The effect of perches and aviary tiers on the mating behaviour of two hybrids of broiler breeders

Sabine G. Gebhardt-Henrich a,*, Anja Jordan a, Michael J. Toscano a, Hanno Würbel b

a Center for Proper Housing: Poultry and Rabbits, Division of Animal Welfare, University of Bern, Burgerweg 22, CH-3052 Zollikofen, Switzerland
b Division of Animal Welfare, VPH Institute, University of Bern, Switzerland

1. Introduction

Aerial perches are among the most valued resources of chickens and are thus required for laying hens e.g. in Europe (EFSA Panel on Animal Health and Welfare (AHAW) (2010)) and Switzerland (Tscher, 2008). Especially at night, chickens use perches (Blokhuis, 1984; Olsson and Keeling, 2005; Odén et al., 2002) while they prefer high structures over low structures (Brendler et al., 2014). Despite the requirements, housing of broiler breeders commonly does not include perches (Gebhardt-Henrich et al., 2017; Riber et al., 2017; Gebhardt-Henrich et al., 2018). It is possible that perches interfere with mating activity when females can perch to avoid males willing to mate as all matings take place on the litter according to producers (personal communications). However, to our knowledge, literature on this topic is missing.

Broiler breeders are the parent generation of broilers which have been successfully selected for high growth rates during the last 5 decades (Zuidhof et al., 2014). These special genetic lines only exist in intensive production systems. Their actual growth rate is dampened from the genetic potential by intense feed restriction during rearing and production. At the same time, females are selected for high egg production and males for frequent mating behaviour. The most important welfare problems in these animals are feed restriction and male aggression (Jong and Guémené, 2011). The severe feed restriction during rearing and the somewhat less severe restriction during production result in a permanent feeling of hunger (Mench, 2002; Dixon et al., 2013, 2014).

Males of broiler breeder hybrids are supposedly more aggressive...
towards females than male layer breeders (Millman and Duncan, 2000b) and more aggressive towards females than an Old English Game breed which had been selected for male/male fighting (Millman and Duncan, 2000c). The cause of the aggression of the male towards the female is that mating events are mainly forced by the male instead of following courtship behaviour. Females are stressed and damaged by the rough mating acts of the males (Mench, 1993; Millman et al., 2000; Millman and Duncan, 2000a; Leone and Estévez, 2008; Jong et al., 2009). To avoid injuries in the females, spurs and the last digit of the hind toe of the males in some hybrids are cut and the beak might be trimmed (Fiks-van Niekerk and Jong, 2007). These mutilations cause suffering in the males and can disturb mating behaviour (Jones and Prescott, 2000).

Courtship and aggressive behaviours share the same origin ontogenetically and aggressive elements remain present during mating to some extent (Krujt, 1964) leading to elevated female mortality in the first weeks after mating commences (Mench, 1993) despite the above mentioned mutilations of males. The aggression of male broiler breeders is not caused by feed restriction (Millman et al., 2000) which led de Jong et al. (2009) to conclude that the mating behaviour in broiler breeders is problematic and needs to be examined in more detail.

As we showed in a previous publication (Gebhardt-Henrich et al., 2018) broiler breeders of a fast (Ross 308) and slower (Sasso) growing hybrid use perches and perches on aviary tiers in an analogous way to laying hens. The aim of this study was to investigate how the presence of aerial perches and perches on aviary tiers influenced the mating behaviour in these animals. We hypothesized that the possibility of females to avoid males by perching would lead to more courtship behaviour in the males and a greater willingness of the hens during mating events.

2. Material, animals and methods

The experiment was approved by the cantonal Food Safety and Veterinary Office Fribourg (2013_26.FR+) and met all cantonal and federal regulations for the ethical treatment of laboratory animals.

