THE EFFECT OF AN AUDIENCE ON THE GAKEL-CALL AND OTHER FRUSTRATION BEHAVIOURS IN THE LAYING HEN (*GALLUS GALLUS DOMESTICUS*)

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Abstract *Animal Welfare 2003, **12**: 315-326*

When thwarted in a behaviour, laying hens show an increase in stereotyped pacing, displacement preening and a specific vocalisation known as the 'gakel-call'. How these behaviours, which might serve as indicators of welfare, are influenced by social factors is not yet known. In this study, we investigated the effect of an audience (another bird or a human) on the expression of the gakel-call and other behaviours indicating frustration. Twenty-four Lohman Brown hens were trained to gain free access to food in a test cage. Sixteen hens were used as test birds and eight as non-test audience birds. The food-deprived test hens were tested for 15 min in a non-thwarting situation (food freely available) and for 15 min in a thwarting situation (food covered but visible). For both situations we investigated four different treatments: no audience in the adjacent cage; a non-thwarted audience bird in the adjacent cage; a thwarted audience bird in the adjacent cage; and finally a human audience. The durations of stereotyped pacing and displacement preening were significantly higher in test birds during thwarting than during non-thwarting; thwarted birds also gave significantly more gakel-calls compared to non-thwarted birds. The test birds, and also the audience birds, gave more gakel-calls when thwarted in the presence of a thwarted conspecific than when in the presence of a non-thwarted bird, but there were no significant differences in stereotyped pacing or displacement preening, which are usually associated with frustration. In conclusion, this study supports the view that the gakel-call signals frustration in laying hens. Furthermore, the state of the audience influences the occurrence of gakel-calls in thwarted hens. Thus, when using the gakel-call as a welfare-indicator, the social aspects of the vocal expression of frustration in laying hens should not be overlooked.

Keywords: *animal welfare, audience, frustration, laying hens, social behaviour, vocalisations*

Introduction

Frustration has been defined as "an aversive motivational state that results from non-reward, reduced reward or delayed reward in the presence of a history of reward" (Amsel 1992). Frustration in the laying hen (*Gallus gallus domesticus*) has been well-studied (eg Duncan &

Wood-Gush 1971, 1972a,b; Wood-Gush 1972; Duncan & Wood-Gush 1974; Jones 1989). These previous studies all applied the thwarting of behaviour to induce a state of frustration and focused mainly on the behavioural effects of frustration. Thwarting of feeding behaviour in laying hens has been found to increase the occurrence of displacement preening and stereotyped pacing (Duncan & Wood-Gush 1972b). Stereotyped pacing is thought to originate from escape movements that become fixed in the bird's behavioural repertoire (Duncan & Wood-Gush 1974). From these studies it is also concluded that thwarting of a behaviour is aversive to laying hens (Duncan & Wood-Gush 1972b, 1974), possibly introducing an element of conflict when a bird repeatedly attempts to perform the blocked behaviour but at the same time tries to escape the situation.

Other studies have focused on vocalisations of laying hens that might indicate frustration (Schenk *et al* 1983; Koene & Wiepkema 1991; Zimmerman & Koene 1998). Bäumer (1962) described a call named 'Gakeln' that, in his opinion, not only indicated the hen's readiness for egg-laying (hence the labels "Legelaut" by Schjelderup-Ebbe [1922] and "[pre]laying-call" by Konishi [1963] and Wood-Gush [1971]), but also in general indicated a behavioural need. Higher numbers of gakel-calls in response to thwarting have also been recorded in contexts other than the pre-laying situation. Higher numbers of gakel-calls have been found upon thwarting of feeding behaviour (Schenk *et al* 1983; Koene & Wiepkema 1991; Zimmerman & Koene 1998), drinking behaviour (Zimmerman *et al* 2000a), dustbathing behaviour (Koene & Wiepkema 1991; Zimmerman *et al* 2000a) and nesting behaviour (Meijsser & Hughes 1989; Schenk *et al* 1983; Zimmerman *et al* 2000a). Furthermore, a longer duration of food- and dustbath-deprivation seems to result in a higher number of gakel-calls (Schenk *et al* 1983; Koene & Wiepkema 1991; Zimmerman *et al* 2000b). This implies that the gakel-call is not only related to the thwarting of behaviour, but also conveys information about the intensity of the frustration.

