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Working for a dustbath: are hens increasing pleasure rather than reducing suffering?

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Abstract

Dustbathing is one of the major behavioural systems of domestic fowl that is constrained by commercial caging systems. Although research conducted over the last 20 years has revealed a great deal about causation of dustbathing, attempts at measuring the importance to hens of having access to dustbathing substrate have proven difficult. Various economic techniques, operant conditioning and learning trials have been used to determine whether hens have a 'need' for dustbathing substrate or 'think' about dustbathing in the absence of substrate. In this study, we measured hens' willingness to work to obtain substrate for dustbathing using a vertically swinging door to which weights could be added. Hens were trained to push through the door to enter a goal box containing peat moss. The hens were subjected to two series of trials to compare the maximum weight that they would push to open the door when living in a cage and deprived of dustbathing substrate, with the maximum weight that they would push when living in a pen furnished with litter and a dustbath (non-deprived). Of the 10 hens that opened the door for access to peat moss, six hens pushed more weight when deprived, three hens pushed more weight when non-deprived and one hen pushed an equal amount of weight. Overall, the hens tended to push more weight (860 ± 95.6 vs. 682.5 ± 83.3 g; $P < 0.10$, one-tailed paired *t*-test) and tended to make more attempts to open the door ($P < 0.10$) when they were deprived than when they were non-deprived. Significantly more trials resulted in dustbathing when hens were deprived ($P < 0.01$) suggesting that following deprivation, the hens were, in fact, more motivated to dustbathe. The results of these trials indicate that although deprived hens may be more motivated to dustbathe, and that most hens may be willing to work to obtain a dusty substrate when they can see it, they are not necessarily willing to work harder when they are in a state of deprivation than when they have recently dustbathed. These results are very difficult to explain using a 'needs' model of motivation in which deprivation leads to a state of suffering. They are much more consistent with

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an ‘opportunity’ model of motivation in which performance of the behaviour, when the opportunity presents itself, leads to a state of pleasure.

Keywords: Domestic fowl; Dustbathing; Motivation

1. Introduction

In natural or rich environments, dustbathing is a common behaviour of domestic fowl that apparently functions to remove feather lipids and maintain plumage (van Liere and Bokma, 1987). The dustbathing behaviour system has been widely studied in jungle fowl and domestic fowl because it provides an interesting model for the study of development and causation of behaviour (Hogan, 1994) and because it is one of the major behavioural systems constrained by commercial caging systems. In the absence of dustbathing substrate, caged laying hens are often observed to perform vacuum dustbathing and therefore, it has been suggested that dustbathing may be important to hens and that they may suffer if they are unable to do so (Beilharz and Zeeb, 1981).

Research conducted over the past 20 years has revealed a great deal about causation of dustbathing. Several lines of evidence indicate a large internal component to its motivation. A bird’s tendency to dustbathe follows a diurnal pattern (Vestergaard, 1982), occurs at regular intervals of 2 to 3 days (Vestergaard, 1980, 1982), and deprivation of dustbathing leads to an increasing tendency to dustbathe over time, suggesting an endogenous rhythm as well as a Lorenzian build-up of motivation (Vestergaard, 1980, 1982; Hogan, 1997; Hogan et al., 1991). External factors also play an important role. Dustbathing can be elicited by exposing birds to visual stimuli such as the sight of a dusty substrate (Petherick et al., 1995) and bright light that simulates sunlight (Hogan and van Boxel, 1993; Duncan et al., 1998). Thermal factors such as ambient temperature and radiant heat also influence hens’ tendencies to dustbathe (Duncan et al., 1998). Dustbathing is very much a social activity, and the sight and sounds of other birds dustbathing can increase a hen’s motivation to dustbathe (Duncan et al., 1998). Surprisingly, peripheral factors, such as lipid accumulation on the feathers, appear to be of minor importance in the causation of dustbathing. Spreading lipids on the feathers caused only marginal increases in dustbathing (van Liere et al., 1991), and removal of the oil gland, which is the main source of feather lipids, had no effect on subsequent dustbathing (Nørgaard-Nielsen and Vestergaard, 1981).

