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Do hens have friends?

Siobhan M. Abeyesinghe[a,*], Julian A. Drewe[a], Lucy Asher[b], Christopher M. Wathes[a], Lisa M. Collins[c]

[a] Department of Production and Population Health, Royal Veterinary College, UK
[b] School of Veterinary Medicine and Science, University of Nottingham, UK
[c] School of Biological Sciences, Queen's University Belfast, UK

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ABSTRACT

Recent interest in positive welfare has encouraged consideration of the formation of socio-positive relationships in farmed species which may provide a means by which to manage positive states. We investigated in detail the existence of dyadic preferential associations in small groups of domestic laying hens. Spatial and temporal associations were examined in two contexts (day activity and evening roosting), within 8 identical pens of 15 laying hens over 8 weeks. Little aggression was observed. Social network analysis was performed to investigate correlations in who associated with whom using weighted degree (number) and binary (presence or absence) data for shared resource areas and proximity to other individuals. No consistent evidence was found for hens actively preferring others in their choice of resource area, or in companion proximity. Perch-roosting positions chosen by the hens were compared with data generated from a random-choice model. Hens showed no position preferences. Most dyads were never observed roosting together and, although some apparently perched together frequently, the low number of nights perching and proportion of nights spent together indicates these findings should be interpreted with caution. Overall, we found no convincing evidence of dyadic preferential relationships expressed by close active and resting proximities. Further work is required to confirm whether these findings hold true in other experimental contexts, are affected by social experience and if they hold in common with the progenitor sub-species.

1. Introduction

Our understanding of the social lives of domestic animals is of increasing importance due to the potential impacts on animal welfare, production and adaptation to the domestic environment. For captive animals diversity in the complexity of social relationships (Kutsukake, 2009) may be shaped by: (i) the evolutionary mechanisms underlying group living in the progenitor species (ecology, life history, etc.); (ii) the discrepancy between natural and artificial environments (lower predation risk, greater and more reliable food and water availability, limitations on space and alterations in social environment); and (iii) the impact of artificial and natural selection in captivity (Price, 1984, 1999).

The functional bases of affiliative behaviour include minimising intra-group aggression and maintaining group cohesion as an anti-predator mechanism (Bekoff, 1977). Thus we may expect selection pressure for affiliative behaviour to be undermined by the significant reduction of predation-risk and resource competition in the domestic environment compared with the environments encountered by progenitor species. Alternatively, selection for increased social tolerance and gregariousness in domesticated species may have maintained affiliative tendencies.

* Corresponding author. Tel.: +44 01707 666947; fax: +44 01707 652090.
E-mail address: sabeyesinghe@rvc.ac.uk (S.M. Abeyesinghe).

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Complex socio-positive relationships may increase fitness and buffer against stress (Hennessy et al., 2009; Cameron et al., 2009; Massen et al., 2010), potentially facilitating adaptation to domestic environments which may differ significantly from the species' biological niche. Such social bonds have also been proposed as a mechanism by which 'positive welfare' can be promoted (Lindberg, 2001), as well as being potentially significant source of stress if disrupted.

Although social bonds between familiar unrelated conspecifics are reported to occur in captive and domesticated ungulates (Guilhem et al., 2000; Durrell et al., 2004; Gygax et al., 2010), relationships are not always consistent (e.g., Durrell et al., 2004), potentially reflecting the degrees of genetic selection or discrepancy between the natural and captive environments. These factors are substantial for the commercial domestic fowl, compared with its progenitor, the Red Junglefowl (RJF; *Gallus gallus spadiceus*), in which inter-female preferential associations have been reported (Sullivan, 1991a). Whether the commercial domestic fowl still forms same sex specific dyadic preferential associations (hereafter referred to as preferential associations) has not previously been investigated, but they can discriminate same sex flock-mates (Abeyesinghe et al., 2009) and show at least one of the attributes underpinning empathy (Edgar et al., 2011), which is associated with complex social relationships. Here we sought evidence for specific dyadic social preferences in domestic fowl by investigating associations amongst small groups of laying hens, using close spatial proximity observed more frequently than expected by chance and maintained across time and across behavioural contexts as a measure of preferential association between individuals (Whitehead and Default, 1999).

