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The relationship between the comb and social behaviour in laying hens

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A B S T R A C T

The question of whether attributes of the combs of laying hens have any consistent relationship with dominance behaviour has yet to be answered unequivocally. This study sought to address this by investigating whether a relationship existed between the competitive ability of hens within stable groups and the size or colour of their combs. Pullets ($n = 120$, Hy-line® Variety Brown) were allocated randomly to eight groups of 15 hens for 32 weeks. Over this period the length and height of each hen's comb was measured regularly to estimate the total comb area and hens were weighed. In weeks 3–10 the aggressive interactions between hens in each group were observed to calculate a behavioural dominance score (David's score) for each hen. This score was based on the outcome of agonistic interactions with other group members; and accounts for the relative strengths of all opponents. Thus dominance scores reflected the competitive ability of hens from their overall within-group fighting success. The luminance, purity and dominant wavelength of the colour of each hen's comb was measured in week 27 using a telespectroradiometer. Hens with higher dominance scores had larger combs than those with lower dominance scores (gradient of slope = 0.008 ± 0.002, $P < 0.001$); this relationship was consistent across the experiment. There was no association between body weight and dominance score but there was a significant inverse relationship between dominance score and the dominant wavelength of the comb (gradient of slope = -0.067 ± 0.023, $P < 0.01$). This indicated that hens with combs perceived by humans as more yellow-red than pure red were generally more successful competitors. Further research is required to ascertain whether or not hens utilise this information on comb size and the underexplored area of comb colour to assess the competitive ability of their opponents.

1. Introduction

It has been well documented in laying hens that as group size increases aggressive behaviour tends to decrease (e.g., Estevez et al., 2003; Hughes et al., 1997; Nicol et al., 1999). This is thought to reflect the fact that in large groups, hens may switch their social strategy from the formation of stable peck-orders, requiring individual recognition, to the use of status signals to assess the competitive ability of other hens, which involves less direct aggression (D'Eath and Keeling, 2003; Pagel and Dawkins, 1997). It has also been noted that hens sometimes appear to settle dominance relationships without overt aggression (Collias, 1943). Wood-Gush (1971) suggested that individuals may avoid physical conflict by using morphological or behavioural cues (later referred to as status symbols) to judge the competitive ability of conspecifics. Since this suggestion, several authors have sought to link physical factors, such as body weight and the characteristics of the comb, to the outcome of agonistic interactions

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between hens (Bradshaw, 1992; Cloutier and Newberry, 2000; Collias, 1943; Forkman and Haskell, 2004; Martin et al., 1997). The general consensus from these studies is that body weight does not have a strong association with dominance rank (Bradshaw, 1992; Collias, 1943; Forkman and Haskell, 2004; Martin et al., 1997) [but see Cloutier and Newberry, 2000]. However, this is likely to be dependant on the magnitude of size discrepancy.

Research into the relationship between the comb and competitive ability has produced more conflicting results. Collias (1943) and Martin et al. (1997) both found that successful hens in dyadic conflicts had larger combs than their opponents. Similarly, Forkman and Haskell (2004) found a significant correlation between ranked comb area and dominance rank in five groups of six laying hens. In contrast, Bradshaw (1992) reported no significant correlation between dominance rank and comb size, and Cloutier and Newberry (2000) found that comb size did not predict attack behaviour and subsequent social rank in newly formed groups of hens. Given the contradictory evidence on the information the comb confers with regards to competitive ability, further investigation is required to determine whether this trait truly is linked to dominance behaviour.

