Contents lists available at SciVerse ScienceDirect





Applied Animal Behaviour Science

journal homepage: www.elsevier.com/locate/applanim

Nest sharing under semi-natural conditions in laying hens

Anja Brinch Riber*

Department of Animal Health and Bioscience, Faculty of Agricultural Sciences, Aarhus University, Blichers Allé 20, Post Box 50, DK-8830 Tjele, Denmark

ARTICLE INFO

Article history: Accepted 6 November 2011 Available online 30 November 2011

Keywords: Domestic fowl Environmental restrictions Genetic selection Gregarious nesting Nest sharing, Semi-natural habitat

ABSTRACT

Under natural conditions, the feral hen (Gallus gallus domesticus) will choose a nest location away from the flock, whereas under commercial conditions, the domestic hen will often choose the same nest as other hens have used or are still using. Simultaneous nest sharing causes several welfare problems to laying hens, and egg production may also be negatively affected. Understanding what causes this difference in nest location selection may provide solutions to the problems associated with simultaneous nest sharing. The aims were to investigate whether a commercial strain of laying hens normally housed in intensive production systems share nests under semi-natural conditions and to describe the behaviour if this behaviour occurred. Twenty 15 weeks old hens were released into an 840 m² enclosure with multiple options for natural and semi-natural nest sites. Over a 63-day period records were made daily of each nest with regard to number of eggs, position, and materials used. On five mornings nesting behaviour was observed. Nest sharing occurred on all but the first 5 days of egg-laying. The majority of hens (n = 14) chose to visit an occupied nest at least once, but no hens exclusively used occupied nests. Visits in shared nests lasted longer than visits in undisturbed nests (13 min 50 s (± 4 min and 57 s) vs 30 min 44 s (± 4 min and 55 s); P < 0.001). Fifteen nests were used. All shared nests (n = 5) were placed up against the borders, whereas the majority of non-shared nests (n = 7 out of 10) were placed more than 1 m away from the borders (P=0.002). Some results indicate that nest sharing was caused by environmental restrictions.

© 2011 Elsevier B.V. All rights reserved.

1. Introduction

Nesting behaviour in feral fowl (*Gallus gallus domesticus*) consists of a sequence of behaviours that includes the selection of a nest location based on suitable habitat, selection of a nest site based on available nesting materials, and nest building (Duncan et al., 1978). Most of the research on nesting behaviour in laying hens has focussed on selection of a nest site (e.g. Duncan and Kite, 1989; Huber et al., 1985; Hughes, 1993; Petherick et al., 1993; Struelens et al., 2005), but much less is known about the selection of nest locations and nest building. One question that remains unanswered is why there is a major difference in nest location

* Tel.: +45 89991318. E-mail address: Anja.Riber@agrsci.dk

selection between feral hens and domestic hens. Under natural conditions, the feral hen will choose a nest location away from the flock (Duncan et al., 1978), whereas under commercial conditions nest sharing frequently occurs, i.e. the domestic hen will often choose the same nest that other hens have used (non-simultaneous nest sharing) or indeed are still using (simultaneous nest sharing), even if she has a choice between the occupied nest and an unoccupied nest (Appleby and Mcrae, 1986). Choosing to nest in an occupied nest in preference to an unoccupied nest is a phenomenon also referred to as gregarious nesting (Riber, 2010). The tendency to perform gregarious nesting may differ between strains of laying hens, but this has not been investigated scientifically. The ancestor of the domestic fowl, the red jungle fowl (G. gallus), behaves in its natural habitat similarly to the feral hen with regard to nest location selection (Collias and Collias, 1967), and has never been observed to

^{0168-1591/\$ -} see front matter © 2011 Elsevier B.V. All rights reserved. doi:10.1016/j.applanim.2011.11.006

perform nest sharing or intraspecific nest parasitism (Geffen and Yom-Tov, 2001).

