,9} = 0.70$, $P = 0.57$) and there was no group size by age interaction ($F_{12,48} = 1.10$, $P = 0.39$). There was a main effect of age on vigilance at each

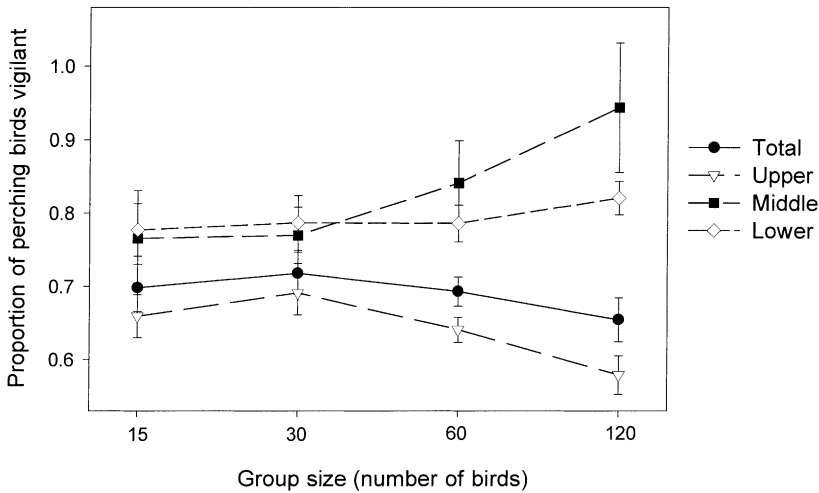


Fig. 3. Effect of group size on the total proportion of birds vigilant of those on perches, and the proportion vigilant at each perch height (upper, 60 cm; middle, 40 cm; lower, 20 cm) of the total on that level (mean \pm S.E.). Group size affected the proportion vigilant on the upper and lower perches ($P < 0.05$).

perch level ($F_{4,48} \geq 9.10$, $P < 0.001$). The proportion of perching birds that were vigilant was lowest at 3–6 weeks of age ($54 \pm 3.1\%$) and rose to a peak at 12–15 weeks ($79 \pm 2.1\%$).

3.3. Preening

The proportion of birds that were preening on the floor of those in the pen increased with group size ($F_{3,9} = 20.52$, $P < 0.001$) and age ($F_{4,48} = 9.39$, $P < 0.001$), especially when the birds were older ($F_{12,48} = 5.05$, $P < 0.001$; Fig. 4). In contrast to the vigilance data, the proportion of birds preening of those present on each perch level increased with increasing group size on the highest perches ($F_{3,9} = 4.26$, $P = 0.039$) and decreased with increasing group size on the middle ($F_{3,9} = 4.27$, $P = 0.039$) and lowest ($F_{3,9} = 45.31$, $P < 0.001$) perches (Fig. 5). The overall proportion of perching birds that were preening was not affected by group size ($F_{3,9} = 2.19$, $P = 0.16$), or the interaction of group size with age ($F_{12,48} = 1.34$, $P = 0.23$), but did vary with age ($F_{4,48} = 8.45$, $P < 0.001$). It was highest at 3–6 weeks of age ($32 \pm 2.0\%$) and lowest at 9–12 weeks ($22 \pm 1.8\%$) and 12–15 weeks ($22 \pm 1.5\%$).

3.4. Disturbances

The frequency of transitions between the floor, the different perch levels and “other” perch locations was not affected by group size, age or their interaction (2.9 ± 0.12 transitions between levels per 5 min focal sample, $F \leq 1.68$, $P > 0.05$). The majority of non-aggressive disturbances received by resting and preening birds occurred on the top

