

at higher stocking densities and fewer birds had the best gaits. However, for the most obvious measures of welfare, i.e. the numbers of birds dying, being culled as unfit or showing leg defects, stocking density had no effect, although there were large differences between producer companies. (Dawkins et al. 2004). This result did not mean that stocking density had no effect on bird welfare, but it did show that, within limits, some effects of high stocking density, at least on physical health, could be mitigated by improving the birds' environment, which some companies did better than others.

However, physical health is only one component of welfare. The other is what the animals themselves want (Dawkins 2003). Paradoxically, a result that shows that physical health can be maintained by good environmental control highlights the importance of then looking at the birds' own responses to different stocking densities. Even if their physical health could be maintained, are the birds distressed by being more crowded? Would they choose to have more space than they have?

There are a number of established methods for discovering whether animals want more space (Fraser & Matthews 1997), including simple preference tests (Mills & Faure 1989; Lindberg & Nicol 1996) and operant conditioning (Lagadic & Faure 1987; Matthews & Ladewig 1994). However, none of these methods are suitable for use on commercial broiler farms, because they involve either complex equipment, removing birds from their peers to test them or working with small groups that do not represent real farm conditions. We circumvented these problems by analysing the behaviour of broiler chickens recorded unobtrusively from video cameras inside commercial houses. By using a simple computer model, we provide an in situ way of identifying how the birds themselves respond to different stocking densities and whether they show evidence of wanting more space at high stocking densities.

Our approach relies on the assumption that the way in which animals distribute themselves in space shows the extent to which they choose to approach or get away from each other, because their current distribution in space is the net result of their previous responses to each other (Guhl & Allee 1944; McBride et al. 1963; Stricklin et al. 1979; Keeling & Duncan 1991; Keeling 1995). Thus, animals that prefer close proximity to other animals will arrange themselves into clusters, leaving unused space between clusters. Such animals will have interindividual distances that are either very small (within a cluster) or very large (between clusters), and there will thus be high variance in interindividual distance. Animals that do not prefer the close proximity of others, on the other hand, attempt to maximize distance between themselves and all other animals and use up all the space available. This results in regular spacing (Barlow 1974) with low variance in interindividual distance. A third possibility is that animals are indifferent to the presence of each other and distribute themselves randomly.

To test between these possibilities, we made video recordings in the same houses from which we already had data on the health and mortality of the chickens and compared the spatial distribution of real chickens with

that produced by a computer simulation of a model of 'social aversion/attraction'. In practical terms, this model gave the probability that a chicken would reject a potential position if it was within a given distance of another bird, conditional on the locations of birds already in position. The two parameters of probability and distance in the social aversion/attraction model correspond to the extent to which a chicken 'wants' more space than it has. We varied the model parameters for simulations of different stocking densities and compared the resulting spatial distributions with those observed in real chickens, using the coefficient of variation in interindividual distances as the statistic for comparison.

We argue that the value of the social aversion/attraction parameter in the model that most closely matches that of broiler chickens on commercial farms for a given stocking density would indicate how aversive or attractive the birds find the close proximity of other birds. If this level varies with stocking density, this result would indicate that birds preferred some stocking densities more than others. If real chickens found crowding aversive, their observed spatial distribution would correspond most closely to simulations from a model with high social aversion, and this result would be more pronounced in houses with higher stocking densities. On the other hand, if real chickens wanted to be close together, their observed spatial distribution would look like simulations from a model with high social attraction. Finally, if chickens were indifferent to each other, then their locations would be randomly distributed. We analysed data on the spatial distribution of chickens at different stocking densities and on their health, mortality, walking ability and behaviour (Dawkins et al. 2004; Jones et al. 2005).

METHODS

Broiler Chicken Houses

Stocking density was experimentally manipulated by each of 10 major broiler producer companies in England, Scotland, Northern Ireland and Denmark. There were five target maximum densities (i.e. the stocking density when the birds were fully grown and just before being taken for slaughter): 30, 34, 38, 42 and 46 kg/m². A typical final weight for a broiler chicken in the U.K. is 2.2 kg (European Commission 2000), so 30 kg/m² corresponds to approximately 13.6 birds/m². A stocking density of 30 kg/m² is the RSPCA's (1995) recommended upper limit and 34 kg/m² is the upper limit recommended by the Farm Animal Welfare Council (1992), while current practice in the U.K. and the E.U. is up to 42.5 kg/m² (European Commission 2000). Thus, the range that we chose covers much current practice. Stocking density was manipulated by altering the numbers of day-old chicks placed in the house, and each stocking density was replicated in at least two houses within each company, with random allocation of stocking density to house within a company. We distinguished between target stocking density, which was calculated in advance from the number of chicks placed and their estimated final weight, and actual stocking density,