2.1. General housing and management

Management during rearing and production followed the recommendations of the breeding companies (Aviagen, 2013) and is described in more detail elsewhere (Gebhardt-Henrich et al., 2017). Briefly, hybrids had to be kept in separated identical (semidetached) houses for management reasons. Each house contained 10 pens of which 9 (3 per treatment: control, aviary, perch) were used for the study. Each pen was 5 × 3.8 m (W × L) and the density was 6.3 hens per m². Control pens (C) consisted of: a litter area, raised slats leading to group nestboxes with male feeders raised above the litter area, and 2 feeding troughs that only females could access on the litter and on the slats. A drinking line was above the litter area until the chicks reached 6 weeks of age (WOA) and was then replaced by a drinking line above the slats in front of the nestboxes. Pens with aerial perches (P) additionally contained 8 wooden perches on the slats. The animals were placed as 1-day-old chicks from the NL (Ross 308) or France (Sasso). Following our request, beaks were not treated, however, the spurs in the Sasso roosters seem to have been clipped. Birds were reared in the pens separated by sex until they were mated at 18 weeks of age. From then onwards, 119 females and 12 males were kept per pen. When distributing birds to pens sex until they were mated at 18 weeks of age. From then onwards, 119 females and 12 males were kept per pen. When distributing birds to pens

2.2. Data collection

Video recordings using IP cameras (Samsung) connected to a Multieye recorder (artec technologies AG, 49356 Diepholz, Germany) of the litter area of the pens at 35 and 40 weeks of age were used because hatching rates of the individual pens were available for the weeks 39 and 45. To determine the optimal time of day for observations, one day per treatment group was randomly picked. From these videos, the first 6 min of every hour during the light period (02:00–16:00 h) were observed (in total 540 min) and the attempted matings plus the actual matings were counted (see definition below). Male-hen interaction, particularly mating behaviour, was analysed with the all-occurrence continuous recording sampling method (Martin and Bateson, 1993), using INTERACT software (Version 14, Mangold International, Arnsdorf, Germany). Frequency, duration and sequence of the behavioural elements were recorded from the videos according to the ethogram (Table 1) by one person (AJ) based on existing ethograms (Engelmann, 1984; Duncan et al., 1990; Millman and Duncan 2000; McGary et al., 2003; De Jong et al., 2009). Supplementary video material on the underlined behavioural elements is available in the digital version.

Table 1

| Ethogram (according to Engelmann, 1984; Duncan et al., 1990; Millman and Duncan 2000; McGary et al., 2003; De Jong et al., 2009). Supplementary video material on the underlined behavioural elements is available in the digital version. |
|---------------------------------|
| Behavioural element | Description |
|----------------------|-------------|
| MALE | Tidbitting | The male pecks and scratches at the ground. |
| | Crowing | The male seems to make a loud singular call. The male moves the head backwards and forwards with neck outstretched and neck feathers ruffled. |
| | Wing flapping | The male’s wings are outstretched and flapped. |
| | Waltzing | The male moves in a semi-circle round the hen with short stumbling steps and has its far wing lowered. |
| | Approach | The male approaches the hen with high steps or positions itself behind or beside the hen, reared up and looks at the hen from above with stretched neck and the neck feathers ruffled. |
| | Running | The male runs after or towards a hen for at least three steps without a particular posture. |
| | Gobbler posture | The male runs towards or after a hen with stretched neck, ruffled feathers and lowered wings. |
| | Put a foot on | The male puts a foot on the hen’s back. |
| | Mounting | The male mounts the hen’s back and thereby has both legs on the back of the hen. |
| | Treating | The male makes small stepping movements with the feet on the hen’s back. |
| | Dismount | The male gets off the hen’s back. |
| | Neck bite | The male grabs the hen’s neck feathers with its beak. |
| | Cloacal contact | The male presses the cloaca against the hen’s cloaca. Good indicators for this: the male stops treading, goes backwards and downwards with a lowered pelvis and tail, while sitting on the hen’s back. |
| | Peck at the head | Vigorous downward blow of the beak of the male directed at the head or the comb of a hen. |
| HEN | Stand | The hen is standing motionless in an upright position before or when the male approaches. |
| | Walk | The hen is walking at a walking pace before or when the male approaches. |
| | Feeding | The hen is feeding at the feeder before or when the male approaches. |
| | Approach | The hen walks towards the male at a walking pace. |
| | Crouching | The hen crouches. |
| | Avoiding | The hen turns away from the male and avoids the male, but does not run away, when the male approaches. Male and hen do not have physical contact. |
| | Running away | The hen runs away from the male for at least three steps. |
| | Escape | The hen escapes the male during the male holds the hen’s neck feathers in its beak or has one or both feet on the hen’s back. It only counts as an escape when male and hen had physical contact, but there was no cloacal contact. |
| | Struggle during neck bite | The hen struggles during the male is holding the hen’s neck feathers in its beak; the hen tries to break away from the neck bite of the male. |
| | Struggle during mating | The hen struggles during mating and tries to shake the male off. |
A behavioural element (such as tidbitting, crowing, wing flapping) was only counted when it was clearly directed at a hen or happened immediately before or after a mating act. In addition, it was recorded whether the male-hen interaction took place on the litter area, on the slatted area or on the aviary tiers.