2. Materials and methods

2.1. Animals and housing

Hyline Brown 15-week-old pullets ($n = 120$), previously brooded and reared in a floor system in a single indoor house containing 20,000 birds, were obtained from a commercial supplier (Noble Foods Ltd., Bilsthorpe). Birds were housed in eight identical, visually isolated pens (3.06 m^2), each containing 15 birds. Although unlikely given the group size, to reduce the possibility of familiar birds caught together being placed as a group, birds were distributed to minimise the number of birds from each crate which were allocated to each of the pens. Pens were bedded with weekly replaced wood-shavings and offered ad libitum commercial pelleted food, water and grit, a 4-hole nest-box and a dual-rail wooden perch (length × height: 1.2 m × 0.5 m). The mean ± SD light intensity was 146 ± 15 lux at bird height and temperature was maintained at 18 ± 2 °C. Two weeks after housing, the photoperiod, encompassing 30 min dawn and dusk periods, was increased by 30 min per week from 11 to 15 h, following standard commercial practice to facilitate egg production. Hens wore coded harnesses, approved for use without regulation by the Home Office, to allow identification. The harness did not impede behaviour; birds could preen under it and the fit was checked regularly, with immediate adjustment or removal as necessary. The birds were re-homed at the end of study.

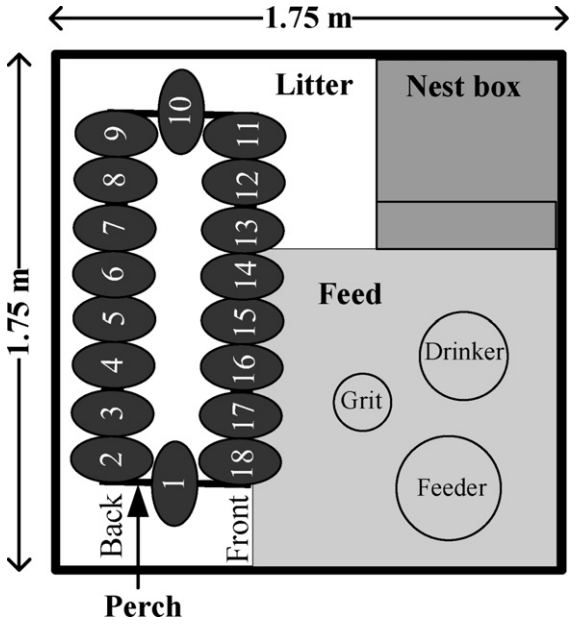

Fig. 1. Plan view of the pen subdivisions (Feed, Nestbox, Perch and Litter areas) and perch locations (1–18) used as a basis for deriving active and roosting spatial associations, respectively. General perch areas were defined as: left [(roosts 1–5, 15–18) vs. right (roosts 6–14)]; front (roosts 11–18) vs. back (roosts 2–9); and edges (roosts 1–3, 8–12, 17–18) vs. middle (roosts 4–7, 13–16).

2.2. Behavioural sampling and analysis

Following the two weeks' acclimatisation, all pens were recorded across eight weeks using an overhead digital CCTV camera system (Milestone Xprotect Client, Ripley, UK). To examine associations during active space use, two 15 min periods commencing immediately and 6 h after the dawn phase on one day of each week were recorded. To examine evening roosting associations the last 15 min of dusk was recorded on three days per week for each of the same eight weeks. Very little aggression was seen during this period, consistent with establishment of stable social groups during acclimatisation.