Simultaneous nest sharing causes several welfare problems to laving hens kept under commercial conditions. Feather loss, scratches, and wounds may result from the struggling that arises when hens squeeze into already occupied nest boxes (Appleby and Smith, 1991). In rare extreme cases, heat stress and suffocation may occur when hens pile on top of each other in nest boxes (Michael C. Appleby, personal communication). Furthermore, increased levels of aggression have been found in front of preferred nest boxes (Meijsser and Hughes, 1989) and between individuals with overlapping pre-laying periods in groups of hens using only one nest site (Freire et al., 1998). The producer suffers loss of income due to eggs being broken or becoming dirty during the struggling in the nest boxes. The excessive expenditure of energy is also likely to increase the amount of feed ingested. With the ban of conventional battery cages from 2012 (CEC, 1999) the occurrence of simultaneous nest sharing and hence the extent of the associated problems are likely to increase for two reasons; (1) group sizes are expected to increase, thus a potential higher number of hens may prefer the same nest boxes and (2) nest boxes must be provided in all types of housing systems for laying hens, including furnished cages. The latter has a large impact, as up till the start of the transition from conventional battery cages to furnished cages the majority of laying hens in the EU have been housed in conventional battery cages without nest boxes.

Research into nest sharing is sparse and as a result knowledge about the phenomenon is limited. However, understanding what causes the difference in nest location selection between feral and domestic hens may help provide a solution. The overall objective of the present study was therefore to investigate whether laying hens from a commercial strain normally housed in intensive production systems exhibit nest sharing under semi-natural conditions. The specific aims were to (a) determine the frequency of nest sharing within a group of hens, both during the phase from point of lav to attainment of full egg-production and during the following phase where egg production was at its maximum, (b) examine the use of shared vs non-shared nests, (c) investigate whether there were common characteristics for the shared nests, and (d) determine whether the common characteristics for the shared nests (if any) differed from the non-shared nests.

2. Materials and methods

2.1. Animals and housing

A total of twenty 15 weeks old hens were released May 26, 2008, into an enclosure measuring $24 \text{ m} \times 35 \text{ m} (840 \text{ m}^2)$ in total; 42 m^2 /hen; see Fig. 3). The hens were supplied by TopÆg Aps, who beak-trimmed the chicks at day-old. The strain used was Isa Warren, which is a commercial egg-laying strain typically used in loose housing systems. The hens were raised under loose housing conditions and had not reached the point of lay upon release into the enclosure. Hens had no previous exposure to outdoor access. For individual recognition the hens were fitted with different

coloured leg bands. The enclosure consisted of a lawn on which trees, shrub and dense vegetation were scattered. In addition, nine low shelters (W: $1.2 \text{ m} \times D$: $1.2 \text{ m} \times H$: 1 m) with branches stuck into wire mesh as roofs were scattered evenly in the enclosure to encourage use of the entire area available (see Zeltner and Hirt (2008) for factors improving use of hen runs). In the enclosure there were no artificial nest boxes, but lush vegetation and plywood sheets (n = 20)offering possibilities of both natural and semi-natural nest sites. The plywood sheets (W: 0.5 m \times H: 0.7 m) were placed up against the fence, trees, and walls at an angle of approximately 45° and distributed evenly in the enclosure (see Fig. 3). This was done to maximise an even distribution of the possibilities of finding a suitable nest in the enclosure, as the dense vegetation (which was assumed to be chosen for natural nest sites) was more clumped in distribution. Hay was added under the plywood sheets and a coniferous branch was placed on each side such that seclusion was created.

