



HAL
open science

Influence of stocking density on some behavioural, physiological and productivity traits of broilers

A Martrenchar, Jp Morisse, D Huonnic, Jp Cotte

► **To cite this version:**

A Martrenchar, Jp Morisse, D Huonnic, Jp Cotte. Influence of stocking density on some behavioural, physiological and productivity traits of broilers. *Veterinary Research*, 1997, 28 (5), pp.473-480. hal-00902495

HAL Id: hal-00902495

<https://hal.science/hal-00902495>

Submitted on 11 May 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Influence of stocking density on some behavioural, physiological and productivity traits of broilers

A Martrenchar*, JP Morisse, D Huonnic, JP Cotte

*Centre national d'études vétérinaires et alimentaires, BP 53,
Zoopôle Beaucemaine, 22440 Ploufragan, France*

(Received 4 December; accepted 13 May 1997)

Summary — In order to investigate the influence of stocking density on broiler welfare, 17 616 Ross chickens were assigned to three different treatments: T_1 , T_2 and T_3 with a final stocking density of 27, 35 and 43 kg/m², respectively (corresponding to an initial density of 12, 16 and 20 birds/m²). Animal welfare was assessed by measuring behavioural, physiological and productivity traits. Behavioural observations included the disturbance frequency of resting birds by other birds, the duration of the lying bouts and the standing/lying ratio. The heterophil/lymphocyte ratios were assessed from blood collected before departure to the slaughterhouse. Main productivity traits were the final live weight and carcass degradation due to foot and pad dermatitis and breast blisters. Most of the observed parameters were adversely affected by the highest density ($P < 0.05$). Between T_1 and T_2 , some traits tended to demonstrate that a better degree of bird welfare existed in T_1 (higher standing/lying postures ratio and final live weight, lower frequency of pododermatitis and hock lesions; $P < 0.05$) whereas other traits showed no differences (frequency of disturbances by other birds during resting, heterophil/lymphocyte ratio). In conclusion, a stocking density of 43 kg/m² seemed to induce poor bird welfare whereas it was not clearly demonstrated that 27 kg/m² was better than 35 kg/m².

broiler / stocking density / behaviour / physiology / productivity

Résumé — Influence de la densité d'élevage sur différents paramètres comportementaux, physiologiques et zootechniques du poulet de chair. Dans le but d'étudier l'influence de la densité d'élevage sur le bien-être du poulet de chair, 17 616 poulets de souche Ross ont été divisés en trois traitements : T_1 , T_2 et T_3 avec, respectivement, une densité finale de 27, 35 et 43 kg/m² (correspondant à une densité initiale de 12, 16 et 20 oiseaux/m²). Le bien-être animal a été estimé en mesurant différents paramètres comportementaux, physiologiques et zootechniques. Les observations comportementales incluaient la fréquence de dérangement des oiseaux au repos par d'autres oiseaux, la durée des périodes de repos et le pourcentage d'oiseaux debouts/couchés. Le rapport hétérophiles/lym-

* Correspondence and reprints
Tel: (33) 02 96 01 62 22; fax: (33)02 96 01 62 23;
e-mail: Arnaud.MARTRENCHAR.CNEVA@zoopole.asso.fr

phocytes a été mesuré sur des échantillons de sang prélevés avant le départ à l'abattoir. Les principaux paramètres zootechniques étaient le poids final et les défauts de carcasse dus aux lésions de pododermatite plantaire et aux ampoules de bréchet. La plupart des paramètres observés ont été affectés d'une manière négative par la densité la plus élevée ($p < 0,05$). En ce qui concerne la comparaison entre T_1 et T_3 , certains paramètres indiquaient un meilleur niveau de bien-être dans T_1 (pourcentage plus élevé d'oiseaux debouts/couchés, poids final plus important, fréquence plus faible de lésions de pododermatite plantaire ; $p < 0,05$) tandis que d'autres paramètres ne montraient pas de différences (fréquence de dérangement des oiseaux au repos par d'autres oiseaux, rapport hétérophiles/lymphocytes). En conclusion, une densité de 43 kg/m^2 semble diminuer le bien-être des animaux alors que la différence entre 35 kg/m^2 et 27 kg/m^2 n'a pas été clairement démontrée.

