Flock size during rearing affects pullet behavioural synchrony and spatial clustering

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Highlights

- Behavioural synchrony and clustering in space decreased with increasing bird group size.
- Preening was the most synchronised over time and feeding the most clustered in space.
- Simultaneous access to resources for all is more important in small than large groups.

Abstract

Animals are often synchronised in their behaviour, with costs and benefits varying according to group size and the behaviour being performed. Making decisions about optimal allocation and distribution of resources to animals in our care therefore poses theoretical and practical challenges. We investigated group size effects on behavioural synchrony and spatial clustering during daytime in pullets of a commercial laying hen strain reared until 18 weeks of age in groups of 15, 30, 60 and 120 (four replicates of each group size). Feeder, drinker, perch and litter space (i.e. floor space allowance) per bird, were constant across group sizes and all resources were continuously available. Even though the absolute numbers of birds performing the same behaviour at the same time or being located together at the same resource patch increased with increasing group size, the relative degree of synchrony of feeding, drinking, perching and preening across the whole flock decreased exponentially with increasing group size ($P < 0.001$ for all behaviours) as did the relative degree of clustering at the same resource patch ($P < 0.001$ for the same four behaviours). Preening was the most synchronous behaviour (more than twice that of the least synchronised behaviour, perching), and feeding the most clustered in space (three times more clustered than the other behaviours). These results imply that it is more important to provide sufficient resource space for all birds to perform daytime activities simultaneously when kept in the smaller group sizes typical of cages, than in the larger flocks typical of birds kept in floor pens and aviaries.

1. Introduction

Animals in the wild often aggregate. If these animals are also synchronised in time, that is to say, they move to a new location at the same time and perform the same behaviour simultaneously, we call the aggregation a social group or flock. Implicit in this concept of a synchronised group is some form of social co-ordination. In fitness terms, synchronisation can increase the probability of finding food or other valuable resources and reduce predation risk. A disadvantage, if all individuals are at the same resource at the same time, is that of competition. These costs and benefits of living in groups are well documented (e.g. Elgar, 1989; Hamilton, 1971; Penning et al., 1993; Pulliam and Caraco, 1984) and have practical importance for predicting how group size and anthropogenic pressures affect social cohesiveness and fission-fusion dynamics (e.g. Chapman and Valenta, 2015; Sueur et al., 2011). Interest in the mechanisms underlying synchrony is increasing (e.g. Dostálková and Spinka, 2010; Sun et al., 2011) and such work is relevant to the welfare of captive animals because of implications for space and resource allocation when different numbers of animals are enclosed within a specific area. There are, however, few empirical studies comparing behavioural synchrony across different imposed group sizes or ages (e.g. Docking et al., 2008; Jørgensen et al., 2009).

Under natural conditions, risk of predation to an individual varies according to the type of behaviour being performed and the proximity of other individuals (Lima and Dill, 1990). Birds that are vigilant have a greater chance of detecting a predator in time to escape than animals performing behaviour where vision is obscured (e.g. feeding and preening). Thus one would expect an individual to minimise its own predation risk by performing a vulnerable behaviour close to a neighbour performing a less risky behaviour that allows greater vigilance, and this has been confirmed in free-ranging domestic fowl (Keeling and Duncan, 1991). In the absence of fitness benefits from altruistic behaviour (e.g. a vigilant mother watching over resting offspring), having such a neighbour could be a disadvantage to the more vigilant animal, who could only minimise its risk of predation by being next to an individual performing an even less risky behaviour. Only when neighbouring individuals with similar characteristics are performing the same behaviour is their risk of predation equalised. A high risk of predation should, therefore, act to increase group synchrony in homogeneous groups. Conversely, given that increased group size theoretically reduces individual predation risk and allows individuals to spend less time being vigilant (Elgar, 1989; Hamilton, 1971; Lima and Dill, 1990; Roberts, 1996), synchrony would be expected to decline with increased group size. Studies of antipredator behaviour suggest that domestic fowl continue to conform to behavioural ecology predictions even when housed indoors in the absence of predators (Cornetto and Estevez, 2001; Newberry and Shackleton, 1997; Newberry et al., 2001) although the magnitude of their antipredator responses may be diminished relative to those of wildlife. There is, for example, evidence that synchrony of perching behaviour is less pronounced in modern laying hens compared to the red jungle fowl, probably because of relaxed selection pressure on antipredator behaviour during domestication (Eklund and Jensen, 2011).