Based on the pilot observations described above, the first 3 min for each of the following 11 h (02:00, 03:00, 08:00–16:00) were chosen for analysis. Thus, for each hybrid, behaviour was analysed for about 10 h (594 min) in total (approximately 33 min per pen and per age of week) after limited technical problems. From the Sasso pen 6 (P) at 35 WOA and the Sasso pen 1 (control) at 40 WOA there were no video recordings available because of camera problems. Thus, at the respective week these two pens could not be used for observation. In case the camera had lost signal at the observation time, the subsequent 3 min were taken. Whenever the behaviour could not be recorded completely, because it was not visible on the video or the video recording paused, incomplete was inserted in place of the missing behavioural element.

Different elements of the ethogram were summarised for analysis. Waltzing, rear up, gobbler posture, wing flapping, crowing, and tidbitting were summarised as courtship behaviour. All male-hen interactions were grouped into five categories: (1) Pecking: The male pecked at the hen’s head or at the hen’s body; no mating and no attempted mating followed before the male walked away from the female, (2) Chasing: The male ran after a hen and the hen ran away from the male; no mating and no attempted mating followed, (3) Courtship: The male showed courtship behaviour; no mating and no attempted mating followed, (4) Attempted mating: The male grabbed the hen’s neck feathers with its beak or put a foot on the hen’s back; no mating followed, (5) Mating: The male mounted and was sitting on the hen’s back. The mating category was subdivided into successful (there was cloacal contact during mating) and failed matings (there was no cloacal contact during mating). In order to measure the duration of a mating, a mating was defined as the period between the male mounting the hen’s back and dismounting. Courtship, attempted matings, and matings were summarised as mating related behaviour. Incomplete mating behaviour was excluded in certain evaluations, depending on the missing behavioural element (success of mating: 20 % unknown, presence of crouching: 29 % unknown).

The behaviour of the hen during mating consisted of the two components crouching and struggling. Crouching was divided into four categories depending if and when the hen showed crouching: (1) Crouching only after the male had mounted on the hen’s back, (2) crouching during the neck bite or after the male had put a foot on the hen’s back, but before the male had mounted, (3) crouching by approach or courtship of the male, but without physical contact of male and hen and (4) hen was in a crouching position already when the male approached (e.g. the hen was sitting on the ground and did not stand up). Struggling was divided into two categories: (1) Struggling and trying to escape first, but no struggling after the male grabbed the hen and (2) struggling during neck bite or mating.

2.3. Statistics

Due to the varied total numbers of certain behaviours between the treatments, most were expressed as a percentage for easier comparison of the categories. For duration, the median was used. If there was more than one treading and cloacal contact per mating, the durations were added for a single value.

