



## Gregarious nesting—An anti-predator response in laying hens

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### ABSTRACT

Gregarious nesting can be defined as a behaviour that occurs when a laying hen (*Gallus gallus domesticus*) given the choice between an occupied and an unoccupied nest site chooses the occupied nest site. It occurs frequently in flocks of laying hens kept under commercial conditions, contrasting the behaviour displayed by feral hens that isolate themselves from the flock during nesting activities. What motivates laying hens to perform gregarious nesting is unknown. One possibility is that gregarious nesting is an anti-predator response to the risk of nest predation emerging from behavioural flexibility in nesting strategy. The aim of the present experiment was to investigate whether gregarious nesting due to behavioural flexibility in nesting strategy is an anti-predator response. Twelve groups of 14–15 Isa Warren hens age 44 weeks were housed in pens each containing three adjacent roll-out nest boxes. Nesting and spacing behaviour were video recorded for 5 days in each of three distinct periods; (a) pre-predator; a pre-exposure period, (b) predator; a period with daily exposure to a simulated attack by a lifelike flying model of a hooded crow (*Corvus cornix*, a potential egg-predator), and (c) post-predator; a post-exposure period. Additional data collected were the behaviour of each hen 5 min prior to and 10 s after the simulated predator attacks. The hens reacted with fear-related behaviour to the simulated predator attacks, e.g. the number of hens engaged in normal non-agitated behaviour decreased from before to after exposure to the predator model ( $P < 0.001$ ), and this did not change with day of exposure ( $P > 0.05$ ). The proportion of gregarious nest box visits of the total number of visits, where the hens had a choice between gregarious or solitary nesting, was found to be higher during the predator period ( $P < 0.01$ ). The general distribution of hens in the pens did not change between periods ( $P > 0.05$ ). In conclusion, evidence was found for the proposed hypothesis that gregarious nesting is an anti-predator response.

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### 1. Introduction

Gregarious nesting can be defined as a behaviour that occurs when a laying hen given the choice between an occupied and an unoccupied nest site chooses the occupied nest site (Appleby et al., 1984). It occurs frequently in flocks of laying hens kept under commercial conditions, contrasting the behaviour displayed by feral hens that isolate themselves from the flock during nesting activities (Appleby, 1997). A laying hen may visit one or more nest

sites several times prior to each oviposition, and gregarious nesting occurs both during visits with and without oviposition (Riber, 2010). There are two possible explanations to the cause of gregarious nesting. One is that the hens possess a preference for the same nest box characteristics (Clausen and Riber, 2012). The other explanation is that the presence of a hen carrying out nesting behaviour may motivate other hens to join her in the activity. The latter, however, leads to another question; why is the presence of another hen a motivating factor? One possibility is that the hen is unable to distinguish between similar nests and therefore in a row of empty nest boxes selects a nest box containing another hen, because the occupied nest box appears different (Appleby and Mcrae, 1986). Early in the laying

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period gregarious nesting may also occur because inexperienced hens select nest locations based on the choice of experienced hens (Riber, 2010).

A third possible explanation to the attraction to other nesting hens is that gregarious nesting may be an anti-predator response emerging from behavioural flexibility in nesting strategy. The secretive nesting behaviour that a feral hen displays can be interpreted as an anti-predator response that minimises the risk of having the nest detected by predators (Duncan et al., 1978). The commercial laying hen does not have the possibility of isolating herself from the flock. Instead she may choose the alternative anti-predator response; choosing a nest already occupied by other hens, i.e. gregarious nesting. This strategy generates a risk-dilution effect as a hen's egg will just be one of many in the nest, i.e. in case of partial nest predation the risk of having her egg predated is reduced by the presence of other eggs (Bertram, 1979).

Gregarious nesting in domestic fowl as an anti-predator response cannot be an evolutionary adaptation in the traditional sense, as no progeny from any nesting strategy involving use of nest boxes is favoured under commercial conditions. However, in a recent review on predators and the breeding bird, Lima (2009) states that although the major influence of predators on avian life histories undoubtedly is expressed at a broad phylogenetic scale, several studies hint at much flexibility on an ecological scale, i.e. within the lifetime of an individual. Predation may vary greatly within a bird's lifetime and behavioural plasticity in response to changes in predation risk will indisputably lead to fitness benefits above those of fixed traits alone. Thus, although not maintained through evolutionary adaptation the possibility exists that gregarious nesting due to behavioural flexibility in nesting strategy is a response to the risk of nest predation. Following this line, more gregarious nesting would thus be expected in the presence of potential predators.