2.2.1. Testing associations during active space-use

Two association measures were recorded for each individual during the active context using one minute scan sampling; simultaneous location in one of four resource-based areas (hereafter 'areas'; Fig. 1) and area-independent conspecific proximity within a single bird-length of the focal bird's head (hereafter 'proximities'). To check for temporal independence of data, contingency tables of transitions from the state at time t against the state at $t-1$, $t-2$, $t-3$, $t-4$, etc. for each observation and day, were created and chi square tests, or where appropriate Fisher's Exact tests, of independence of transitions were performed until the criteria for temporal independence had been satisfied. When test results were combined, results were considered to be significant overall when the cumulative binomial

probability was $p < 0.05$ (Cross and Chaffin, 1982); this required twelve or more significant results (cumulative binomial probability ($r \geq 12$, $n = 128$, $p = 0.05$) = 0.03). Data collected at time points 0, 5, 10 and 15 min in each active observation period were considered independent of each other and used in subsequent analyses.

Area association networks were constructed whereby ≥2 birds simultaneously located in the same resource area were considered to be associating. For each time period, a weighted adjacency matrix was constructed; for each pair of hens *i* and *j*, the *ij*th entry of the matrix took the value of the number of times that hens *i* and *j* associated. Thus, x_{ij} was greater than zero when association occurred and zero if it did not. Matrices were symmetric about the diagonal because associations were not directed, i.e. $x_{ij} = x_{ji}$ (if hen A was in close proximity to hen B, then hen B must have been close to hen A). As a hen could not associate with itself, all diagonal values were zero, i.e. $x_{ii} = 0$. The analysis was repeated using binary networks to assess the presence or absence of any associations rather than a count of associations present. The stability of repeated associations between individuals was examined by testing networks where pairs of hens (i) associated any number of times and (ii) associated at least half the time (≥4 out of 8 possible time points per week) using the quadratic assignment procedure (QAP) in UCInet for Windows (Borgatti et al., 2002). QAP involves computation of Pearson's correlation coefficients for corresponding cells of two data matrices (each matrix coding for one network), followed by random permutation of one matrix and re-computation of Pearson's correlation coefficients. This was repeated 50,000 times to calculate the proportion of times that coefficients from randomly arranged networks were larger or equal to the observed Pearson's coefficient and thus generate an associated probability value that the relationship between the networks was due to chance (Hanneman and Riddle, 2005). The method allowed searching for temporal correlations between networks constructed from data collected over various time intervals within the study period. To account for multiple testing of the same networks, we applied a Bonferroni correction and considered relationships significant where $p < 0.007$ for tests comparing seven time periods (e.g., when comparing week 1 with each of the other seven weeks) and $p < 0.002$ for tests comparing 28 time periods (e.g., when comparing all weeks with all other weeks).

To evaluate hens' associations based on proximities irrespective of area location, simple ratio association indices were computed for each pen using SocProg (Whitehead, 2009). The null hypothesis was that individual hens associated at random with other hens within their pen. For each pen, the standard deviation (SD) of observed association indices for all within-pen dyads was compared against randomised association indices generated via a Monte Carlo test, involving 50,000 permutations of an observation-by-individual matrix with 100 flips per permutation (keeping constant the number of individuals per pen and observations in which each individual was recorded; Bejder et al., 1998). Preferred or avoided companionships were evidenced by significant differences (at $p < 0.0005$; equating to significance at the 5% level in a two-way test after Bonferroni correction for multiple comparisons; Hanneman and Riddle, 2005), but individual dyadic relationships were considered significant only if the overall pen-level test was also significant (Whitehead, 2008).

2.2.2. Testing associations during roosting

To determine roosting associations, each hen's occupancy of one of 18 individual perch roost locations (hereafter 'roosts', based on a space allocation of 15 cm per bird; Fig. 1) was recorded at the end of dusk. A sampling-without-replacement, random-choice model, developed in Microsoft Excel using AbleBits™ Random Generator add-in function, was used to simulate random roost selection by individual hens; running the simulation for 1000 iterations, each ending once all 15 birds had chosen. Once a location had been selected by a bird, it was no longer available to others. As there were more roosting locations than hens, all hens had a choice of available locations (minimum 4). The random-choice model was then compared with the observed roosting location data for each pen in three ways to allow discrimination of location from flock-mate preferences.