In general, full models included all interactions which were successively removed from the model when their P-values exceeded 0.2. Plots of residuals were used to evaluate the fit of the models. Post-hoc multiple comparisons were adjusted according to Scheffe’s procedure. The number of matings was analysed with a generalized linear model (Proc Glimmix, SAS®) using the Dual Quasi-Newton optimization technique with a log-link function and corrected for over dispersion. The pen nested in treatment and hybrid was taken as the subject factor. A logit-link function for binary data was used to analyse whether matings: were successful, took place on the litter, involved hens crouched without force, and involved hens struggling.

The percentage of matings with preceding courtship behaviour was analysed with a mixed general model (Proc Mixed, SAS®) on arc sine transformed percentages with pen as the repeated factor. Back transformed least squares with 95 % confidence intervals are presented.

The intra-observer reliability was assessed using Cohen’s Kappa-test within INTERACT. For this the observer coded a randomly chosen video clip (10 male-hen interactions) with INTERACT according to the ethogram twice.

3. Results

3.1. Intra-observer reliability

Intra-observer reliability was very high. The κ for hen behaviour and for location was 1.00 (number of codings: 25 and 14, respectively), that of male behaviour was 0.96 (number of codings: 29).

3.2. Frequency and success of matings

Although broiler breeders in pens with aerial perches and aviary tiers used the elevated structures during the light hours (Gebrhardt-Henrich et al., 2018) the frequency of matings did not differ among the treatments or hybrids (hybrid: F_{1,14} = 1.50, P = 0.24; treatment: F_{2,14} = 0.00, P = 0.99; age: F_{1,14} = 2.18, P = 0.16). However, there was a significant interaction between hybrid and age (F_{1,14} = 6.93, P = 0.02) (Fig. 1), namely the Ross hybrid tended to have fewer matings in the 40. than in the 35. week of age (t_{14} = 2.75, adj. P = 0.07).

Most matings (79.5 %) of the Ross hybrid were successful and only 20.5 % failed. Likewise in the Sasso hybrid, 80.4 % were successful and 19.6 % failed. If only the successful matings were compared, there were no differences due to hybrid, treatment, or age (hybrid: F_{1,73} = 0.67, P = 0.417; treatment: F_{2,73} = 0.61, P = 0.55; age: F_{1,73} = 0.80, P = 0.37).

3.3. Location

The equipment of the pens with aerial perches and aviary tiers affected the location of matings differently in the two hybrids (hybrid: F_{1,13} = 12.45, P = 0.004; treatment: F_{2,13} = 6.37, P = 0.01). The Ross hybrid mated most often on the litter area (75 % in control pens, 94.4 % in pens with perches) and the rest of the matings took place on the slatted area. In the pens with aviaries, matings were only observed on the litter area. In contrast, the Sasso hybrid mated more often on the slatted area in control pens (66.7 %) and pens with perches (62.5 %) than on the litter area. In the pens with aviaries, matings took place most often on the litter area and 18.2 % on the aviary tiers (Fig. 2).

3.4. Male mating behaviour

The male showed courtship behaviour before mating in only 24.5 % (95 % confidence interval: 11.2, 41.1) (Ross) and 25.8 % (12.4, 42.0) (Sasso) cases, respectively. No courtship means that the male approached or chased the hen without a particular posture or simply stood beside and grabbed the hen without previous interaction. In most cases, 74.3 % (54.5, 89.9) in Ross and 85.5 % (65.35, 97.7) in Sasso no mating followed when courtship was shown. Hybrids did not differ for these measures.

The most frequently observed courtship behaviours were rear up and waltzing, followed by the gobbler posture (see videos in the supplementary file). Matings occurred more after rear up than after waltzing and gobbler posture without a difference between hybrids or age (hybrid: F_{1,15} = 0.41, P = 0.53; age: F_{1,62} = 0.19, P = 0.67; courtship: F_{2,62} = 4.99, P < 0.01). The courtship elements crowing, wing flapping and tidbitting were rarely observed in connection with mating. No
courtship behaviour was observed between two males in the Ross hybrid. In contrast, 62.5 % of the waltzing and 30 % of the gobbler posture of Sasso males were directed at another male.