The aim was to test the prediction that simulated attacks by a model of a potential egg-predator would increase the frequency of gregarious nesting. Furthermore, the effect of the simulated attacks on a number of other parameters of nesting and spacing behaviour were analysed to provide background information for the results on gregarious nesting behaviour.

## 2. Material and methods

### 2.1. Animals and housing

A total of 177 Isa Warren hens were housed in 12 experimental pens (Fig. 1; 2 m × 2.6 m) in groups of either 14 ( $n=3$ ) or 15 hens ( $n=9$ ). The hens were supplied by TopÆg Aps, Viborg, Denmark, who beak-trimmed the chicks at day-old. The experiment started when the hens were 44 weeks old and ended at 48 weeks of age. The pens housing the hens were identical; three adjacent nest boxes with identical design were placed in each pen 95 cm above the ground. The nest boxes only differed in position (left + corner, middle, and right) and could be accessed from a five-step ladder that also functioned as perches. The two upper perches were as long as the total width of all three

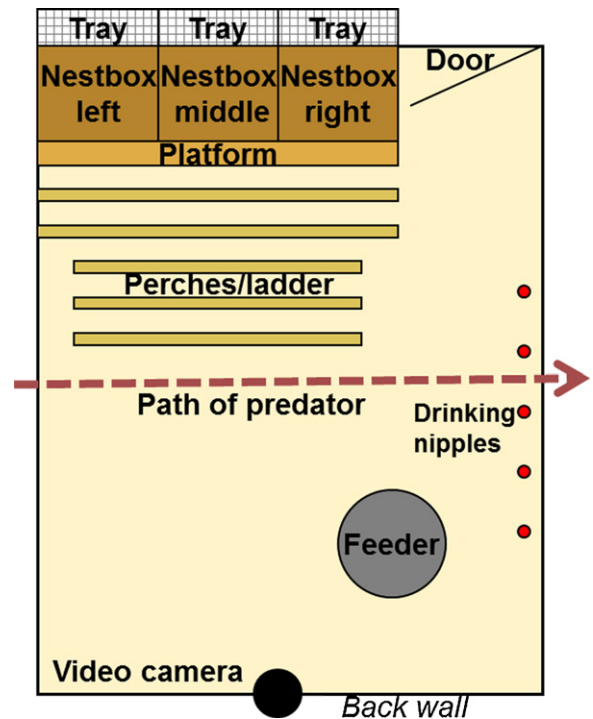


Fig. 1. Design of the experimental pens.

nest boxes. In front of the nest boxes there was a 15 cm wide platform. The three covered nest boxes each measured 40 cm × 30 cm × 34 cm ( $W \times D \times H$ ) and contained mats of Astroturf. The nest boxes were designed in a way that the eggs rolled into a separate tray for each nest box. The experiment was conducted in continuation of two other experiments aimed at describing (1) characteristics of laying hens performing gregarious nesting behaviour (Riber, in preparation) and (2) development with age of nest box use and gregarious nesting (Riber, 2010). The animals and housing conditions in the present experiment were therefore identical to that described in Riber (2010), i.e. for more details about animals and housing consult *ibid*. The two previous experiments were observational studies, i.e. no treatments were applied.

### 2.2. Treatment

In weeks 44, 45, 47, and 48 of age the hens received no treatment and were only subjected to normal husbandry procedures (i.e. feeding, egg collection, surveillance). During week 46 of age the hens were exposed to a simulated attack by a lifelike flying model of a hooded crow (*Corvus cornix*, a potential egg-predator) during five consecutive mornings approximately 10 min after lights-on. The crow was made of plastic, stuffed with concrete, and had dimensions (e.g. wing span 84 cm) and colours similar to a live crow (Fig. 2). It was attached via snap hooks to two pulleys on a 36 m long wire that was stretched from one end to the other in the room housing the hens such that it followed the centre of the pens (all 12 pens were placed in one row). To ease the “flight”, the wire was attached at 4 m height at the starting point and at 3 m height at the end



**Fig. 2.** The applied model of a potential egg-predator, the hooded crow.

point such that a slope was created. With a hard manual push the crow “flew” from the starting point to the ending point passing all the pens on its way. This was done once every morning, and it took about 8 s for the crow to pass all 12 pens. The starting and ending point, and with that the person handling the crow, were not visible to the hens.

