Thwarting of behaviour in different contexts and the gakel-call in the laying hen

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Abstract

Earlier studies have shown that thwarting of feeding behaviour in the laying hen is expressed through a specific vocalisation, the gakel-call. The first aim of this study was to investigate whether the effect of deprivation per se on the occurrence of gakel-calls can be distinguished from the effect of the additional frustration. Frustration is defined as the state of an animal that results from nonreward in the expectancy of reward. The second aim was to investigate whether the occurrence of gakel-calls is restricted to a food context or whether it can be regarded as an expression of frustration in general. For this purpose, 20 hens were deprived of food, water and dustbath. After deprivation at a fixed time, a cue was given and the hens were rewarded with access to food, water or dust during a 15-min session on 4 consecutive days. On the fifth day, they were thwarted in the associated behaviours by blocking the access to these commodities, after the hens had been presented the signal that previously preceded the reward. We then recorded behaviours that might reflect the state of frustration in three 15-min periods. The period ‘Pre-Frustration’ started 15 min before ‘Frustration’. This, in turn, was followed by the period ‘Post-frustration’ in which the hens were rewarded again. Nesting behaviour was thwarted by blocking the access to the nest (Frustration) after a hen had reached the last stage of its prelaying behaviour.

In the food, water and dustbath context, deprivation elicited gakel-calls. The additional frustration resulted in a higher number of gakel-calls in all contexts except the food context. However, together with the findings of previous experiments, the results of this study suggest that frustration, in general, is expressed through the gakel-call. Frustration in the nest context elicited more gakel-calls than the other contexts. This latter finding is discussed in the light of the
occurrence of the gakel-call under natural circumstances. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

In domestic laying hens, an increase in behaviours such as stereotyped pacing, displacement preening and the occurrence of a specific vocalisation, the gakel-call, is associated with thwarting of feeding (Duncan and Wood-Gush, 1972a,b; Schenk et al., 1983; Zimmerman and Koene, 1998a), dustbathing (Koene and Wiepkema, 1991) and nesting behaviour (e.g. Schenk et al., 1983; Meijsser and Hughes, 1989; Freire et al., 1996). Thwarting a behaviour that ensures fulfillment of ethological needs impairs welfare. Animal welfare is the state of the animal regarding its attempt to fulfill its needs (Broom, 1996). A number of studies suggests that the gakel-call is given in reaction to the thwarting of behaviour (Schenk et al., 1983; Meijsser and Hughes, 1989; Koene and Wiepkema; 1991; Zimmerman and Koene, 1998a). Behaviours, which are given in response to the thwarting of behaviour, can be used as indicators of the subsequent state of frustration and may, therefore, qualify as measures of welfare (Dawkins, 1990; Duncan, 1992). Frustration has been defined as “an aversive motivational state that results from nonreward, reduced reward or delayed reward in the presence of a history of reward” (Amsel, 1992). From this definition, it follows that the effect of mere thwarting of behaviour might be distinguishable from the effect of frustration. The first aim of the present study was to investigate whether the effect of deprivation on the occurrence of gakel-calls could be distinguished from the effect of the additional frustration.

Under natural conditions, it has been described that a female hen, which is about to leave the group to find a suitable nest site, utters the gakel-call. As a rule, the dominant male responds to the gakel-call by escorting the female hen to a nest site (McBride et al., 1969; Thornhill, 1988). The advantage for the female of the presence of the male probably is a better protection against predators, while the male might benefit by the chance to copulate with the female on the way back to the group (McBride et al., 1969; Thornhill, 1988). However, the occurrence of the gakel-call is not restricted to the prelaying context (Bümer, 1962; Schenk et al., 1983; Meijsser and Hughes, 1989; Zimmerman and Koene, 1998a). The second aim of the present study was to investigate whether frustration in different contexts (food, water, dust and nest) results in a higher number of gakel-calls. For this purpose, hens were thwarted in their feeding, drinking, dustbathing and nesting behaviour in a situation in which they previously had access to these commodities. Furthermore, we examined whether the various contexts of thwarting affected temporal characteristics of the gakel-call in different ways. Schenk et al. (1983) found some indication that an increasing deprivation of dustbath resulted in a higher number of gakel-calls given in response to the thwarting of dustbathing behaviour. He found that these gakel-calls also tended to be longer in duration and consisted of fewer notes. So, an increase in the motivation level may be reflected in temporal characteristics of the gakel-call.
We formulated the following research questions: Does frustration give rise to a higher number of gakel-calls than the mere thwarting of behaviour? Is a state of frustration, in general, caused by the omission of reward in different contexts (feeding, drinking, dustbathing and nesting), expressed through the gakel-call and other behaviours indicative of frustration? Are there any differences between the contexts of frustration in the number and temporal characteristics of gakel-calls?