3.5. Female mating behaviour

The frequency when the hen crouched by approach or courtship of the male without physical contact between male and hen was greater in the Ross than in the Sasso hybrid \( (F_{1,99} = 11.57, P = 0.001) \) and varied between treatments \( (F_{2,99} = 3.03, P = 0.05) \) (Fig. 3). It was lower in the control treatment than in aviaries or pens with perches (least square means: control -2.3 ± 0.56, aviary -0.77 ± 0.38, perch -0.78 ± 0.40). Ross hens crouched like this in 44.7 % of all matings and Sasso hens only in 13.7 %. Instances when the hen did not crouch or the hen crouched after the male had mounted on the hen’s back were shown more frequently by the Sasso (13.7 %) than the Ross hens (2.1 %). The hen crouching after the neck bite or the male placed one foot on the back happened in 48.9 % cases in the Ross and 66.7 % in the Sasso hybrid.

Instances when the hen struggled during neck bite or mating were less frequent in the Ross (mean 6.7 %) than in the Sasso hybrid (mean 42.2 %) \( (F_{1,98} = 5.93, P = 0.02) \) and tended to be greater in 40 compared to 35 WOA \( (F_{1,98} = 3.11, P = 0.08) \). There was no difference between treatments \( (F_{2,98} = 0.84, P = 0.44) \).

4. Discussion

Most important for production, the presence of aerial perches or aviary tiers did not reduce the number or success rate of matings. These results are in agreement with the data on hatchability of brood eggs which did not differ among treatments (Gebhardt-Henrich et al., 2018).
The reduction in the number of matings of Ross 308 at 40 WOA corresponds to the lower hatching rate at 45 WOA in this hybrid (Gebhardt-Henrich et al., 2018). The relationship between the observed hatching rates and matings indicates that the behaviour observations were sufficiently accurate and valid. The lower mating activity in Ross 308 at 40 WOA could be caused by the high body mass of the males (5.7 ± 0.4 kg) (McGary et al., 2003). Besides the reduced mating activity in Ross 308, transfer of sperm (McGary et al., 2003), as well as sperm quantity and quality (Bilkic and Estevez, 2005) could have played a role but were not assessed in the current study. Hatchability rates were between 90.8 and 94 % in the Sasso and between 74.3 and 81.2 % in the Ross 308 at 35 and 45 WOA. These rates were lower than predicted from the breeding company for Ross 308 and could be due to the above average body mass of the males. Until depopulation at 48 WOA, we obtained on average 72.6 chicks per Ross 308 hen and 118.5 chicks per Sasso hen (Gebhardt-Henrich et al., 2018). The production figures of Ross 308 were unusually low and cannot only be explained by the low hatchability rates. Part of the reason was that Ross 308 males entered the nest boxes and ate eggs (pers. observation). The hen mortality was approximately 5% and the male mortality was about 24 % over the production cycle.

Although the number of matings was not affected by the provision of perches or aviary tiers, the location of the matings differed among treatments and hybrids. In contrast to Ross 308, Sasso males were mostly patrolling in the litter area which was devoid of females. It seemed that the Sasso females were actively avoiding the males and even hardly used the feeder in the litter area (Candelotto, 2015). Possibly, the large dimorphism in size between the dwarfed Sasso hen and the normal sized Sasso male caused fearful behaviour of the females towards the males. The size dimorphism in Ross 308 is much smaller and the hens avoided the males much less in this hybrid. The fearful behaviour of the Sasso hens towards the males is problematic because the Sasso hybrid is particularly used in management systems with high animal welfare standards like free-range and organic flocks. The dwarfing of hens requires less feed restriction in this sex which improves their welfare (Decuyper et al., 2010) though needs to be balanced against the possible negative aspect of fear of females towards males. Alternatively, sometimes the Sasso male stood on the litter instead of on the hen’s back during copulations which might be more comfortable for the hen.