### 2.3. Data collection

Digital video recordings were obtained daily from lights-on till 5 h later from three periods; (a) pre-predator; a 5 days pre-exposure period (age 44 weeks), (b) predator; a 5 days period with daily exposure to a simulated attack by the predator model (age 46 weeks), and (c) post-predator; a 5 days post-exposure period (age 48 weeks). The hens thus functioned as their own controls (pre-predator period), and waning of the effect of the simulated predator attacks on gregarious nesting could be observed (post-predator). The day before each video recording period all hens were fitted with distinct back marks ( $L$ : 10 cm  $\times$   $W$ : 7.3 cm) enabling individual identification of the hens on the recordings. The back marks were fitted using a loop of elastic band that was slipped over each wing, and all hens quickly habituated to the marks. The material used for the back mark was soft 3 mm thick rubber with a base attached on the back side where to the elastic bands were attached. Hens were inspected from a distance several times daily to ensure that the back marks remained in place. Only a few times did the back marks flip upside down, but the movements of the hens brought them back in place. The back marks were taken off again immediately after finishing video recordings. Putting the back marks on and off three times with 1 week intervals instead of leaving them on for the entire experiment was done in order to avoid abrasions. Observations of hens using the nest boxes after the first 5 h of light were few and often the purpose of these visits were resting or preening; consequently video recordings were limited to the first 5 h after lights-on.

Data collected from all three video recording periods were (1) time and identity of each hen for all entries and exits from each of the three nest boxes (left + corner, middle, or right), (2) time of oviposition of each hen, and (3) distribution of hens in the pens. Entries were scored when the hen put one leg and the head inside the nest box, and likewise exits were scored when the hen put one leg and the head outside the nest box. Time of oviposition was noted either on direct view of egg-dropping or when the hen assumed the characteristic position for egg-laying, the penguin position (Fölsch and Vestergaard, 1981). The location within the pen of each hen was recorded by scan sampling

twice a day at 4½ and at 5 h after lights-on. Locations were defined by dividing the on-screen area into equal sized squares (0.65 m  $\times$  0.66 m); 12 squares at floor level and 10 squares at the vertical space available to the hens (i.e. the five step ladder and the nest boxes). Additional data collected from the predator period were the behaviour of each hen (a) 5 min prior to and (b) 10 s after the simulated predator attacks. Three categories of behaviour were defined: (1) normal non-agitated behaviour; no response at all, (2) alerted behaviour; the hen stands or walks with the neck stretched and eyes opened, and (3) panic behaviour; the hen tries to escape by running, jumping, or flying. Data on behaviour prior to and after the simulated predator attacks were collected using instantaneous sampling, i.e. records were made of whether or not the behaviour occurred at the sample point (Martin and Bateson, 1993). The number of eggs laid in each nest box and the number of floor eggs laid in each pen were recorded daily around 14:00 h during the duration of the experiment. It was noted if the eggs were cracked.

Some of the data from the pre-predator period have also been used for describing development with age of nest box use and gregarious nesting in Riber (2010).

### 2.4. Data treatment

When a nest box received a visit, it was assigned to one of four possible types of occupancy status depending on both its own occupancy and the occupancy of the two other nest boxes;

1. “occupied” = the nest box visited was occupied by one or more hens, whilst at least one other nest box was unoccupied. This corresponds to *gregarious* nesting.
2. “all occupied” = all nest boxes, including the one visited, were each occupied by one or more hens,
3. “unoccupied” = the nest box visited was unoccupied, whilst at least one other nest box was occupied by one or more hens. This corresponds to *solitary* nesting.
4. “all unoccupied” = all nest boxes, including the one visited, were unoccupied.

The proportion of gregarious nesting at the three different periods was calculated using only visits directed to nest boxes when there was a choice of “unoccupied” and “occupied” nest boxes. Visits directed to nest boxes with a status of “all unoccupied” or “all occupied” were excluded.

The duration of pre-laying period was defined to start with a hen’s first entry into a nest box and ended with her oviposition, i.e. the duration of the pre-laying period is a minimum estimate, because before a hen enters a nest she has gone through preceding pre-laying phase of searching for possible nest sites without entering them followed by nest inspections where she puts only her head in nest boxes (Wood-Gush, 1971).

### 2.5. Statistics

All data were subjected to repeated measurements analysis of variance (ANOVA) in the SAS<sup>®</sup> statistical program using the Mixed procedure (SAS, 2000). Data were tested

and found to meet the assumptions of ANOVA, i.e. normal distribution and homogeneity of variance, though log-transformation of the data on the duration of the pre-laying period and the data on the behavioural activity prior to and after the simulated predator attack was necessary to meet these requirements. The statistical unit used in all analyses was pen. Pen-specific random effects were included in all analyses to account for the repeated measurements of the response over time from each pen. In addition to period the following explanatory variables were used each in their separate analysis: time (before/after the simulated attacks), day of exposure, occurrence of oviposition, and use of nest boxes according to their occupancy status or position. The qualitative factors used differed according to the analysis conducted but were in addition to period and pen one or more of the following: nest box position, occupancy status, day, time, identity of hens, occurrence of oviposition, and number of (a) individuals, (b) eggs, (c) hens using nest boxes, and (d) squares occupied.