It is possible that inconsistencies in findings between studies may have arisen because more than one characteristic of the comb is associated with dominance: comb colour may be of importance in this respect. Laying hens have been shown to be particularly sensitive to red, suggesting that red colouration could be of special significance (Barbur et al., 2002). Yet relatively few studies have investigated whether comb colour is linked to competitive ability in laying hens. Bradshaw (1992) tested the relationship between a hen's position in a linear dominance hierarchy and comb colour in a group of six hens by visually appraising comb colour and assigning ranks based on the depth of redness. The hen with what they judged to be the 'darkest red' comb was ranked 1 and the individual with the 'lightest pink' comb ranked 6. They reported a positive correlation between this colour rank and dominance rank. However, this result should be treated with caution as the colorimetric method was strongly subjective and it is unclear whether or not the observer scoring the combs was aware of the social rank of hens. Martin et al. (1997) tested whether comb colour predicted the outcome of dyadic conflicts. They utilised the more conventional method of photographing combs and using Munsell chips to match visually the combs to a known colour chart (Munsell, 1929). They reported no variation in comb colour between any of the 150 hens assessed, which is surprising as it is extremely unlikely that all the combs were identical in colour. This suggests that the sensitivity of this colorimetric method may have been inadequate. Potentially important information may be lost when comb colour is estimated from photographic representations as colour reproduction can differ considerably from actual colour. Cloutier et al. (1996) also utilised the Munsell system to determine whether comb colour estimated from photographs was associated with the outcome of competitive interactions. They found that individuals with 'darker' combs tended to defeat opponents with 'paler' combs. However, it is unclear whether 'darker' referred to colour saturation or brightness. Therefore, although some studies have touched on the relationship between comb colour and hen social behaviour, we argue that this topic has yet to be adequately investigated. Spectroradiometry offers a more objective approach to colorimetry than the Munsell system and is better able to distinguish fine-scale colour differences as it is not constrained by the availability of known colour chips (Zuk and Decruyenaere, 1994). In a comparison between these two approaches Zuk and Decruyenaere (1994) found that spectroradiometry detected much greater variation between the comb and feather colour of red jungle fowl roosters, and was better able to explain observed differences in mating success, than the Munsell system.

The aim of this study was to test whether or not comb size and/or colour (measured using spectroradiometry) are related to the competitive ability of laying hens by investigating these traits in eight small groups of hens. This provides an insight into whether the comb conveys information that could be of potential use to a hen judging the relative fighting ability of conspecifics. Comb size was examined shortly after the formation of social groups and again at later times when the groups were more established to test the temporal dynamics of the putative relationship between comb size and dominance behaviour. This experiment was conducted alongside a larger behavioural experiment, which only enabled a single measurement of comb colour to be conducted at the end of the experiment. Therefore, it was only possible to test for a general association between colour and competitive ability.

2. Materials and methods

One hundred and twenty pullets (Hy-line® Variety Brown) were obtained from a commercial farm (Noble Foods Ltd., Blisthorpe) at point-of-lay (∼15 weeks of age). On arrival, all hens were leg-tagged and fitted with lightweight lycra™ harnesses for identification on overhead video cameras. Fifteen hens were allocated at random to each of eight identical visually isolated pens (1.75 m × 1.75 m × 2 m, $w \times d \times h$). Pens were bedded with wood-shavings (replaced weekly) and contained two wooden perches (L = 1.2 m), a nest-box with four nests, a feed hopper, grit tray and water trough. Hens had *ad libitum* access to commercial food pellets, water and grit throughout the experiment. At the start of the trial, rooms were illuminated by fluorescent lighting for 11 h a day, inclusive of dawn and dusk periods each of 30 min. From 2 weeks after arrival, the photoperiod was increased by 30 min a week until it reached 16 h a day, in line with standard commercial practice to induce egg laying. To facilitate observations the mean light intensity in the pens was 146 ± 15 lux at hen head-height and the temperature was maintained at 18 ± 2 °C. The hens were kept for 32 weeks.

2.1. Comb measures

Hens were weighed in each of weeks 1–19 and again at the end of the experiment (week 32). The first day of weighing was the third day after arrival and mixing. On the same days as they were weighed, the maximum length and breadth of each hen's comb was measured to the nearest mm and their product calculated to estimate total comb area for each individual. This approximation of comb area does not account for the saw-tooth shape of the comb, but provides a proximate measure of total area which is an established approach in studies linking comb size and behaviour (D'Eath and Keeling, 2003; Forkman and Haskell, 2004)