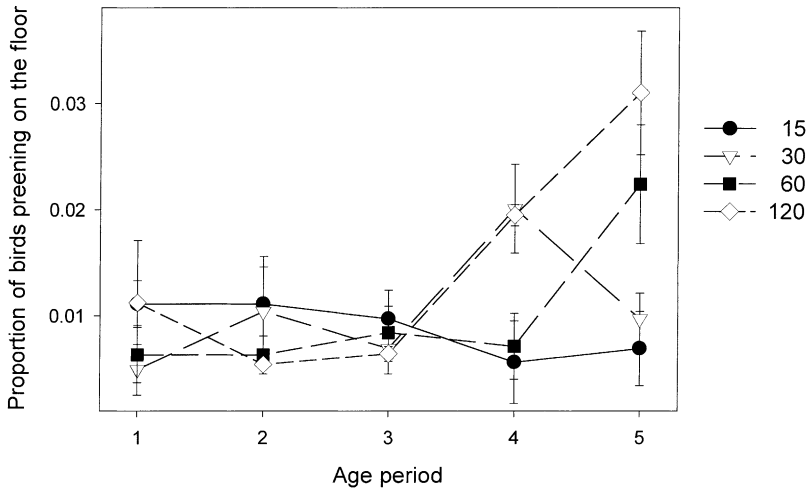


Fig. 4. Effect of age period ((1) 3–6 weeks; (2) 6–9 weeks; (3) 9–12 weeks; (4) 12–15 weeks; (5) 15–18 weeks) and group size (15, 30, 60 or 120 birds) on the proportion of birds preening on the floor of those in the pen (mean ± S.E.). There were significant group size, age and group size by age effects ($P < 0.001$).

perch level (Fig. 6). The proportion of disturbances received was higher in the larger groups on the top perch level ($F_{3,9} = 4.03, P = 0.045$) and tended to decline with increasing group size on the middle perch level ($F_{3,9} = 3.67, P = 0.056$). Disturbances on the floor, lowest perch level and “other” perch locations fluctuated inconsistently with age ($F_{4,48} \geq 4.47, P \leq 0.004$).

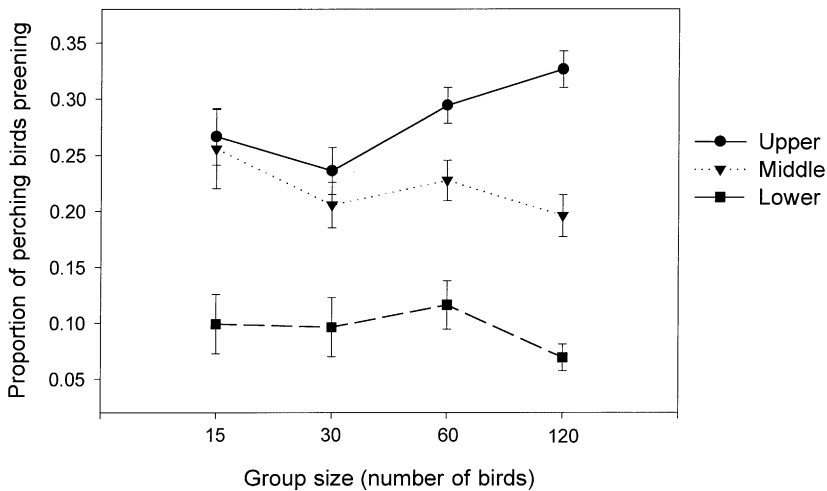


Fig. 5. Effect of group size on the proportion of birds preening at each perch height (upper, 60 cm; middle, 40 cm; lower, 20 cm) of the total on that level (mean ± S.E.). Group size affected the proportion preening at all heights off the floor ($P < 0.05$).