To prevent the hens from laying their eggs in "unnatural" locations, access to indoor facilities were not offered. Instead, a primitive shelter (W: $1.5 \text{ m} \times D$: $2.0 \text{ m} \times H$: 2.2 m) offering protection against rain and wind was provided. It consisted of corrugated fibre cement roofing sheets and sides of white tarpaulin from the top to 1 m above ground. In the shelter the hens had ad libitum assess to commercial layer feed, water, crushed shells, and three perches (up to 1.4 m height). During daytime birds were observed to feed and drink in the shelter. Perching in the shelter was only observed during nights. The enclosure also included an area with bare ground ideal for dust-bathing. Most of the eastern border of the enclosure was comprised by a building, and a hedgerow ran along the western side of the enclosure. The enclosure was fenced off with chicken wire that did not provide any cover. There were no human-made disturbances in the area during the periods of nesting activities, and only few the remaining part of the days (e.g. passing cars, surveillance, feeding, and egg collection). The study ended July 28, 2008, when the hens were 24 weeks old. During the study period the temperature ranged from 4.8 °C (minimum at night time) to 30.2 °C (maximum at daytime) with an average of 15.7 °C. The light hours were at maximum 17 h and 20 min and at minimum 16 h and 6 min. One hen became ill with inflammation of the oviduct on July 13 (age 22 weeks old) and was euthanized. Successful predation on hens did not occur, and attacks or potential predators were not observed. Egg shells were never found, egg-predators were never observed in or near the enclosure, and there were no species of predator in the area capable of moving entire eggs from the enclosure, thus, predation on eggs was unlikely to have occurred.

2.2. Data collection

The data collection was done in two phases: (a) phase 1; the initial phase of egg laying, where egg production increased from 0 to full egg production and (b) phase 2; the full egg production phase, where egg production was at its maximum. This distinction between two phases was done because it has previously been found that hens kept under experimental settings simulating commercial conditions engage in more nest sharing at point of lay than when older and more experienced (Riber, 2010).

The point of full egg production was defined to be on the day when ≥ 0.9 eggs were laid per hen.

2.2.1. Registration of eggs and nest locations

During both phases the enclosure was searched thoroughly for eggs following a specified route at 17:00 h. The number of eggs laid was counted and all eggs were removed daily. The daily removal of eggs was done in order to avoid attraction to nests on following days due to the presence of eggs. It was noted whether the eggs were laid in a nest. A nest was defined as a shallow depression on the ground, moulded by the hen(s) and containing egg(s). The position of each nest was marked on a map of the enclosure, and each nest was described as either natural (in existing vegetation) or semi-natural (behind the provided plywood sheets or low shelters).

2.2.2. Direct observations

On five mornings in phase 2 (July 16, 17, 22, 23, and 28; age 22-24 weeks old) direct observations of the nesting behaviour of all 19 hens was conducted using continuous recording. Observations started at 4:20 h (approximately 40 min before sunrise) and ended at 9:30 h when most nesting activity had terminated. The observer sat elevated 3.5 m high close to the southern border of the fence to have an overview of the entire enclosure. The only area with dense vegetation that was large enough for a hen to choose between several nest sites was close to the observer and consisted mainly of 0.8-1.2 m tall stinging nettle (Urtica dioica), cow parsley (Anthriscus sylvestris), and curled dock (Rumex crispus). Due to the elevated position of the observer it was possible to follow hens entering the area by observing the vegetation moved by the hens; this allowed the observer to identify entries and exits to nests. Hens were identified from colour of feathers, size and shape of combs, and colour and placement (left/right leg) of leg bands (sometimes with aid from a binocular). The hens were habituated to the observer through normal husbandry procedures, and approximately 5 min after the observer had placed herself in the observation position the hens did not pay attention to her (hens neither avoided nor were they attracted to the observer, and they resumed their behavioural activities). Records were made of the time of each hen's entry to and exit from a nest, the location of the nest, and if possible whether oviposition occurred. The latter was identified on either the characteristic egg-laying position, the penguin position (Fôlsch and Vestergaard, 1981), which was only possible to observe if a full view of the nest was given, or on emission of post-oviposition calls upon leaving the nest (McBride et al., 1969) followed by cessation of nest-seeking behaviour.

Non-standardised direct observations were made at different times of the day in both phases in order to record the qualitative spatial use of the enclosure.

