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Rearing without early access to perches impairs the spatial skills of laying hens

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Abstract

The effect of rearing with and without perches on the spatial ability of domestic hens (*Gallus gallus domesticus*) was investigated. No access or late access to perches during rearing has been shown to increase the later prevalence of floor eggs and cloacal cannibalism in loose-housed laying hens. This may be explained by either the birds reared without perches have difficulty using perches due to low muscle strength, lack of motor skills, and inability to keep balance, or they have impaired spatial skills necessary for moving around in three-dimensional space. These alternative explanations are not mutually exclusive.

Thirty, day-old chicks were randomly allocated into two equal groups and reared in litter pens, one with access to perches (P+) and one without (P-). At 8 weeks of age, all birds were given access to perches, and by 15 weeks, all birds were using perches for roosting at night. At 16 weeks, 10 birds from each group were tested in pens where food was presented on a wire mesh tier 40 cm above the ground (T40). Three consecutive tests, with increasing difficulty for the bird to reach the food, were then performed. Firstly, the food was presented at 80 cm above the ground but with the tier at 40 cm still present; secondly, food was presented on the tier at 80 cm; and then, finally, with the food on a 160 cm high tier with the tier at 80 cm still present. All birds were food deprived for 15 h before each test and the time from the bird entering the pen until reaching the food was recorded. There was no difference in the time to reach the food between P+ and P- birds in the T40 test. But as the difficulty of the task increased, the difference between the P+ and P- birds became significant, with the P- birds taking a longer time to reach the food or not reaching it at all. Since there was no difference between P+ and P- in the T40 test, it

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seems reasonable to suppose that the later differences did not depend on differences in physical ability. Therefore, the results may imply that rearing without early access to perches, in some ways, impairs the spatial cognitive skills of the domestic hen. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Perching and roosting high off the ground is important as a predator defense for many ground-dwelling birds, including the red junglefowl (*Gallus gallus*), from which our domestic hen (*Gallus gallus domesticus*) originated (McBride et al., 1969; Wood-Gush and Duncan, 1976; Wood-Gush et al., 1978). The ability to use perches is also important for domestic hens in their present environment, not least because food and water are often provided off the ground in commercial aviary systems. However, under commercial conditions, the opportunity to learn how to move between different levels is missing since chicks are usually reared in brooding cages.

Since predator defense behaviour almost always contains a large innate part and, in most cases, functions without any prior training (Bolles, 1970), the finding that young chicks reared without access to perches are less adept at using them later in life is something of a surprise (Appleby et al., 1983; Appleby and Duncan, 1989). Although there are no predators in commercial poultry systems, abnormal behaviours by one bird towards another, such as injurious pecking and cannibalism, are common. In a previous study, Gunnarsson et al. (1999) showed that rearing young chicks without access to perches and giving them access only after 4 weeks of age, doubled the prevalence of cloacal cannibalism in the adult flocks. Furthermore, the prevalence of floor eggs in these flocks was three times higher. A high level of floor eggs has previously been related to birds' impaired ability to perch (Appleby et al., 1983, 1988).

Early access to perches may influence the behaviour of adult hens in two different ways. The first alternative is that the use of perches at an early age increases the muscle mass and bone strength of the birds so that they are able to use the perches better, later in life. The second alternative is that the use of perches helps the bird to develop the cognitive skills necessary for moving around in three-dimensional space.

In the literature, there are several reports of how the lack of early experience of specific stimuli can have long-lasting or semi-permanent effects on brain development and behaviour (Inglis, 1975; Rosenzweig and Bennett, 1996). Research in this area seems to indicate that in several species, the newborn or newly hatched individual has the neural preparedness for normal development, but if exposure to critical stimuli is obstructed at sensitive periods, neural structures, in particular, and also certain behaviours, do not develop normally. Male zebra finches (*Taeniopygia guttata*), for example, must have social contact and must be exposed to singing from adult males at the age of 5–10 weeks, to be able to develop species typical singing later in life (Jones at al., 1996). Kittens (*Felis catus*), exposed to a one-directional visual environment, do not develop a normal visual cortex or normal spatial cognition (Blackmore and Cooper, 1970).