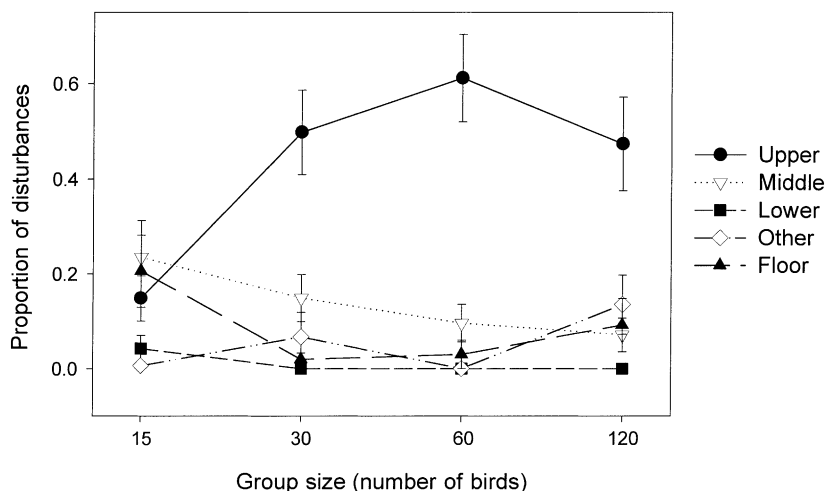


Fig. 6. Effect of group size on the proportion of disturbances occurring at each perch height (upper, 60 cm; middle, 40 cm; lower, 20 cm), on “other” perching locations such as on the water lines and feeders, and on the floor of the total disturbances to focal birds while resting and preening (mean \pm S.E.). Group size affected the proportion of disturbances occurring on the upper perches ($P < 0.05$).

4. Discussion

The strong preference for the highest perches is consistent with our assumption that use of perches by domestic fowl in indoor housing represents antipredator behaviour. This result is consistent with the findings of Keeling (1997), who exposed laying hens to a ground predator model, and suggests that the birds had a greater sense of security when perching higher off the ground even in the absence of non-human predators. From the first age period (3–6 weeks), the birds used the top perch level by hopping up via the lower and middle perches, although, perching did increase with age. The birds used the perches without any encouragement from a mother hen. Presumably, this early perching behaviour was related to the design of our perching “trees”. In the wild, trees would not be as likely to have such conveniently spaced branches leading in a stair-step fashion up to the canopy. Also, such trees would provide an easy access route for predators and would presumably not be selected as roosting sites by adults in the wild. That young domestic fowl reared without adults make use of relatively low and easily accessible perches in indoor housing is well known, although, the propensity to perch varies between strains and individuals (Faure and Jones, 1982; Appleby and Duncan, 1989; Newberry et al., 1995; Fiscus-LeVan et al., 2000). The proportion of birds perching during our scans was within the range of daytime perch use reported for adult laying hens (25%, Appleby et al., 1992; 32–37%, Appleby and Hughes, 1995; 30%, Abrahamsson et al., 1996; 47%, Carmichael et al., 1999).

As predicted, perch use decreased with increasing group size. This effect of group size was independent of stocking density and occurred at all ages under conditions in which the floor space allocation per bird was generous. Therefore, the birds in our study were not

“forced” to use the perches due to inadequate space on the floor, although this may happen at high stocking densities (Hughes and Elson, 1977).

There was a relatively large increase in perch use after 12 weeks, and a drop in the use of “other” perch locations, coinciding with the doubling of perch space from 10 to 20 cm per bird. The “other” perches (the wire over the water lines and edges of the feeders) could be considered more costly perching sites because they were narrow and swung in response to bird movement, resulting in birds tending to lose their balance and falling off them. These results suggest that the availability of space on “preferred” upper perches was a limiting factor, especially at 9–12 weeks and for birds in the smaller groups that were more motivated to use the perches. Upper perch space limitation probably explains why the reduction in perch use with increasing group size was observed at the lower and middle perch levels but not at the upper level.

From a practical perspective, Appleby (1995) suggested that 14 cm of perch space per bird was sufficient for adult laying hens in cages provided with a single short perch between two walls. In loose-housing systems where multiple perches are provided at different levels, our results indicate that emphasis should be placed on upper perch space, with lower perches being provided for access to upper perches and other resources. We only observed perching behaviour during the daytime. At night, almost all the birds will perch if sufficient, accessible perch space is available (Appleby, 1995; Appleby and Hughes, 1995; Abrahamsson et al., 1996). Based on the maximum numbers of birds that we observed perching together on a single perch at the top level and averaging over all group sizes, it appears that about 10 cm of accessible upper perch space per bird would have been required for all birds to perch at the upper level at 3–6 weeks of age (range 8–11 cm), and about 18 cm would have been needed at 15–18 weeks of age (range 14–25 cm). The precise amount of perch space used varied with perch length because a bird could not make use of vacant perch space that was less than her full body width unless, perhaps, it was located at the end of a free-standing perch. The above numbers are based on apparent full occupancy of perches during the daytime. We cannot discount the possibility that birds would squeeze together tighter on perches at night.