When there was an overall statistically significant difference, pair wise comparisons were made using the *t*-test. Results are reported as least square means and standard errors. When log-transformation was used to meet the assumptions of ANOVA, the least-square means and standard errors reported were back-transformed for presentation.

### 2.6. 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). All hens were re-homed to families as pets after completion of the experiment.

## 3. Results

In total 7401 nest visits and 2133 ovipositions were registered on the video recordings. The latter corresponded to 88.8% of all eggs laid in nest boxes throughout the video recording periods. The eggs for which oviposition was not registered were laid either outside the first 5 h of light, i.e. after the video recording was terminated, or they were laid within the video recording period, but oviposition could not be observed due to other hens blocking the view of the nest box entrance.

### 3.1. Immediate response to predator

The hens reacted with fear-related behaviour to the simulated predator attacks (Fig. 3). The number of hens engaged in normal behaviour decreased from before to after exposure to the predator model ( $F_{1,107} = 11,283.6$ ,  $P < 0.001$ ), and this did not change with day of exposure ( $F_{4,103} = 1.88$ ,  $P = 0.12$ ). Furthermore, there was an effect of the interaction between time (before/after exposure to the predator model) and day of exposure on alerted behaviour ( $F_{4,99} = 5.98$ ,  $P < 0.001$ ) and panic behaviour ( $F_{4,99} = 7.90$ ,  $P < 0.001$ ), i.e. the fear reaction to the simulated attacks

decreased in strength with day of exposure or in other words the hens started to habituate to the simulated attacks.

### 3.2. Effect on occurrence of gregarious nesting

The mean proportion of gregarious nest visits differed between the three periods ( $F_{2,337} = 5.21$ ,  $P = 0.006$ ). During the predator period it was higher than during the pre-predator period ( $0.44 \pm 0.04$  vs.  $0.38 \pm 0.04$ ;  $t_{338} = -3.01$ ,  $P = 0.003$ ), and during the post-predator period the proportion of gregarious nest visits remained at the level found in the predator period ( $0.43 \pm 0.04$ ;  $t_{337} = 0.47$ ,  $P = 0.64$ ). The number of gregarious nest visits depended both on period ( $F_{2,524} = 5.08$ ,  $P = 0.007$ ; Fig. 4) and on nest box position ( $F_{2,524} = 206.7$ ,  $P < 0.001$ ), i.e. more gregarious nest visits were directed to the left nest box than the other two nest boxes during all periods and more during the predator and post-predator periods than during the pre-predator period. The general distribution of hens in the pens did not differ between periods ( $F_{2,346} = 0.17$ ,  $P = 0.84$ ).

### 3.3. Effect on use of nest boxes according to their occupancy status

Visits were directed to nest boxes of all four types of occupancy status, but the number of visits depended on the interaction between nest box status and period ( $F_{6,697} = 3.10$ ,  $P = 0.005$ ; Fig. 5), i.e. the number of visits to occupied nest boxes increased from the pre-predator period to the predator period ( $t_{697} = -4.09$ ,  $P < 0.001$ ) and remained at this level during the post-predator period ( $t_{697} = 0.78$ ,  $P = 0.43$ ).

A comparison between the periods of the proportions of visits directed to the four types of occupancy status divided into those with and those without oviposition revealed that there was an overall effect ( $F_{17,264} = 1.99$ ,  $P = 0.01$ ; Fig. 6). Pair wise differences between periods were only found for visits to occupied nest boxes without oviposition, where more visits were directed to occupied nest boxes during the predator period than during the pre-predator period ( $t_{264} = -2.15$ ,  $P = 0.03$ ).

### 3.4. Effect on use of nest boxes according to their position

The use of the three nest boxes was also affected by the simulated predator attacks (Fig. 7). There was a tendency to an overall effect of period on the number of visits to nest boxes ( $F_{2,166} = 2.47$ ,  $P = 0.09$ ). The number of visits to nest boxes was higher during the predator period than during the pre-predator period ( $t_{360} = -2.07$ ,  $P = 0.04$ ). During the post-predator period the number of nest box visits decreased to a level in between the pre-predator ( $t_{360} = -1.34$ ,  $P = 0.18$ ) and predator period ( $t_{360} = 0.73$ ,  $P = 0.46$ ). There was an overall effect of nest box position on number of visits received ( $F_{2,358} = 127.39$ ,  $P < 0.001$ ); more visits were directed to the left nest box than to the other two nest boxes (left vs. middle,  $t_{358} = 14.52$ ; left vs. right,  $t_{358} = 13.00$ ;  $P < 0.001$ ), whereas there was no difference between the middle and right nest boxes in number of nest visits received ( $t_{358} = -1.53$ ,  $P = 0.13$ ).