In this experiment, we aimed to investigate whether early access to perches enhances spatial skills in laying hens by equalising as much as possible the physical skills of birds reared with and without the opportunity to move between different levels. If there is a difference in spatial skills dependent on early experience, then birds reared with early access to perches should be able to perform tasks in three-dimensional space, in this case, finding food presented on different levels more quickly than birds without early access to perches.

2. Materials and methods

2.1. Animals and housing

Thirty, day-old non-beak-trimmed female chicks (G. gallus domesticus; Hisex brown hybrid) from a commercial hatchery, were randomly allocated into two home pens of $150 \times 250 \times 270$ cm (length \times width \times height) (Fig. 1a). The pens had a solid wall between them, whereas the other walls were solid up to 110 cm above the floor and then wire mesh up to the roof. The stocking density was 4 hens/ m^2 and wood-shavings were provided as litter material on the floor.

One pen (P +) contained five perches (10, 30, 60, 90 and 120 cm) above the floor). The perches were $60 \times 60 \text{ mm}$ and 150 cm long, making a total perch length of 750 cm, i.e., 50 cm/bird. The other pen (P -) had no perches for the first 8 weeks.

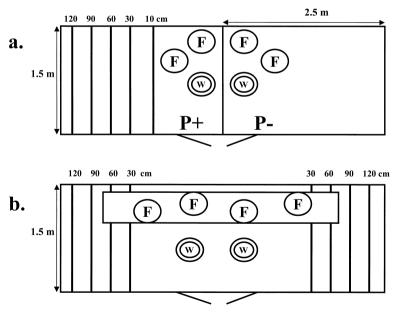


Fig. 1. (a) Pen layout during the first 10 weeks (F = food troughs, W = water). Pen P + contained perches whereas pen <math>P - did not contain perches. (b) Pen layout from 15 weeks onwards after the central partition had been removed, the perch arrangement modified and the food troughs placed on a tier at 60 cm above floor level.

The room was lit with light bulbs (60 W, white light) and the chicks were given 12 h of full light per day. The lighting regime was the same throughout the experiment. One infrared heat lamp (175 W) was placed in each group during the first 8 weeks to ensure an area with suitable and constant climate for the chicks. Standard commercial food (crumbled) and water were supplied ad libitum. The birds were never given coccidiostats or any other medication.

At 8 weeks of age, both home pens were provided with an identical perch arrangement. Thus, the three lowest perches (10, 30 and 60 cm) were removed from the P+ pen and two perches (at 90 and 120 cm) were put into the P- pen. The perch length in each pen was 20 cm/bird. The heat lamps were removed from the home pens. In the room, we installed a shielded 60-W light bulb, which was turned on and off 1 h before and after the ordinary light program, to create dusk and dawn light. The birds were also weighed and marked with plastic leg rings and wing clips for identification. Ten birds from each group were randomly selected as test birds and weighed.

2.2. Perch training

The birds were checked after dark every night, from 8 weeks of age, to see how many of them were roosting on the perches. No birds in the P- group were observed perching spontaneously for the first 4 days after they were given access to perches. Since a criterion for starting the experiment was that all birds, irrespective of rearing treatment, should able to roost on the perches at night-time, we began training the birds to perch at 9 weeks of age, i.e., 1 week after the perches were reorganised. All birds were lifted onto the perches two to four times a day. At 10 weeks, all birds were weighed again and the partition between the two compartments was taken away, so the P- and P+ birds were housed in one group. All birds moved between the two semi-compartments, and we observed no increase in aggression. At 11 weeks of age, we put perches at 30 and 60 cm above the floor into both semi-compartments to promote spontaneous use of perches. The perch length then became 40 cm/bird. Perch training, by lifting the birds onto the two highest perches, was continued until the birds were 15 weeks old.