2.3. Statistics

All data were subjected to analysis in the SAS[®] statistical programme (SAS, 2000). Test for homogeneity in data

collected in phase 2 on number of eggs laid daily, the average proportion of eggs laid daily in shared nests, and the average daily proportion of shared nests were either carried out using a Pearson chi-square test (χ^2) or a Fisher's exact test. A Pearson chi-square test was used when all expected numbers were more than 5 and Fisher's exact test was used when some of the expected numbers were less than 5. Similarly, a Fishers exact test was used to test for homogeneity in data collected in phase 2 on nest location selection in relation to the border of the different types of nests (Table 1). In the analysis of (a) whether the duration of nest visits differed between visits in non-disturbed and disturbed nests and (b) whether choice of nest type differed between visits ending or not ending with oviposition, the data were subjected to repeated measurements analysis using the mixed procedure. By using this statistical method with individual (a) or day (b) as random effects the dependency between days/within individuals were taken into account during the analysis.

Results are reported as raw means and standard deviations, except in the analyses of (1) duration of nest visits, where the result is presented as least square mean and standard deviation, and (2) time spent (a) on each nest visit, (b) in nests on each nest-using day, and (c) from first entry to a nest to last exit from a nest, where the results are presented as medians and ranges.

2.4. Ethical note

All procedures involving animals were approved by the Danish Animal Experiments Inspectorate in accordance with the Danish Ministry of Justice Law no. 382 (June 10, 1987) and Acts 333 (May 19, 1990), 726 (September 9, 1993) and 1016 (December 12, 2001). The study fulfilled the requirements of the ethical guidelines of the International Society of Applied Ethology (Sherwin et al., 2003). After completion of the study all hens changed status from experimental animals to backyard hens, and stayed in the same enclosure, though with access to indoor facilities.

3. Results

In total 631 eggs were laid during the study (Fig. 1); 142 eggs were laid during phase 1 and 489 eggs were laid during phase 2. The number of eggs laid per day did not differ in phase 2 ($\chi^2 = 8.8$, df = 5; P = 0.12). Egg-eating did not seem to occur; thin-shelled or cracked eggs (n = 11) were not eaten or moved from nests by the hens. The non-standardised direct observations revealed that the hens used the entire area available to them, and stereotypic pacing along the borders was never observed.

Table 1

Distance between the border of the enclosure and the different types of nests.

Type of nest	<1 m	>1 m
Shared nest	5	0
Non-shared nest	3	7
No well-defined nest	0	6

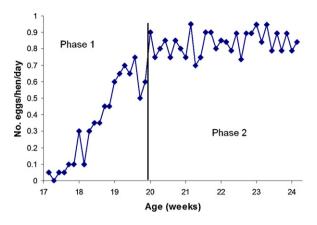


Fig. 1. Mean number of eggs produced per hen per day during phases 1 and 2.

3.1. Nest sharing

Nest sharing occurred on all days of egg-laying, except the first 5 days in phase 1 with more than one egg collected (Fig. 2). The proportion of eggs laid in shared nests increased during phase 1 concurrently with the increase in egg production. During phase 2 the average proportion of eggs laid daily in shared nests was 0.83 (\pm 0.09) and did not differ between days (Fishers exact test; *P* > 0.05). Similarly, the proportion of nests shared to the total number of nests used increased during phase 1 concurrently with the increase in egg-production. During phase 2 the average daily proportion of shared nests was 0.54 (\pm 0.15) and did not differ between days (Fishers exact test; *P* > 0.05).

During the five days of direct observations 18 hens were observed using nests, and 14 of them chose an occupied nest at least once. None of the hens exclusively used occupied nests. In total, 185 nest visits were recorded (37.0 ± 6.4/day). Of these nest visits 71 were directed to nests already occupied by another hen ($14.2 \pm 8.1/day$), i.e. the hens chose simultaneous nest sharing 38.4% of the times they visited a nest. The proportion of times a shared nest was chosen did not depend on whether the visit ended in oviposition ($F_{1,4} = 1.30$, P = 0.32). The median time spent (a) on each nest visit was 5 min and 21 s (range: 2 h and

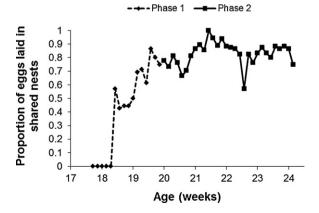


Fig. 2. Proportion of eggs laid daily in shared nests during phases 1 and 2.