In week 27, each hen was removed from its pen and the spectral reflectance of the comb from 380 to 780 nm was measured using an ocean telespectroradiometer. A telespectroradiometer is a spectroradiometer with modified telescoping input optics that enable the spectral irradiance of objects to be measured from larger distances (Blass, 2009). Colour measurements were conducted over two days in a room without daylight. The room was lit on both days with the same artificial light source (Osram L 58 W/830 Lumilux Warm White), which had been left on overnight to ensure a standard level of light output. On removal from its pen, each hen was held in a similar position against a white background whilst the telespectroradiometer image was taken. The telespectroradiometer was focused on a 5 mm diameter circular area in the centre of the comb to take each measurement. Efforts were made to complete this procedure in under a minute before hens were returned to their home pens. This was to reduce the possibility of changes in comb colour in response to handling. Comb colour is influenced by blood supply, which can be altered by stress. However, as the hens were habituated to handling, such a response to this intervention was not anticipated or observed visually. The spectral reflectance data enabled three main colour characteristics to be quantified for each comb: (1) the luminance of each comb relative to a reference white, (2) the dominant wavelength reflected by each comb (which relates to the perceived hue) and (3) the purity of the comb colour, i.e., the colour saturation (expressed as a ratio).

2.2. Behavioural observations

An overhead CCTV camera system (Panasonic colour CCTV camera WV-CL270/G, Milestone XProtect Remote Client, Sony and Milestone IP video management software, Ripley, UK) was used to record the behaviour of the hens in each group, on a day when they were not disturbed in each of weeks 3–10. On recording days, the hens were videoed remotely for 15 min in the morning (immediately after the dawn period) and afternoon (6 h after the dawn period). All aggressive interactions between hens were recorded by two experienced observers. The observers watched the same number of videos from each pen as well as 10% of the same recordings to enable the inter-observer reliability to be calculated. There was a high degree of correlation between the two observers in their recording of aggressive behaviour (Spearman's rank correlation test: $r_s = 0.940$, $n = 44$, $P < 0.001$). The total number of aggressive interactions observed during these sessions between all hens was used to construct a matrix for each pen, detailing the proportion of aggressive interactions won and lost by each hen between all dyads in that pen. An aggressive interaction was defined as an aggressive peck directed from one bird to another that resulted in retreat or avoidance by the recipient (the actor being defined as the winner and the recipient the loser). By calculating the proportion of aggressive interactions won and lost, this approach takes into account the win/loss asymmetry resulting from the total number of interactions recorded between different dyads. This approach is more suitable for situations where multiple interactions between individuals are witnessed than methods such as Clutton-Brock et al.'s index (1979). The latter index treats any number of losses or wins between dyads in the same manner as a single loss or win, which can disproportionately raise or lower the dominance index of an individual based on a single win or loss (Gammell et al., 2003). Using the aggression matrices constructed for each pen, a David's score was calculated for each hen so that the relative score of each hen within a pen reflected its within-group competitive ability (David, 1987). Thus a hen with a higher David's score than another hen within the same group would be considered to have a greater competitive ability, as based on the number of agonistic interactions they won and lost with all other hens in the group. To correct for any missing data, a modification was applied whereby a dyadic dominance index based on chance was allocated to any dyads between which no interactions were witnessed during observations (de Vries et al., 2006). In this experiment, David's scores were not used to assign an absolute dominance rank to each individual as there was no assumption of a linear dominance hierarchy.

2.3. Ethical note

Approval for the harnesses to be worn for identification was given by the Home Office Inspector with regular inspection by the Royal Veterinary College's Named Animal Care and Welfare Officer. The harnesses did not impede behaviour; a hen could preen underneath it and fit was checked regularly to ensure the size remained appropriate as the hen grew. There was no evidence of any discomfort resulting from harnesses. At the end of the experiment, the harnesses were removed and the hens were re-homed.