At 15 weeks of age, a wooden tier $(25 \times 157 \text{ cm})$ was placed 60 cm above the floor in the home pen, and the four feeders were all put on the tier (Fig. 1b). Thus, food was only available on the tier. This was to get the birds used to finding food above floor level as the birds could reach the tier either by jumping up to the tier directly from the ground or via the 30 and 60 cm high perches. The body weight of all birds was checked everyday during the following week, to control that all birds were fed properly. By 16 weeks of age, all birds were roosting spontaneously at night.

2.3. Habituation to the test pens

At 11 weeks, we started to habituate the birds to finding food on the floor in the two test pens. The test pens each measured $100 \times 100 \times 270$ cm (length \times width \times height) (Fig. 2). The test pens were placed in the same room as the home pen and the floors were covered with wood-shavings. All walls of the test pens were solid except for the

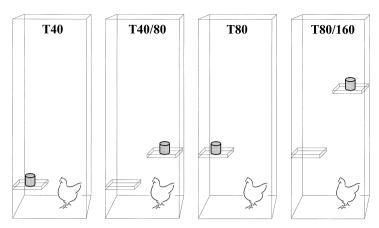


Fig. 2. Test pen arrangements. The tier was made of wire mesh $(30 \times 30 \text{ cm})$ and the feeder was identical to those in the home pen. In test T40, the food was presented on a tier 40 cm above the floor. In test T40/80, the food was presented 80 cm above the ground but with the tier at 40 cm still present. In T80, the lower tier was removed and the testing repeated with food present on the tier at 80 cm, and in T80/160, the food was on a 160-cm-high tier with the tier on 80 cm still present.

door, which was made of wire mesh from 30 cm and above. The birds were food-deprived for 1 h before the habituation sessions started and were then fed in the test pen. The birds were habituated in groups of three or four for 4 consecutive days with the individuals in the groups changing everyday. The observers sat quietly, approximately 2 m from the doors of the test pens, during the habituation as they would during the test sessions. Birds were then habituated singly until all birds were feeding in the test pens.

2.4. Testing

At 16 weeks of age, we started testing the individual birds with food presented on a tier 40 cm above the floor (T40). The tier was made of wire mesh $(30 \times 30 \text{ cm})$ and the feeder was identical to those in the home pen. The side of the 50-cm-high feeder was visible from the floor when it was placed on the 40- and 80-cm tiers, and the bottom of the feeder was visible through the wire mesh at all heights. The placement of the tier was varied systematically between the left and right side of the test pen.

During the test, we recorded the time (s) until the bird jumped up onto the tier and started to peck the food. The maximum session length was 600 s. The number of attempts to reach the tier was recorded, as well as the quality of the jumps, that is if the bird kept its balance after jumping up on the tier. The quality of the jump was according to the following scale: (1) attempted to jump up to the tier but did not reach the tier with its feet; (2) attempted to jump up to the tier, touched it with at least one foot but then fell down again; (3) jumped up on the tier and stayed there, but had difficulties in balancing; and (4) jumped up onto the tier easily and with good balance.

The birds were first tested after a 3-h food deprivation time and then followed by a 15-h food deprivation. The reason for this was to find a suitable food deprivation time, where most birds would try to jump up onto the tier to reach the food. In all the following sessions, only the 15-h food deprivation time was used.

In a subsequent test, the food was placed on the tier at 80 cm above the ground, but with the tier at 40 cm still present (T40/80). At 19 weeks of age, the lower tier was removed and the testing repeated with food present on the tier at 80 cm (T80) and then, finally, with the food on a 160-cm-high tier with the tier at 80 cm still present (T80/160) (Fig. 2).

We performed clinical examination and scoring of all individual birds at the same time as the birds were weighed at 16 and 19 weeks, respectively. The examination was performed according to a method presented in Gunnarsson et al. (1995), which involved scoring of body features such as general condition, keel bone condition, status of integument, comb status, foot condition, and status of the cloaca; in total 36 different variables were scored.