which was the product of the actual numbers of birds in the house at maximum stocking density and their actual weights. Differences between target and actual stocking densities were due to the difficulty of estimating how fast birds would grow, because actual growth rate depends on stocking density (Dawkins et al. 2004). At as close to maximum target stocking density as possible (average age and weight: 35 days and 1.78 kg, range 1.49–2.27 kg), birds were assessed for gait and leg health and body weight. Fresh faecal samples were collected for analysis of corticosteroid levels. We also recorded in-house readings of air ammonia and litter moisture at predetermined sites across the house. Producers supplied full records of mortality over the growing period, including the numbers of birds culled. They record mortality on a daily basis. We recorded temperature and humidity continuously throughout the life of the birds using Tiny Tag data loggers (four per house at a height of 60 cm). We studied 114 chicken houses on 20 farms between August 2000 and November 2002. A full description of the experimental design, methods, mortality rates and details of husbandry and management is given elsewhere (Dawkins et al. 2004; Jones et al. 2005).

Video Recordings

Video cameras were installed in each house before the day-old chicks arrived. Four wide-angle lens cameras and their operating batteries (Tracksys Ltd, Nottingham, U.K.) were installed at predetermined, randomly chosen points in each house at a height of 155 cm and at an angle of about 70° to the vertical. Each camera battery had a unique switch code and sent a radio signal to a receiver linked to a VCR and switch gear in the anteroom of the house. Adjacent houses operated at different radio frequencies to prevent interference, and the view from cameras at the same location in each house was standardized as much as possible. The cameras were switched on at close to maximum stocking density, and the birds were video recorded between 1000 and 1200 hours. Video was recorded from one camera for 10 min before an automatic switch to the next camera. We recorded 80 min of video per house in eight 10-min sequences (two switching cycles). Neither researchers nor stockmen entered the houses during the recording period.

Image Capture

We chose a static image, at a random time from the start of recording, from each of the four camera records/house from one of their switching cycles. Some video records were unsuitable (e.g. through poor image quality or interference from other equipment), so we analysed 327 of a possible 368 images from 92 houses. This gave a possible four images/house; however, the houses contained 7000–50 000 birds and the cameras were spaced in different parts of the house, so a single bird could not have been picked up by more than one camera. For each image, an acetate sheet with a 4.5-cm square drawn on it was placed over the video screen, towards the bottom of the

screen (nearest to the camera). We avoided, where possible, feeders and drinkers, and we used data of birds that were neither feeding nor drinking. The position of the head and centre of the body of every chicken within the square was recorded by using (unpublished) software that gave *X* and *Y* coordinates for each mouse click. The positions were recorded on a fixed scale set by the software, and we called the spatial units that the program delivered 'software units' (approximately 25 cm in the real world). In addition, the position of any feeders or drinkers, either inside or outside the square, was recorded. For the 327 images that we analysed, the following information was attached to each one: company, farm, house, target stocking density and actual stocking density. The area occupied by the bodies of single chickens on different parts of the screen was measured by a separate analysis in which the positions of head, midbody, left extremity and right extremity were measured on screen.

Adjustment for Parallax and Image Size

To correct for distortion on the screen caused by parallax, we used two separate procedures as a check on each other. The first involved placing four balls (each 10.5 cm diameter, with their centres 25 cm apart in a square configuration) on a pavement consisting of square, 61 × 61-cm concrete slabs, then filming the square of balls repeatedly at three distances from a camera placed at the same height (1.55 m) and angle (70°) as in the broiler houses. This gave an empirical scaling factor that could be applied to the software images. The second method involved taking the known height and camera angle, then estimating focal length and scaling factor by trial and error on a number of images so that the stocking density on an image after adjustment matched the known target stocking density of that image. The focal length and scaling factor were estimated as 0.4 m and 0.0116, respectively. The scaling factors were used to convert these to real-world measures. The two methods gave comparable results: when we double-checked by applying the calculated scaling factor to the video footage of the balls, the calculated and empirical scaling factors were similar. Each camera covered an area of the chicken house floor that was irregularly shaped because of the camera angle, but the area used for the analysis corresponded to approximately 4 m².