A second factor affecting flock synchrony is competition for resources. The degree of competition will vary according to the distribution of the resources in time and space and the number of individuals competing for them, and will be fine-tuned by zeitgebers (e.g. dawn and dusk, sounds signalling food availability, etc.). When resources are clumped, some individuals in the group may prevent others from using a resource at the same time, through either physical obstruction or aggressive threat (Leone and Estevez, 2008; Thogerson et al., 2009). As a result, synchrony of resource use will decrease. The presence of more individuals at a resource implies greater competition for access to that resource. Unless the resource is quickly depleted and difficult to defend (Estevez et al., 2002), increased group size, especially in combination with clumped resource distribution, would therefore be expected to reduce behavioural synchrony. These conditions apply when pullets of domestic fowl strains selected for egg production are reared commercially. Feed and water are usually provided ad libitum but clumped at feed troughs and drinkers, and perch space, if any, may be sufficient in total length but limited at preferred upper levels (Newberry et al., 2001).

Caged laying hens feeding from a single trough exhibit a higher degree of feeding synchrony at greater feeding trough space allocations (Hughes, 1971; Thogerson et al., 2009; Webster and Hurnik, 1994). Based on such observations, it is often recommended that feeders should be long enough to allow all birds to feed simultaneously under the assumption that the birds are socially motivated to coordinate their behaviour and frustrated if unable to do so. However, when Collins et al. (2011)

investigated both feeding synchrony and clustering in groups of four adult laying hens in floor pens with one feed trough, it appeared that clustering resulted primarily from independent attraction to the feeder rather than social cohesion. In contrast, Collins and Sumpter (2007) reported marked social facilitation of feeding behaviour in time and space among young broiler chickens in large commercial flocks. These results suggest that there may be group size and age differences in behavioural synchrony over time and spatial clustering around resources in domestic fowl. In commercial layer houses, group sizes in cages are more similar to those found in nature whereas in loose housing systems there can be several thousand birds in a flock. Moreover, the groups are highly uniform, comprising females only, all of the same age and usually of the same genetic strain. According to the arguments presented above, birds competing for clumped but non-depleting resources should become less synchronised with increasing group size. With the trend to keep laying hens and pullets in larger groups with multiple feeding, drinking and perching locations, the manner in which group size affects whole flock synchronisation and local clustering around resources is of practical importance when deciding on appropriate allocation and distribution of resources. For a discussion of some of the consequences of different space, resource allocations and group sizes for laying hens kept in furnished cages, based on theoretical models, see Appleby (2004).

In this study, we investigated the effects of group size on flock synchrony and clustering at resource patches in layer pullets reared in floor pens. Based on theoretically reduced predation risk and increased competition for resources with increased group size, we hypothesised that behavioural synchrony and spatial clustering would decline with increasing group size. We also evaluated the frequency with which one bird disturbed another as a possible consequence of lack of behavioural synchrony in larger groups. We chose to work with pullets because there is limited information about appropriate allocation of resources during rearing and because effects of pullet age on synchrony and clustering have not, to our knowledge, been reported previously.

2. Materials and methods

2.1. Animals, housing and husbandry

Four group sizes were used in this study; 15, 30, 60 and 120 pullets per pen. Each group size was replicated four times. The pens were arranged in randomised blocks within the same environmentally controlled building. Pen walls were constructed of plywood to a height of 1.5 m to provide a visual barrier between pens, with chicken wire above for ventilation. The 900 pullets (of a commercial strain of White Leghorn laying hens with intact beaks) were randomly assigned to these floor pens at 1 day of age, with continuous access to standardised feed, water, perches and litter. There were four feeders and three rows of drinking nipples in each pen and, initially, there were two three-tiered wooden perch units but this was increased to four units per pen at 12 weeks. The layout of these resources was the same for each group size (Fig. 1). The stocking density was 5 birds per m2 in all group sizes, and the amount of feeding space (4 cm per bird), the number of nipple drinkers (one for every 5 birds) and the perch space (10 cm, increased to 20 cm per bird) were also constant across group size. To achieve this consistency of stocking density and resource allocation, the size of the pen, feeders, drinkers and perches was increased proportionally with increasing group size while keeping the pen shape consistent. The photoperiod was 23 h during the first week, gradually lowered to 8.5 h by 3 weeks of age, and raised to 10.5 h from 12 to 18 weeks of age. Light intensity was a mean of 11 lx on perches and 5 lx on the floor and the scotoperiod was completely dark as typical of some commercial poultry housing. The building was heated by hot water pipes along the walls and the concrete floor was covered with wood shavings litter. Management was according to routine practice for rearing laying hen pullets in Sweden and the study was approved by the regional ethics board. Prior to commencing behavioural observations the number of birds in each pen was adjusted, by adding chicks if necessary. During the experimental period, between 3 and 18 weeks, total mortality was 0.4% and no further adjustments to group numbers were made.