The influence of a bird audience on laying hen vocalisations such as the food-call and alarm-call has been extensively studied (Gyger *et al* 1986; Gyger & Marler 1988; Evans & Marler 1991, 1992; Evans *et al* 1993a,b; Evans & Marler 1994). These studies showed that, depending on the type of audience (ie male or female, same or different species), the production of food-calls and alarm-calls can be either stimulated or inhibited. The effect of a human audience on laying hen vocalisations in general is not well documented. Humans can act as a fear stimulus for domestic hens (for a review, see Duncan 1992). On the other hand, regular handling of birds can be a reliable and potent method of reducing hens' fear of humans (Jones 1993, 1994). Because in poultry husbandry the appearance of a human is often a signal that food is about to arrive, one can imagine that the gakel-call, as an indicator of frustration, can equally well be directed toward a human audience.

Thwarting of a behaviour induces an unsatisfied motivational state (Fraser & Duncan 1998), here called 'frustration'. Prolonged thwarting of a behaviour, the performance of which would have satisfied certain behavioural needs of the animal, may have a negative impact on the animal's welfare. The gakel-call, as an indicator of frustration, might then serve as an additional indicator of welfare in laying hens (Zimmerman & Koene 1998). However, because laying hens are almost always kept in groups, it is necessary to determine how the mere presence and the possible state of frustration of a conspecific influences the occurrence of the gakel-call.

The following two research questions were formulated to investigate this possible social effect: first, does the presence of an audience (bird or human) affect behaviour and

vocalisations indicative of frustration during thwarting of feeding behaviour? Second, does the state of frustration of the audience bird affect behaviour and vocalisations?

Methods

Animals and test conditions

We used 24 Lohman Brown hens that were 47 weeks of age when the experiment began. We subdivided the hens in two groups of 12 hens. Each group was housed in a littered pen that measured 3.0 × 1.5 × 2.0 m (l × w × h) with a feeder, a drinker, perches and a communal nest-box. When not stated otherwise, the hens had access to pelleted food and water *ad libitum*. The light period was 0730h–1930h. Eight hens out of each group served as test hens. For the audience hens, we selected four individuals of average weight and with average plumage condition from the same group. Test hens were always tested with the same audience hen.

We used two adjacent wire-mesh cages (0.5 × 0.5 × 0.5 m), a 'test' cage and an 'audience' cage, the adjacent sides of which were made of Plexiglas. At the front of each cage, a feeder and a drinker (both 10 × 5 × 5 cm) were attached to the outside. Hens could reach the food and water through two holes in the wire mesh (see Figure 1).