poulet de chair / densité d'élevage / comportement / physiologie / zootechnie

INTRODUCTION

The optimal stocking density of broilers is a question that is currently very much under debate. At present, there is no European regulation fixing an upper limit. In France, the average stocking density used by producers varies from 20 to 23 birds per square metre. This has been largely determined by economic considerations (Magdelaine, 1995). From a welfare point of view, high stocking densities may create various problems (reviewed by Ekstrand, 1993), such as a decrease in the average distance travelled per day by the birds, a deleterious effect on the quality of the atmosphere and of the litter resulting in an increase in the incidence of dermatitis. Other changes in the behavioural pattern have also been described. In particular, Lewis and Hurnik (1990) have shown that as the stocking density increased, chickens spent less time resting. It could be assumed that this modification of the resting behaviour was due to disturbances by other birds, but this hypothesis needs to be investigated. The purpose of this study was to study the effect of stocking density on different broiler welfare traits with special attention being given to the resting behaviour.

MATERIALS AND METHODS

Experimental design

A total of 17 616 Ross broiler chicks were assigned to three treatments (T_1 , T_2 , T_3). The

three pens each had an area of 367 m^2 . They were part of a single shed that was divided into three isolated compartments. The floor was cemented and the litter was made of straw, about 7 cm thick. The main ambience parameters (temperature, hygrometry, concentration of ammonia in the air) were controlled by heating and ventilation and were the same for each of the three treatments (table I). Ventilation was controlled by fans in the roof, which extracted the inside air coming from apex ridge vents on either side of the house. The study was conducted during the early spring when the average daily temperature range for the region was from 8 to 15°C . The sex ratio in each pen was equal to 1. Birds were introduced into the pens as day-old chicks and were slaughtered at d42. Initial stocking densities in T_1 , T_2 and T_3 were 12, 16 and 20 birds per square metre, respectively. Litter dry matter content was analysed the day after slaughter by taking five samples from each of the three pens.

All chickens were fed ad libitum on a standard dietary regimen (3 040 kCal/kg and 22.2% protein, 1–21 days; 3 110 kCal/kg and 20.3% protein, 22–42 days). The living conditions are described in tables I and II.

Behavioural traits

Bird behaviour was studied by video recording. The available space per bird was assumed to be sufficient during the first 2 weeks of age and a video camera was installed in each pen from week 3. The field of vision covered by the camera had an area of approximately 8 m^2 , which included a feeder, a nipple drinker and a side wall. Recordings were performed weekly, the same day of the week for the three treatments, between 1 am and 8 am during the light period, 1 h after the light had been switched on, with a 15

Table I. Main livestock conditions according to treatment day (T_1, T_2, T_3).

	<i>Treatment day</i>						
	<i>1</i>	<i>6</i>	<i>8</i>	<i>17</i>	<i>21</i>	<i>27</i>	<i>35</i>
Artificial 10 lux cycle (light/dark in h)	24/0	19/5	17/7	19/5	20/4	22/2	22/2
Air temperature ($^{\circ}\text{C}$)	30	30	29	28	26	23	20
Ventilation ($\text{m}^3 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$)	0.3	0.5	0.5	0.6	0.7	0.9	1.3

Table II. Main livestock conditions applied to the three experimental treatments (T_1, T_2, T_3).

	<i>Treatments</i>		
	T_1	T_2	T_3
Stocking density (birds/ m^2)	12	16	20
Feeding space/bird (cm)	1.2	1.2	1.2
Birds/drinking nipples	17	17	17
Litter dry matter content ^a (%; $n = 5$)	71.38	65.6	64.1

^a This parameter was analysed the day after slaughter.

min on/30 min off recording cycle. During video playback, the first bird that was seen lying down was observed. The following parameters were recorded: total duration of the lying bout (LB, in seconds, continuous variable), number of disturbances by another bird (numeric variable) and whether or not the termination of the LB was due to a disturbance by another bird (dichotomous variable). Disturbance was defined as an event when a lying bird held up its head, or stood, or slightly moved the whole body without standing because another bird was walking in front or over it, or was touching it, or was flapping his wings close to it. The lying duration time was stopped when the bird stood up. The video tape was then rewound until the beginning of the observation and the next bird that was seen lying down was chosen.