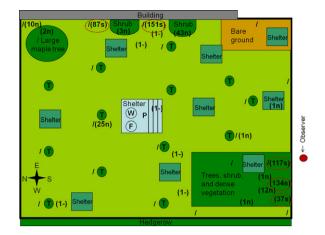


Fig. 3. The enclosure and the number of eggs (in brackets) laid at the noted sites. n = non-shared nest, s = shared nest, also marked with a red stippled circle, - = no nest characteristics, but an egg was found. / = plywood sheets, P = perches, W = water, F = feed, and T = young fruit trees. Figure not to scale.

28 min and 21 s), (b) in nests on each nest-using day was 40 min and 47 s (range: 2 h and 28 min and 5 s), and (c) from first entry to a nest to last exit from a nest was 56 min and 10 s (range: 4 h and 18 min and 12 s). The duration of undisturbed nest visits was shorter than the duration of nest visits where at least two hens were in the nest at the same time at some point (13 min 50 s (\pm 4 min and 57 s) vs 30 min 44 s (\pm 4 min and 55 s); *F*_{1,164} = 17.73, *P*<0.001).

3.2. Characteristics of nests

Most eggs (n = 625) were laid in well-defined nests, i.e. in shallow depressions, always concealed either by dense vegetation or plywood sheets. A total of 234 eggs were laid in nine natural nest sites and 391 eggs were laid in seminatural nest sites, i.e. behind six of the plywood sheets (Fig. 3). Six eggs were found on sites that could not be classified as nest sites (no depression, no concealment, on short grass). One of these eggs had been dropped from a perch in the large primitive shelter, whereas the five remaining eggs may have been scratched out of nests.

Five of the 15 nests used were shared, and the majority of eggs were laid in these nests (n = 526). All five shared nests were placed up against the borders, whereas the majority of non-shared nests were placed more than 1 m away from the borders (Table 1). A significant relationship was found between the type of nest and the distance to the border (Fishers exact test; P=0.002). The first two nests shared were both behind provided plywood sheets along the eastern border of the enclosure, separated by 9 m. The last three nests shared were all in the dense vegetation along the southern border of the enclosure, and again they were closely placed together, separated by a maximum of 6 m. In general, nests lost popularity after a period of time and new nests were built, and this process occurred continuously. In phase 1 the total number of nests and the number of shared nests used daily increased concurrently with the increase in egg production. In phase 2 a total of 6.1 (± 1.0) nests were used daily and 3.3 (± 0.7) nests were shared daily.

4. Discussion

Domestic hens from a commercial egg-layer strain kept under semi-natural conditions were found to share nests, both simultaneously and non-simultaneously. Not only did nest sharing occur, but the majority of hens participated in this type of nest use. The observed behaviour has not been reported in field studies of feral hens or red jungle hens. Feral hens and red jungle hens adopt a completely different nesting strategy in that they isolate themselves from the flock during egg-laying (Collias and Collias, 1967; Duncan et al., 1978). Domestic hens kept in commercial conditions share nests as observed in the present study, although attempts to isolate themselves during pre-laying behaviour may also be observed in some individuals (especially floor layers), expressed as stereotyped escape behaviour such as pacing, orientation away from the flock, and attempts to escape out of the pen (Riber, 2010: Rietveld-Piepers, 1987). This difference in nest location selection between feral/red jungle hens and domestic hens may involve changes in two behavioural aspects; the domestic hen may have a higher propensity to choose an occupied nest and she may also be more tolerant to sharing the nest with intruding hens. There are at least two explanations to the difference in nest location selection behaviour between feral/red jungle hens and the domestic hens in the present study. One is that the enclosure offered in this study provided insufficient possibilities for isolation during nesting behaviour, i.e. environmental restrictions. Another is genetic differences between the few strains that have been investigated for occurrence of nest sharing.