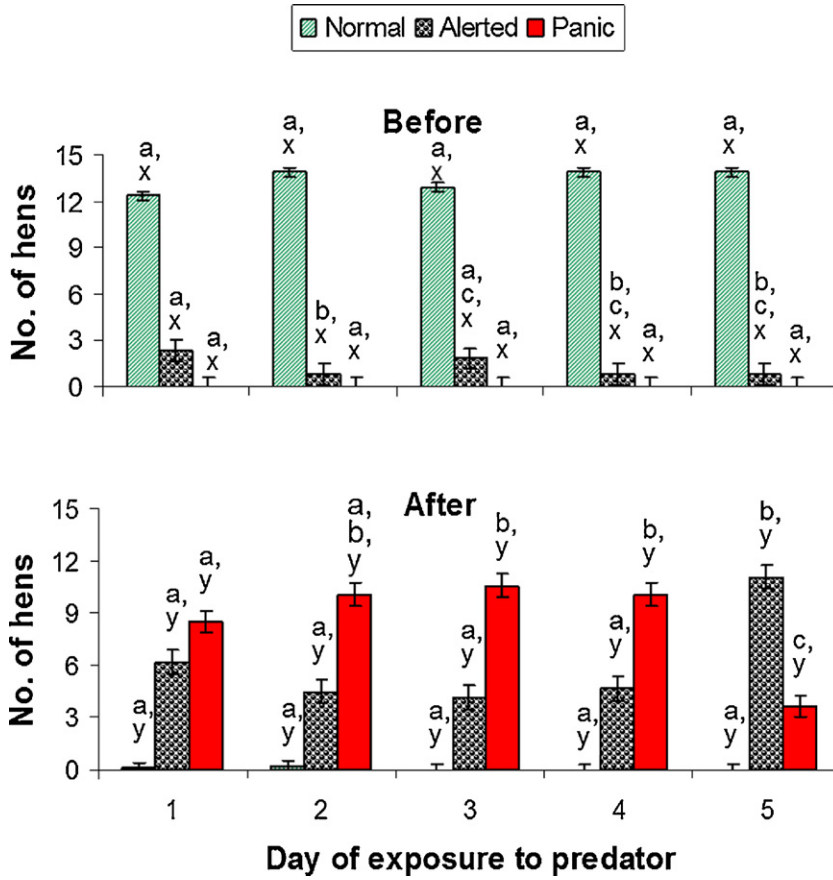


Fig. 3. Mean number ( $\pm$ SE) of hens engaged in normal, alerted, and panic behaviour, respectively, before and after the simulated predator attacks. Letters a, b, and c indicate differences within time and behaviour and letters x and y indicate differences within days and behaviour.

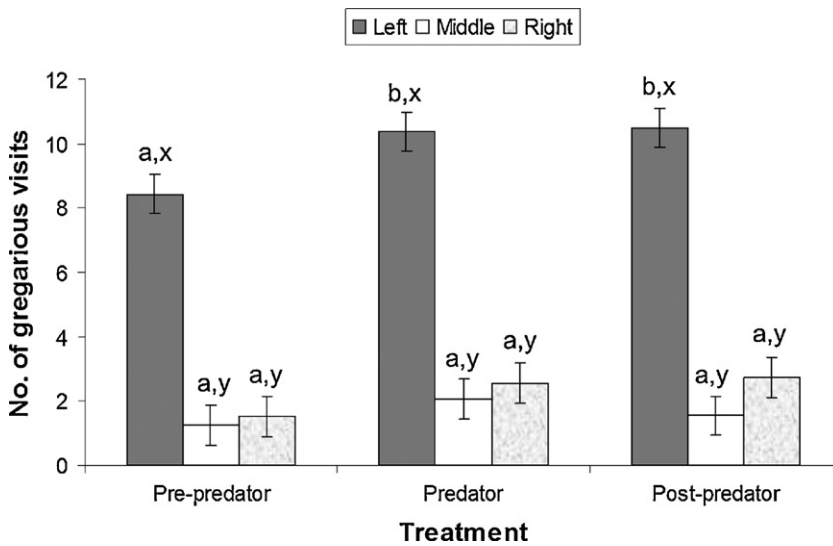


Fig. 4. Mean frequency ( $\pm$ SE) of number of gregarious nest visits per day according to nest box position during the three periods. Letters a and b indicate differences within nest box position and letters x and y indicate differences within period.