Behaviour of Focal Birds

One randomly chosen focal bird from each 10-min section of video was analysed for 5 min for the following: frequency and duration of stand, lie, feed, drink, preen, rest (eyes closed), lie stretched out; frequency of walk, run (including number of strides), peck litter, peck other bird, scratch litter, scratch head, stretch head, wing or leg, shake body, shake head, dustbathe, wing flap, aggressive interactions, perch (on drinker line), changes of posture (up/down), jostling or being jostled by other birds, and being disturbed or walked on by other birds (*N* = 741 from 107 houses).

Simulations

Social aversion/attraction model

Simulations were run with Microsoft Visual Basic 6.3 from Microsoft Excel 2002 for Windows. Each simulation began with an empty chicken house of known dimensions and a known number of chickens to fit into it and then placed the chickens one by one into the house. As each chicken was introduced, it either accepted or rejected its randomly selected position, based on the positions of the chickens already in the house. If the chicken accepted the randomly chosen position, then the simulation continued with the placement of the next chicken. However, if the chicken rejected the position, then new positions in the house were selected at random until the chicken accepted one. The simulation ended when each chicken had accepted positions. Once a chicken accepted a potential position, it did not change position in response to the placement of additional chickens later in the simulation. This is potentially a structural limitation of the simulation compared to real chicken behaviour. However, all chickens in a given simulation were identical with respect to their attraction/aversion, so this approximation should not have affected the key results.

The social aversion/attraction model had two parameters chosen before a simulation began, a 'distance x ' and a second parameter, \emptyset , which ranged from 1 (most aversive) to -1 (most attracted). Fully aversive chickens rejected any position that was within distance x of any other chickens already in the house, with a probability of 1. Partially aversive chickens rejected any position in the house if any other chicken was within distance x of the proposed position, with a probability equal to \emptyset , where $0 < \emptyset < 1$. If \emptyset was negative ($-1 \leq \emptyset < 0$), the chickens accepted any position that was less than distance x from another bird; otherwise, they sought a new position with a probability equal to $-\emptyset$. We called such chickens socially attracted chickens. Indifferent chickens always accepted their position, regardless of the positions of chickens already placed in the simulated house. Their spatial distribution was the spatial distribution of randomly chosen points and occurred when $\emptyset = 0$.

Statistics

Spatial distribution

Stocking density (even locally, as measured by the number of chickens in a particular image) will affect both the mean and variance of the interindividual distances, so we focused on the coefficient of variation (CV, i.e. the standard deviation divided by the mean of all pairs of interindividual distances). We compared the simulations with the observed data, taking for comparison the distribution of indifferent (randomly distributed) chickens. For each of the 327 images, 1000 simulations were performed, using the number of birds actually in the image within the area of screen used. The mean of the CV values from the 1000 simulations of indifferent chickens was considered to be the expected CV if the birds were distributed at random within that image. This mean was

then subtracted from the observed coefficient of variation to obtain an adjusted coefficient of variation (CV residual). A positive CV residual (observed minus expected) would suggest social attraction (CV greater than that expected for indifferent chickens), and a negative CV residual would suggest social aversion (CV less than that expected for indifferent chickens). We used a sign test to evaluate the distribution of these CV residuals for significant evidence of attraction or aversion. The distribution of these residuals was approximately normal and similar for different stocking densities, so we tested for the effect of target stocking density with a one-way ANOVA. We also regressed the same data against the actual number of birds on the screen (giving an idea of the local density experienced by the birds) and tested for the significance of the regression.

In addition, we varied the distance x parameter within the model to find the value that best fitted the observed spatial distribution of real chickens, to find either the best-fit minimum distance (if chickens were socially aversive) or the best-fit maximum distance (if chickens were socially attracted). We did this by considering strongly aversive chickens with $\emptyset = 0.99$. (With fully aversive chickens, the simulations can become infinitely long because they never settle down.) Using a random 5% sample of the images ($N = 14$) and their test statistics, we ran 100 simulations for each of the following distance x values: 2.8, 3.0, 3.2, 3.4, 3.6, 3.8 and 4.0 screen units (equal to 70, 75, 80, 85, 90, 95 and 100 cm, respectively). The mean CV (derived from the 1000 simulations of indifferent chickens) for each distance was calculated and regressed against the distance x parameter values to give the best-fit value. From the regression line, the optimal value of distance x was obtained to give test statistics closest to that observed in each image sampled. The mean of these best-fit values over all the images was then calculated to give a global average.