2.5. Statistical analysis

Statistical analysis of bodyweight at 8, 10, 16 and 19 weeks of age was performed using Student's *t*-test (Altman, 1994). As the observation time when the birds were in the test pens was interrupted after 600 s, the time to reach the food was analysed with Wilcoxon generalised test for truncated data (SAS Institute, 1990). Wilcoxon rank sum tests were used to analyse the jump scores, as well as the time to reach the food when only the birds reaching the food were included in the data set (SAS Institute, 1990).

3. Results

In the P + group, the first chicks were seen perching on the lowest perch 8 days after hatching. Perching chicks were observed on the second perch 11 days after hatching and on the highest perch, 22 days after hatching.

The body weight (mean \pm SD) was at 8 weeks of age, 842 ± 83 g; at 10 weeks, 977 ± 96 g; at 16 weeks, 1273 ± 102 g; and at 19 weeks, 1496 ± 100 g. There was no significant difference in mean body weight between the P + and the P - birds at any of the four times they were weighed (8 weeks, t = -0.92, df = 19, P = 0.37; 10 weeks, t = -1.64, df = 19, P = 0.12; 16 weeks, t = -0.36, df = 19, t = 0.72; 19 weeks, t = 0.18, t = 0.18, t = 0.18, t = 0.86. All birds were scored as normal for all body features during clinical examinations at 16 and 19 weeks of age. Thus, these results were not analysed further.

No bird lost weight when the feeders were placed on the raised tier in the home pen and all birds were roosting on the perches at night-time by 16 weeks of age. Casual observations showed no apparent differences in how P + and P - birds moved about the pen or used the perches. Thus, we concluded that when the testing in the experimental pens started, all birds could jump at least 30 cm off the ground and that they could jump from this perch to another perch 60 cm above the ground.

When 3-h food deprivation was used, only five out of 20 birds reached the food and there was no significant difference between P + and P - birds (Fig. 3a; Table 1). Furthermore, there was no difference between P + and P - birds when the deprivation time was increased to 15 h, although in this test, all birds except three jumped

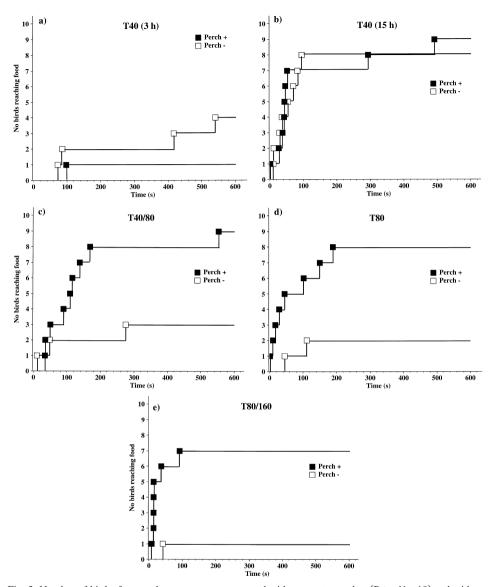


Fig. 3. Number of birds, from each treatment group; reared with access to perches (P+, N=10) and without perches (P-, N=10), reaching the food in the different test situations. (a) T40(3h) = food on 40 cm tier and 3 h food deprivation time. (b) T40 (15h) food on 40 cm tier and 15 h food deprivation time. (c) T40/80 = food on 80 cm tier and 15 h food deprivation time. (d) T80 = food on 80 cm tier and 15 h food deprivation time. (e) T80/160 food on 160 cm tier and 15 h food deprivation time.

immediately up to the tier to reach the food (Fig. 3b; Table 1). But, when the difficulty of the task increased, the birds from P + were significantly faster in reaching the tiers and in pecking the food than the P - birds (Fig. 3c-e; Table 1). In the most difficult

Table 1 Results for birds reared with perches (P+; N=10) and birds reared without perches (P-; N=10); median time and number of hens reaching the food and distribution of jump scores. Time to reach the food was analysed with Wilcoxon generalised test for truncated data and the jump scores (4 = most successful jump) were analysed using Wilcoxon rank sum test