2. Materials and methods

2.1. Animals and housing

Twenty laying hens, 10 ISA Brown and 10 ISA White Leghorns, of 23 weeks old were housed individually in cages (139 × 50 × 50 cm; L × W × H). The cages were positioned in a row, approximately 15 cm apart. The front and top side of a cage were made of wire-netting and the sides adjacent to the other cages contained a small wire-netting window (20 × 20 cm). Hens could have visual and auditory contact with other hens, and the side windows allowed neighbouring hens to have tactile contact. Each cage contained a nest (39 × 50 × 40 cm) and dust area (50 × 50 cm). Food (commercial pellets) and water were freely available outside experimental treatments. The light period fell between 2:00 AM and 18:00 PM.

2.2. Experimental procedure

The 20 hens were subdivided in four groups containing either three ISA Brown hens and two White Leghorns or the reverse. All groups received four treatments: they were successively thwarted in their feeding (Food), drinking (Water), dustbathing (Dust) and nesting (Nest) behaviour in a randomised way, to prevent an effect of order of treatments. The procedure for training and testing in the treatments Food, Water and Dust was as follows. The hens were deprived of food or water for 23 h prior to training and testing by closing the feeder or drinker. Twenty-three hours of food deprivation had appeared to be sufficient to elicit an increase in gakel-calls and other behaviours indicative of frustration (Zimmerman and Koene, 1998a,b). We figured that 23-h dust deprivation would not be sufficient, because hens normally take a dustbath every 2 days (Vestergaard, 1982). Therefore, the dust area was covered up with a wooden lid for 72 h. After deprivation, the hens were trained to get access to food, water or dust at a fixed time on 4 consecutive days. For this purpose, the feeder and drinker were opened for 45 min. The entrance of the experimenter and the marked removal of the cover of feeder, drinker and dustbath served as conditioned stimuli. Because a dustbathing cycle under unrestricted circumstances typically lasts about 30 min (Vestergaard, 1982), the hens were accustomed to receive 15-min access to the dust area during training. Fifteen minutes access to dust was short enough to maintain the need to perform dustbathing behaviour on the consecutive training and test days. After 4 days of training, a test day
followed. A test session in all treatments lasted 45 min and was subdivided in three 15-min periods:

Pre-Frustration: This period started 15 min before the time the hen was used to get access to one of the commodities on a training day;
Frustration: At the start of this 15-min period, feeder, drinker or dust area were opened and immediately closed again;
Post-frustration: Feeder, drinker and dust area were opened.

Training and testing in these treatments were carried out from 1200 h onwards after all hens had laid their eggs.

The procedure of training and testing in treatment Nest was different from the other treatments. Egg-laying occurs in a 25-h cycle and 1–2 h before egg-laying hens typically are engaged in prelaying or nesting behaviour. The hen performs a number of nest inspections before it finally settles on the nest (McBride et al., 1969; Wood-Gush and Gilbert, 1969). Because it is impossible to predict the precise time of nesting behaviour, it was impracticable to train hens to have access to the nest at a certain time and then block this access during testing. This was the reason we thwarted the last stage of prelaying behaviour in which the hen finally settles on the nest. For this purpose, the hens of a group were scanned on 2 consecutive days, every 30 min from the onset of the light period, to determine the approximate time of oviposition. On the third day, a hen that had entered a nest was observed for 15 min (Pre-Frustration) and after that, pushed off the nest and the nest box was closed for 15 min (Frustration). After 15 min, the nest was opened again (Post-frustration).