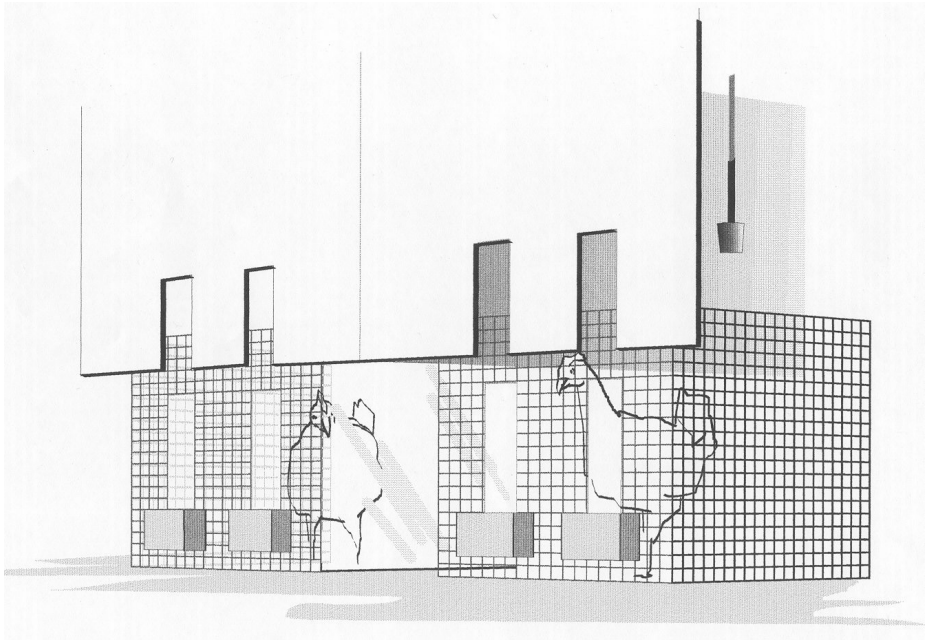

Figure 1 **Drawing of the test cages. In both cages the feeder is the bowl closest to the Plexiglas.**

A T-shaped wooden barrier was hanging from the ceiling and, when lowered, prevented the birds from seeing the feeder and drinker and the adjacent cage before a training or test session started. We used two directional microphones, hanging from the ceiling, to record sound. Both microphones were connected to a Canon UC20 video-8 camera that was positioned 1.85 m away from the cages at the side of the feeders. Pictures and sound were recorded onto video-tape (Salerna SV900).

Experimental procedure and treatments

We first habituated all hens to the test room and test cages by placing them in one of the cages for 30 min on two consecutive days. During these two sessions the experimenter put food in the feeders to indicate the location of the food and lowered and pulled up the barrier twice. After habituation the training period started.

During training and testing, all hens in one group were food-deprived by removal of the feeder at 1900h on the day before training. Each hen received two training sessions per day, one in the morning and one in the afternoon, and the eight test hens in each group were always trained in the same order. The following procedure was used for training: the experimenter took a hen out of its home pen, carried it to the test room, put it in the test cage and then pulled up the barrier, after which the hen was allowed to feed for 15 min. Test hens were subjected to three different training sessions: individual training, training with an audience bird, and training with a human audience. The audience birds received their training in the sessions with the test hens. We considered both the test and the audience hens to be sufficiently trained when on three consecutive afternoon training sessions all hens started feeding immediately after the barrier had been pulled up. All hens met this criterion within a total of nine training sessions.

During testing, the test hens were subjected to eight different treatments, as shown in Table 1. All hens were tested in the afternoon from 1400h onwards, with the final test session ending at around 1630h. Each hen was tested once per day at approximately the same time, and each hen received a different order of treatments according to a balanced design. In the mornings, in between afternoon test sessions, hens were subjected to a training session and allowed to feed for 15 min. The test procedure was the same as the training procedure. After having placed the test hen in the test cage, the experimenter returned to the pen, collected the audience bird, returned again to the test room and placed the audience hen in the adjacent cage. When a test bird was going to be tested without an audience, the experimenter still returned to the pen and then walked back to the test room to deny the test hens any clues about the treatment before the test session started. After the audience bird had been placed in the cage (or after this had been shammed), the video-recording was started, the barrier was lifted and the experimenter left the room. In the human audience condition, the experimenter stayed in the room on the side of the adjacent cage. The human wore the same type and colour of clothing during training and testing as during the normal husbandry routine of the hens.

Table 1 Treatments of the test birds during testing.

		Contrast		
State of the test hen	**Type of treatment**	**A**	**B**	**C**
Non-thwarted test hen	1. Empty cage	–1		
	2. Non-thwarted audience hen	–1		
	3. Thwarted* audience hen	–1		
	4. Human audience	–1		
Thwarted test hen*	5. Empty cage	+1	–3	
	6. Non-thwarted audience hen	+1	+1	–1
	7. Thwarted audience hen	+1	+1	+1
	8. Human audience	+1	+1	

* Thwarting of feeding behaviour for both test and audience hens consisted of the feeder being covered with Plexiglas. In the non-thwarting treatment the hens had free access to food during the 15 min session. Contrasts A–C represent the comparisons between specific treatments. The treatments with a minus sign are compared with the treatments with a plus sign (see also Statistical analysis section).