In pens with aviaries mounted on the slats there was limited space for mating on the slats. The limited space is probably the reason why no matings were observed on the slats in aviary pens. Clearly, males had flexibility in deciding where to mate and also how they gained access to the females. Matings were also observed on aviary tiers in both species (unsystematic personal observations). Sasso males were seen to jump up onto the slats, drag females forcefully from perches and copulate with them. Hens falling from perches or aviary tiers were often mounted by several males in the vicinity (unsystematic observations).

In agreement with other published reports, most matings were not initiated by courtship behaviour of the male (Millman et al., 2000; Jong and Guémené, 2011). A reason for the low frequency of courtship behaviour could be the low responsiveness of the hens to males displaying courtship behaviour. The posture ‘rear up’ was almost the only male behaviour that was followed by the female’s response of crouching and thus initiating copulation. Alternatively, high body mass in males might limit the ability to show courtship behaviour (McGary et al., 2003). Strong directional selection for high mating activity in the male lines at the expense of courtship behaviour (Millman et al., 2000; Millman and Duncan, 2000b) could have favoured aggressive behaviour towards females and females might avoid males with aggressive behaviour (Millman and Duncan, 2000a). On the other hand, a misclassification of so-called courtship behaviour could also contribute to the supposedly low response of broiler breeder hens to male courtship displays. Waltzing which is an anthropomorphic expression and the gobbler posture might not belong exclusively to courtship behaviour but may indicate territoriality or a general state of arousal (Wood-Gush, 1971; Zuk et al., 1990). In at least in a third to half of all cases the male showed rear up, the hen responded with crouching, in contrast to waltzing or the gobbler posture which were rarely or never followed by a copulation. Wing flapping and crowing are also described as courtship behaviour (Kruitt, 1964; Wood–Gush, 1971; Chappell et al., 1997) but these behavioural elements were never observed in connection with copulations or directed towards a hen. Tidbitting is described as highly attractive to females (Wood-Gush, 1971; Millman and Duncan, 2000b; Millman and Duncan, 2000a) but was actually never observed in this study. Possibly, feed-restricted males would not share feed as much as non-deprived males and thus do not display tidbitting.

Besides a misclassification of a type of behaviour as courtship behaviour, other factors could be responsible for the lack of mating receptivity of the females. Compared with the ancestral species, broiler breeders are kept in large groups and thus might not be able to recognize each other as individuals and interfere with courtship behaviour (Millman et al., 2000; Jong et al., 2009). Other causes like separate rearing
are also reported (Jong et al., 2009). In this study, female and male chicks were reared under visual contact, but only the females in the pen next to the male’s pen had a good view of the opposite sex.

Ross hens rarely struggled during mating, in contrast to Sasso hens that struggled three times as much. Sasso hens mostly crouched only after the neck bite or after the male had put a foot on the hen’s back, compared with the Ross hens that already crouched by approach or courtship of the male in half of all cases. When the hen struggled and crouched only after the male had mounted on the hen’s back, it was considered a forced mating. Previous studies reported high frequencies of forced matings in broiler breeders (50 %: Millman et al., 2000, or even 82 %: Jong et al., 2009). In this study, forced matings were often observed in the Sasso hybrid (13.7 %), but they were very rare in the Ross (2.1 %). Possibly, the definition of a ‘forced’ mating differed between the studies. Usually, when the Ross hen struggled, the hen escaped the male, compared with the Sasso, where the male was often able to mate despite the struggling of the hen. A reason for the difference in escape success rate could be the large difference in size between Sasso males and hens, which allows the males to push the hen in a crouching position with its weight and force matings (Millman and Duncan, 2000a).

In the Ross 308 hybrid forced matings were more common in the absence of perches and aviaries. Maybe, the hens not willing to copulate escaped the males by sitting on the perches and on the aviary tiers.

In conclusion, this study confirmed that aggressive male behaviour and forced matings represent a welfare problem of (female) broiler breeders. However, the presence of perches and aviaries allowed the hens to withdraw from the males to a certain extent and reduced the number of forced matings at least in the Ross 308 hybrid. Therefore, due to the fact that there were no negative effects on mating activity or productivity, perches or aviaries can be recommended as environmental enrichment to improve the welfare of broiler breeders.