Vigilance is usually reported in the context of foraging and, to our knowledge, has not previously been investigated in birds while resting on perches away from a food source. Given the ease of obtaining food and water, the birds in this experiment could be considered to have had considerable spare time for vigilance (Illius and Fitzgibbon, 1994), unlike wild animals that pay a cost for vigilance by having less time for other activities such as foraging (Berger, 1978). Vigilance may be attributed to monitoring conspecifics, monitoring for food or monitoring for predators (Robinson, 1981). A report on monkeys indicated no effect of group size on within-group surveillance (Treves, 1999). If our birds were primarily monitoring conspecifics when vigilant, we would expect vigilance to increase with group size as occurred on the lowest perches. However, we observed the opposite trend for birds on the upper perches, among whom vigilance declined with increasing group size as is typically reported in wild animals monitoring for predators (e.g. Cresswell, 1994). Although, the frequency of transitions between floor and perches was not affected by group size, birds in the larger groups received more disturbances from other birds when on the top perch level. Thus, the decline in vigilance with increasing group size on the top perch level occurred despite greater disturbance from

other birds. This result is consistent with monitoring for predators rather than within-group surveillance. The greater frequency of disturbances in larger groups was probably due to the increased numbers of birds on the longer perches provided to larger groups. It is unlikely that monitoring for food affected vigilance in our experiment. Food was available *ad libitum* in predictable locations and should have been accessible to the same extent in all group sizes because all groups had the same amount of feeder space per individual.

With regard to vigilance associated with monitoring for predators, it is unclear how birds should respond to predation risk in an indoor enclosure with solid walls to a height of 1.5 m, wire mesh above, a solid ceiling and exposed perches without surrounding foliage. The birds were not exposed to overhead movements that could signal an approaching aerial predator. Observer presence could have been a source of perceived predation risk, although, it appeared that the birds paid minimal attention to people unless they entered the pen. We did not control for observer proximity or distance of perches from walls. We did, however, control for other potentially confounding factors in studies of vigilance, including age, sex, temperature, availability of food, flock density and actual predation risk (Elgar, 1989).

Theoretically, the amount of vigilance required per animal to detect predators declines as group size increases. This reduced need for vigilance allows animals to perform other activities during the time that would otherwise be spent in vigilance. The benefit of reduced time spent vigilant in a larger group is high when comparing relatively small groups but reaches an asymptote above which there are diminishing returns from being in even larger groups. Theoretical models, and some experimental data, suggest that the greatest benefits in terms of reduced vigilance occur as group size increases from two, to about 5–10, animals (e.g. Berger, 1978; Dehn, 1990). Although our group sizes were above this range, we found that, in our larger groups, synchronisation of preening and perch use occurred at a local level among neighbouring birds rather than over all birds in the group (Keeling *et al.*, 2001) and the same probably applied to vigilance. When considering vigilance as a proportion of the numbers of birds present locally on each perch, the numbers were in the range where the strongest group size effects on vigilance would be expected. It is possible that there were edge effects on heavily occupied perches such that birds on the ends of perches were more vigilant than those in the centre, as reported for other species (e.g. Robinson, 1981). If so, we would predict higher vigilance in the smaller groups due to the shorter perches in those pens. Our results are consistent with this prediction for birds on the upper perch level.