The animals were treated according to the Guidelines for the Use of Animals in Research, the legal requirements of Sweden and the guidelines of the Swedish University of Agricultural Sciences.

The following behaviours of the hens were regarded as potential indicators of frustration and were recorded continuously: the number of gakel-calls, alarm-cackles (Collias 1987), head-flicks, and yawns. Yawning is a comfort behaviour that occurs also in conflict situations (Kruijt 1964), and head-flicking is an alertness response in a situation inducing increased attention (Hughes 1983). The duration of stereotyped pacing was also recorded (Duncan & Wood-Gush 1972b). Furthermore, the time spent by a hen 'interacting' with the feeder (ie head in feeder in the non-thwarting treatment; looking through or pecking at the Plexiglas in the thwarting treatment) was studied. The time it spent trying to escape through the holes in the wire mesh (ie the bird moving back and forth with head and neck through the hole, sometimes with one foot in the wire) was also recorded. The duration of preening directed at the breast and neck was recorded as an indicator of displacement preening (Duncan & Wood-Gush 1972a), and the duration of preening at other parts of the body was also recorded.

Statistical analysis

We used the general linear model procedure in SAS (SAS Institute 1996) to carry out an analysis of variance. Data were tested for normality (PROC Univariate) and when necessary the data were square-root or log-transformed to obtain normality. We first tested whether there was a significant effect of the factors 'group', 'time period' (ranging from 1 to 8), 'weight of bird' and 'carry over' (factor that tested for an effect of a particular treatment on the subsequent one). We then tested the effect of the factors 'hen' and 'treatment' on the behavioural elements described in the previous paragraph. When a significant effect of treatment was found we used the Contrast Statement to compare the means of specific treatments.

We combined the thwarting treatments and statistically compared them to the lumped non-thwarting treatments to test the effect of the thwarting of behaviour (contrast A, Table 1). To investigate the audience effect we compared the combined audience treatments with the non-audience treatments (contrast B, Table 1). The effect of the state of the audience bird on frustration behaviours and vocalisations in test birds was investigated by the comparison of the treatments 'non-thwarted audience hen' with 'thwarted audience hen' (contrast C, Table 1).

Results

The effect of thwarting

We found a significant effect of group on the number of gakel-calls (ANOVA: $F_{1,13} = 5.45$, $P < 0.05$). The hens from one pen (group two) gave more gakel-calls (mean ± SEM: 17.8 ± 2.2) than the hens from the other pen (group one; 6.50 ± 1.0). No effects of carry over, time period or body weight were found.

Test birds gave significantly more gakel-calls (non-thwarting 5.0 ± 1.0 versus thwarting 19.3 ± 2.2; ANOVA: $F_{1,13} = 86.01$, $P < 0.001$; Figure 2) and showed more head-flicks (non-thwarting 2.4 ± 0.5 versus thwarting 11.2 ± 2.1; ANOVA: $F_{1,13} = 46.28$, $P < 0.001$) and yawns (non-thwarting 0.8 ± 0.5 versus thwarting 7.0 ± 1.2; ANOVA: $F_{1,13} = 48.38$, $P < 0.001$) when thwarted than when non-thwarted (contrast A, Table 1). In the thwarting treatments, significantly more time was spent in stereotyped pacing (non-thwarting 1.9 ± 1.1

versus thwarting 35.1 ± 5.5; ANOVA: $F_{1,13} = 39.2$, $P < 0.001$), trying to escape (non-thwarting 0.3 ± 0.2 versus thwarting 3.3 ± 1.0; ANOVA: $F_{1,13} = 9.4$, $P < 0.010$) and displacement preening (non-thwarting 0.9 ± 0.5 versus thwarting 9.9 ± 0.6; ANOVA: $F_{1,13} = 35.77$, $P < 0.001$) than in the non-thwarting treatments. These differences were also significant when the separate thwarting treatments were tested against their respective non-thwarting counterparts (ie treatments 1 versus 5, 2 versus 6, 3 versus 7, and 4 versus 8; Table 1). No alarm cackling was recorded.