Test situation	P+					P —						Wilcoxon generalised test for comparing time to reach food		Wilcoxon rank sum test for comparing jump scores		
	Median time (s)	No. of hens reaching the food	Jump score distribution ^a				Median time	No. of hens reaching	Jump score distribution ^a				χ_1^2	P-value	S	P-value
			4	3	2	1	(s)	the food	4	3	2	1				
T40 (3-h food deprivation)	600	1	1	-	-	_	600	4	1	3	-	-	2.22	0.14	4.5	0.41
T40 (15-h food deprivation)	45	9	7	2	-	-	62	8	6	1	1 ^b	-	0.05	0.82	70	0.84
T40/80	112	9	9	_	_	_	600	3	3	_	_	_	4.41	0.04	19.5	1.00
T80	73	8	8	_	_	-	600	2	2	-	_	_	6.93	0.008	11	1.00
T80/160	25	7	7	_	_	_	600	1	4	_	_	_	8.03	0.004	4.5	1.00

^aWhen two jumps were needed for reaching the food (T40/80 and T80/160), average score is presented.

^bThis bird scored 3 in the second trial.

task (T80/160), only one of the P – birds reached the food compared to seven of the P + birds (Fig. 3e). However, of the birds that jumped up to the tiers, there was no significant difference in the quality of the jump (Table 1) or in the time to start pecking in the food between P + and P – birds (Wilcoxon rank sum test; T40 (3 h), S = 3, df = 4, P = 1.00; T40 (15 h), S = 70, df = 16, P = 0.88; T40/80, S = 16, df = 11, P = 0.58; T80, S = 13, df = 9, P = 0.70; T80/160, S = 7, df = 7; P = 0.38).

There were no occasions when a bird managed a more difficult task when it had not also achieved the task immediately preceding it. That is to say, all birds reaching food in T80/160 had reached food in T80. All birds reaching the food in T80 had reached the food in the T40/80 and so on. In the situations with two tiers (T40/80 and T80/160, birds not reaching the food did not even make any attempts to reach the lower tier.

4. Discussion

There was a significant difference between the P + and the P - birds in their ability to gain access to food placed on high tiers, but not low tiers.

Previously, the general development of perching in laying hens, as well as individual differences in perching behaviour, has been reported. There are studies where the birds have been reared with early access to perches (Faure and Jones, 1982b; Appleby et al., 1988) or late access, i.e., from the time they became adult (Faure and Jones, 1982a; Appleby et al., 1992; Lambe and Scott, 1998). Nevertheless, it has not been clear how to explain the beneficial effect of this early experience of access to perches on later utilisation of three-dimensional space. The results from our experiment suggest that the effect is on the individual's development of cognitive spatial skills.

It may be argued that the difference between P+ and P- birds could be explained by the lack of physical ability among the P- birds due to low muscle strength, lack of motor skills for jumping, or inability to keep balance. It would be difficult to completely prove that the physical ability is the same for birds from both treatments as their early rearing was different. However, it seems reasonable to suppose that there was no major difference between the bird groups, as there was no significant difference in average body weight or clinical features between P+ and P- birds, and all birds were perching spontaneously and moving easily between the perches in their home pen at 16 weeks of age. Perhaps, most importantly, there was no difference between P+ and P- birds in the time taken for those who did succeed in jumping up to the food in the test situations or in the quality of the jump.