Although our understanding of the complex of factors involved in causation of dustbathing has advanced considerably, measuring the strength of motivation to dustbathe, or its importance to hens, has proven to be much more problematic. Several very different approaches have been used to determine whether hens have a ‘need’ for dustbathing substrate (Dawkins, 1983; Lagadic and Faure, 1987; Faure, 1991) or whether they even ‘think’ about dustbathing in the absence of substrate (Petherick et al., 1990b). A number of studies have indicated that when given a simple choice between wire or a substrate that permits scratching and dustbathing, hens readily choose the latter (Dawkins, 1981, 1983), although their initial choices may be influenced by their rearing environment or previous experience with dustbathing substrate (Hughes, 1976; Petherick et al., 1990a; Sanotra et al., 1995). However, when hens have been asked either to perform some task or to pay a price in order to obtain access to litter, they have generally been either unable or unwilling to do so.

In her landmark paper introducing consumer demand theory as a measure of ethological 'need', Dawkins (1983) presented data indicating that hungry hens were not willing to pay a price (sacrifice time spent feeding) for access to litter. Dawkins suggested that hens did not regard litter for scratching and dustbathing as a necessity but cautioned that her results should only be viewed as preliminary because of the stringency of her tests; these initial tests simply indicated that in hungry birds, the need for litter to scratch and dustbathe in was not as strong as the need for food. Along a similar line, Faure and Lagadic (1994) used varying wind speeds to impose increasing costs to hens and measure demand curves. In order to validate their technique, they showed that birds were willing to withstand increasing wind speeds to obtain food during periods of food deprivation. However, when birds deprived of dustbathing had to pay a similar price for access to sand, they were no more willing to withstand wind for sand than they were for bare wire floors.

Using a different approach, Dawkins and Beardsley (1986) employed operant conditioning techniques to determine whether hens found access to litter reinforcing. They found that hens would not learn to peck a key to open a door to gain access to litter (mixture of sand, sawdust and wood shavings). The birds did learn to break a photo beam to open the door, but only after a large number of trials. They suggested that access to litter was not reinforcing to hens when the operant task required of them was to peck a key and suggested that the task might have been incompatible with the behaviour system of dustbathing. Lagadic and Faure (1987) and Faure (1991) found that hens would learn to peck at a key to move a solid wall to enlarge their cage, but that the number of key pecks was not significantly increased when enlargement resulted in access to wood shavings instead of a wire floor. The authors argued that since hens would perform the task for space but not for litter, their results indicated that hens lack a need for substrate. In contrast to these other reports, Matthews et al. (1993) found that hens would peck at a key to move a wire cage over an area of peat moss, and they used increasing fixed ratio schedules to increase the cost of obtaining peat moss. Their results suggest that access to litter is not only reinforcing, but that the relatively shallow demand functions that they obtained indicate that the material is a highly important commodity.

In order to determine whether dustbathing is stimulus-bound, or whether hens 'think' about dustbathing when substrate is out of sight, Petherick et al. (1990b) tested hens' abilities to associate a colour cue with gaining access to peat moss in a Y-maze. They found that only 1 of 12 hens would learn the association when trials were separated in time, but 6 of 15 hens were able to learn the task when massed trials were used. The fact that birds ran significantly faster to the choice point when their previous choice had resulted in them gaining access to peat, along with the improvement in learning performance with a change in testing procedure, suggested that birds might have had some cognitive representation of peat moss when it was out of sight.

In the study reported here, we tried yet another approach to measuring the strength of hens' motivation for dustbathing. We used an obstruction test to determine whether hens would be willing to push through a weighted door (Duncan and Kite, 1987) in order to gain access to dustbathing substrate. We compared their willingness to work in order to open the door when they were deprived of the opportunity to dustbathe and their motivation for dustbathing was presumably very high, with their willingness to do so when they were non-deprived and had recently dustbathed.