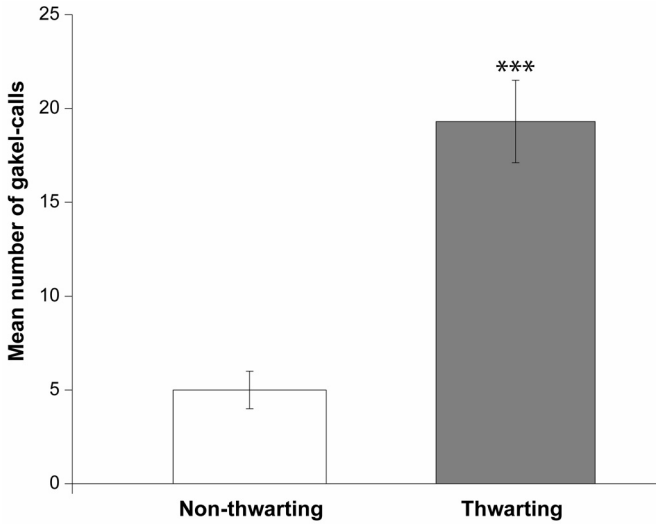

Figure 2 **Mean (± SEM) number of gakel-calls in the test birds in the non-thwarted and thwarted treatments. ***$P < 0.001$.**

The effect of an audience

Thwarted test birds showed a tendency to give more gakel-calls in the treatments with an audience (bird and human) than in the treatments without an audience (no audience 16.3 ± 4.1 versus audience 20.2 ± 2.5; ANOVA: $F_{1,13} = 3.66$, $P = 0.058$). In the presence of an audience, thwarted test birds showed more head-flicking (no audience 4.3 ± 1.8 versus audience 13.4 ± 2.6; ANOVA: $F_{1,13} = 13.68$, $P < 0.001$) and spent more time in stereotyped pacing (no audience 20.0 ± 6.5 versus audience 40.2 ± 6.9; ANOVA: $F_{1,13} = 5.63$, $P < 0.05$) than when without an audience.

We also made separate comparisons between the no-audience treatment (empty cage) and each of the audience treatments (ie treatments 5 versus 6, 5 versus 7, and 5 versus 8). The presence of a non-thwarted audience bird compared to an empty cage did not significantly affect the number of gakel-calls (Figure 3) but it significantly increased the number of head-flicks (no audience 4.3 ± 1.8 versus non-thwarted audience bird 12.6 ± 3.9; ANOVA: $F_{1,6} = 9.84$, $P < 0.01$), the number of yawns (no audience 4.5 ± 1.9 versus non-thwarted audience bird 11.8 ± 3.0; ANOVA: $F_{1,6} = 5.55$, $P < 0.05$) and the time spent in stereotyped pacing (no audience 20.0 ± 6.5 versus non-thwarted audience bird 53.3 ± 14.0; ANOVA: $F_{1,6} = 10.19$, $P < 0.001$).

The presence of a thwarted audience bird compared to no audience resulted in a significantly higher number of gakel-calls (ANOVA: $F_{1,6} = 5.56$, $P < 0.05$, Figure 3) and a