Declarations of Competing Interest

The authors report no declarations of interest.

Acknowledgements

We acknowledge funding from the Federal Food Safety and Veterinary Office FSVO (project number 2.13.10), Bell Schweiz AG, Micarna SA and Wüthrich Brüterei AG. Fritz Schwab did an excellent job caring for the broiler breeders. Maurice Sander (Aviagen™) gave valuable advice on the management of broiler breeders. We thank the extended Schwab family for hospitality on their farm during the study. Numerous helpers were involved in this project and without them this study would not have been possible. This publication is based on the MSc. thesis of Anja Jordan submitted to the Vetsuisse Faculty of the University of Bern.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.japplanimbei.2020.105145.

References

Aviagen, 2013. Management Handbook: Parentstock Ross. Aviagen. Bilcik, B., Estevez, I., 2005. Impact of male–male competition and morphological traits on mating strategies and reproductive success in broiler breeders. Appl. Anim. Behav. Sci. 92, 307–323.

Blokhuis, H.J., 1984. Rest in poultry. Appl. Anim. Behav. Sci. 12, 289–303.

Brendler, C., Kipper, S., Schrader, L., 2014. Vigilance and roosting behaviour of laying hens on different perch heights. Appl. Anim. Behav. Sci. 157, 93–99.

Candiletto, L., 2015. Floor Egg Rates In Different Housing Systems Of Two Broiler Breeder Strains (Ross 308 and Sasso) and Possible Measures to Reduce Floor egg. BSc, Bern, Switzerland.

Chappell, M.A., Zuk, M., Johnsen, T.S., Kwan, T.H., 1997. Mate choice and aerobic capacity in red junglefowl. Behaviour 134, 511–529.

Decypierre, E., Bruggeman, V., Everaert, N., Li, Y., Boonen, R., Tavernier, J.de, Janssens, S., Buys, N., 2010. The broiler breeder paradox: ethical, genetic and physiological perspectives, and suggestions for solutions. Br. Poult. Sci. 51, 569–579.

Dixon, L.M., Sandilands, V., Bateson, M., Brocklehurst, S., Tolkamp, B.J., D’Eath, R.B., 2013. Conditioned Place Preference or Aversion as animal welfare assessment tools: limitations in their application. Appl. Anim. Behav. Sci. 148, 164–176.

Dixon, L.M., Brocklehurst, S., Sandilands, V., Bateson, M., Tolkamp, B.J., D’Eath, R.B., 2014. Measuring motivation for appetitive behaviour: food-restricted breeder broiler chickens cross a water barrier to forage in an area of wood shavings without food. PloS One 9, e102252.

Duncan, L.J.H., Hocking, P.M., Sewright, E., 1990. Sexual behaviour and fertility in broiler breeder domestic fowl. Appl. Anim. Behav. Sci. 26, 201–213.

EFSA Panel on Animal Health and Welfare (AHAW), 2010. Scientific opinion on welfare aspects of the management and housing of the grand-parent and parent stocks raised and kept for breeding purposes. EFSA J. 8, 1667.

Engelmann, C., 1984. In: Neumann-Neudamm, J. (Ed.), Leben und Verhalten unseres Haußgeflügels, 1st ed. Radebeul, Germany.

Fiks-van Nierkerk, T., Jong, L.G.de, 2007. Mutillations in poultry in European poultry production systems. Lohmann Information 42, 35–46.

Gebhardt-Henrich, S.G., Toscano, M.J., Würl, B., 2017. Perch use by broiler breeders and its implication on health and production. Poult. Sci. 96, 3539–3549.

Gebhardt-Henrich, S.G., Toscano, M.J., Würl, B., 2018. Use of aerial perches and perches on aviary tiers by broiler breeders. Appl. Anim. Behav. Sci. 203, 24–33.