2. Materials and methods

2.1. Animals and housing

Twelve mature medium hybrid (Amberlink) hens that had been reared on litter and had experience with peat moss as a dustbathing substrate were used in the experiment. The hens were housed in a large floor pen that was furnished with wood shavings, perches, nest boxes, a bell drinker and a feeder. In one corner of the pen was a covered wooden box ($0.16 \times 0.8 \times 0.08$ m) filled with peat moss to a depth of 8 cm that was opened periodically to stimulate dustbathing. The home pen was illuminated by fluorescent tubes maintained on a 15:9 h light:dark cycle (lights on 0600–2100 h) and giving an average illumination at bird height of 3 lx.

Four individual cages and the experimental apparatus were located in an adjoining area of the room next to the floor pen. The individual wire mesh cages ($92 \times 61 \times 39$ cm) were positioned approximately 20 cm above the floor and spaced 25 cm apart. In order to prevent vacuum dustbathing in the cages, three dowel rods, 2.5 cm in diameter, were fixed horizontally 5 cm above, and spaced 15 cm apart along the length of, the cage floor. Ad libitum access to water and to food in crumb form was provided in the cages. When housed in the cages, the birds had visual contact with birds in the other cages and auditory contact with all of their flockmates. This area of the room was also illuminated by fluorescent tubes on the same schedule as the floor pen but gave an average illumination of 130 lx in both the cages and the experimental apparatus. The entire room was maintained between 18°C and 23°C.

2.2. Experimental apparatus

The experimental apparatus was constructed of white painted plywood that was covered by plastic mesh to prevent the birds from flying out. It consisted of a runway (0.56×1.5 m) and a goal box (0.88×0.91 m) separated by a one-way vertically swinging door. At the end of the runway farthest from the swing door was a covered start box that was used to release the birds at the start of trials. The swing door was made of 3-mm stainless steel rods soldered together and suspended from a 5-mm rod that was attached to the top of the door frame (Follensbee, 1992). The doorframe was made of plywood and had a door hole that measured 42×20 cm ($h \times w$). The door could be made progressively more difficult to open by adding weights to wire rods that extended from each side of it. The door could be swung from its resting position with varying levels of force applied by the hen. When a hen pushed at the weighted-door with sufficient force it would swing away from the frame, and with the weight of the door pressing along the hen's back, would allow her to pass underneath and enter the goal box.

During the trials, peat moss was placed in the goal box in a blue, wooden container measuring 61 × 61 × 23 cm. The side of the container facing the swing door was made of a 7.5-cm high piece of Plexiglas that allowed the birds to see the peat moss from the runway. The floor of the runway was bare concrete. To improve the birds' footing, four strips of non-skid material (100 Grade sandpaper) were glued to the floor at the entrance to the door.

2.3. Training procedure

During the month preceding the start of the experiment, the birds were trained to open the swinging door to obtain food after a short period of food deprivation. Food was removed from the home pen at approximately 1630 h on days preceding training. At 1030 h the following day, the feeder was placed in the goal box and birds were individually placed in the runway directly in front of the swinging door. On the first day, the birds were gently guided through the door and allowed to feed for a short time. The procedure was repeated two to three times on 8 different days until all of the birds learned to consistently leave the start box and push through the swinging door to obtain food. No weight was added to the door during the training periods.

2.4. Testing procedure

Testing began for the first set of birds within a few weeks of training. Each testing series involved four hens. During the first part of the testing series, two of the hens were held in the cages to deprive them of dustbathing while the other two hens remained in the floor pen (non-deprived). Each bird was subjected to a series of trials to determine the maximum amount of weight she would push to obtain access to peat moss in the goal box. After the maximum door weight was determined for each bird, the bird's home environments were switched and the series of trials repeated to establish maximum door weight birds would push to obtain access to peat moss when living in the other home environment. The series of trials were conducted with three groups of hens so that a total of twelve birds were tested, each bird under both the dustbathing deprived and non-deprived condition. Order of condition was balanced across hens.