For comparison purposes, the number of disturbances (n) was expressed for a standard lying bout duration of 3 min, ie, the frequency of disturbances was equal to $(n/d) \times 180$ where d was the duration of the lying bout in seconds. The

frequency was calculated only for the bouts during which at least one disturbance occurred.

The sex of the observed birds remained undetermined. Six birds per 15 min session were observed and ten sessions per treatment and per week were recorded. All the observation data obtained by the focal technique were averaged by session in order to obtain ten average values per treatment and per week. Each recording session was considered as a pseudo-replication.

The video playback was stopped using the pause button at the beginning and at the end of each session, (twenty observations per week and per treatment) to estimate the standing/lying ratio: number of birds not lying/total number of birds seen on the picture.

Physiological traits

On day 41, the blood of 30 randomly selected birds (15 males and 15 females) per treatment

was collected from the wing vein in heparinised tubes. In order to minimise the stress due to the handling procedure, 15 birds were held in a holding crate in two opposite corners of each pen for a period not exceeding 10 min before blood sampling. After Giemsa staining, the heterophil/lymphocyte (H/L) ratio was assessed by counting 50 white blood cells.

Productivity traits

One hundred and twenty randomly chosen birds per pen (60 males and 60 females) were individually weighed the day before slaughter. The food conversion ratio and the mortality rate was then calculated for each pen.

The presence or absence of pododermatitis and hock lesions, breast blisters and scabby hip syndrome was checked at the slaughterhouse on 60 birds per treatment. A lesion had to be at least about 0.5 cm large to be scored, and the intensity of the lesions was not recorded. An animal showing both pododermatitis and hock lesions received the same score as an animal showing one or other of these lesions.

Statistical method

A chi-square test was used to compare percentages between treatments (mortality rates, pododermatitis lesions, breast blisters). The Mann-Whitney test was used to test the effect of density on the percentage of lying bouts without disturbances and the percentage of lying bouts terminated because of a disturbance. The frequencies of disturbances were log-transformed and the standing/lying ratios were square rooted to fit a Gaussian distribution before being analysed by an analysis of variance. Comparisons of means of duration of lying bouts, bodyweights and H/L ratios were also achieved by the analysis of variance but without any prior transformation.

RESULTS

Behavioural traits

Globally, resting birds were significantly more disturbed in the highest density

whereas the differences between T_1 and T_2 were not significant (table III). Except for an increase in T_2 during week 3, which was not confirmed during the following weeks, the duration of LB did not appear to be related to stocking density. The standing/lying ratio tended to be higher in T_1 compared with T_2 and T_3 , especially from week 4.

Physiological traits

The stocking density had no significant influence on the H/L ratio (table IV).

Productivity traits (table IV)

Birds were significantly heavier on d41 by about 100 g in T_1 than in T_3 whereas T_2 had intermediate results. This difference was more pronounced for the males. The food conversion ratio tended to be reduced at the highest densities.

The pododermatitis and hock lesions were much more frequent in the highest densities. Nevertheless, the lesions were mild and involved only some brownish to black-brown discoloration of the hocks and feet, with light damage to the skin. A low incidence of mild breast blisters was recorded and this was not related to the livestock density. No case of scabby hip syndrome was observed.

DISCUSSION

Treatments were chosen according to practical considerations. T_3 corresponded to the average stocking density used by French farmers. T_1 is a density used in the French "red label" production system, which is usually considered satisfactory for bird welfare (Koehl, 1995). T_2 was selected as an intermediate density.

Table III. Influence of three stocking densities on broiler behavioural traits (mean \pm SEM).