The durations of deprivation used in the different treatments were chosen arbitrarily, but we expected that they would motivate the animals sufficiently to try to perform the behaviour when being thwarted. So, although we were not able to precisely assess the intensity of thwarting in the different treatments, we assumed that the intensities would not differ too much.

During the three experimental periods, the number of gakel-calls and alarm-cackles were recorded. Furthermore, the durations of stereotyped pacing (Duncan and Wood-Gush, 1972b), displacement preening (Duncan and Wood-Gush, 1972a) and number of escape attempts were recorded. We defined an escape attempt as the hen sticking its head out the front of the cage, through the wire, while moving its body backwards and forwards.

Gakel-calls were digitised using Signal® software. From gakel-calls that were not disturbed by background noises, the mean duration, the mean number of notes and the mean duration of the first note were determined.

2.3. Statistical analysis

We used a repeated measures analysis in the GLM-procedure in the SAS® statistical program (SAS Institute, 1989) with strain, group and treatment as factors. Whenever a significant effect of one of the factors was found, a post hoc test (LSMEANS) was carried out to find the statistical differences between the levels of a factor.
The effect of strain, group and treatment on mean duration and number of notes per gakel-call were determined in a repeated measures analysis in SAS.

3. Results

No effect of strain or group on any of the behaviours recorded was found.

In treatment Food, the number of gakel-calls in period Frustration was not significantly higher than in period Pre-Frustration (ANOVA: $F_{1,17} = 2.60$, $P = 0.13$; Fig. 1). There were also no significant differences in the number of cackles (Mean ± S.E.M.: Pre-Frustration: 0.1 ± 0.1 vs. Frustration: 1.0 ± 0.5) and escape attempts (Pre-Frustration: 9.6 ± 2.4 vs. Frustration: 11.6 ± 3.9) between the periods Frustration and Pre-Frustration in treatment Food. In the period Frustration, the time spent in stereotyped pacing was significantly less than in period Pre-Frustration (Pre-Frustration: 299 ± 42.4 vs. Frustration: 240 ± 41.1; ANOVA: $F_{1,17} = 13.46$, $P < 0.01$). We found no significant difference in the duration of displacement preening between the periods Pre-Frustration and Frustration (Pre-Frustration: 15.6 ± 14.5 vs. Frustration: 44.8 ± 12.3).

In treatment Water, the hens gave significantly more gakel-calls in period Frustration than in period Pre-Frustration (ANOVA: $F_{1,17} = 4.90$, $P < 0.05$; Fig. 1). We found no significant differences between periods Pre-Frustration and Frustration in the number of cackles (Pre-Frustration: 0.8 ± 0.4 vs. Frustration: 0.6 ± 0.5), escape attempts (Pre-Frustration: 11.3 ± 3.1 vs. Frustration: 8.8 ± 2.2) and the duration of pacing (Pre-Frustration: 285 ± 39.7 vs. Frustration: 300 ± 46.3) and preening (Pre-Frustration: 16.8 ± 6.4 vs. Frustration: 7.3 ± 2.2).

![Fig. 1. The mean number of gakel-calls in the three experimental periods in all treatments. Signs indicate the level of significance of the difference between periods Pre-Frustration and Frustration; N.S.: nonsignificant, * $P < 0.05$, ** $P < 0.001$.](image)
Table 1
The mean number of alarm-cackles, escape attempts and the mean duration of stereotyped pacing and displacement preening in all the treatments in period Frustration