Each test day, the four birds were randomly assigned a testing order. One hour before testing began, the dustbath in the home pen was opened to give the birds access to peat moss. Opening the dustbath always resulted in stimulating bouts of dustbathing in some of the birds in the pen. This was done so that if test birds were at all motivated to dustbathe, they would likely have engaged in a dustbathing bout immediately prior to testing. Therefore, when birds were living in their pen they were not only non-deprived but were likely to have been 'dustbathing satiated'. Birds were tested on alternate days because the tendency to dustbathe is known to increase over time and shows an endogenous rhythm of 2 to 3 days (Vestergaard, 1982). Birds were tested in the middle of the day, to avoid periods of egglaying and because motivation to dustbath is known to be highest at mid-day (Vestergaard, 1982).

At the beginning of each test day, birds were weighed, examined for dust in the feathers, (an indication of recent dustbathing) and placed in the start box. After being released, the hen was allowed 10 min to open the door to obtain access to peat. Each testing series began with zero weight added to the door. If the hen successfully opened the door and entered the goal box, she was allowed 200 s in contact with the peat. After 200 s, the hen was returned to the start box, and additional weight (100 g) was added to the door. The procedure was repeated up to four times in 1 day with weight progressively increased by 100 g each time. On the fourth trial of the day, hens were allowed to remain in the goal box for 20 min to complete a full bout of dustbathing before returning to their home pen or cage.

When a hen did not attempt to open the door, testing was over for that day. On the next day of testing, the previous weight at which a hen had last successfully opened the door was used for trial 1 and then weight was increased progressively with each trial. When opening the door appeared to become difficult for a hen, smaller weights (25 g) were added to the door until the maximum weight that a hen could or would push to open the door was determined. When a hen attempted to push the door open a total of 10 times but was unsuccessful, she was returned to the start box, and tested again at her previous successful weight. When a hen failed to open the door at a given weight on two successive test days, the previous weight at which she successfully opened the door was considered the maximum weight for that condition (deprived vs. non-deprived).

2.5. Data collection and statistical analyses

In addition to obtaining the maximum door weights that hens would push to enter the goal box, other behaviour patterns that we thought might reflect hens' motivation to dustbath were measured. The latency to open the door, number of unsuccessful attempts to open the door, and the latencies from opening the door to begin pecking at the peat moss and to begin dustbathing were recorded for each trial. Onset of dustbathing was deemed to occur when the first vertical wing shake was observed. Vertical wing shakes, squatting and side-lying (elements of vacuum dustbathing) performed in the runway were also recorded.

The maximum door weights obtained when hens were deprived vs. non-deprived were analysed using a paired *t*-test. The proportions of successful trials (when hens pushed through the door) that resulted in dustbathing were subjected to an arcsine transformation for proportions (Zar, 1984) so that paired *t*-tests could be used to compare the proportion of trials resulting in dustbathing when hens were deprived vs. non-deprived. The latencies to begin pecking in the peat and to begin dustbathing were calculated from the time that the birds opened the door. All data from Trial 4 of each of the days were truncated at 200 s so that they could be analysed together with data from all other trials. The average numbers of attempts to open the door, and latencies to open the door, to begin pecking in the peat and to begin dustbathing were subjected to logarithmic transformations, and transformed data were analysed using analyses of variance to determine any differences between deprived and non-deprived conditions (SAS Institute, 1996). Hen was included in the model to account for the repeated measures and the unequal numbers of trials across hen. Spearman's rho was used to determine whether latencies to open the door were correlated with the amount of weight on the door (SAS Institute, 1996).