4.1. Environmental restrictions

The only common characteristic for the shared nests was their placement along the borders of the enclosure. and this common characteristic differed from that of nonshared nests. This finding is comparable to the common observation under commercial conditions that nest boxes at the end of rows are preferred to those in the middle. The concentration of nest-seeking hens in the area along the borders may well have been higher here than in the rest of the enclosure during the main laying period. Thus, the chance of nest-seeking hens coming across nests containing eggs and/or hens has been higher in this area. It is well-known that the presence of eggs and hens in a nest functions as a stimulus for domestic hens to use the same nest (Appleby et al., 1984; Freire et al., 1998). This may be a plausible explanation to why all the shared nests were placed along the borders in contrast to the non-shared nests. The higher concentration of nest-seeking hens along the borders may be due to one of two reasons; (1) borders provide natural lines in the environment to be investigated or (2) the placement of nests along the borders may be interpreted as attempts at moving as far as possible in the enclosure from the flock during nest location selection, i.e. it may indicate that the quantity of area offered in this study provided insufficient possibilities for isolation during nesting behaviour. However, stereotypic pacing along the borders was never observed, neither during nest location selection nor during the remaining active period. Placing the eggs along the borders of an enclosure has been found in a previous study of Japanese quail kept in semi-natural conditions (Schmid and Wechsler, 1997). Corners have often been found to be preferred nest locations in domestic fowl and quail (Kite et al., 1980; Lundberg and Keeling, 1999; Schmid and Wechsler, 1997, 1998), but this was not confirmed in the present study.

In addition to the finding that all shared nests were placed along the borders, it was also found that a high proportion of all eggs, regardless of the type of nest they were laid in, were laid along the border. One could argue that the placement of these eggs along the border could be due to the border providing protection against aversive climatic conditions (wind and rain). This is supported by the fact that one third of the nests and almost half of the eggs were laid on the part of the eastern border comprised by a building. However, this can only be part of the explanation, as the southern border was as popular as the eastern border, and the fence here was chicken wire, which did not provide any protection against aversive climatic conditions. The high proportion of eggs placed along the borders is in contrast to results found in wild birds. Wallander et al. (2006) found that wader nests were placed farther away from man-made structures, including barbed wire fences and stone walls, than expected by chance. It has often been found that avian nest predation increases near habitat edges (reviewed by Paton, 1994; Batáry and Báldi, 2004, but see Lahti, 2001), i.e. it would be irrational to consider the placement of the high proportion of eggs along the borders as an anti-predator strategy. Also, it does not explain the observed difference in placement of shared and non-shared nest in relation to distance to border.

Both the quality and quantity of the area has an influence on nest location selection. It was anticipated that given the degree of cover and complexity of the enclosure (i.e. amount of dense vegetation, semi-natural nests, shelters, trees, etc.), the area would provide sufficient possibilities for the hens to seek isolation during nest location selection. Only one study has investigated nest location selection of feral hens (though the hens were only feral if using the ontogenetic approach to feralization proposed by Daniels and Bekoff (1989), because they had reverted to the wild, but had not been hatched in wild). Duncan et al. (1978) reported that the individual nests used by 10 feral hens, who never shared nests, were separated by as little as 20 m, but distributed on an area of various habitat types of approximately $150 \text{ m} \times 150 \text{ m}$, excluding two outlier nests. A comparison of the qualities of areas offered is complicated by a lack of detailed information about degree of cover and complexity of study area. Some records from the ring-necked pheasant (Phasianus colchicus torquatus) also suggest that nest sharing is a response to overcrowded conditions. In this gallinaceous species that has been found to perform intraspecific nest parasitism it seems as if nest sharing under natural conditions becomes more frequent with increasing breeding densities (Baskett, 1947).