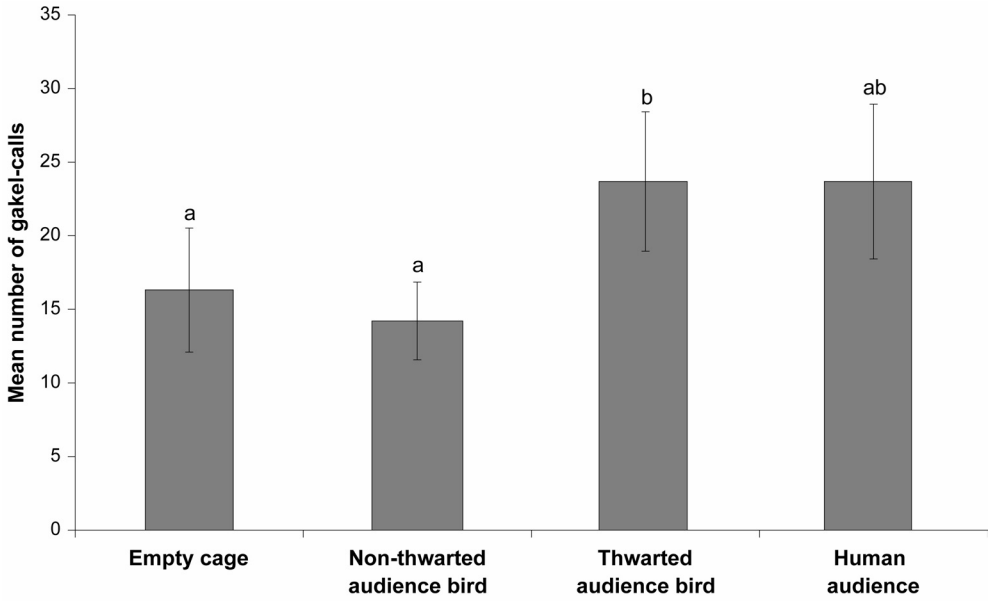

Figure 3 **Mean (± SEM) number of gakel-calls in thwarted test birds with the empty cage and the three different types of audience. Different letters indicate significant differences ($P < 0.05$).**

significantly higher number of head-flicks (no audience 4.3 ± 1.8 versus thwarted audience bird 23.6 ± 6.0; ANOVA: $F_{1,6} = 29.25$, $P < 0.001$) in test birds. There were no significant effects on any other behaviour.

In the presence of a human audience, test birds tended to show more gakel-calls (ANOVA: $F_{1,6} = 3.59$, $P = 0.06$, Figure 3) and to spend more time in stereotyped pacing (no audience 20.0 ± 6.5 versus human audience 38.3 ± 12.7; ANOVA: $F_{1,6} = 3.29$, $P = 0.07$) than when thwarted without an audience. Furthermore, test birds exhibited longer durations of preening (no audience 40.1 ± 18.8 versus human audience 84.0 ± 26.6; ANOVA: $F_{1,6} = 5.29$, $P < 0.05$) and displacement preening (no audience 7.5 ± 2.2 versus human audience 14.1 ± 4.6; ANOVA: $F_{1,6} = 4.48$, $P < 0.05$) in the presence of a human audience compared to the empty cage treatment.

The effect of the state of the audience bird

Thwarted test birds gave significantly more gakel-calls in the presence of a thwarted audience bird than when in the presence of a non-thwarted audience bird (non-thwarted audience bird 14.0 ± 2.7 versus thwarted audience bird 23.5 ± 6.0; ANOVA: $F_{1,13} = 6.86$, $P < 0.05$). In the presence of a thwarted audience bird, thwarted test birds tended to show fewer yawns (non-thwarted audience bird 11.8 ± 3.0 versus thwarted audience bird 7.7 ± 2.5; ANOVA: $F_{1,13} = 3.18$, $P = 0.07$), performed more head-flicks (non-thwarted audience bird 12.6 ± 3.9 versus thwarted audience bird 23.6 ± 6.0; ANOVA: $F_{1,13} = 8.42$, $P < 0.01$) and spent less time in stereotyped pacing (non-thwarted audience bird 53.3 ± 14.0 versus thwarted audience bird 28.4 ± 8.6; ANOVA: $F_{1,13} = 5.70$, $P < 0.05$) than when with a non-thwarted neighbour.