2.4. Statistical analyses

A generalised linear mixed model (GLMM) was used to investigate the relationship between comb size and David's score at three discrete time points in the experiment; three days after the hens were mixed (week 1), in week 10 (the final week of behavioural observations) and at the end of the experiment (week 32). Comb area was the response variable with a log normal error distribution. The fixed effects in the model were David's score, body weight and week. David's score and bodyweight were both covariates and week was a fixed factor with three levels (weeks 1, 10 and 32). Including body weight in the model controlled for differences in comb size attributable to mass. An interaction between David's score and week was included to test whether the relationship between comb area and David's score differed across weeks. Pen and hens nested within pen were specified as random effects to account for the non-independence of individuals within the same pen and repeat measures on the same individuals across weeks. The same model, but with body weight as the response variable (and not a fixed effect), was used to test the relationship between hen size and David's score over the experiment with a normal error distribution.

To test the relationship between comb colour and competitive ability, three separate general linear mixed models were run. Each model had David's score as a fixed effect with luminance, dominant wavelength or purity as a response variable. In each case, the error distribution was normal. Pen was specified as a random factor, again to account for the non-independence of measures conducted on hens within the same pen. To check for any association between comb colour and comb size a GLMM was performed with comb size in week 32 as the response variable and luminance, dominant wavelength and purity as covariate fixed effects. Pen was specified as a random factor and the error distribution in this case was normal.

In all cases the model assumptions of homogeneous variance across fixed effects and normality of response variables were checked by visually inspecting model residuals using residual frequency distributions and *Q*–*Q* plots.

3. Results

There was a highly significant association between comb size (i.e., area) and David's scores; hens with a larger comb area generally had higher David's scores (GLMM: $F_{1,110} = 13.68$, $P < 0.001$, gradient of slope = 0.008 ± 0.002, Fig. 1). Although this association did not vary significantly across weeks 1, 10 or 32 (GLMM: $F_{2,225} = 2.72$, $P = 0.07$), there was a trend for it to become stronger over the experiment (week 1: gradient of slope 0.006 ± 0.003, $P = 0.03$; week 10: gradient of slope 0.008 ± 0.003, $P < 0.01$; week 32: gradient of slope 0.012 ± 0.003, $P < 0.001$). There was no significant association between body weight and David's score (GLMM: $F_{1,111} = 0.01$, $P = 0.91$) and this did not differ across the weeks observed (GLMM: $F_{2,228} = 1.05$, $P = 0.35$).

Although there was a trend for hens with higher David's scores to have combs with a higher luminance (or reflectance), this association was not significant statistically (GLMM: $F_{1,100} = 2.75$, $P = 0.10$). However, there was an inverse association between the competitive ability of hens and the dominant wavelength of their combs (GLMM: $F_{1,107} = 8.03$, $P < 0.01$); hens with higher David's scores had combs with lower dominant wavelengths (gradient of slope = -0.067 ± 0.023, Fig. 2). The dominant wavelengths ranged from 603 to 616 nm. There was no evidence of a relationship between the purity of comb colour and David's scores (GLMM: $F_{1,107} = 0.04$, $P = 0.85$).

There was no relationship between comb size and any aspect of comb colour examined (GLMM: luminance: $F_{1,41} = 0.01$, $P = 0.93$; dominant wavelength: $F_{1,105} = 1.10$, $P = 0.30$; and purity: $F_{1,105} = 2.12$, $P = 0.14$).

4. Discussion

This study identified a strong positive association between the size of a hen's comb and her competitive ability. Hens with higher David's scores had larger comb areas than those with lower David's scores. This relationship was consistent over time. An important implication of this result is that comb size in week 1 (just 3 days after mixing) was significantly associated with a hen's competitive performance in weeks 3–10. This raises the possibility that comb size predicted competitive ability; although dominance relationships may have been established by day 3, it seems unlikely that comb size would have altered substantially in response to newly established social positions in this timeframe. However, to our knowledge, there are no published data on the time taken for the comb to change size. If comb size is predictive of competitive ability it could convey useful information to hens judging an unfamiliar opponent.

The association between comb size and competitive ability was stable as it was still evident at the end of the experiment (22 weeks after the behavioural observations). The peck-order between hens in small groups has been reported to persist for more than a year without change (Collias, 1943). Therefore, we can assume that the dominance behaviour of hens based on behavioural observations between weeks 3 and 10 continued to reflect the relative competitive ability of hens at the end of the trial.