4.2. Genetic influence

Nest sharing in domestic hens as a response to environmental restrictions instead of a behaviour developed during domestication would be in accordance with the common finding that behaviour in general has remained the same during domestication and presumably feralization, i.e. behavioural elements are not lost and new behavioural patterns are not added due to the genetic alteration (Price, 1984). However, behaviours may be suppressed or enhanced phenotypically (Price, 1984). This is indeed true with regard to broodiness in the domestic strain used in the present study, suggesting that genetic alteration during domestication may also have influenced nest location selection. Normally, domestic hens from commercial strains never or very seldom become broody, because they have been genetically selected for highyielding egg production. The feral hens studied by Duncan et al. (1978) were from a bantam strain (see Savory et al., 1978), i.e. they were not genetically selected for highyielding egg production in contrast to the strain used in the present study. The feral hens reached a state of broodiness within the first generation of release into the wild and were described as birds that were "hardy and known for their good parental values" (see Wood-Gush and Duncan, 1976). In contrast, broodiness has been suppressed during domestication in the strain of hens used in the present study. Thus, the possibility continues to exist that heredity may play a role in the propensity of nest sharing.

5. Conclusion

In conclusion, nest sharing was found to occur in the majority of the domestic hens kept under semi-natural conditions. Nest sharing was partially caused by environmental restrictions; all shared nests were placed along the borders in contrast to non-shared nests. However, due to the difference in degree of genetic selection for high-yielding egg production of the strains compared, the possibility exists that heredity plays a role in the propensity of nest sharing.

Acknowledgements

I am grateful to Dr. Erik Jørgensen for statistical advice. I thank Dr. Birte L. Nielsen, Dr. Liat Romme Thomsen, and Kathryn Proudfoot for commenting on the manuscript. This work was financed by The Danish Research Council for Technology and Production Sciences.

References

- Appleby, M.C., Mcrae, H.E., 1986. The individual nest box as a superstimulus for domestic hens. Appl. Anim. Behav. Sci. 15, 169–176.
- Appleby, M.C., Mcrae, H.E., Duncan, I.J.H., Bisazza, A., 1984. Choice of social conditions by laying hens. Br. Poult. Sci. 25, 111–117.
- Appleby, M.C., Smith, S.F., 1991. Design of nest boxes for laying cages. Br. Poult. Sci. 32, 667–678.
- Baskett, T.S., 1947. Nesting and production of the ring-necked pheasant in North-Central Iowa. Ecol. Monogr. 17, 1–30.
- Batáry, P., Báldi, A., 2004. Evidence of an edge effect on avian nest success. Conserv. Biol. 18, 389–400.