3. Results

3.1. Maximum weights pushed to enter the goal box

Two of the original 12 hens would not open the door to enter the goal box during the tests, although they did push through at zero weight to obtain food during the training sessions. Data from these two hens were eliminated from the analyses. Of the 10 hens that did open the door during our trials, six pushed more weight to open the door when deprived, three pushed more weight when non-deprived and one hen pushed an equal amount of weight (Fig. 1). Overall, the mean ($\pm$SE) maximum weights pushed tended to be greater when hens were deprived of dustbathing (860 ± 95.6 g) than when hens were non-deprived (682.5 ± 83.3g) ($0.05 < P < 0.10$, one-tailed paired t-test). The numbers of trials conducted to determine the maximum weights were highly variable (range = 6 to 29) depending on the amount of weight pushed and the individual hen's pattern of performance during the trials. Some hens continued to attempt to open the door after repeatedly being returned to the start box while others stopped performing the task after one or two trials.

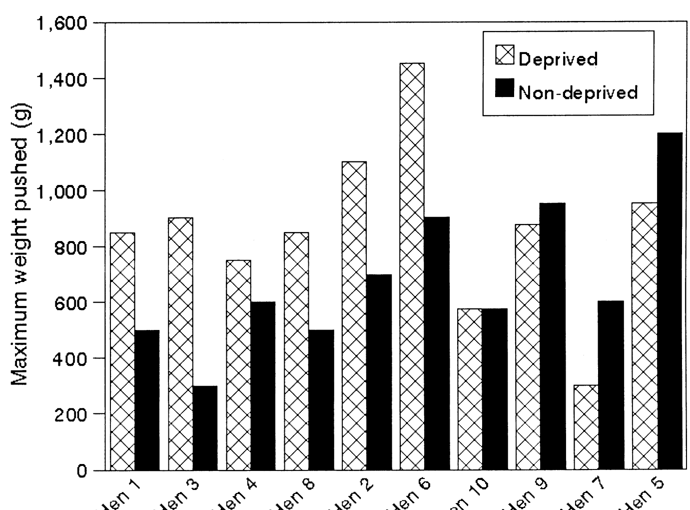

Fig. 1. The maximum weights that hens would push in order to obtain access to peat moss when deprived (hatched) and non-deprived (solid) of dustbathing. Values are for individual hens.

Table 1
Means (±SE) for behaviour patterns recorded during the trials. The number of hens used to derive the mean for a given condition is given in the column preceding the mean (*n*). Probability values are for comparisons between deprived and non-deprived conditions

Behaviour	*n*	Deprived	*n*	Non-deprived	*P*
Latency to open door (s)	10	82.0 ± 8.9	10	69.9 ± 11.3	> 0.10
Latency to peck at peat moss (s) after opening door	10	29.6 ± 10.7	9	32.6 ± 7.7	> 0.10
Latency to dustbathe (sec) after opening door					
All hens	9	80.5 ± 9.4	6	85.5 ± 7.4	> 0.10
Only hens that dustbathed in both conditions	5	66.4 ± 8.9	5	87.8 ± 8.6	$0.05 < P < 0.10$
Unsuccessful attempts to open door	10	1.4 ± 0.3	10	0.75 ± 0.3	$0.05 < P < 0.10$

3.2. Behaviour in the runway

The behaviour measured during the trials was also highly variable across hens (Table 1). It was originally hypothesised that latency to open the door would be shorter when birds were deprived of dustbathing and presumably more highly motivated to get to the peat moss. This was not the case. The average latency to open the door was numerically greater when hens were deprived of dustbathing (Table 1). Latency to open the door was significantly correlated with the amount of weight on the door, indicating that it took birds longer to push open the door when the task was more difficult. The birds tended to have more weight on the door during a greater number of trials when they were deprived of dustbathing (Table 2). Correlations between the latency to open the door and the amount of weight on the door are given in Table 2 for individual hens and for all hens combined. When hens were deprived of dustbathing there was a significant positive correlation between door weight and latency to open the door in eight of 10 hens. When