Behavioural observations

The independent statistical unit was house. Where multiple measurements were made within a house, we used a single house-specific mean in the analysis. Behaviour and other variables were first analysed for effects of target stocking density, actual stocking density and company, using analysis of variance. Where actual density effects were significant, they were further analysed by linear regression analysis and post hoc Tukey comparison.

Univariate linear correlations were examined between outcome variables and predictors treated as continuous variables. Multivariate linear models were constructed using a stepwise model selection procedure (starting from a model with no predictors), with possible predictors including both categorical predictors and those continuous predictors that were linearly correlated (with correlation coefficients < -0.2 or > 0.2) with the response variable. Both models with and without effects of company were used to allow within-company differences to be clearly identified, while giving insight into the extent to which between-company differences could be explained by the recorded variables. The overall level of variation that can be explained for each outcome measure is given

(R^2), along with the partial level of explanation by each predictor (partial R^2). With such a large number of statistical tests, one or more of the comparisons may produce a significant result by chance. For this reason, we discuss effects only when $P < 0.01$. Replication of the observed results in an independent study will be needed to strengthen the evidence for the observed associations between house attributes (including both stocking density and other variables such as environmental conditions) and observed behaviour.

Ethical Note

The stocking densities used in this study were all within the range in commercial use within northern Europe. All companies were given the option of not stocking at the highest densities if they thought that doing so would compromise the welfare of the birds; one company took this option. In summer, when there was a potential danger of the houses overheating, we instructed the companies to terminate a trial rather than risk exposing the birds to unacceptably high temperatures. This measure did not occur, and mortality levels throughout this study were generally within or lower than the industry average.

RESULTS

Spatial Distribution

The CV residuals (observed minus expected) are shown in Fig. 1a for all target stocking densities. If there were no differences between observed and simulated indifferent birds, the data would vary evenly around zero, but most of the points were well above zero, indicating that observed CV was consistently higher than expected; i.e. the birds were more clustered than would be expected at random (two-tailed sign test: $P < 0.001$). Clustering was significant over the range of stocking densities studied ($F_{4,317} = 1.17$, $P = 0.322$).

A similar result was obtained by plotting the results as a function of the number of birds within the square drawn on the video screen, a local measure of the number of birds within a given area and therefore the one actually experienced by the birds (Fig. 1b). There was no significant trend relating CV residuals to number of birds present ($R^2 = 0.002$, $P > 0.01$).

The first set of simulations treated chickens as point locations. To compare these points to birds occupying real space, we introduced the further restriction in the simulation model that birds could not land on top of each other or occupy each other's physical space. Measuring the surface area covered by a bird from the videos was difficult, because chickens change both their apparent size and shape depending on what they are doing. For example, a bird sitting down appears larger than one standing up, because the wings are rested on the floor, and chickens rest so close together that they appear to be compressed. Measured widths of birds ranged between 15 and 50 cm. The test statistic, CV residual, was robust despite wide variations in the assumptions about chicken

size and did not vary with stocking density (Fig. 2). The larger the body size was assumed to be, the lower was the CV of distances, but the conclusion that birds tended to cluster remained the same.

In the social attraction simulations, the best-fit value of distance x was three software units (approximately 75 cm). Thus, the behaviour of real chickens most closely resembled the output from a model in which the chickens rejected their assigned positions if they were more than 75 cm from another bird, although the fact that 75 cm is only approximate means that we cannot rule out the possibility that the chickens might also move when separated by smaller distances.

Behaviour and Health at Different Stocking Densities

On average, the birds spent 72% of the observation time lying down and 34% of their time resting (eyes closed). Resting bouts were generally short ($\bar{X} = 56$ s, range 9–264 s). Feeding and drinking accounted for 16% of their time and preening 4%. Preening bouts were also short ($\bar{X} = 13$ s, range 0–68 s). Much of the rest of the chickens' time (45%) was spent being alert, performing small comfort movements (e.g. stretching head or body, body shake) or walking.

Stocking density had little effect on most of the behaviour seen and significantly affected only two behavioural measures, jostling (Fig. 3) and number of steps taken (Table 1). The incidence of birds jostling increased significantly from the lowest to the two highest stocking densities ($F_{4,90} = 4.6$, $P = 0.002$). Birds were mostly jostled while they were at the feeders and drinkers or while they were huddled together resting. After being jostled, the birds sometimes repositioned themselves (29% of cases) or continued with their previous behaviour (21% of cases). However, jostling did interrupt resting bouts and caused the jostled bird to stand (15% of cases), and led to short preening or sitting down (5% and 4% of cases, respectively).