Weeks of treatment (No)	Stocking density (birds/m ²)		
	12 (T ₁)	16 (T ₂)	20 (T ₃)
Frequency of disturbances of a resting bird by other birds/3 min (n = 10)			
3	4.6 \pm 0.3 ^a	4.6 \pm 0.8 ^a	5.9 \pm 0.6 ^{a*}
4	3.2 \pm 0.4 ^a	3.2 \pm 0.3 ^a	5.6 \pm 0.6 ^b
5	2.7 \pm 0.5 ^a	3.2 \pm 0.4 ^{ab}	3.7 \pm 0.4 ^b
6	2.4 \pm 0.3 ^a	2.7 \pm 0.2 ^a	3.9 \pm 0.5 ^b
% of lying bouts without disturbances (n = 10)			
3	22 \pm 5 ^a	26 \pm 8 ^a	8 \pm 5 ^b
4	25 \pm 4 ^a	25 \pm 7 ^a	20 \pm 6 ^a
5	35 \pm 4 ^a	22 \pm 6 ^{ab}	17 \pm 6 ^b
6	22 \pm 5 ^a	15 \pm 4 ^a	3 \pm 2 ^b
% of lying bouts terminated because of disturbance (n = 10)			
3	43 \pm 8 ^a	45 \pm 11 ^a	62 \pm 17 ^a
4	34 \pm 7 ^a	35 \pm 7 ^a	50 \pm 10 ^a
5	25 \pm 7 ^a	48 \pm 10 ^{ab*}	58 \pm 7 ^b
6	39 \pm 5 ^a	57 \pm 7 ^a	74 \pm 7 ^b
Duration of lying bouts (second; n = 10)			
3	111 \pm 15 ^a	153 \pm 11 ^b	102 \pm 19 ^a
4	163 \pm 19 ^a	179 \pm 12 ^a	160 \pm 21 ^a
5	186 \pm 18 ^a	233 \pm 29 ^a	208 \pm 18 ^a
6	230 \pm 11 ^a	254 \pm 35 ^a	223 \pm 26 ^a
Standing/lying ratio (n = 20)			
3	47 \pm 2 ^a	41 \pm 3 ^{a**}	42 \pm 2 ^a
4	40 \pm 3 ^a	30 \pm 2 ^b	31 \pm 4 ^b
5	29 \pm 1 ^a	19 \pm 2 ^b	22 \pm 1 ^b
6	18 \pm 2 ^a	15 \pm 1 ^{ab}	13 \pm 1 ^b

Data in a row with no common superscript differ significantly ($P < 0.05$). * $P = 0.07$ between T₂ and T₃; ** $P = 0.06$ between T₁ and T₂.

The treatments not only differed from each other by the stocking density but also by the size of the bird population. The respective influences of these two factors could not be dissociated. If a regulation concerning broiler production is applied in the

near future, it is unlikely that producers will change the size of their sheds. Hence, if the stocking density changes, the size of the bird population will change too. The aim of the authors was to point this out. This does not however preclude the use of studies on

Table IV. Influence of three stocking densities on physiological and productivity traits of broilers.

	Stocking density (birds/m ²)		
	12 (T ₁)	16 (T ₂)	20 (T ₃)
Physiological traits			
Heterophil/lymphocyte ratio (mean ± SEM, n = 30)	45.2 ± 3.4 ^a	39.4 ± 3.7 ^a	40.6 ± 3.8 ^a
Productivity traits			
Live weight at d41 (g; mean ± SEM)			
Males (n = 60)	2,475 ± 26 ^a	2,402 ± 26 ^b	2,327 ± 23 ^c
Females (n = 60)	2,049 ± 25 ^a	2,023 ± 23 ^{ab}	1,969 ± 23 ^b
Males + Females	2,262 ± 27 ^a	2,209 ± 25 ^{ab*}	2,148 ± 23 ^b
Food conversion ratio	1.77 [‡]	1.74 [‡]	1.72 [‡]
Pododermatitis and hock lesions (% ± 95% CI, n = 60)	32 ± 7 ^a	69 ± 6 ^b	94 ± 3 ^c
Breast blisters + pustules + haematoma (% ± 95% CI, n = 60)	4.1 ± 2.6 ^a	4.4 ± 2.6 ^a	4.2 ± 2.6 ^a
Mortality (% [‡])	3.3 ^a	3.6 ^a	3.6 ^a

*: $P = 0.06$ between T₂ and T₃; †: the amount of data is too low to allow a statistical comparison; ‡: data collected on the whole sample. Data in a row with no common superscript differ significantly ($P < 0.05$).

the influence of group size on bird behaviour, which has already been proven to be important (Newberry and Hall, 1990).