The finding that comb size is positively correlated with competitive ability substantiates the observations of Collias (1943), Forkman and Haskell (2004) and Martin et al. (1997) but is in contrast to those of Bradshaw (1992) and Cloutier and Newberry (2000). Cloutier and Newberry (2000) suggested that an average difference in comb area of >25% may be necessary for this trait to reflect social rank. The mean difference in comb area in our study ranged from 25.5% to 44.7%. It is possible that the variation in comb size in the experiments conducted by Bradshaw (1992) and Cloutier and Newberry (2000) was insufficient to detect a significant association between comb size and dominance behaviour. To our knowledge, the current study is the largest in terms of sample size, to investigate the association between comb size and dominance behaviour in laying hens. Furthermore, by comparing relative dominance scores with comb area, as opposed to ranking dominance and comb size, our approach was more sensitive than previous studies. Therefore, the weight of evidence supports the notion that there is a relationship between comb size and dominance behaviour in laying hens.

It is less clear how such an association between comb size and competitive ability has come about. There is some evidence from early research that comb size in domestic hens is influenced by testosterone concentrations (Luck, 1982; Williams and McGibbons, 1956), which could be a mechanistic link between comb size and aggression (Allee et al., 1939). Comb size does not appear to be related to dominance behaviour in female red jungle fowl and it has been suggested that a relationship between comb size and dominance in laying hens may be more likely a result of inadvertent selection for larger and more pronounced combs size during domestication (Kim and Zuk, 2000). In line with findings of several previous studies, fighting ability did not appear to be related to body weight in the current experiment (Bradshaw, 1992; Collias, 1943; Forkman and Haskell, 2004; Martin et al., 1997).

Hens with combs of a lower dominant wavelength generally had higher David's scores than those possessing