In total, we could explain 35.2% of the variation in jostling behaviour. Stocking density explained 11.3%, and 19.2% of the variation was correlated with the incidence of a particular leg abnormality, angle-out deviation (outward twist at intertarsal joint $>30^\circ$ between legs (Dawkins et al. 2004)). Birds afflicted in this way might have had less control of movement, leading them to bump into one another. The number of strides walked per walking bout decreased from the lowest two stocking densities to the highest density ($F_{4,90} = 3.5$, $P = 0.01$; Fig. 3), but the number of walking bouts was unaffected by stocking density and averaged 0.43/bird per min. We could explain 16.9% of the variation in walking strides per walking bout, 9.3% of it by the effect of stocking density, 3.1% by mean relative humidity (RH) in week 3 and 4.5% by company.

The behaviour of the birds was correlated with variations between companies associated with different environmental conditions, that in turn affected the condition of the birds' feet and legs. However, these differences are difficult to relate to welfare differences between companies (see Supplementary Material). Birds were more likely

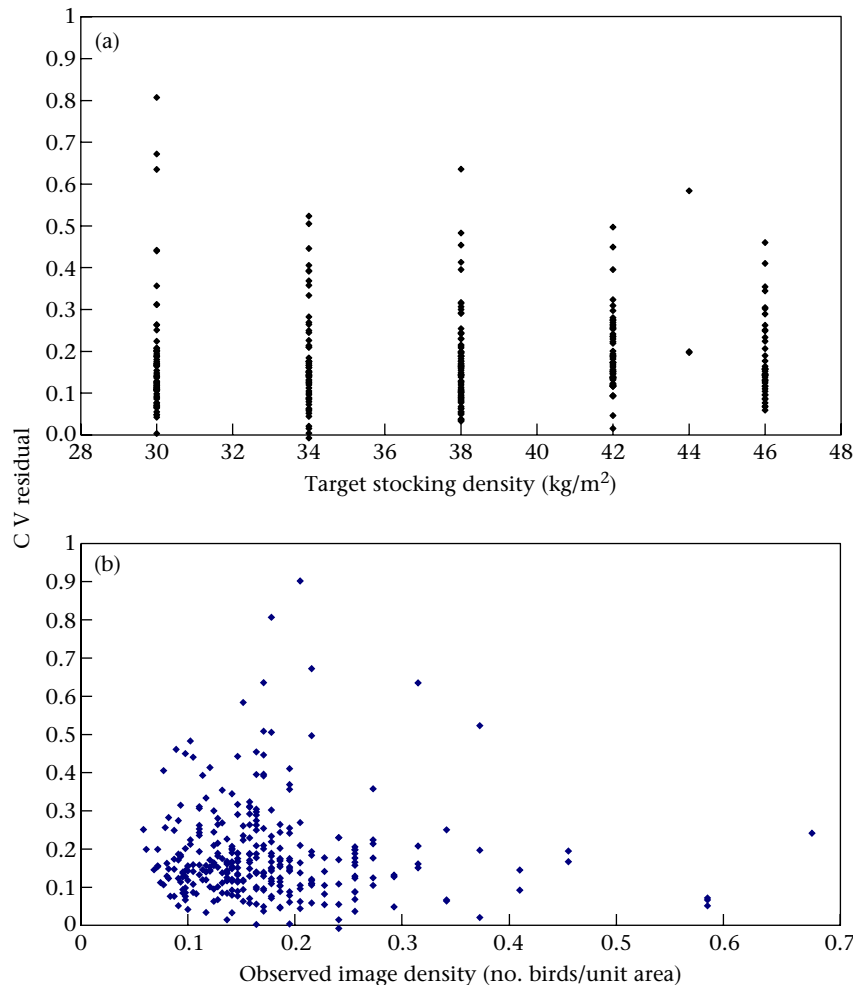


Figure 1. (a) Spatial distribution of chickens in relation to target stocking density, expressed as a CV residual (calculated for each video image by taking the observed coefficient of variation of distances between all chickens and subtracting the simulated CV of distances between the same number of chickens. If real chickens were indifferent to the presence of other birds, the CV residuals would centre around zero. (b) Spatial distribution of chickens as a function of the number of birds immediately surrounding them (number in standard square on video screen/square area), expressed as the same CV residual as in (a).

to stand with heaters spread evenly through the house (partial $R^2 = 7.0\%$) and less likely to peck at litter with heaters down the centre line or at opposite ends of the house (partial $R^2 = 19.7\%$). Birds fed more in the winter months (partial $R^2 = 14.0\%$), showed more leg stretching (partial $R^2 = 6.9\%$) and aggression (partial $R^2 = 5.3\%$) when stockmen visited less and showed more drinking in houses with fan-assisted ventilation (partial $R^2 = 12.8\%$). Fewer disturbances were recorded in houses with more drinkers per unit area (partial $R^2 = 9.2\%$).