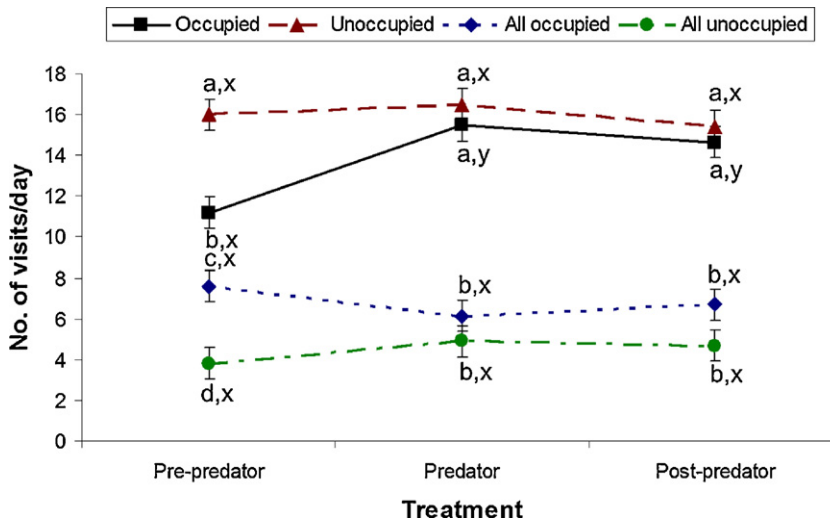


Fig. 5. Mean frequency ( $\pm$ SE) of number of visits per day according to nest box occupancy status during the three periods. Letters a, b, c, and d indicate differences within period and letters x and y indicate differences within nest box occupancy status.

Moreover, the number of eggs laid in each of the three nest boxes differed ( $F_{2,502} = 432.4, P < 0.001$ ), but this did not differ between periods ( $F_{2,22} = 0.03, P = 0.97$ ). More eggs were laid in the left nest box ( $7.9 \pm 0.1$  eggs/day) than in the other two nest boxes (middle:  $2.4 \pm 0.1$  eggs/day, right:  $3.1 \pm 0.1$  eggs/day;  $23.6 < t_{526} < 27.1, P < 0.001$ ). Also, more eggs were laid in the right nest box than in the middle nest box ( $t_{526} = -3.5, P < 0.001$ ).

3.5. Effect on general nesting behaviour parameters

The mean time of day of oviposition was affected by the simulated predator attacks ( $F_{2,22} = 4.30, P = 0.03$ ),

with later ovipositions during the predator period ( $06:21:42 \pm 00:05:40$ ) than during the pre-predator period ( $06:08:12 \pm 00:05:44; t_{22} = -2.33, P = 0.03$ ). During the post-predator period the mean oviposition time ( $06:15:21 \pm 00:05:38$ ) decreased to a level in between the pre-predator ( $t_{22} = -1.24, P = 0.23$ ) and predator period ( $t_{22} = 1.10, P = 0.29$ ).

A number of general nesting behaviour parameters did not differ between the three periods; number of (a) hens using nest boxes ( $13.4 \pm 0.3$  hens/day;  $F_{2,22} = 0.10, P = 0.91$ ), (b) eggs laid in nest boxes ( $13.4 \pm 0.2$  eggs/day;  $F_{2,166} = 0.42, P = 0.66$ ), and (c) floor eggs ( $1.16 \pm 0.07$  eggs/day;  $F_{2,166} = 0.54, P = 0.58$ ). Neither did the duration of the pre-laying period differ between the three periods ( $41 \text{ min } 49 \text{ s} \pm 1 \text{ min } 33 \text{ s}; F_{2,2119} = 2.10, P = 0.12$ ). Registrations of cracked eggs in nest boxes were few throughout the experiment ( $< 0.1$  eggs/day).