It is obvious that the welfare of broilers in commercial pens is strongly dependent on the actual space available and, hence, on the weight of the animals. Moreover, the weight of broiler chickens at slaughter has considerably increased over these last years and the future evolution of this tendency is difficult to predict. For this reason, it seemed appropriate to take into account the value of kg/m² rather than the number of birds/m². The weight densities on the day before slaughter were 27, 35, 43 kg/m² at T₁, T₂ and T₃, respectively.

The definition of disturbances of resting birds by other birds was, to some extent, subjective. Stating that what was observed was actually perceived by the lying bird as a true disturbance was an assumption. It was based on the authors' personal experience of observation of broilers resting behaviour.

The authors have already shown (unpublished data) that similar results using the same method could be obtained in different strains of broilers. Nevertheless, it cannot be excluded that the observed reaction of the lying bird was not triggered by the proximity of another bird, but by specific needs (eating, drinking, thermoregulating, etc). Moreover, the exact effect of these disturbances on bird welfare requires further investigation.

The level of activity decreased at the highest densities; this has already been observed by other authors (Blokhuys and van der Haar, 1990; Lewis and Hurnik, 1990) in small pens. Scherer (1989) cited by Bessei (1992) observed an increased activity at the highest density in the first weeks of age. However, our observations only began during the third week of age and this latter aspect could not be compared. Other studies have demonstrated that activity level increased at densities of 7 and 10

birds/m² compared with 12 birds/m² (Lewis and Humnik, 1990). Further studies involving densities lower than the ones used in our study should be undertaken to assess different aspects of the birds resting behaviour.

Gross and Siegel (1983) claimed that the H/L ratio was a good indicator of avian responses to stress in the environment. In our experiment, no significant influence of stocking density on the H/L ratio could be demonstrated. One explanation could be that the increase in stocking density did not create a sufficient stress to produce a strong alteration in this indicator and hence, that a high stocking density was not perceived by the birds as a stress factor. However, it can also be assumed that this parameter is not adequate for testing the chronic stress that can be induced by a change in livestock density. The present data did not allow us to choose between these two possible explanations.

Results of productivity trait measurements are in agreement with the work of other authors. Higher stocking density increased the incidence of dermatitis (Greene et al, 1985; McIlroy et al, 1987; Bruce et al, 1990) and decreased the final live weight (Proudfoot et al, 1979; Scholtyssek and Gschwindt-Ensinger, 1983; Shanawy, 1988; Grashorn and Kutritz, 1991; Elwinger, 1995). In the present study, the individual weight decreased by about 7 g when the stocking density increased by 1 kg/m². In another study, Elwinger (1995) found this reduction in weight to be about 3 g.

It is generally accepted that high stocking densities increase litter moisture content (Proudfoot et al, 1979; McIlroy et al, 1987; Shanawy, 1988; Gordon and Tucker, 1993), and this was confirmed in the present study. Furthermore, high stocking densities may be associated with a hot and humid climate and with high values of atmospheric ammonia or airborne dust whose effect on bird performance and health has already been

proven to be deleterious (Quarles and Fagerberg, 1979; Greene et al, 1985; Martland, 1985; McIlroy et al, 1987; Algers and Svedberg, 1989). Such conditions may induce poor animal welfare. For instance, birds may be obliged to stand up more frequently to thermoregulate and hence have insufficient rest periods. Hence it should be emphasized that high stocking densities (more than 27 kg/m²) should not be recommended if the level of technical management is not high enough to provide satisfactory ambience parameters.

A possibility of reducing the value of kg/m² could be to remove the heaviest birds a few days before the others. For instance, in western France, it is a usual practice to remove the birds intended for exportation at about d37 (light chicken) when the average weight is 1.44 kg (Magdelaine, 1995). In this situation, if a stocking density of 35 kg/m² is to be achieved by the first day of bird removal (removal of 8 birds/m²), the initial density would be $35/1.44 = 24.3$ birds/m². The remaining birds could be kept until d42 at a reasonable density. The average final weight would be 1.9 kg (Magdelaine, 1995) and the resultant stocking density would be $1.9 \times 16.3 = 31.0$ kg/m². In this case, the value would never exceed 35 kg/m², but is the welfare of the birds maintained at an acceptable level during the whole growing period? In our study, we saw in the third treatment that the frequency of disturbances was higher during week 4 when the value in weight/m² was inferior to 35 kg/m². The influence of this practice on bird welfare should be investigated including the effect of the potentially stressful removal process.