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Mutual effects of treatments

Even though this experiment was not designed to include the audience birds in the analysis, their behaviour was also recorded on videotape and analysed, and the behavioural data of the audience birds supported the findings in the test birds. Audience birds gave significantly more gakel-calls (ANOVA: $F_{1,6} = 28.62$, $P < 0.001$) and showed more head-flicks (non-thwarting 4.2 ± 0.9 versus thwarting 9.9 ± 0.6; ANOVA: $F_{1,6} = 8.73$, $P < 0.01$) and yawns (non-thwarting 1.2 ± 0.6 versus thwarting $5.2 \pm 0.1.3$; ANOVA: $F_{1,6} = 7.71$, $P < 0.05$) when thwarted in their feeding behaviour than when non-thwarted. Furthermore, stereotyped pacing (non-thwarting 0.7 ± 0.5 versus thwarting 66 ± 20; ANOVA: $F_{1,6} = 18.12$, $P < 0.001$) and displacement preening (non-thwarting 0 ± 0 versus thwarting 13.2 ± 3.1; ANOVA: $F_{1,6} = 22.59$, $P < 0.001$) both had longer durations during thwarting than during non-thwarting.

Thwarted audience birds also gave more gakel-calls in the presence of a thwarted test bird than when in the presence of a non-thwarted test bird (non-thwarted test bird 15.1 ± 3.2 versus thwarted test bird 27.8 ± 4.9; ANOVA: $F_{1,6} = 5.71$, $P < 0.05$).

Discussion and conclusions

The thwarting of feeding behaviour resulted in an increase in the number of gakel-calls and other behaviours indicative of frustration. We also found an audience effect on the gakel-call and other frustration behaviours in thwarted test birds. This audience effect depended on the type of audience (bird or human) and on the state of the audience (thwarted or non-thwarted).

In line with previous studies (Kruijt 1964; Duncan & Wood-Gush 1972b; Hughes 1983; Schenk *et al* 1983; Koene & Wiepkema 1991; Zimmerman & Koene 1998), we found that thwarting of feeding behaviour resulted in a higher number of gakel-calls and an increase in the time that the test and audience birds spent performing stereotyped pacing and displacement preening. Also, conflict behaviours such as head-flicking and yawning were shown more frequently in the thwarting than in the non-thwarting treatments.

The first research question was whether the presence of an audience affects the gakel-call and other frustration behaviours during thwarting of feeding behaviour. Our results show that there was indeed such an audience effect. Depending on the type of audience, thwarted test birds showed more behaviours associated with frustration than when tested alone. Thwarted test birds exhibited more yawning behaviour (Kruijt 1964) and showed more stereotyped pacing in the presence of a non-thwarted, feeding audience bird than when faced with an empty cage. A possible explanation for the increase in yawning is that the presence of a feeding audience bird might have been interpreted by the test bird as the presence of a successful competitor, which, together with the absence of food in her own cage, might have elicited conflict between attempting to get to her own food and, at the same time, to the food in the adjacent cage. Thwarted test birds persisted in trying to reach their own food by pecking at the Plexiglas, but at the same time exhibited stereotyped 'escape' pacing. This pacing was performed mainly in front of the Plexiglas, closest to the other cage, and could be a demonstration of the thwarted test bird trying to reach the food in the neighbouring cage.

The presence of a thwarted audience bird increased the number of head-flicks in thwarted test birds. This is possibly expressed in the positive correlation between the number of head-flicks in the thwarted test birds and the number of gakel-calls in the thwarted audience birds (Spearman rank correlation: $r = 0.99$, $P < 0.001$). We had the strong impression that calls given by the audience bird elicited head-flicking in the test bird and *vice versa*. This impression supports Hughes (1983), who described head-flicking as an alertness response.

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However, in the reverse comparison, a positive correlation between the number of gakel-calls given by thwarted test birds and the number of head-flicks in audience birds was found only in the treatments where audience birds were non-thwarted (both test and audience bird non-thwarted: $r = 0.80$, $P < 0.05$; test bird thwarted, audience bird non-thwarted: $r = 0.80$, $P < 0.05$). We know that subordinate hens pay more attention to dominant hens (Nicol & Pope 1994, 1999) but by choosing 'average' hens as audience birds we assumed we had ruled out an effect of rank. This cannot be precluded, however, since we did not determine the dominance relationships of test and audience birds.