It would have been desirable to measure the muscle strength of the birds' legs as well as their wings to rule out any effect of differences in motor capability for jumping. We found difficulties in developing such tests and reviewing the literature, we found no study of muscles dynamics in laying hens. As increased muscle activity stimulates the calcification of bone tissue (Guyton 1986) and muscle strength is recovered faster than bone mineral density (Sievanen et al., 1994), an increase in bone strength would imply an increase in muscle strength. There are studies comparing the bone strength of hens housed in battery cages and alternative systems at the end of the laying period. Birds

housed in aviary systems with perches or tiers have stronger bones than those kept in cages (Nørgaard-Nielsen, 1990; Fleming et al., 1994). However, Newman and Leeson (1998) found no difference in tibia bone strength between old, previously caged, laying hens kept in an aviary for 20 days and their contemporaries maintained in the aviary the whole time. In our experiment, all birds were housed under the same conditions from 8 weeks of age, i.e., 8 and 11 weeks before the tests were carried out. Thus, differences in bone strength, as well as in muscle strength, between P + ADP - BDP - B

As there was no difference between P+ and P- birds in their time to reach the food in T40 after 3- or 15-h food deprivation, the P+ and P- birds probably had the same physical ability to jump from the ground to the 40-cm tier. There is no obvious reason to believe that the physical effort required to jump from 40 to 80 cm was substantially different, as the length and the angle required for the jumps were the same. Nevertheless, since there was a significant difference in the number of birds reaching the 80-cm tier in the T40/80 treatment, it implies that there were other aspects to the task than solely the physical capacity that made it more difficult. We propose that it is the cognitive aspect of the task that is causing problems for the birds reared without perches. That is to say, firstly, the food is higher up off the ground, and so above eye-level to the bird, and, secondly, that it cannot be reached directly, but requires a two-step process whereby the bird first jumps away from the food.

Regolin and Vallortigara (1995) have investigated detour behaviour in two-dimensional problems. In contrast with our experiment, the reward in their experiment was not visible for the chicken when the detour was made; this has previously been shown to facilitate detour problem solving. In this sense, our problem might have been harder for the animals to solve; something that is also evident from our results. Nevertheless, we consider our setup to be based on the commercial situation for laying hens, where food is raised up on tiers and is often visible from the ground.

Our results, put into context of previous studies of perches in laying hens (Faure and Jones, 1982b; Appleby et al. 1988; Gunnarsson et al., 1999), showed the importance of early access to perches for utilisation of raised tiers. However, it can be argued that the usage of perches may decrease the welfare of laying hens, as birds that have access to perches have more keel bone deformations, and that prevalence of deformations increases with age (Platt, 1933; Carstens et al., 1936; Appleby et al., 1993; Abrahamsson et al., 1996). The usage and design of perches influence the incidence of keel bone deviations (Tauson and Abrahamsson, 1996) and, to a minor extent, the disorder has been attributed to strain (Abrahamsson et al., 1996) and insufficient calcium metabolism (Carstens et al., 1936; Appleby et al., 1993). However, in our study, no keel bone deviations were found during the clinical scoring of the birds.

As far as we know, this is the first time that provision of perches for the development of spatial skills in the domestic hen has been investigated. From our results, it seems reasonable to suppose that the early access of perches affects the cognitive ability of the birds and that this effect is not confounded with the birds' physical ability. However, from our results, it is not possible to distinguish whether this effect is due to a development of a specific spatial skill in relation to perches and tiers or to a more general development of spatial cognition.

5. Conclusion

Rearing without early access to perches seems to impair the cognitive spatial skills of the domestic hen and the effect is both pronounced and long-lasting. It affects how easily birds move about in an aviary system and this, in turn, has practical and welfare implications.