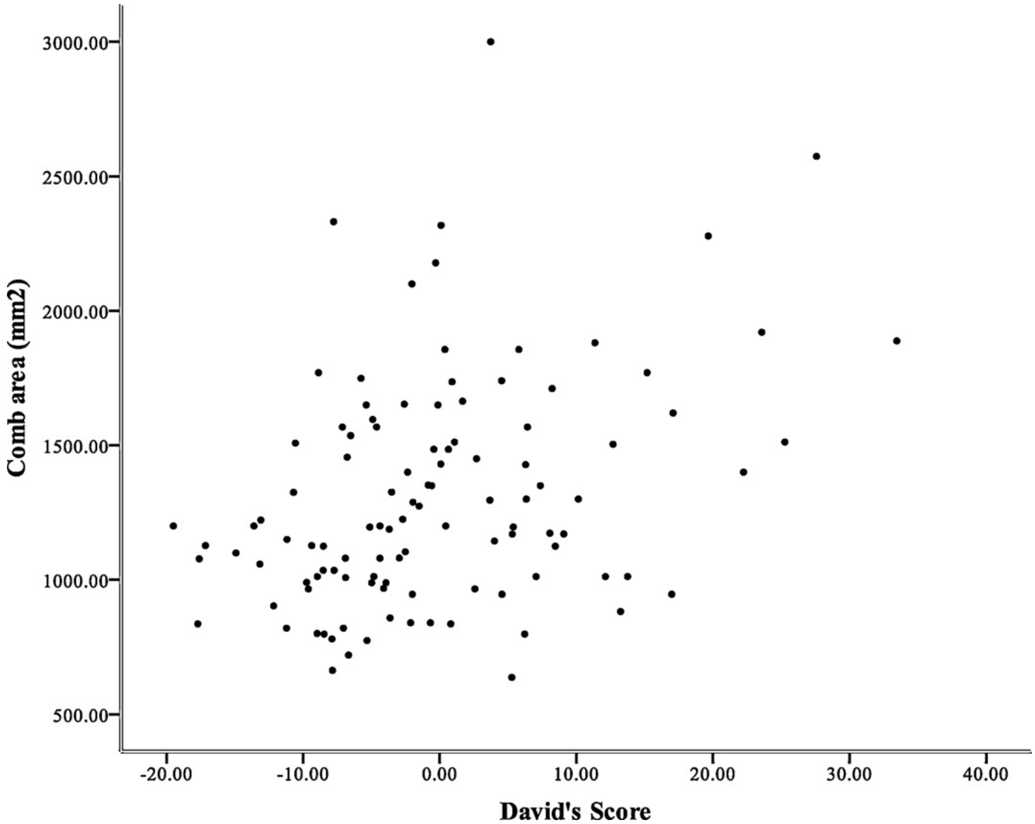

Fig. 1. The association between comb area and David's score in laying hens in week 32 (week 32 given as an example as there was no significant difference in this relationship between weeks 1, 10 and 32).

combs with a higher dominant wavelength. The dominant wavelengths of combs ranged from 603 to 616 nm. Therefore, hens with a comb that had a hue perceived by humans as closer to yellowish-red than pure-red tended to have a higher competitive ability. Comb colour is controlled primarily by blood supply, suggesting that differences in this trait are likely to reflect variation in blood components such as carotenoids. In other species, such as the red grouse, *Lagopus lagopus scoticus*, comb redness has been shown to be linked to carotenoids, high concentrations of testosterone, and overall body condition (Mougeot et al., 2007). There was a non-significant tendency for hens with higher David's scores to have combs of a higher luminance, but no observable relationship between the purity of comb colour and competitive ability. It is difficult to place the results of this study in the context of the few previous studies that have investigated comb colour and dominance behaviour in hens (Bradshaw, 1992; Cloutier et al., 1996; Martin et al., 1997). This is partly due to methodological inconsistency, but also because the two studies that reported an association between these traits used ambiguous terminology to describe colour (Bradshaw, 1992; Cloutier et al., 1996). Although colour measurements made using spectroradiometry are likely to be more accurate and objective than those with the Munsell system, they should be broadly comparable if accurate and unambiguous terminology is used. Therefore, we encourage future studies to report the luminance, dominant wavelength and purity of colours as these are the main characteristics that can be quantified from the standard C.I.E. chromaticity system

There is an inevitable limitation of using colorimetric methods based on human vision to quantify the colour characteristics of a trait of interest in another species in that we can never be absolutely certain how such characteristics are perceived by the latter. Particularly luminance, as this characteristic is based on the human spectral sensitivity curve. However, Saunders et al. (2008) have demonstrated that the inherent error in the equations used to calculate luminance is greater than any perceptual difference in luminance expected between hens and humans based on their relative spectral sensitivity. Therefore the improvement in accuracy achieved by tailoring luminance measures to the chicken spectral sensitivity curve would be negligible. Purity and dominant wavelength are also based on a model of human vision; the values are taken from the C.I.E. chromaticity system. As the perceptual descriptions relating to dominant wavelength, i.e., perceived hue, and in the case of purity, colour strength, are based on a human perspective it is advisable to limit the use of human-biased descriptive terms associated with these characteristics until we know whether there is a significant difference between human and hen perception in this context.

The comb colour measures were conducted 17 weeks after the behavioural observations. As previously stated, it is reasonable to assume that the dominance relationships