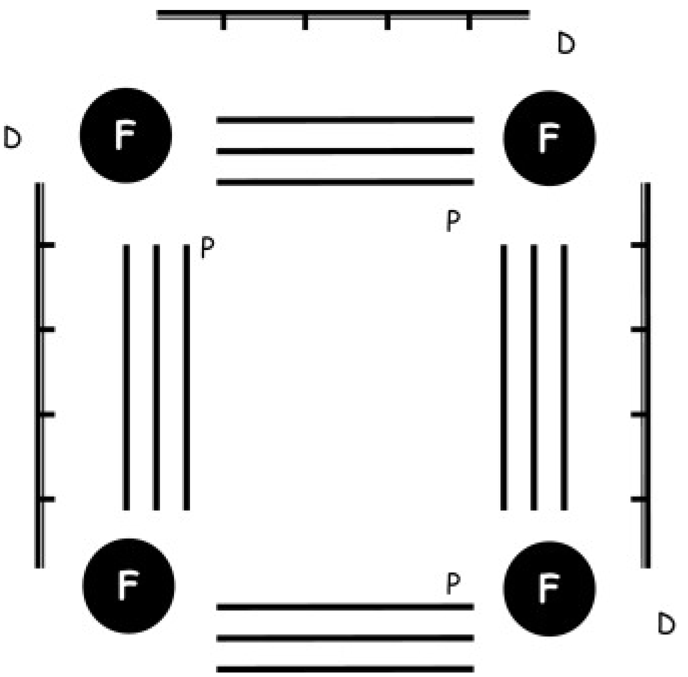

Fig. 1. The pen shape and layout of resources in the pen were the same for all group sizes. The size of the resource patch at each location was increased with increasing group size so that the allocation per bird remained constant. F = feed trough, D = row of drinking nipples, P = perch unit with perches at three different levels. Wood shavings were used as litter material. For more details of the perch design, see Newberry et al. (2001).

2.2. Behaviour observations

Observations were made by experienced observers standing outside the pen and comprised scan observations of all birds in the pen and focal observations of 12 birds per group. Frequent checks were made to ensure high inter-observer reliability. The observations were made during five, 3-week periods when the birds were 3–18 weeks old. All observations were balanced across time of day and period, and no management procedures that might affect bird behaviour were carried out immediately before or during the observations. For each pen and period, 12 scan observations were carried out, six in the morning and six in the afternoon, at intervals of 30 min so that data from successive scans were effectively independent. During each scan, the total number of birds feeding (beak in or above feed trough), drinking (beak raised towards water nipple), perching (located on a wooden perch), and preening (self-grooming with beak) while on a perch were counted separately for each feeder, each drinker and each perch unit. The number of birds dust bathing (including dust application, absorption and shaking-off phases) or preening on the floor was also recorded.

For focal samples, 12 birds from each group were selected at random and individually marked with blue dye. At 12 weeks, these focal birds were marked with large plastic numbered wing tags. For each period and time of day (morning or afternoon), each focal bird in a pen was observed for 5 min in a pre-determined random order and during this time interruptions in its behaviour that were clearly caused by another bird were recorded. Disturbances, by definition, were not aggressive but were always caused by physical contact (Cornetto et al., 2002; Estevez, 1994). A moderate disturbance was defined as causing the focal bird to stop the behaviour it was performing for between 1 and 2 s. A severe disturbance was recorded when the focal bird had not returned to its original behaviour after 2 s. Disturbances could occur when the focal bird was preening or sitting/lying in any location, but they usually occurred when it was perching and another bird was trying to get onto the perch or to change its perching position.