<table>
<thead>
<tr>
<th>Treatment</th>
<th>No. of alarm-cackles</th>
<th>No. of escape attempts</th>
<th>Duration of pacing (s)</th>
<th>Duration of displacement preening (s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Food</td>
<td>1.0 ± 0.5&lt;sup&gt;a,b&lt;/sup&gt;</td>
<td>11.6 ± 3.9&lt;sup&gt;b&lt;/sup&gt;</td>
<td>240 ± 41&lt;sup&gt;a&lt;/sup&gt;</td>
<td>44.8 ± 12.3&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Water</td>
<td>0.6 ± 0.5&lt;sup&gt;b&lt;/sup&gt;</td>
<td>8.8 ± 2.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>300 ± 46&lt;sup&gt;a&lt;/sup&gt;</td>
<td>7.3 ± 2.2&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Dust</td>
<td>0.3 ± 0.1&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.1 ± 0.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>104 ± 11&lt;sup&gt;b&lt;/sup&gt;</td>
<td>16.1 ± 6.0&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Nest</td>
<td>8.0 ± 3.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>11.4 ± 2.5&lt;sup&gt;b&lt;/sup&gt;</td>
<td>306 ± 32&lt;sup&gt;a&lt;/sup&gt;</td>
<td>29.8 ± 7.4&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

Different letters indicate differences between the treatments.

In treatment Dust, hens gave significantly more gakel-calls in period Frustration than in period Pre-Frustration (ANOVA: $F_{1,17} = 5.18, P < 0.05$; Fig. 1). They spent significantly less time pacing in period Frustration than in period Pre-Frustration (Pre-Frustration: $157 ± 25.2$ vs. Frustration: $104 ± 11.2$; ANOVA: $F_{1,17} = 5.86, P < 0.05$). No significant differences were found in the number of cackles (Pre-Frustration: $0.6 ± 0.3$ vs. Frustration: $0.3 ± 0.1$), escape attempts (Pre-Frustration: $2.9 ± 1.1$ vs. Frustration: $1.1 ± 0.3$) and the duration of displacement preening (Pre-Frustration: $8.8 ± 3.6$ vs. Frustration: $16.1 ± 6.0$).

In treatment Nest, the hens gave significantly more gakel-calls in period Frustration than in period Pre-Frustration (ANOVA: $F_{1,17} = 30.83, P < 0.001$; Fig. 1). Also, the hens gave significantly more cackles (Pre-Frustration: $0.0 ± 0$ vs. Frustration: $8.0 ± 3.2$; ANOVA: $F_{1,17} = 6.07, P < 0.05$) and performed more escape attempts (Pre-Frustration: $0.0 ± 0$ vs. Frustration: $11.4 ± 2.5$; ANOVA: $F_{1,17} = 22.03, P < 0.001$) in the period Frustration than in the period Pre-Frustration. Furthermore, more time was spent in pacing (ANOVA: $F_{1,17} = 84.79, P < 0.001$) and displacement preening (ANOVA: $F_{1,17} = 13.25, P < 0.01$) in period Frustration (duration of pacing: $306 ± 32.7$; duration of preening: $29.8 ± 7.4$) than in period Pre-Frustration (pacing: $0.0 ± 0$; preening: $1.8 ± 1.6$).

The number of gakel-calls given in period Frustration was significantly higher in treatment Nest than in the other three treatments (ANOVA: $F_{1,17} = 15.84, P < 0.001$). The number of gakel-calls in period Frustration did not differ between treatments Food, Water and Dust (Fig. 1). The number of alarm-cackles given in period Frustration was significantly higher in treatment Nest than in treatment Dust (ANOVA: $F_{1,17} = 3.80, P < 0.05$; Table 1). Significantly, more escape attempts were performed in period Frustration in the treatments Food and Nest than in treatment Dust (ANOVA: $F_{1,17} = 4.10, P < 0.05$; Table 1). The time the hens spent pacing in period Frustration was significantly lower in treatment Dust than in the other three treatments (ANOVA: $F_{1,17} = 16.79, P < 0.001$; Table 1). The duration of displacement preening in period Frustration did not differ between treatments (Table 1).