To test whether specific roosts were occupied by birds more frequently than expected by random choice, the observed proportion of evenings ($n = 24$) that each of the 18 roosts was occupied by any bird was calculated. To test whether general perch areas were chosen more or less often than expected with random choice, the number of evenings an individual was observed occupying a roost in specified areas of the perch (Fig. 1: left vs. right; front vs. back; and edges vs. middle) as a proportion of the total number of evenings that individual was recorded on the perch was calculated. For statistical analysis the observed results for both specific locations and general areas, were compared with expected (random-choice model) medians per pen using 1-sample Wilcoxon Signed Rank tests.

To test whether individual hens chose to roost next to a specific companion more or less often than would be expected at random, the number of evenings any dyad occupied immediately adjacent roosts (maximum of two; one either side), as a proportion of the total number of evenings that both birds were perching simultaneously, was calculated. A random choice model distribution of SDs, calculated from 42 subsets of the original model (each containing model roosting data over a hypothetical 24-night period), was then compared with the observed pen SDs of the proportion of evenings dyads roosted adjacently, using one-sample *t*-tests (the model distribution met parametric test assumptions). All data were corrected for multiple testing (Haccou and Meelis, 1992).

3. Results

3.1. Associations during active space use

Hens in only one of the eight pens (pen 1) showed an overall significant level of association when considering resource area use ($SD_{observed} = 0.077$, $SD_{random} = 0.060$; $p = 0.00002$ cf. Bonferroni-corrected $p_{Bc} < 0.0005$ equating to significance at the 5% level in a two-way test), with two dyads preferentially associating (mean simple-ratio association indices 0.45 and 0.52) and one showing avoidance

Table 1
Descriptive analysis of roosting companion preferences comparing the 'expected' random model output, with the observed (from the video footage of 8 hen groups) proportion of evenings that any within-pen dyad perching simultaneously also occupied immediately adjacent roosts (possible number of dyads per pen = 105).

	Mean proportion	Standard error of the mean	Minimum proportion	Maximum proportion	Skewness
Expected	0.12	0.00	0.09	0.15	0.07
Observed by pen					
1	0.07	0.01	0.00	0.40	1.31
2	0.10	0.01	0.00	0.50	1.42
3	0.09	0.01	0.00	0.33	0.81
4	0.10	0.01	0.00	0.67	1.78
5	0.07	0.01	0.00	0.50	1.62
6	0.10	0.01	0.00	0.75	2.25
7	0.07	0.01	0.00	0.50	2.07
8	0.10	0.02	0.00	1.00	2.96

(0.13) relative to the pen mean simple-ratio association index of 0.30. We found no evidence of temporal stability in association networks. No significant correlations occurred when the structure of weighted networks from one week was compared with those of any other week (overall mean correlation across all pens $r = 0.035$, $p = 0.265$), or within-day networks of morning compared to afternoon sessions (overall mean correlation across all pens $r = 0.077$, $p = 0.225$). For binary networks of birds associating more than 50% of the time, a significant correlation occurred in only pen 1, between the structure of the association networks in weeks 3 and 4 (QAP with 50,000 permutations, $r = 0.297$, $p = 0.006$; overall mean correlation across all pens $r = 0.022$, $p = 0.281$), suggesting that birds tended to associate in an area with the same other individuals across this narrow time period, but not longer timeframes.

No pen showed an overall significant level of preferred or avoided proximity-based associations ($p \geq 0.002$ cf. $p_{Bc} < 0.0005$).