2.3. Statistical analysis

2.3.1. Behavioural synchrony

If a behaviour was highly synchronised in time, then a high degree of variability in the number of birds performing such behaviour would be expected across scans. On the other hand, low levels of synchrony would be characterized by little across-scan variability in the number of birds performing the behaviour. To assess the degree of behavioural synchrony, we calculated a Synchrony Index (SI) as a measure of the difference between the observed number of birds performing each behaviour within each scan and period (Oi scan) and the expected number, which was the mean number across the 12 scans (M12 scans) assuming that the behaviour was performed at a constant rate. This approach of comparing observed and expected levels controlled for concurrent behaviour resulting simply because a behaviour occurred frequently (Asher and Collins, 2012; Rook and Penning, 1991). Variation in group size, and large group sizes that rendered individual identification and gathering of fine-grained behavioural sequences from all group members impractical, precluded use of existing agent-based and oscillator formulas (e.g. Engel and Lamprecht, 1997; Rook and Penning, 1991; Sun et al., 2011). Our SI was calculated for each behaviour as follows:

$$SI = \frac{15}{N}\sum_{i=1}^{12}\left[O_{iscan} - M_{12scans}\right]^2 / M_{12scans}$$

where N is the number of birds in a pen. With division by N, SI no longer depended on group size, and because synchrony per bird was not intuitive, we multiplied by the constant, 15 (the number of birds in the smallest group size). When comparing treatments where the number of birds within pens varies, such standardisation is critical. Thus, when the same proportion of birds engaged in a given behaviour in all 12 scans, SI was zero whereas SI was maximized when the variability in proportion of individuals engaged in a specific behaviour was greatest.

The standardised SI values were entered into an analysis where we investigated effects of group size, period (as a repeated measure) and their interaction on synchrony of feeding, drinking, perching, overall preening, preening on a perch, preening on the floor and dust bathing using a mixed model analysis of variance (Proc Mixed in SAS 9.4, SAS Institute Inc., Cary, NC, USA). For variables with residuals that were not normally distributed, the mixed linear model was applied to ranked data. Means comparisons were made based on differences in least-squares means, with p-values adjusted for multiple comparisons using the Tukey option.

2.3.2. Spatial clustering

If birds were clustering at resources, then many birds would be present at a particular resource site within the pen whereas few or no birds would be present at other sites providing the same resource. Thus, to assess the degree of clustering during feeding, the total number of birds feeding at each scan was divided by four to obtain the mean number of birds at each of the four feeders. Similarly to the calculation of the SI, a Clustering Index (CI) value, standardised as described above so that clustering at resources was comparable across group sizes, was calculated using the observed number of birds at each of the four feeders per scan, and the mean as the expected value. A CI value of zero meant that the birds were showing no clustering at resources (i.e. they were evenly distributed between the feeders) whereas a high CI value indicated high clustering at resources (i.e. more birds at some feeders and fewer at others). This process was repeated for each of the 12 scans of that group for each period, and the mean CI (for all 12 scans) was calculated. These mean CI values were then subjected to mixed model analysis of variance using methods described above. The analysis was repeated for the three lines of drinking nipples and each of the perch stations, accounting for the fact that there were only two perch units in the pen during periods 1, 2 and 3, and four perch units during periods 4 and 5. The number of birds preening on each perch unit was also analysed. Preening on the floor and dust bathing were not included in this analysis.

2.3.3. Time budget and disturbance frequencies

The time budgets for feeding, drinking, perching, dust bathing and preening on the perches or on the floor were calculated as the mean proportion of birds performing each behaviour over the 12 scans for each pen and period. The data for disturbances were taken from the focal bird observations. Severe and moderate disturbances were analysed separately but the frequencies were low and the trends were similar, so these data were pooled for the final analysis. The data were subjected to mixed model analysis of variance as described above.