4. Discussion

Support was found for the hypothesis that gregarious nesting is an anti-predator response. The prediction was that if gregarious nesting in laying hens is an anti-predator response to the risk of nest predation then simulating attacks by a potential egg-predator would increase the frequency of gregarious nesting, and this in fact did happen in the present experiment with regard to nest visits without oviposition. From this it can be concluded that laying hens are capable of directly assessing variation in the risk of nest predation. However, selection of the final nest sites where the eggs were laid did not seem to be affected accordingly, i.e. predation risk affected the early part of pre-laying behaviour. Lack of sufficient space in the gregarious nest boxes for settling down for the sitting phase prior to egg-laying may have forced some hens about to lay an egg to leave the gregarious nest boxes and select nest boxes with more space available as the final nest sites for oviposition. Hens may withhold their eggs as a response to increased predation risk (Lundberg and

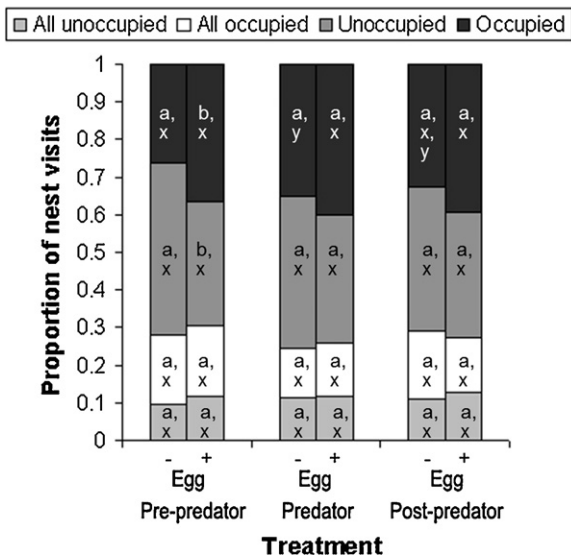
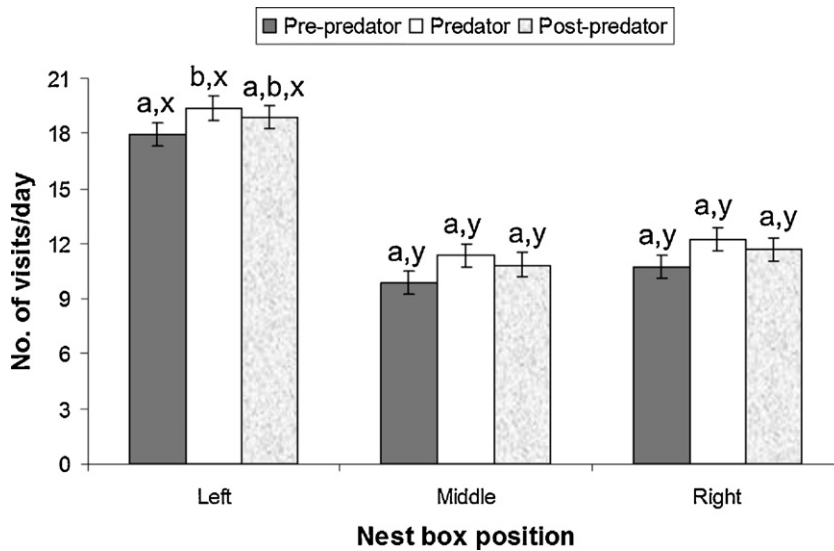


Fig. 6. Mean proportion of number of visits without (-) and with (+) oviposition, according to nest box occupancy status during the three periods. Letters a and b indicate differences within period and nest box occupancy status, and letters x and y indicate differences within oviposition category (-/+) and occupancy status.



**Fig. 7.** Mean frequency ( $\pm$ SE) of number of visits per day to each of the three nest boxes according to their position during the three periods. Letters a and b indicate differences within nest box position and letters x and y indicate differences within period.

Keeling, 1999). Individual variation in the reaction to the simulated predator attacks was observed, and it is likely that those hens that reacted most strongly to the simulated attacks also responded with short delays of oviposition. As the capability to withhold an egg is limited, hens may have reached a point where they were no longer able to wait for a possibility of laying the egg in the occupied nest boxes and have been forced to find nest boxes with sufficient space. The simulated attacks by the predator also resulted in later ovipositions and in a tendency of the hens to increase the number of nest visits. The increase in frequency of gregarious nest visits during the predator period could not be due to the tendency to a general increase in number of nest visits, because there was no increase in number of visits to nest boxes with other statuses than occupied. It is well documented that domestic and red jungle fowl react with anti-predator behaviour to simulated attacks by a model of a hawk (Håkansson and Jensen, 2008) and respond with fearfulness to less lifelike models of predators, e.g. black silhouettes on computer screens (Evans et al., 1993). The described procedure of simulating attacks was therefore considered sufficient to elicit possible anti-predator responses in the hens, and indeed the simulated attacks by the predator had the expected effect on immediate behaviour, i.e. the hens reacted with fear-related behaviour.