Jones, E.K.M., Prescott, N.B., 2000. Visual cues used in the choice of mate by fowl and their potential importance for the breeder industry. Worlds Poult. Sci. J. 56, 127–138.

Jong, L.G.de, Guzméni, D., 2011. Major welfare issues in broiler breeders. Worlds Poult. Sci. J. 67, 73–82.

Jong, L.G.de, Wolthuis-Fillerup, M., van Emous, R.A., 2009. Development of sexual behaviour in commercially-housed broiler breeders after mixing. Br. Poult. Sci. 50, 151–169.

Kruijt, J.P., 1964. Ontogeny of social behaviour in burmese red junglefowl (Gallus gallus spadiceus). Behav. Suppl. 1–201. No. 12.

Leone, E.H., Estevez, I., 2008. Economic and welfare benefits of environmental enrichment for broiler breeders. Poult. Sci. 87, 14–21.

Martin, P., Bateson, P., 1993. Measuring Behaviour, 2nd ed. Cambridge University Press, Cambridge, p. 222.

McGary, S., Estevez, I., Ruzek-Cohen, E., 2003. Reproductive and aggressive behavior in male broiler breeders with varying fertility levels. Appl. Anim. Behav. Sci. 82, 29–44.

Mench, J.A., 1993. Problems associated with broiler breeder management. Proceedings of the Fourth European Symposium on Poultry Welfare. 4th European Symposium on Poultry Welfare, Edinburgh. 18 – 21. September 1993. Universities Federation for Animal Welfare, The Old School, Brewhouse Hill, Wheathampstead, Herts AL4 8AN, UK, Herts, Great Britain, pp. 195–207.

Mench, J.A., 2002. Broiler breeders: feed restriction and welfare. Worlds Poult. Sci. J. 58, 603–609.

Millman, S.T., Duncan, L.J.H., 2000a. Do female broiler breeder fowl display a preference for broiler breeder or laying strain males in a Y-maze test? Appl. Anim. Behav. Sci. 69, 275–290.

Millman, S.T., Duncan, L.J.H., 2000b. Effect of male-to-male aggressiveness and feed restriction during rearing on sexual behaviour and aggressiveness towards females by male domestic fowl. Appl. Anim. Behav. Sci. 70, 63–82.

Millman, S.T., Duncan, L.J.H., 2000c. Strain differences in aggressiveness of male domestic fowl in response to a male model. Appl. Anim. Behav. Sci. 66, 217–233.

Millman, S.T., Duncan, L.J.H., Widowski, T.M., 2000. Male broiler breeder fowl display high levels of aggression toward females. Poult. Sci. 79, 1233–1241.

Oden, K., Keeling, L.J., Algers, B., 2002. Behaviour of laying hens in two types of aviary systems on 25 commercial farms in Sweden. Br. Poult. Sci. 43, 169–181.

Olsson, I.A., Keeling, L.J., 2000. Night-time roosting in laying hens and the effect of thwarting access to perches. Appl. Anim. Behav. Sci. 68, 243–256.

Riber, A.B., Jong, I.C.de, van de Weerd, H.A., Steenfeldt, S., 2017. Environmental enrichment for broiler breeders: an undeveloped field. Front. Vet. Sci. 4, 86.

Tsch, 2008. Tierschutzverordnung CH., Wood-Gush, D.G.M., 1971. The Behaviour of the Domestic Fowl. Heinemann Educational, London viii,147 st.

Zuidhof, M.J., Schneider, B.L., Carney, V.L., Verker, D.R., Robinson, F.E., 2014. Growth, efficiency, and yield of commercial broilers from 1957, 1978, and 2005. Poult. Sci. 93, 2970–2982.

Zuk, M., Thornthill, R., Ligon, J.D., Johnson, K., Austad, S., Ligon, S.H., Wilmont, N.T., Cristin, C., 1990. The role of male ornaments and courtship behavior in female mate choice of red JungleFowl. Am. Nat. 136, 459–473.