The proportion of birds preening on the floor increased with group size and age, suggesting that older birds in larger groups were more likely to feel sufficiently safe to engage in vulnerable activities on the floor. It appeared that birds in larger groups either moved straight up to the preferred top perch level to rest and preen or stayed on the floor whereas, because birds in smaller groups were more motivated to get off the floor, they made use of lower perch levels to rest and preen when the top level was occupied. Although the birds had ample opportunity to habituate to their predictable indoor environment, predatory attacks usually occur by surprise and birds should not take risks unless they are energetically compromised, which was not the case in our birds. In evolutionary terms, conservatism in the rate of loss of antipredator behaviour under conditions of relaxed predation pressure might be expected. Given the relatively limited number of generations

that have passed since most domestic fowl kept for commercial egg production have been fully protected from non-human predators in indoor housing, one would still expect to find that their antipredator behaviour follows patterns evolved under pressure from wild predators. The changes in the perching behaviour that we have observed in young domestic fowl with increasing group size are consistent with those hypothesised to result from predation pressure in wild animals.

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References

- Abrahamsson, P., Tauson, R., Appleby, M.C., 1996. Behaviour, health and integument of four hybrids of laying hens in modified and conventional cages. *Br. Poult. Sci.* 37, 521–540.
- Appleby, M.C., 1995. Perch length in cages for medium hybrid laying hens. *Br. Poult. Sci.* 36, 23–31.
- Appleby, M.C., Duncan, I.J.H., 1989. Development of perching in hens. *Biol. Behav.* 14, 157–168.
- Appleby, M.C., Hughes, B.O., 1995. The Edinburgh modified cage for laying hens. *Br. Poult. Sci.* 36, 707–718.
- Appleby, M.C., Duncan, I.J.H., McCrae, H.E., 1988. Perching and floor laying by domestic hens: experimental results and their commercial application. *Br. Poult. Sci.* 29, 351–357.
- Appleby, M.C., Smith, S.F., Hughes, B.O., 1992. Individual perching behaviour of laying hens and its effects in cages. *Br. Poult. Sci.* 33, 227–238.
- Berger, J., 1978. Group size, foraging, and antipredator plays: an analysis of bighorn sheep decisions. *Behav. Ecol. Sociobiol.* 4, 91–99.
- Bilčík, B., Keeling, L.J., Newberry, R.C., 1998. Effect of group size on tonic immobility in laying hens. *Behav. Proc.* 43, 53–59.
- Brake, J., 1987. Influence of presence of perches during rearing on incidence of floor laying in broiler breeders. *Poult. Sci.* 66, 1587–1589.
- Carmichael, N.L., Walker, A.W., Hughes, B.O., 1999. Laying hens in large flocks in a perchery system: influence of stocking density on location, use of resources and behaviour. *Br. Poult. Sci.* 40, 165–176.
- Collias, N.E., Collias, E.C., 1967. A field study of the Red Jungle Fowl in north-central India. *Condor* 69, 360–386.
- Collias, N.E., Joos, M., 1953. The spectrographic analysis of signals of the domestic fowl. *Behaviour* 5, 176–188.
- Crawford, R.D., 1990. Origin and history of poultry species. In: Crawford, R.D. (Ed.), *Poultry Breeding and Genetics*. Elsevier, Amsterdam, pp. 1–41.
- Cresswell, W., 1994. Flocking is an effective antipredation strategy in redshanks, *Tringa totanus*. *Anim. Behav.* 47, 433–442.
- Dehn, M.M., 1990. Vigilance for predators: detection and dilution effects. *Behav. Ecol. Sociobiol.* 26, 337–342.
- Elgar, M.A., 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev. Camb. Philos. Soc.* 64, 13–33.