Table 2
Correlation coefficients (Spearman's rho) and probability values for the correlations between latencies to open the door and the amount of weight on the door for individual hens and overall for each condition. The number of trials used to derive the data for each hen is given in the column preceding the r_s

	Deprived			Non-Deprived		
	n	r_s	*P*	*n*	r_s	*P*
Hen 1	19	0.52	< 0.03	10	0.09	> 0.50
Hen 2	16	0.62	< 0.01	12	0.14	> 0.50
Hen 3	16	0.50	< 0.05	4	−0.04	> 0.50
Hen 4	14	0.50	< 0.04	8	0.80	< 0.02
Hen 5	16	0.76	< 0.01	18	0.48	< 0.05
Hen 6	27	0.24	< 0.01	12	0.41	> 0.10
Hen 7	4	0.40	> 0.10	11	−0.62	< 0.05
Hen 8	15	0.36	> 0.10	7	−0.34	> 0.10
Hen 9	16	0.58	< 0.02	16	0.58	< 0.02
Hen 10	18	0.64	< 0.01	16	0.53	< 0.03
Overall	161	0.53	< 0.001	114	0.31	< 0.01

they were non-deprived, only four of the hens had significant positive correlations, while one had had a significant negative correlation. When data from the 10 hens were pooled, overall correlations were significant when hens were in both conditions, but r_s values

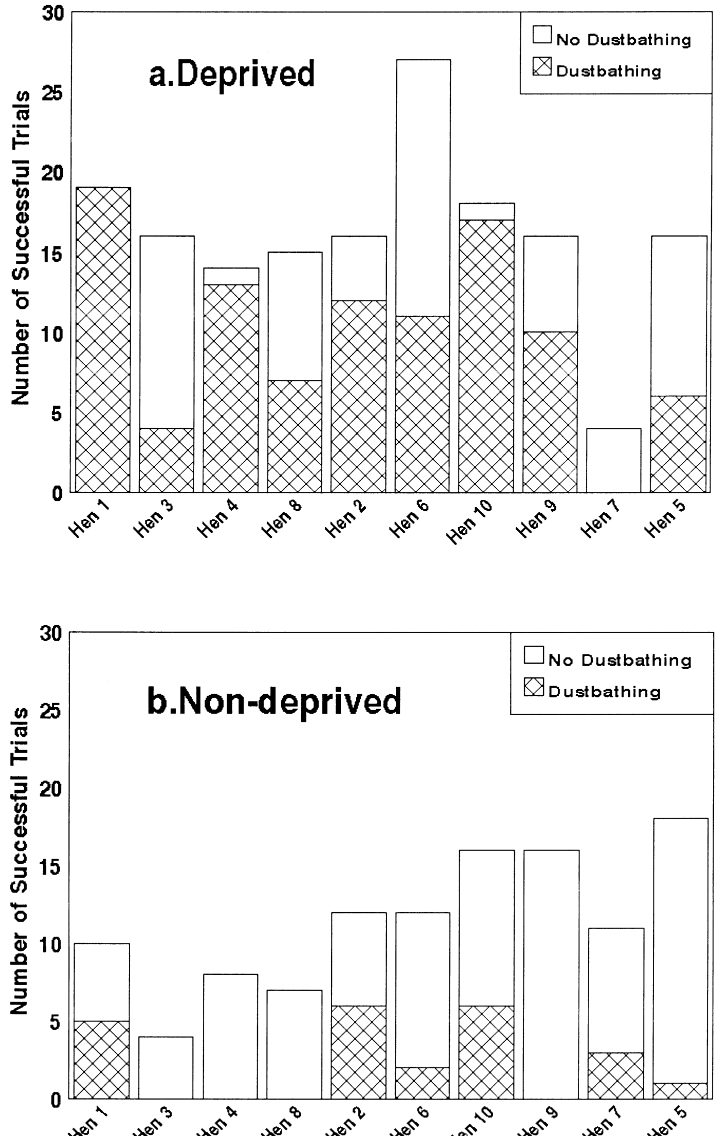

Fig. 2. The total number of successful trails (hatched + solid) and the number of those trials that resulted in dustbathing (hatched only) when hens were deprived (a) and non-deprived (b) of dustbathing. Values shown are for individual hens. The proportion of trials resulting in dustbathing was greater when hens were deprived ($P < 0.001$).

were generally higher when hens were deprived. This suggests that behaviour was more consistent when hens were deprived of dustbathing.