- Collias, N.E., Collias, E.C., 1967. A field study of red jungle fowl in North-Central India. Condor 69, 360–386.
- CEC (Commission of the European Communities), 1999. Council Directive 1999/74/EC of July 19 1999. Laying Down Minimum Standards for the Protection of Laying Hens, http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=OJ:L: 1999:203:0053:0057:EN: PDF.
- Daniels, T.J., Bekoff, M., 1989. Feralization: the making of wild domestic animals. Behav. Process. 19, 79–94.
- Duncan, I.J.H., Kite, V.G., 1989. Nest site selection and nest-building behavior in domestic fowl. Anim. Behav. 37, 215–231.
- Duncan, I.J.H., Savory, C.J., Woodgush, D.G.M., 1978. Observations on reproductive behavior of domestic fowl in wild. Appl. Anim. Ethol. 4, 29–42.
- Fôlsch, D.W., Vestergaard, K., 1981. The behaviour of fowl. In: The Normal Behaviour and the Effect of Different Housing Systems and Rearing Methods. Animal Management, vol. 12. Birkhäuser Verlag, Basel.
- Freire, R., Appleby, M.C., Hughes, B.O., 1998. Effects of social interactions on pre-laying behaviour in hens. Appl. Anim. Behav. Sci. 56, 47–57.
- Geffen, E., Yom-Tov, Y., 2001. Factors affecting the rates of intraspecific nest parasitism among Anseriformes and Galliformes. Anim. Behav. 62, 1027–1038.
- Huber, H.U., Folsch, D.W., Stahli, U., 1985. Influence of various nesting materials on nest site selection of the domestic hen. Br. Poult. Sci. 26, 367–373.
- Hughes, B.O., 1993. Choice between artificial turf and wire floor as nest sites in individually caged laying hens. Appl. Anim. Behav. Sci. 36, 327–335.
- Kite, V.G., Cumming, R.B., Wodzicka-Tomaszewska, M., 1980. Nesting behaviour of hens in relation to the problems of flor eggs. In: Wodzicka-Tomaszewska, M., Edey, T.N., Lynch, J.J. (Eds.), Reviews in Rural Science IV. Armidale, New South Wales, Australia, pp. 93–96.
- Lahti, D.C., 2001. The "edge effect on nest predation" hypothesis after twenty years. Biol. Conserv. 99, 365–374.
- Lundberg, A.S., Keeling, L.J., 1999. The impact of social factors on nesting in laying hens (*Gallus gallus domesticus*). Appl. Anim. Behav. Sci. 64, 57–69.
- McBride, G., Parer, I.P., Foenander, F., 1969. The social organization and behaviour of the feral domestic fowl. Anim. Behav. Monogr. 2, 125–181.
- Meijsser, F.M., Hughes, B.O., 1989. Comparative analysis of pre-laying behaviour in battery cages and in three alternative systems. Br. Poult. Sci. 30, 747–760.
- Paton, P.W.C., 1994. The effect of edge on avian nest success: how strong is the evidence? Conserv. Biol. 8, 17–26.
- Petherick, J.C., Seawright, E., Waddington, D., 1993. Influence of quantity of litter on nest box selection and nesting behaviour of domestic hens. Br. Poult. Sci. 34, 857–872.
- Price, E.O., 1984. Behavioral aspects of animal domestication. Q. Rev. Biol. 59, 1–32.
- Riber, A.B., 2010. Development with age of nest box use and gregarious nesting in laying hens. Appl. Anim. Behav. Sci. 123, 24–31.
- Rietveld-Piepers, B., 1987. The development of egg-laying and nest-site selection in a strain of white laying hens. PhD thesis, Wageningen University.
- Savory, C.J., Wood-Gush, D.G.M., Duncan, I.J.H., 1978. Feeding behaviour in a population of domestic fowl in the wild. Appl. Anim. Ethol. 4, 13–27. SAS, 2000. SAS OnlineDoc1, Version 8 with PDF Files.
- Schmid, I., Wechsler, B., 1997. Behaviour of Japanese quail (*Coturnix japonica*) kept in semi-natural aviaries. Appl. Anim. Behav. Sci. 55, 103–112.
- Schmid, I., Wechsler, B., 1998. Identification of key nest site stimuli for Japanese quail (Coturnix japonica). Appl. Anim. Behav. Sci. 57, 145–156.
- Sherwin, C.M., Christiansen, S.B., Duncan, I.J., Erhard, H.W., Lay, D.C., Mench, J.A., O'Connor, C.E., Petherick, J.C., 2003. Guidelines for the ethical use of animals in applied ethology studies. Appl. Anim. Behav. Sci. 81, 291–305.
- Struelens, E., Tuyttens, F.A.M., Janssen, A., Leroy, T., Audoorn, L., Vranken, E., De Baere, K., Odberg, F., Berckmans, D., Zoons, J., Sonck, B., 2005. Design of laying nests in furnished cages: influence of nesting material, nest box position and seclusion. Br. Poult. Sci. 46, 9–15.
- Wallander, J., Isaksson, D., Lenberg, T., 2006. Wader nest distribution and predation in relation to man-made structures on coastal pastures. Biol. Conserv. 132, 343–350.
- Wood-Gush, D.G.M., Duncan, I.J.H., 1976. Some behavioural observations on domestic fowl in the wild. Appl. Anim. Ethol. 2, 255–260.
- Zeltner, E., Hirt, H., 2008. Factors involved in the improvement of the use of hen runs. Appl. Anim. Behav. Sci. 114, 395–408.