The reason why the experiment was conducted was a desire to test all three possible explanations to the cause of gregarious nesting mentioned in the introduction. The expectations to a confirmation of the hypothesis in the present experiment were low, and the results are therefore surprising. However, the results cannot be explained away by a general tendency in all animals to increase the group size or the density of an aggregation during periods of increased predation risk, as the distribution of the hens in the pens in general, unlike that in the nest boxes, did

not differ between the periods. Instead the results seem to fit well into the growing topic in behavioural ecology that birds are capable of responding on an ecological time scale to changes in predation risk with behavioural plasticity in nesting behaviour (Lima, 2009). Nest predation is repeatedly reported as the most important source of reproductive failure for the great majority of birds (e.g. Ricklefs, 1969), and since predation can vary greatly within a bird's lifetime, flexibility in the response to predators will unquestionably lead to fitness benefits. Several examples of such flexibility have been found (Lima, 2009). For example, increased nest predation risk has been found to affect next breeding attempts in great tits (*Parus major*) by altering the clutch size (Julliard et al., 1997), and dark-bellied brent geese (*Branta bernicla bernicla*) has been found to completely forego breeding if predator abundance is high (Spaans et al., 1998). These examples of behavioural changes in reproduction in response to increased predation risk are unlikely to happen in domestic fowl that is highly selected for egg-production and lay large clutches only separated by one or a few days (Gilbert and Wood-Gush, 1971). More resembling the observed response in the present experiment, dusky warblers (*Phylloscopus fusca-tus*) and orange-crowned warblers (*Vermivora celata*) have been found to select different nest locations depending on the abundance of mammalian predators (Forstmeier and Weiss, 2004) or following the simulated appearance of a model of an unfamiliar avian predator (Peluc et al., 2008). Like in the present experiment, short simulated attacks by a predator not leading to the loss of eggs or young have been found to result in changes in nesting strategy, e.g. in Tengmalm's owls (*Aegolius funereus*) where simulating a nest predation attempt induced breeding dispersal (Hakkarainen et al., 2001).

Behavioural plasticity in nesting behaviour in response to changes in predation risk has also previously been found

in laying hens; Lundberg and Keeling (1999) found that the overall number of eggs laid during an observation period of 3 h decreased if all eggs were removed every 5 min, which can be interpreted as the hen withholds her egg if there is a predator around. This is in correspondence with the later mean time of oviposition found during the predator period in the present experiment. Furthermore, the tendency found to increase the number of nest visits in response to the simulated attack by the predator can be interpreted as increased indecision in nest selection leading to more nest visits before a choice was made. This could be a variety of the often observed inconsistency in nest choice by commercial laying hens, which has been suggested to be an anti-predator response to the continued removal of eggs in production systems, corresponding to the observation that having the nest predated under natural conditions leads to abandonment of the nest (Duncan et al., 1978). There was, however, no indication of true inconsistency, as no shifts between periods in preference of nest box position were observed within groups, making it unlikely that shifts in individual preferences occurred.

A possible proximate cause of the increase in the frequency of gregarious nest visits after the simulated predator attacks could be that exposure to the predator model caused the hens to base their selection of nest location more on the choice of other hens, either because being in a group whilst nesting reduced the fear induced by the predator or because they during nest selection used a simple reasoning such as “another hen have chosen that particular nest box, ergo it must be safer than the unoccupied nest box(es)”. Social influence on behaviour has been reported previously in laying hens, e.g. in choice of feeding site (Mcquoid and Galef, 1992, 1993) and in learning new skills (Nicol and Pope, 1992). Furthermore, obtaining knowledge on the nesting success of conspecifics has been found in bird species living under natural conditions, where such information amongst other things is used to decide where to place the succeeding nest (e.g. Doligez et al., 2004). Another possibility could be that the higher predation risk stimulated the hens to seek out a more hidden nest site and this led them to explore and look under other hens. This behaviour has been recorded in hens without access to nest boxes (Freire et al., 1998).

## 5. Conclusions

The present paper did find evidence for the proposed hypothesis that gregarious nesting is an anti-predator response. Seeing this result in a production perspective, the majority of laying hens are housed in predator-free environments, but some incidents may be perceived by the hens as an increase in predation risk and result in increased frequencies of gregarious nesting. Good management may therefore be effective in reducing the frequency of gregarious nesting. Gregarious nesting has also been found to be more common early in the egg-laying period (Riber, 2010), which is difficult to explain using the anti-predator response hypothesis, but is more likely explained by a tendency of inexperienced hens to select nest locations based on the choice of experienced hens (Riber, 2010). Knowledge

about the cause of gregarious nesting is still sparse and until proved otherwise gregarious nesting should be considered as a behavioural activity influenced by multiple factors.

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