- Evans, C.S., Evans, L., Marler, P., 1993. On the meaning of alarm calls: functional reference in an avian vocal system. *Anim. Behav.* 46, 23–38.
- Faure, J.M., Jones, R.B., 1982. Effects of age, access and time of day on perching behaviour in the domestic fowl. *Appl. Anim. Ethol.* 8, 357–364.
- Fiscus-LeVan, N.F., Estevez, I., Stricklin, W.R., 2000. Use of horizontal and angled perches by broiler chickens. *Appl. Anim. Behav. Sci.* 65, 349–365.
- Gallup Jr., G.G., Nash, R.F., Donegan, N.H., McClure, M.K., 1971. The immobility response: a predator-induced reaction in chickens. *Psychol. Rec.* 81, 513–519.
- Gunnarsson, S., Keeling, L.J., Svedberg, J., 1999. Effect of rearing factors on the prevalence of floor eggs, cloacal cannibalism and feather pecking in commercial flocks of loose-housed laying hens. *Br. Poult. Sci.* 40, 12–18.
- Hamilton, W.D., 1971. Geometry for the selfish herd. *J. Theor. Biol.* 31, 295–311.
- Hughes, B.O., Elson, H.A., 1977. The use of perches by broilers in floor pens. *Br. Poult. Sci.* 18, 715–722.
- Illius, A.W., Fitzgibbon, C., 1994. Costs of vigilance in foraging ungulates. *Anim. Behav.* 47, 481–484.
- Johnson, R.A., 1963. Habitat preference and behaviour of breeding jungle fowl in central western Thailand. *Wilson Bull.* 75, 270–272.
- Keeling, L.J., 1997. A comparison of two basic characteristics of a perch for laying hens. In: Hemsworth, P.H., Špinká, M., Kostal, L. (Eds.), *Proceedings of the 31st International Congress of the ISAE. Research Institute of Animal Production*, 13–16 August 1997, Prague, CZ, p. 83.
- Keeling, L.J., Duncan, I.J.H., 1991. Social spacing in domestic fowl under semi-natural conditions: the effect of behavioural activity and activity transitions. *Appl. Anim. Behav. Sci.* 32, 205–217.
- Keeling, L.J., Newberry, R.C., Estevez, I., 2001. Effects of group size on the behavioural synchronisation of laying hens. *Appl. Anim. Behav. Sci.*, submitted for publication.
- Landeau, L., Terborgh, J., 1986. Oddity and the “confusion effect” in predation. *Anim. Behav.* 34, 1372–1380.
- Lima, S.L., Dill, L.M., 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68, 619–640.
- McBride, G., Parer, I.P., Foenander, F., 1969. The social organisation and behaviour of the feral domestic fowl. *Anim. Behav. Monogr.* 2, 127–181.
- Newberry, R.C., Shackleton, D.M., 1997. Use of cover by domestic fowl: a Venetian blind effect. *Anim. Behav.* 54, 387–395.
- Newberry, R., Blair, R., Gill, S., Knott, M., 1995. Health of broilers reared under two patterns of increasing light and with access to perches. *Poult. Sci.* 74 (Suppl. 1), 84.
- Nishida, T., Hayashi, Y., Shotake, T., Maeda, Y., Yamamoto, Y., Kurosawa, Y., Douge, K., Hongo, A., 1992. Morphological identification and ecology of the Red Jungle Fowl in Nepal. *Anim. Sci. Technol. Jpn.* 63, 256–269.
- Pulliam, H.R., Caraco, T., 1984. Living in groups: is there an optimal group size? In: Krebs J.R., Davies, N.B. (Eds.), *Behavioural Ecology: An Evolutionary Approach*, 2nd Edition. Blackwell, Oxford, pp. 122–147.
- Robinson, J.G., 1981. Spatial structure in foraging groups of wedge-capped capuchin monkeys *Cebus nigrivittatus*. *Anim. Behav.* 29, 1036–1056.
- SAS Institute, 1989. *SAS/STAT[®] User's Guide*, Version 6, 4th Edition, Vol. 2. SAS Institute Inc., Cary, NC.
- Stanford, C.B., 1995. Influence of chimpanzee predation on group size and antipredator behaviour in red colobus monkeys. *Anim. Behav.* 49, 577–587.
- Treves, A., 1999. Within-group vigilance in red colobus and redbelted monkeys. *Am. J. Primatol.* 48, 113–126.
- Wood-Gush, D.G.M., Duncan, I.J.H., 1976. Some behavioural observations on domestic fowl in the wild. *Appl. Anim. Ethol.* 2, 255–260.
- Wood-Gush, D.G.M., Duncan, I.J.H., Savory, C.J., 1978. Observations of the social behaviour of domestic fowl in the wild. *Biol. Behav.* 3, 193–205.