Variation within companies (Supplementary Material) accounted for more wing stretching (partial $R^2 = 15.7\%$), walking (partial $R^2 = 10.7\%$) and feeding (partial $R^2 = 6.8\%$) when there were fewer stockman visits, more feeding with manual control over temperature (partial $R^2 = 7.4\%$), more walking with heaters spread evenly through the house (partial $R^2 = 18.1\%$), and more dustbathing when heaters were placed midway in the house (partial $R^2 = 11.8\%$). Birds stood more (partial $R^2 = 13.1\%$) and rested less (partial $R^2 = 10.1\%$) in older

houses, lay down less (partial $R^2 = 10.4\%$) and pecked more (partial $R^2 = 11.2\%$) at other birds with nipple drinkers and perched less (partial $R^2 = 29.5\%$) with nipple and cup drinkers (compared to nipple-only drinkers).

There was less feeding (partial $R^2 = 8.6\%$) and walking (partial $R^2 = 12.7\%$), with more variation in RH during week 1; more resting (partial $R^2 = 16.2\%$) and more disturbance (partial $R^2 = 13.3\%$), with more variation in temperature in week 3; more walking on other birds, with increasing RH in week 2 (partial $R^2 = 23.0\%$) and more aggression when RH in week 2 was out of range (partial $R^2 = 6.5\%$). The behaviour of the birds was also correlated with some measures of physical health, such as the state of their feet and legs. Birds stood less with increasing levels of the healthiest foot pads (score 0, partial $R^2 = 4.1\%$) and lay down more with increasing levels of foot pads with lesions (score 2, partial $R^2 = 4.7\%$) and rotation of the legs (partial $R^2 = 9.4\%$).

Birds were more likely to lie stretched out when the incidence of angle-in leg deviation was higher (partial

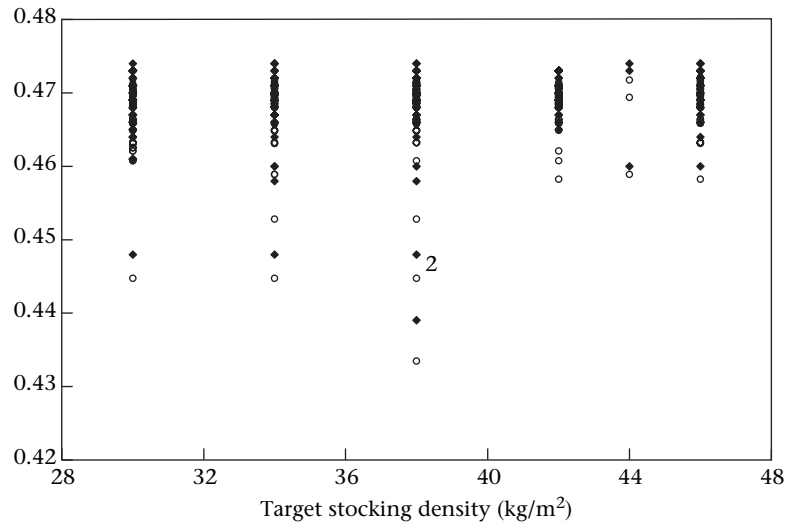


Figure 2. The coefficient of variation of interindividual distances between all pairs when chickens were regarded as points (◆) and when they were regarded as occupying a circle with a 25-cm diameter (○). The clustering effect was independent of stocking density regardless of whether the chickens were treated as points or as having an appreciable size.

$R^2 = 4.3\%$), and increased dustbathing with a higher incidence of angle-out leg deviation (partial $R^2 = 8.3\%$). Higher levels of faecal corticosteroid were associated with increased levels of drinking and walking (partial $R^2 = 6.4\%$ and 10.2% , respectively).

DISCUSSION

The model developed here provides an easy way to use observed distributions of animals to infer how they respond to the presence of each other (Clark & Evans 1954; Simberloff 1979; Stricklin et al. 1979; Keeling & Duncan 1991; Keeling 1995; Krebs 1999). By finding a setting of the social aversion/attraction parameter in the model that corresponded to the observed distribution of real animals, we can see whether broiler chickens chose to approach other animals or are trying to avoid them,

important information when evaluating their welfare, particularly on farms where other ways of measuring preference and aversion may be logistically difficult to use.