3. Results

3.1. Behavioural synchrony

There were significant group size effects on synchrony of feeding ($F_{3,12} = 29.6$; $P < 0.001$), drinking ($F_{3,12} = 83.3$; $P < 0.001$), perching ($F_{3,12} = 23.7$; $P < 0.001$), preening anywhere in the pen ($F_{3,12} = 67.0$; $P < 0.001$), preening only on the perches ($F_{3,12} = 53.1$; $P < 0.001$), and preening on the floor ($F_{3,12} = 10.1$; $P < 0.001$). In all cases, synchrony decreased with increasing group size (Fig. 2). Synchrony of perching also declined with increasing age (mean ± SE, 6.39 ± 0.799, 4.33 ± 0.577, 3.88 ± 0.573, 3.89 ± 0.515 and 3.15 ± 0.581 from periods 1–5, respectively; $F_{4,48} = 7.9$; $P < 0.001$). There was a significant group size by period interaction for preening on the floor ($F_{12,48} = 4.0$; $P < 0.05$), with the decline in synchrony with increasing group size being more consistent in periods 1 and 3 than at other ages (Fig. 3). There were no significant effects of group size or age on synchrony of dust bathing (overall mean ± SE, 7.05 ± 0.795, $P > 0.05$).

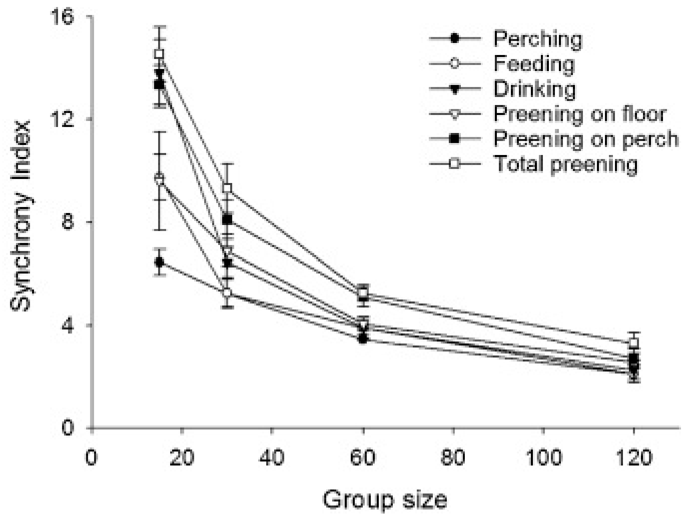

Fig. 2. Synchrony index (mean ± SE) for the number of birds feeding, drinking, perching, preening on the floor, preening on perches, and preening anywhere in the pen, at the same time according to group size.

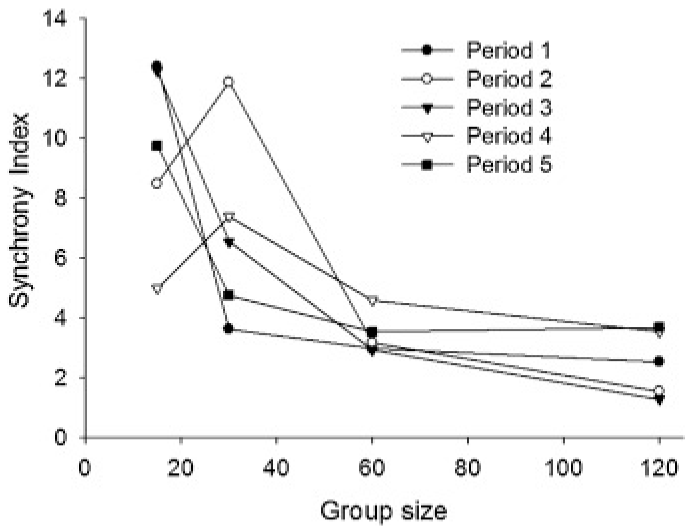

Fig. 3. Synchrony index (mean) for the number of birds preening on the floor at the same time in each period, according to group size.

3.2. Spatial clustering

With increasing group size, there were significant decreases in the relative degree of clustering of birds when feeding from the four feeders ($F_{3,12} = 43.1$; $P < 0.001$), drinking from the three rows of water nipples ($F_{3,12} = 26.3$; $P < 0.001$), perching on the different perch units ($F_{3,12} = 36.9$; $P < 0.001$), and preening while perching on the different perch units ($F_{3,12} = 52.5$; $P < 0.001$; Fig. 4). There was an age effect on clustering when feeding ($F_{4,48} = 36.0$; $P < 0.001$) and preening on perches ($F_{4,48} = 74.0$; $P < 0.001$), and an age by group size interaction for perching ($F_{12,48} = 2.3$; $P < 0.05$; Fig. 5). Birds were most clustered at feeders in periods 1–2, less in period 3 and least in periods 4 and 5 (means comparisons, $P < 0.05$). They were most clustered on perch units when perching in periods 4 and 5, less clustered in period 1, and least clustered in periods 2 and 3 (means comparisons, $P < 0.05$). The magnitude of the increase in clustering when perching between periods

2–3 and 4–5 was greater in smaller than larger groups. When preening on perches, the birds were more clustered in periods 4 and 5 than when younger (means comparisons, $P < 0.05$).