The number of attempts to open the door also varied a great deal during the trials (Table 1). We had thought that hens might show some persistence in goal-directed activity by repeatedly pushing at the door until opening it, as had been observed by Follensbee (1992) for hens working for nest boxes. While some hens appeared to adopt this strategy to open the door, others would exert a great deal of force and push the door open during a single prolonged effort. Overall, hens did tend to make more attempts to open the door when they were deprived of dustbathing than when they were non-deprived ($0.05 < P < 0.10$).

3.3. Behaviour in the goal box

Mean latencies to begin pecking at the peat moss after entering the goal box were the same when hens were deprived of substrate as when they were non-deprived ($P > 0.10$) (Table 1). Mean latencies to begin dustbathing were also similar when data were derived from all hens that exhibited the behaviour after entering the goal box ($P > 0.10$). Nine hens dustbathed in the goal box when they were deprived, while only six hens performed the behaviour when non-deprived. When paired comparisons were made of values from only the five hens that dustbathed in both conditions, latencies to begin dustbathing tended to be shorter when those hens were deprived than when they were non-deprived ($0.05 < P < 0.10$).

The total number of successful trials and the number of those trials that resulted in dustbathing are illustrated for each hen in Fig. 2. Most hens completed more successful trials when deprived of dust with a significantly greater proportion of those trials resulting in dustbathing ($P < 0.001$). When hens were deprived of dustbathing, 61% of the successful trials resulted in dustbathing, whereas hens dustbathed in only 20% of the trials when they were non-deprived.

3.4. Vacuum dustbathing

Elements of vacuum dustbathing were observed in the runway by six of the birds in a total of 15 different trials. Ten of the 15 instances of vacuum dustbathing were performed when hens were deprived of dustbathing. Eleven of the 15 were observed when hens were near or at their maximum weight, when the task of opening the door had become difficult for the hens. Fourteen of the 15 instances occurred immediately following a successful trial during which the hens had begun dustbathing and were interrupted to begin a new trial. In most of these cases, the hens had peat moss on or under their feathers, and some of the peat moss became scattered on the floor of the runway during the trial.

4. Discussion

The results of our experiment suggest that hens are not willing to work harder by pushing open a heavier door to obtain access to peat moss when they have been deprived of dustbathing compared to when they are non-deprived, but the data are equivocal. The majority of hens did push more weight and tended to attempt to open the door more times when deprived of dustbathing. The hens also tended to begin dustbathing more quickly and during a significantly higher proportion of trials when deprived, indicating that they were, in fact, more motivated to dustbathe. However, some of the hens had higher maximum weights when non-deprived. During some of the trials, hens worked extremely hard to open the door immediately following a dustbath in the home pen, as indicated by the presence of dust under their feathers. Perhaps they had been interrupted in the middle of a dustbathing bout when taken for testing, and were still motivated to dustbathe, or the sight of a brightly-lit box filled with fresh peat moss increased their motivation to dustbathe.

An alternative explanation is that the hens worked to enter the goal box for some other reason, such as to get out of the runway or to go home. This might explain the number of successful trials that did not result in dustbathing. However, the 200-s time limit in the goal box may have not been enough time to finish the preliminary pecking phase of dustbathing before the onset of vertical wing shakes which was used as our indicator of the start of dustbathing.