Fig. 2. The mean duration per gakel-call (A), the mean number of notes per gakel-call (B) and the mean duration of the first note (C) in all treatments. Different letters or combinations of letters indicate significant statistical differences between treatments below the 0.05 level for both the mean length and number of notes.
We found a significant effect of treatment on both the mean length per gakel-call (ANOVA: $F_{1,16} = 6.41, P < 0.001$; Fig. 2A) and the mean number of notes per gakel-call (ANOVA: $F_{1,16} = 13.84, P < 0.001$; Fig. 2B) in period Frustration. Both mean length and number of notes per gakel-call were significantly higher in treatment Nest than in treatments Water and Dust. No effect of treatment was found on the length of the first note (Fig. 2C).

No significant positive correlation (Spearman rank correlation) between mean length and number of notes per gakel-call was found in any of the treatments. A significant positive correlation between the length of the first note and the total length per gakel-call was found in treatment Dust ($r = 0.78, P < 0.05$). This tended to be the case in treatment Water ($r = 0.67, P = 0.9$).

4. Discussion

The present study shows that deprivation plus additional frustration in a water and dustbath context is reflected in a higher number of gakel-calls compared to deprivation alone. We did not find such an increase in the number of gakel-calls in the food context, unlike very clear results in previous studies (Zimmerman and Koene, 1998a,b). An explanation for the major difference between the previous and the present study might be the procedure of frustration. In our previous experiments, hens were thwarted in their feeding behaviour in a conditioning paradigm. In a control session, every 30 s hens were rewarded with 5-s access to food after the conditioned stimulus or operant response. In a 15-min frustration session, the food reward was omitted by presenting the hens an empty feeder. Such a session typically consisted of approximately 23 trials in which the hens were presented the empty feeder in every trial. The state of frustration elicited in the frustration session in the previous experiment might have been more intense than in the period Frustration in the present study. The difference in mean number of gakel-calls in both 15-min periods of frustration in the food context (present study: 6.9, previous study: 22) might be a reflection of the difference in the degree of frustration between the experiments. Furthermore, in the present study, the comparison was made between deprivation and frustration treatment; while in the previous study, a frustration session was compared to a control session. This difference in type of comparison also might have accounted for the nonsignificant difference in the number of gakel-calls between frustration and its “control”, in contrast to previous findings.

In the period Frustration, the number of gakel-calls was higher in treatment Nest than in the other treatments. This might mean that in this treatment the level of frustration was higher. However, this is not supported by higher levels of other behaviours indicative of frustration in treatment Nest compared to the other treatments. An alternative explanation for the higher number of gakel-calls in treatment Nest is suggested by the occurrence of the gakel-call under natural circumstances. The gakel-call is given before oviposition and probably has evolved as a signal towards the rooster (McBride et al., 1969; Thornhill, 1988). According to Meijsser and Hughes (1989), the performance of the gakel-call is related to finding a suitable nest site, also under husbandry conditions. Another explanation is offered by the motivational model.
proposed by Wiepkema (1987). It implies that the gakel-call under these circumstances is an emotional expression of the detection of a prolonged mismatch between actual (“no nest site found”) state and desired state (“find a suitable nest site”) and is an indication of frustration. Both oviposition and the detection of a prolonged mismatch could at the same time contribute to the occurrence of gakel-calls. The surplus of gakel-calls in treatment Nest compared to the other treatments might be the gakel-calls specifically related to oviposition.

This latter finding might account for the difference in temporal characteristics of gakel-calls between treatment Nest and the treatments Water and Dust. Gakel-calls in treatment Nest lasted longer and consisted of more notes than in the treatments Water and Dust. Schenk et al. (1983) found that the mean duration of a single gakel-call was longer when dustbathing was thwarted stronger by longer deprivation. However, from the present study, nothing decisive can be concluded about the relation between the number of gakel-calls and their temporal characteristics on the one hand, and the intensity of thwarting in the different treatments on the other.

5. Conclusions

In conclusion, the results from the present and previous studies suggest that both deprivation and the additional frustration, in general, in laying hens is expressed through the gakel-call. The higher number of gakel-calls in the nest context merits further research into the functional aspects of this frustration call.

References