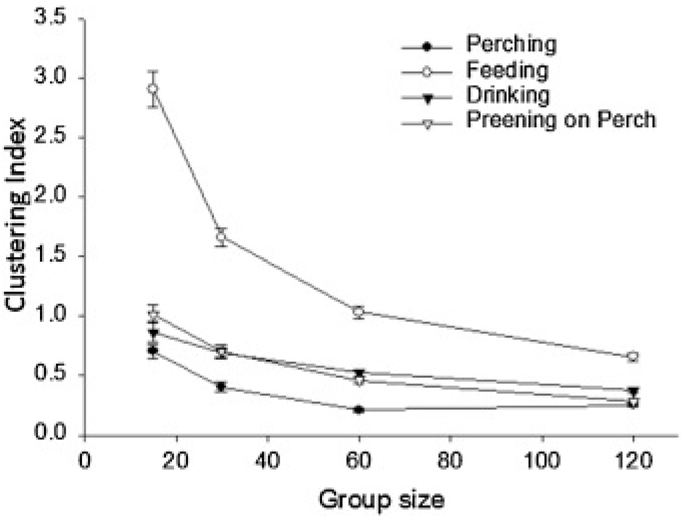

Fig. 4. Clustering index (mean ± SE) for the number of birds feeding, drinking perching and preening while perching at the same location at the same time according to group size.

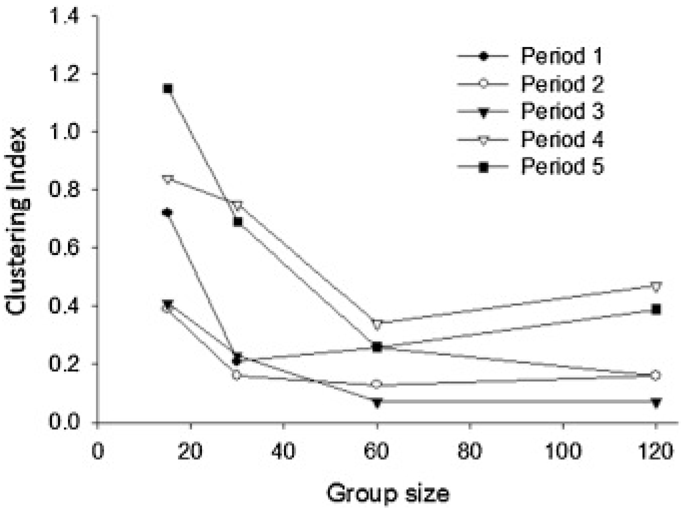

Fig. 5. Clustering index (mean) for the number of birds perching at the same location at the same time in each period, according to group size.

3.3. Time budget and disturbance frequencies

The percentage of time spent performing each of the behaviour patterns of interest is presented in Table 1 together with significant group size, age and group size by age effects. A significant group size main effect was found only for perching behaviour, which decreased with increasing group size. Age effects were significant for several behaviour patterns. Birds spent the greatest proportion of their time perching and feeding and most of the preening was performed on the perches. A small amount of perching on waterlines and feeders was not included in this analysis.

Table 1. Percentage (mean ± SE) of time spent performing each behaviour according to group size (GS). Perching time decreased with GS, feeding and drinking time decreased with age period, and perching and preening on floor time increased with period (PER). GS by age effects showed no consistent pattern.