The results of the present study demonstrated that birds reared at 43 kg/m² were more disturbed during resting than birds reared at 35 or 27 kg/m². Moreover, we observed a decrease in the level of activity and in the final bodyweight, and an increase in the incidence of pododermatitis and hock

lesions in T₃ compared with T₁ and T₂. In this respect, the welfare of birds seemed to be poorer in T₃. The same conclusion could be drawn with the comparison between T₁ and T₂, except that there was no difference in the frequency of disturbances by other birds during resting. The differences in terms of welfare between these latter treatments was not clearly demonstrated.

REFERENCES

- Algers B, Svedberg J (1989) Effects of atmospheric ammonia and litter status on broiler health. *Proc 3rd Europ Symposium on Poultry Welfare*, Tours, France, 237-241
- Bessei W (1992) Das Verhalten von Broilern unter intensiven Haltungsbedingungen. *Arch Gefluegelkde* 56, 1-7
- Blokhuis HJ, van der Haar J W (1990) The effect of the stocking density on the behaviour of broilers. *Arch Gefluegelkde* 54, 74-77
- Bruce DW, McIlroy SG, Goodall EA (1990) Epidemiology of a contact dermatitis of broilers. *Avian Pathol* 19, 523-537
- Ekstrand C (1993) *Effects of stocking density on the health, behaviour and productivity of broilers*. A literature review. Report 32. Swedish Univ Agricultural Sciences, Faculty Veterinary Medicine, Dept Animal Hygiene, PO Box 345, S-532 24, Skara, Sweden
- Elwinger K (1995) Broiler production under varying population densities - a field study. *Arch Gefluegelkde* 59, 209-215
- Gordon SH, Tucker SA (1993) Effect of broiler stocking density on litter condition and hockburn. *Proc 4th Europ Symposium on Poultry Welfare*, Edinburgh, UK, 290
- Grashorn M, Kutritz B (1991) Der Einfluss der Besatzdichte auf die Leistung moderner Broilerherkünfte. *Arch Gefluegelkde* 55, 84-90
- Greene JA, McCracken RM, Evans RT (1985) A contact dermatitis of broilers - clinical and pathological findings. *Avian Pathol* 14, 23-38
- Gross WB, Siegel HS (1983) Evaluation of the heterophil/lymphocyte ratio as a measure of stress in chicken. *Avian Dis* 27, 972-979
- Koehl PF (1995) Evolution des performances techniques et des coûts de production en élevage de volailles de chair. *Broiler national day*, Rennes 10/24/95. Institut technique de l'aviculture, Paris, France
- Lewis NJ, Hurnik FJ (1990) Locomotion of broiler chickens in floor pens. *Poultry Sci* 69, 1087-1093
- Magdelaine P (1995) Eléments de compétitivité des filières volailles de chair. *Broiler national day*, Rennes 10/24/95. Institut technique de l'aviculture, Paris, France
- Martland MF (1985) Ulcerative dermatitis in broiler chickens: the effect of wet litter. *Avian Pathol* 14, 353-364
- McIlroy SG, Goodall EA, McMurray CH (1987) A contact dermatitis of broilers - epidemiological findings. *Avian Pathol* 16, 93-105
- Newberry RC, Hall JW (1990) Use of pen space by broiler chickens: effects of age and pen size. *Appl Anim Behav Sci* 25, 125-136
- Proudfoot FG, Hulan HW, Ramey DR (1979) The effect of four stocking densities on broiler carcass grade, the incidence of breast blisters, and other performance traits. *Poultry Sci* 58, 791-793
- Quarles CL, Fagerberg DJ (1979) Evaluation of ammonia stress and coccidiosis on broiler performance. *Poultry Sci* 58, 465-468
- Scholtysek S, Gschwindt-Ensinger B (1983) Leistungsvermögen einschliesslich Befiederung und Belastbarkeit von Broilern bei unterschiedlicher Besatzdichte in Bodenhaltung. *Arch Gefluegelkde* 47, 3-8
- Shanawy MM (1988) Broiler performance under high stocking densities. *Br Poult Sci* 29, 43-52