3.2. Associations during roosting

The proportion of evenings that a specific roost location in each pen was occupied did not differ significantly from random choice (p's > 0.191). The expected probability of a location being chosen assuming all hens were roosting was 83%, but for most observations, some hens were not roosting (mean number of hens roosting over 24 nights ± standard error (SE) in pens 1–8: 6.0 ± 1.0, 8.5 ± 0.6, 9.0 ± 0.44, 7.9 ± 0.61, 7.4 ± 0.41, 9.25 ± 0.46, 6.7 ± 0.41, 8.1 ± 0.43). Hens did not have a general area preference: the observed proportions of evenings individuals within each pen chose roosting locations on the left over the right (p's > 0.116), the back over the front (p's > 0.074) or in the middle rather than the edge of perches were no different from random choice (p's > 0.065). However hens did not appear to choose roosting neighbours at random (1-sample t-tests, t for pens 1–8: −28.860, −35.080, −24.990, −43.614, −25.984, −31.500, −47.485, −73.776; d.f. = 41, $p < 0.0001$). There was greater variance and more skew in the hens' proportional roosting partner choices than expected if choice was random; some dyads were seen together frequently, though most were never observed sitting together (Table 1). No weighting was incorporated into the expected model due to lack of data on which to base assumptions of positive association, thus proportions do not reflect numbers perching and should be interpreted with caution.

4. Discussion

To our knowledge this is the first systematic examination of evidence for within-group specific dyadic preferential associations in laying hens using different behavioural contexts. We hypothesised true preferences would be characterised by specific dyads reliably spending greater time in close proximity across active and roosting contexts than would be expected by chance. However we found no consistent evidence for this. The small number of apparent associations did not hold across contexts, suggesting they were chance occurrences rather than true pair-wise social preferences. There are a number of possible explanations for our findings.

It is possible that experimental factors in this study influenced expression or identification of preferential associations and therefore, in the absence of further evidence it is appropriate to assume the current findings are context specific. Since the aim of this study was to seek evidence for the ability of domestic fowl to form specific preferential dyadic social relationships, group size was deliberately kept relatively small, consistent with the progenitor's natural history (Collias and Collias, 1967, 1996). We considered that, if hens were capable, preferential social relationships would be facilitated via greater opportunity for familiarity and reduced cost to memory. Our area-association measure assumed, on the basis that fowl show strong social facilitation of much behaviour (Mench and Keeling, 2001), that preferentially associating hens would be concurrently using the same resources (Massen et al., 2010). However, if social facilitation is socially indiscriminate, i.e. any bird is equally likely to join any other in an activity; shared resource areas would not indicate social preference.

Unlike the progenitor, hens in this study were kept in a relatively confined space. However sufficient pen space was available for birds to distribute themselves such that none were within close proximity (as we defined it) with another bird. By adopting a proximity threshold close to that necessary for social recognition (Dawkins, 1995), a necessary pre-requisite for specific social preference, we defined close proximity in a biologically and socially

relevant manner. While a larger pen size would have facilitated greater spatial distribution, it is not anticipated to have altered meaningful associations; even if certain birds were to be found relatively more close together than others, if inter-individual distances exceeded those necessary for social recognition it is unlikely this would be meaningful in terms of a specific social preference rather than simply general social motivation. Since behaviour most likely to be affected by space allowance (walking and ground-pecking; Keeling, 1994) was still observed, even if social preferences were expressed primarily during specific types of behaviour, frequency of proximity observations is not anticipated to have been spatially constrained. One limitation of our study is introduced by the fixed observation periods during active contexts. It was not possible to observe bird activity throughout the day and therefore we tested our experimental data for temporal independence to ensure we did not find false positives for preferential associations. Although this increased confidence in any associations identified, it correspondingly reduced the chances of observing any associations by reducing our sample size to 64 observations per bird per pen. The social network analysis accounts for the probabilities of finding birds together at greater than chance levels given this number of observations, but it is conceivable that the numbers of observations limited our ability to detect associations. If it is reasonable to assume that the strength of preferential associations would be reflected in the amount of time spent in close proximity, then this experimental limitation would reduce the chances of finding preferential associations of moderate to low strength.

Given the prolonged, close proximity and contact involved in roosting (Wood-Gush et al., 1978), we expected individuals to be selective of their neighbours. Apparent associations could not be explained by specific individuals consistently roosting early and thus being more frequently found together. However, proportional choice based on a greater number of nights is more notable than the same proportion of fewer nights perched together. To illustrate, assuming simultaneous perching by a dyad on $\geq$25% of recorded nights ($n \geq 6$) and being recorded in close proximity $\geq$50% of those nights is a plausible minimum indicator of preferential association; only one dyad (pen 7) of 840 met this criterion. The low numbers and variation in which birds perched each night suggests our roosting partner findings should be interpreted with caution and requires further investigation when all birds are perching.