Behaviour	**Group size**				**Factors**		
	15	30	60	120	GS	PER	GS × PER
Feeding	11.3 ± 1.16	12.9 ± 0.17	11.9 ± 0.40	10.9 ± 0.31	ns	***	ns
Drinking	3.9 ± 0.12	4.0 ± 0.19	3.7 ± 0.18	3.7 ± 0.12	ns	*	*
Perching	31.6 ± 1.04	30.7 ± 1.57	28.8 ± 0.60	25.8 ± 1.02	*	***	ns
Preening	8.8 ± 0.33	8.2 ± 1.00	8.9 ± 1.00	8.9 ± 0.66	ns	ns	ns
Preening on perch	7.9 ± 0.38	7.2 ± 0.87	7.9 ± 0.51	7.4 ± 0.69	ns	ns	ns
Preening on floor	0.9 ± 0.20	1.0 ± 0.21	1.0 ± 0.12	1.5 ± 0.18	ns	***	***
Dust bathing	0.7 ± 0.30	0.5 ± 0.04	1.0 ± 0.25	0.7 ± 0.19	ns	ns	ns

*P < 0.05.

*** P < 0.001.

The mean number of disturbances received per focal bird per 5 min was 0.12 ± 0.077. There was no significant effect of group size but the number of disturbances decreased with increasing age ($F_{4,48} = 7.0$; $P < 0.001$; Fig. 6).

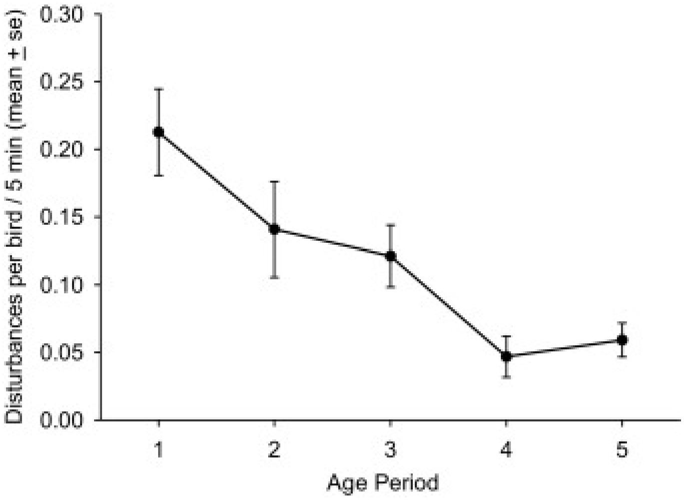

Fig. 6. Differences in the frequency of non-aggressive disturbances (mean ± SE) between birds that resulted in the recipient interrupting its ongoing behaviour at different periods.

4. Discussion

As predicted, proportionally fewer birds performed the same behaviour at the same time and in the same location in larger than in smaller group sizes. This was true for all the behaviour patterns we studied, with the exception of dust bathing, which may not have been recorded sufficiently often for differences in synchrony to be detected. At all group sizes, daytime perching was the least synchronised behaviour and preening the most synchronised. Comparisons of clustering at resources showed that the birds clustered most when feeding. These differing patterns may reflect the vulnerability of young fowl to predation under natural conditions. Birds in the wild would generally have a lower predation risk in larger groups, with less need to synchronise behaviour across the whole group. Within a group size, birds could be considered most safe when perching, so least likely to synchronise this behaviour during daytime, but more vulnerable when preening, so more likely to synchronise preening bouts. Consequently, birds should preen in the safest place, on perches, as supported by the finding that preening on the perches was between four and eight times more frequent in the time budget than preening on the floor. Clustering at feeders is consistent with Collins and Sumpter's (2007) finding that young broilers choose to feed close together.

Period effects were found for synchrony in perching and preening on the floor and for clustering at feeders, perching and preening on the perch. As discussed previously, young birds are more vulnerable to predation in nature and so may be expected to be more synchronised, particularly when conducting highly risky behaviours such as preening and feeding. Results in our study, however, may also be explained in part by the fact that, although space per bird was constant throughout the whole experiment, the birds had relatively more space at the resources when younger (and thus smaller) allowing greater cohesion. The reduced synchrony of perching and the higher clustering during perching and preening on perches in periods 4 and 5, suggests that perch space was insufficient until we added two additional perch units to each pen at the end of the third period. A preference for the highest perch level and relatively low use of the two lower levels except as ladders to the top level (Newberry et al., 2001) means that effective daytime perch space was probably only about one third that provided. We would, nevertheless, predict high synchrony of perching at night when all birds could be expected to roost off the floor especially after gaining early experience jumping on and off perches during the day and occasional night time observations confirmed this.