When we applied the model to the key issue of whether broiler chickens found higher stocking densities more aversive than lower ones, we found no evidence that the birds attempted to get away from each other at any of the five commercial stocking densities studied. On the contrary, broiler chickens consistently spaced themselves closer together than expected at random, that is, closer than did the 'indifferent' chickens in the simulations. They appeared to be attracted to each other even when local space was available. Our analysis excluded birds that were feeding or drinking, so the clustering effect cannot be explained by their use of these resources. Clustering appears to be an attraction to other birds while sitting, resting or performing comfort behaviours. Furthermore, birds showed no difference in their tendency to space out

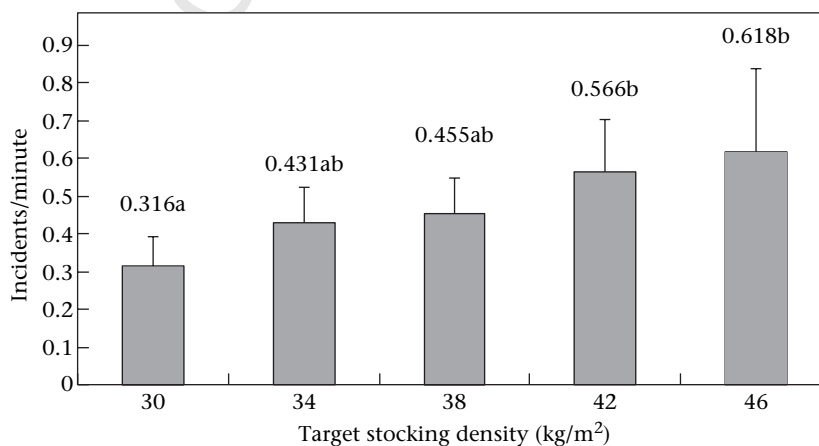


Figure 3. The effect of target stocking density on the incidence of jostling (number of incidents/bird per min). Values with different superscripts are significantly different (Tukey post hoc comparison: $P < 0.01$).

Table 1. Effect of target stocking density on the number of strides/walking bout

Target stocking density (kg/m ²)	Mean±SE	Range
30	5.01 ^a ±0.33	2.0–8.2
34	5.02 ^a ±0.42	2.8–12.5
38	4.08 ^{ab} ±0.16	2.1–5.3
42	4.05 ^{ab} ±0.28	1.7–6.3
46	3.62 ^b ±0.32	1.3–6.3

Values with different superscripts are significantly different (Turkey test: $P < 0.01$).

and occupy all available space at higher and lower stocking densities, suggesting that they did not find higher stocking densities more aversive.

The spatial distribution of the chickens is best explained by a social attraction model in which simulated birds reject potential positions, not when other birds are too close, but when they are not close enough. The distance x model parameter that best fitted the observed data was estimated to be about 75 cm.; i.e. the chickens had a 0.99 probability of rejecting a potential position if the nearest chicken was more than about 75 cm away. It was difficult to estimate accurately distances between real chickens from the video that we used, so this is a rough estimate and should be further tested using better equipment with better calibration. The model also has the structural simplification that, once a simulated chicken has accepted its potential position, it cannot change its position in response to what later chickens do. However, given that the model specifies that all chickens have the same parameter settings for a given simulation, each successive chicken will behave in a way that best suits all previously placed chickens as the simulation places more and more chickens. Future models that have more complex assumptions or incorporate more parameters, such as environmental heterogeneity, might give a closer fit to the real data. However, that possibility is the case with all models.

Nevertheless, this simple model, with just two biologically meaningful parameters (distance to another bird and probability of choosing another position), resulted in spatial distributions that were similar to those observed in real broiler chickens. This finding at least poses a challenge to the widespread view that crowding is always aversive for broiler chickens, and that they would prefer to have more space than they commonly have in commercial broiler houses. We are investigating how spatial distribution is related to the behaviours that the birds are doing at the time; perhaps birds choose varying amounts of space for different behaviours. Differences in spatial distribution may also depend on time of day, a factor outside the scope of this study. However, within the limits of the data collected in over 100 commercial broiler chicken houses, we found no evidence of aversiveness and considerable evidence of attraction, even at the highest stocking densities. Perhaps this finding is not as surprising as it might seem. Broiler chickens, despite their large size, are juveniles and are killed by 6 weeks of age, well before they reach reproductive age. Domestic chicks reared by their

mothers are brooded under her wings, and physical contact is important to them, in addition to the temperature benefits of being brooded. They show no signs of avoidance of each other until 6–10 weeks of age, when dominance hierarchies begin to be established (Kruijt 1964; Dawson & Siegel 1967; Wood-Gush 1971). At least, the results of this study should lead us to question whether the close proximity to other birds that is often described as ‘crowding’ is always, from the birds’ point of view, as aversive as is often assumed.