The mere presence of an audience bird did not affect the number of gakel-calls in thwarted hens, but the presence of another thwarted bird did. Both test and audience birds showed a higher number of gakel-calls when both were thwarted. This suggests that the gakel-call is subject to social facilitation. Social facilitation has been described as "an increase in the frequency or intensity of responses already in an animal's repertoire, when shown in the presence of others engaged in the same behavior at the same time" (Clayton 1978). Test birds showed such an increase, but only when they were already thwarted themselves. It has been described that under natural conditions the gakel-call has evolved as a signal from the hen to entice the rooster to accompany her to a nest site (McBride *et al* 1969; Thornhill 1988). This company apparently benefits the hen. One can imagine that this brings about competition between hens for the rooster's attention, so explaining why gakel-calls of one hen stimulate another hen to show an increase in the number of gakel-calls. Increased head-flicking suggests that thwarted test birds in the presence of thwarted audience birds were more alert than when with non-thwarted audience birds. If competition occurs between hens giving gakel-calls before egg-laying, then it seems reasonable to expect that in this experiment a thwarted hen should focus on another thwarted hen.

The presence of a human audience increased the time thwarted test birds spent on both displacement preening and normal preening. Displacement preening in domestic fowl has been described in conflict situations in which two strong incompatible tendencies are balanced (Duncan & Wood-Gush 1972a). The incompatible tendencies in the present experiment could be trying to escape from the aversive situation (food visible but covered) and still expecting food because of the presence of the human observer, which used to be a signal for food. In this case, one would expect the thwarted test birds to show higher levels of gakel-calls in this treatment. Indeed, the thwarted test birds tended to show such an increase.

Because the gakel-call is a vocalisation indicative of frustration, one could expect other behaviours indicative of frustration to be subject to social facilitation too. This was not found. Nevertheless, if we accept that the gakel-call has a social function, such as alerting the rooster to accompany a hen to a nest site, then it is not surprising that in our study we found an effect of an audience on the gakel-call and not on the other frustration behaviours. However, we found that a thwarted test bird spent less time in stereotyped pacing in the presence of a thwarted audience bird than when with a non-thwarted audience bird. As explained previously, the sight of a feeding audience bird elicited stereotyped pacing in the thwarted test birds, probably because the test birds were trying to reach the food in the adjacent cage.

In conclusion, the thwarting of feeding behaviour in the domestic laying hen is not only expressed through behaviours such as stereotyped pacing and displacement preening, but is also reflected in an increase in a specific vocalisation, the gakel-call. The presence of an audience influences the performance of this gakel-call, but it does not necessarily imply a corresponding change in underlying frustration. Increased gakel-calling in the presence of a

conspecific could be related to competition, reflecting the origin of this call in nesting behaviour. Nevertheless, in addition to affecting this vocalisation, audience effects also influence the performance of other specific behaviours.

The sight of a feeding audience bird elicits yawning and stereotyped pacing in the thwarted hen, probably as a result of the conflict between trying to reach her own covered food and the food of the other hen. A human audience, being a signal for food, elicits a similar conflict in thwarted birds between trying to reach food and approaching the human. This is demonstrated by higher levels of displacement preening and a tendency to give more gakel-calls with a human audience than with no audience or a bird audience.

Animal welfare implications

This study supports other work (Schenk *et al* 1983; Koene & Wiepkema 1991; Zimmerman & Koene 1998) in which it is suggested that the gakel-call is an expression of frustration in laying hens. It has also been found that an increasing number of gakel-calls reflects an increasing degree of frustration (Zimmerman *et al* 2000b). From these two findings we conclude that the gakel-call, as a measure of frustration, might be used as an easy-to-measure, non-invasive indicator for the welfare of laying hens. However, in the present study we found that a thwarted test hen gave more gakel-calls in the presence of another thwarted hen than in the presence of a non-thwarted conspecific. This higher number of gakel-calls suggests a higher intensity of frustration. The fact that the occurrence of other behaviours indicative of frustration did not increase in the presence of a thwarted conspecific nevertheless counters this suggestion. We suggest that social facilitation of the gakel-call stems from the original context of this vocalisation. In using the gakel-call as a welfare-indicator, the social aspects of the vocal expression of frustration in laying hens should not be overlooked.

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