Acknowledgements

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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.
- Altman, D.G., 1994. Practical Statistics for Medical Research. 1st edn. Chapman & Hall, London, 611 pp.
- Appleby, M.C., Duncan, I.J.H., 1989. Development of perching in hens. Biol. Behav. 14, 157-168.
- Appleby, M.C., Duncan, I.J.H., McRae, 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., McRae, H.E., Duncan, I.J.H., 1983. Nesting and floor-laying by domestic hens: effects of individual variation in perching behaviour. Behav. Anal. Lett. 3, 345–352.
- 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.
- Appleby, M.C., Smith, S.F., Hughes, B.O., 1993. Nesting, dust bathing and perching by laying hens in cages: effects of design on behaviour and welfare. Br. Poult. Sci. 34, 835–847.
- Blackmore, C., Cooper, G.F., 1970. Development of the brain depends on the visual environment. Nature 228, 477–478.
- Bolles, R.C., 1970. Species-specific defence reactions and avoidance learning. Psychol. Rev. 71, 32-48.
- Carstens, P., Wenzler, G., Prüfer, J., 1936. Untersuchung über die Verkrümmungen des Brustbeins beim Huhn (Investigation of keel bone deformation in the domestic fowl). Arch. Gefluegelkd. 10, 97–129.
- Faure, J.M., Jones, R.B., 1982a. Effects of sex, strain and type of perch on perching behaviour in domestic fowl. Appl. Anim. Ethol. 8, 281–293.
- Faure, J.M., Jones, R.B., 1982b. Effects of age, access and time of day on perching behaviour in domestic fowl. Appl. Anim. Ethol. 8, 357–364.
- Fleming, R.H., Whitehead, C.C., Alvey, D., Gregory, N.G., Wilkins, L., 1994. Bone structure and breaking strength in laying hens housed in different husbandry systems. Br. Poult. Sci. 35, 651–662.
- Gunnarsson, S., Keeling, L.J., Svedberg, J., 1999. Effects 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.
- Gunnarsson, S., Odén, K., Algers, B., Svedberg, J., Keeling, L., 1995. Poultry health and behaviour in a tiered system for loose housed layers, Department of Animal Hygiene, Swedish University of Agricultural Sciences, Skara, Sweden. Report 35, 142 pp.
- Guyton, A.C., 1986. Textbook of Physiology. 7th edn. Saunders, Philadelphia, PA.
- Inglis, I.R., 1975. Enriched sensory experience in adulthood increases subsequent exploratory behaviour in the rat. Anim. Behav. 23, 932–940.
- Jones, A.E., Ten Cate, C., Slater, P.J.B., 1996. Early experience and plasticity of song in adult male zebra finches (*Taeniopygia guttata*). J. Comp. Psychol. 110, 354–369.

- Lambe, N.R., Scott, G.B., 1998. Perching behaviour and preferences for different perch designs among laying hens. Anim. Welfare 7, 203–216.
- McBride, G., Parer, I.P., Foenander, F., 1969. The social organization and behaviour of the feral domestic fowl. Anim. Behav. Monogr. 2, 126–181.
- Newman, S., Leeson, S., 1998. Effect of housing birds in cages or an aviary system on bone characteristics. Poult. Sci. 77, 1492–1496.
- Nørgaard-Nielsen, G., 1990. Bone strength of laying hens kept in an alternative system, compared with hens in cages and on deep-litter. Br. Poult. Sci. 31, 81–90.
- Platt, C.S., 1933. Crooked keels in relation to width of perches. Poult. Sci. 12, 333-334.
- Regolin, L., Vallortigara, G., 1995. Detour behaviour of the domestic chick: searching for a disappearing prey and disappearing social partner. Anim. Behav. 50, 203–211.
- Rosenzweig, M.R., Bennett, E.L., 1996. Psychobiology of plasticity: effects of training and experience on brain and behavior. Behav. Brain Res. 78, 57–65.
- SAS Institute, 1990. In: SAS/STAT User's Guide. 4th edn. SAS Institute, Cary, NC, USA, p. 1686.
- Sievanen, H., Kannus, P., Heinonen, A., Oja, P., Ivuori, I., 1994. Bone mineral density and muscle strength of lower extremities after long-term strength training, subsequent knee ligament injury and rehabilitation: a unique 2-year follow up of a 26-year-old female student. Bone 15, 85–90.
- Tauson, R., Abrahamsson, P., 1996. Foot and keel bone disorders in laying hens. Effects of artificial perch material and hybrid. Acta Agric. Scand., Sect. A: Anim. Sci. 46, 239–246.
- Wood-Gush, D.G.M., Duncan, I., 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 on the social behaviour of domestic fowl in the wild. Biol. Behav. 3, 193–205.