So far we have discussed reasons for not detecting preferential associations which existed in our experimental population; however it is also possible that we did not detect preferential associations because they did not occur. In this case, while not precluding the possibility of strong and equal social preference for all group members, given the increased cognitive load associated with complex socio-positive bonds (Croney and Newberry, 2007) our findings would support the possibility of social 'indifference', whereby hens in this study did not place value on individual-specific relationships and were equally tolerant of close proximity by any group member. This interpretation is consistent with preferences for resources explaining domestic hens' movements better than generalised sociality in recent research (Collins et al., 2011), yet conflicts with a previous report of specific intra-flock female–female associations in the RJF progenitor (Sullivan, 1991a).

If preferential associations did not occur in our study sample, one plausible explanation may be provided by the birds' previous social experience. Birds housed in large groups, do not discriminate familiar from unfamiliar individuals (D'Eath and Keeling, 2003) and may acquire weaker conspecific social bonds (Gygax et al., 2010; Schweitzer et al., 2011). It has been proposed that the majority of individuals in large flocks will adopt a strategy of 'social tolerance' in order to avoid the costs associated with defending resources against large numbers of competitors (Estevez et al., 2007). It is possible that birds acquired from such a large flock for this study continued to behave in this socially tolerant fashion rather than altering to a strategy requiring social recognition when re-housed in small groups, rendering development of specific dyadic social preferences unlikely. Further, RJF females naturally brood small clutches of eggs alone (Collias and Collias, 1996) and hatched chicks remain with the hen, independent of the flock, for around 12 weeks (Wood-Gush, 1955; Sullivan, 1991b) during which all early socialisation occurs. Studies comparing brooded and non brooded chicks support an influence of the parent bird on social behaviour. For instance, Fält (1978) found greater aggression in non-brooded Swedish bantams and Bertin and Richard-Yris (2005) found social motivation, measured by social reinstatement behaviour, to be greater in brooded Japanese quail. Commercial fowl are reared in large groups in the absence of an adult on which to imprint, constraining opportunities for social learning which may conceivably contribute to the likelihood of forming certain social bonds. Thus future study should examine maternally reared birds which have been housed continuously in small groups.

Another explanation for lack of preferential associations in the current study assumes that the progenitor subspecies is capable of forming such social bonds, but that social behaviour in the domestic fowl has altered via functional adaptation to the modern domestic environment (Price, 1984), where such bonds are unnecessary and high metabolic demand requires energy conservation (Schutz and Jensen, 2001) possible by minimising cognitive load. An alternative explanation for the lack of evidence for preferential associations in the current study is that they do not occur in fowl. Previously reported RJF associations (Sullivan, 1991a) were based upon proximities within 5 m (in a 0.65 ha area) which significantly exceeds the minimum distance necessary for social recognition in hens (Dawkins, 1995) and thus require confirmation with a proximity measure relevant to dyadic preferential associations. Although such social relationships cannot be ruled out, observational studies of RJF and feral fowl indicate basic sociality appears to be derived from food location and anti-predator strategies rather than more invested mechanisms such as parental care (Collias and Collias, 1967, 1996; McBride et al., 1969; Sullivan, 1991b).

In this study, using a range of measures and a relatively large number of groups, we found no convincing evidence for specific dyadic preferential associations based

on socially relevant close proximities in small groups of adult commercial-strain laying hens. Further work is required to determine whether these findings for domestic hens are specific to our experimental context or alter with social experience of hens and to re-examine evidence for specific dyadic preferred associations in the progenitor subspecies. This information is essential to better understand the nature of social relationships in domestic fowl and determine the validity of using socio-positive relationships as a means to promote positive welfare and buffer against stress in this farmed sub-species.

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