It is important, however, not to consider what the animals themselves choose in isolation from other measures of welfare, in particular from the effect that stocking density (crowding) may have on other aspects of bird behaviour and physical health. Higher densities led to an increase in incidence of poor gait at the two highest stocking densities, a reduction in growth rate (Dawkins et al. 2004) and an increase in relative humidity in week 6 (Jones et al. 2005). On the other hand, we found no significant effects of stocking density on the most obvious measures of bird health: the numbers of birds dying, being culled as unfit or showing leg defects (Dawkins et al. 2004), so there is no simple connection between stocking density and bird welfare. Birds may choose to sit in clusters (‘rafting’: Appleby 2004), which may result in overheating or other detrimental effects on the birds’ physical health. We did find some effects of stocking density on behaviour such as jostling, which may be important for welfare because it disrupts rest, and where we did find effects of stocking density, they were largest at the two highest stocking densities. However, for logistical reasons, the numbers of feeders and drinkers in this experiment were not altered with stocking density, so the increased jostling at higher densities might have been simply because of increased competition for resources. Less jostling occurred when a house contained more drinkers/unit area; on the other hand, with more drinkers, the moisture levels of the litter were higher (Jones et al. 2005), which has potential implications for foot pad dermatitis and hockburn (Broom & Reefman 2005). The connections between behaviour, stocking density and environment are thus complex. Apparently minor factors, such as the position of the heaters or the number of times a day that a stockman visits a house can affect behaviour (Jones et al. 2005). Heaters that give rise to hot spots within the house, for example, might lead the birds to crowd together and jostle more than with heaters that spread heat more evenly. Alternatively, birds might become calmer and jostle less if they become used to humans because the stockman visits regularly.

Different companies have different systems of heating and ventilation and different ways of delivering drinking water, and these are associated with major differences in the health and mortality of the birds (Dawkins et al. 2004; Jones et al. 2005). For example, fan-assisted ventilation led to lower levels of ammonia within the house. Ammonia in high concentrations is aversive to birds (Kristensen & Wathes 2000) and so could potentially affect their behaviour, either directly or through indirect effects on litter quality and the discomfort the birds might feel from walking or sitting on it. Our results are comparable with those

of other studies showing that broilers spend much of their time sitting down (Weeks et al. 2000), and that there are small but significant effects of stocking density on behaviour (Hall 2001). However, our results also show that, even taking into account the effects of the two highest stocking densities on gait and jostling, stocking density may not be the most important factor to affect behaviour or other aspects of broiler welfare. Thus, reductions in stocking density do not necessarily improve bird welfare unless other factors are considered.

The European Union is in the process of adopting standards for broiler welfare that would include legislation on the minimum amount of space each bird should have (European Commission 2005; e.g. see defra.gov.uk/portal/site/defraweb). To avoid expensive changes that satisfy well-meaning humans but that result in little or no real change in bird welfare, proposed legislation needs to be based on evidence. Although stocking density ('crowding') seems the most obvious area for change in broiler chicken farming, our evidence suggests that, even if there were a major reduction in stocking density, the improvement in bird welfare might be much less than those pressing for change lead us to believe. We have examined two criteria of chicken welfare: the physical health of the birds and whether they choose more space, as judged by a model in which this choice is represented by the probability of rejecting a potential position if too close to another bird. Based on both of these criteria, stocking density, often seen as a key factor to animal welfare, had less effect than did other factors, such as control of temperature and humidity, which in turn lead to higher standards of air and litter quality. Pressing for change in these aspects of broiler farming, while also urging major changes in feed and, above all, in the genetics of the birds themselves, is more likely to improve broiler welfare than is concentration on stocking density alone.

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SUPPLEMENTARY MATERIAL

Supplementary material can be found, in the online version, at [doi:10.1016/j.anbehav.2006.03.019](https://doi.org/10.1016/j.anbehav.2006.03.019).

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