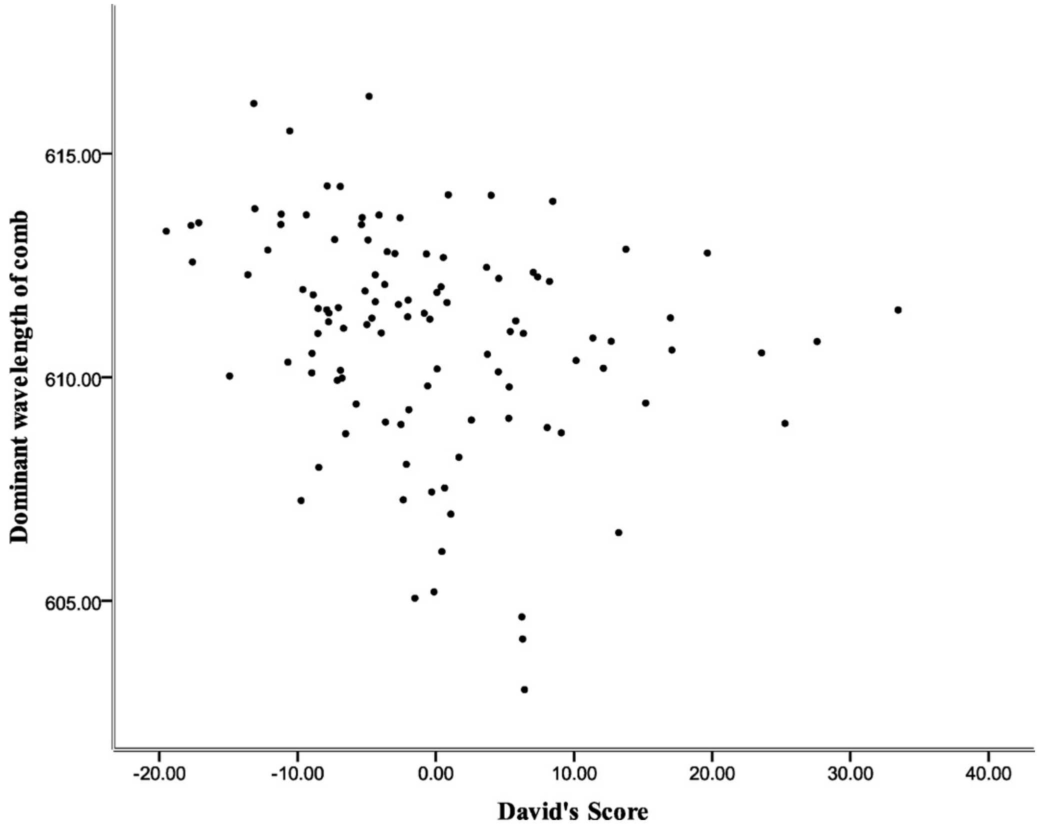

Fig. 2. The association between the hue (i.e., dominant wavelength) of the comb and the David's score of laying hens.

between hens were stable over this period (Collias, 1943), but it is not known whether comb colour is similarly stable over time. However, the fact that there was a significant association between dominance behaviour between weeks 2 and 10 and comb colour in week 27, suggests that the relationship between these two traits, at least, may be stable. Furthermore, the telespectroradiometer did not measure spectral reflectance across the entire ultraviolet range ($320 < \lambda < 400$ nm), though hens are sensitive to this range of wavelengths (Prescott and Wathes, 1999). As the dominant wavelengths of the combs were all above 603 nm, it is likely that this does not represent a significant information deficit.

It is important to acknowledge that even though there was a significant relationship between both the size and colour of the comb and dominance behaviour, hens do not necessarily use these traits in social contexts. It is possible that individuals cannot perceive the relative differences in size and colour, which could provide useful social information. Or even if they can perceive such differences, they may not glean any social cues from this information. However, these traits are used in other social contexts; both comb size and colour are known to influence mate choice in red jungle fowl (Cornwallis and Birkhead, 2007; Zuk et al., 1995). Furthermore, in the case of comb colour, the dominant wavelengths reported in this study are within the range of longer wavelengths to which chickens are particularly sensitive (Prescott and Wathes, 1999). This makes it likely that hens can perceive the differences in the dominant wavelengths of different combs. Finally, it is pertinent to remember that the comb measures were not conducted at the same time points as the behavioural observations. Therefore, any conclusions drawn from this study rely upon the assumption that the behavioural observations made during weeks 3–10 generally reflected stable social relationships and that the association between comb traits, particularly colour, and these social relationships was relatively consistent throughout the experimental period.

5. Conclusions

This study examined the relationship between dominance behaviour and the size as well as colour of domestic laying hens' combs. We found that hens with a greater competitive ability had larger combs with a colour that tended to be characterised by lower dominant wavelengths than less competitive hens. To date, conflicting evidence has been reported on this topic. As this is the largest study of this kind, we believe that these results provide strong evidence that the comb is linked to dominance behaviour. This raises the possibility that hens utilise attributes of an opponent's comb to judge competitive ability. Further research is required to fully investigate this possibility.

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