Changes in patterns of behavioural synchrony with increased group size might come about in three possible ways. The first could be because of a fundamental change in how birds behave in social groups of different sizes. Such changes in social organisation are well known in some species (e.g. pumpkinseed sunfish, Blanckenhorn, 1992) and, in domestic fowl, there is evidence that the hierarchical social system breaks down as group size increases and birds become less aggressive (D'Eath and Keeling, 2003; Estevez et al., 1997, 2002). Our choice of group sizes in this study seem to span this range for laying hens (Keeling et al., 2003). Secondly, our results could be explained by a distance effect, because larger groups were spread over a greater area. Larger groups were kept in larger pens (to control density) and so the behaviour of a bird in one area of the pen may have been less likely to influence the behaviour of other birds at the other side of the pen. Lying in cows is most influenced by near neighbours (Stoye et al., 2011) as is nursing in sows (Špinka et al., 2004), and Febrer et al. (2006) estimated that broilers choose to position themselves within 75 cm of another bird, suggesting that behavioural synchrony would be greatest among birds within this range. However, even large congregations of animals can be highly synchronised when flying or schooling as a result of a 'wave' effect in which the behaviour of individuals in one part of the group influences that of individuals elsewhere in the group (Parrish and Turchin, 1997). An example of this in laying hens is the panic reaction occasionally seen in practice in large flocks. A third explanation is that, as long as birds are synchronised with a sufficient number of neighbours to minimise predation risk, there is no additional benefit of being synchronised with all flock members since this would increase competition for resources (Pulliam and Caraco, 1984). In bighorn sheep vigilance decreases significantly as group size increases up to five, but there is no additional decline as groups become larger than this (Berger, 1978). A similar effect could be occurring in synchronisation, resulting in proportionally fewer birds performing the same behaviour in the larger flocks. The point at which no additional benefits are gained by synchronising with an increasing number of birds may vary according to the behaviour being performed and the level of competition for the resources. These three explanations for the changes in synchrony and in clustering, with increasing group size are not mutually exclusive and all may be contributing to the results of this study.

Even if reduced synchrony and clustering with increasing group size would be adaptive under natural conditions, from an animal husbandry perspective, it is necessary to question whether it is associated with any negative effects on the welfare of the birds. We found no significant effect of group size on the overall number of disturbances of resting or preening birds, indicating that larger group sizes per se, in the absence of a corresponding increase in bird density (Febrer et al., 2006; Ventura et al., 2012), did not cause birds to interrupt the behaviour of others more often. Although birds were more clustered in space in smaller groups, their behaviour was also more synchronised, reducing the chance that resting and preening birds would be disturbed by more active birds. There was a significant decrease in the number of disturbances with age, possibly because increased familiarity with their environment resulted in older birds reacting less when jostled by other birds, or simply due to a decline in bird activity with age. Similarly, we have not found proportionately increased levels of aggression in larger groups (Estevez et al., 2002).

Here we have presented synchronous behaviour in terms of variation in the relative number of birds performing the same behaviour at the same time (SI), or at the same time and the same location (CI), based on the view that the degree of synchrony in two groups of differing size is equal when the same proportion of birds is performing the same behaviour at the same time in each group. However, it could be argued that, from a cost-benefit standpoint, both perceived predation risk and competition for resources are affected by the actual number of nearby birds that are vigilant or exploiting a resource rather than by the proportion. It is evident from the proportions in Table 1 that the actual number of birds engaged in different behaviours increased with increasing group size, thus increasing the likelihood that more birds were performing the same behaviour concurrently in larger groups. We can therefore question whether the relative proportion or actual number of individuals performing behaviour concurrently, or perhaps a combination of both, is relevant to the welfare of captive birds. Considering ongoing discussions about optimal group sizes and allocation of resources for animals under human management, this seems an important question to be resolved (Appleby, 2004). Meanwhile, the results of this study would not lead us to anticipate that birds in large groups experience problems, provided that producers allocate sufficient feeders, drinkers and perches at different locations in the pens to allow birds to synchronise and cluster with their immediate neighbours. In small groups, however, it appears that birds do synchronise their behaviour in time and cluster together with the whole group and so sufficient total resources to allow them to do this should be provided. On the basis of the results of this study we suggest that resource space allocations per bird should be greater when birds are kept in small groups, where sufficient resources have to be allocated to permit the entire group to synchronise their behaviour, than in large groups.

Acknowledgements

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