Another possibility is that dustbathing is not motivated by negative affect. Fraser and Duncan (1998) suggested that natural selection will have favoured negative affective states to motivate animals in ‘need situations’ in which the fitness benefit of an action has increased because the action is needed to cope with a threat to survival. They postulated that positive affective states, on the other hand, have evolved in ‘opportunity situations’ in which the fitness benefit of an action has increased because the cost of performing it has declined. Dustbathing would seem to fall into the latter category of actions. Thus, failure to perform dustbathing does not pose an immediate threat to survival, whereas dustbathing when other immediate needs are met and when the opportunity arises will result in a fitness benefit. It may be, then, that dustbathing is largely motivated by a positive affective state (pleasure). During the course of the current experiment, the hens may have come to associate the pleasurable state accompanying dustbathing with pushing open the door. Once this association was made, pushing open the door alone may have elicited feelings of pleasure and accounted for hens pushing open the door without subsequently dustbathing. Supporting evidence for this possibility is the fact that the three hens that pushed more weight when non-deprived, had first been tested when deprived.

The behaviour of the hens during the trials was highly variable, and there was little concordance among our measures of motivation (i.e., latencies and frequencies of attempts to open the door). Some of the inconsistencies in our data were due to our testing procedures. We chose to use massed trials, four per day, rather than separate trials in order to reduce the time required to complete a testing sequence, and because Petherick et al. (1990b) had found an improvement in learning in hens when massed rather than separate trials were used. Some hens did not appear to be affected by an interruption in dustbathing between trials. However, some hens failed to complete more than one trial per day after dustbathing was interrupted and they were returned to the start box. Although this study did not involve an economic technique per se, it has been strongly recommended that animals be allowed to schedule their own bout length as interruption may devalue activities for the performer (as cited in Mason et al., 1998).

We attempted to ensure that hens were highly motivated to dustbathe when deprived (we allowed 2 days since their last exposure to dust and tried to prevent vacuum dustbathing in the cages) and were not motivated to dustbathe when non-deprived (we stimulated dustbathing in the home pen immediately prior to testing). However, we could not be absolutely certain that this strategy worked, and some variation in the motivational states of the hens in this study probably affected our results. It is known that, not only is there a build-up of dustbathing motivation with deprivation, but motivation for dustbathing seems to have an endogenous rhythm over the course of the day. While we tested birds at the time when they are known to be most highly motivated to dustbathe, day-to-day or time-of-day variation in motivation to dustbathe may have affected our results. This is one disadvantage to using this type of scheduled test that measured motivation at a specific time on the experimenter's schedule rather than the bird's. Using more of a closed economy (Mason et al., 1998) that would allow birds to work to access the dustbath at different times of day according to their own schedule would eliminate this problem.

Although we tested the birds under standard conditions, some external stimuli may also have influenced the birds' tendency to dustbathe. In order to control feather pecking, the floor pen was more dimly lit than the cage and testing apparatus. Non-deprived hens, therefore, were exposed to peat moss in brighter light during the trials, which probably changed the visual stimulus properties of the peat. It is known that visual stimuli are important in dustbathing motivation, with both sight of a dusty substrate (Petherick et al., 1995) and illumination (Duncan et al., 1998) able to stimulate dustbathing. In addition, the characteristic scratching sounds of hens dustbathing in the floor pen could occasionally be heard during our trials. Although the importance of auditory stimuli has never been tested with regard to dustbathing motivation, we do know that the sight/sound of other birds dustbathing increases a hen's tendency to dustbathe (Duncan et al., 1998).

When all studies attempting to measure the importance of dustbathing are considered, discrepancies among the results can probably be explained by two factors. Whether or not test birds can see a dry dusty substrate seems to make a huge difference to their motivation; studies in which the substrate has been out of sight, have generally concluded that dustbathing motivation is not very important (e.g., Dawkins and Beardsley, 1986; Petherick et al., 1990), whereas studies in which the birds have been able to see the substrate have concluded that dustbathing is important (e.g., Vestergaard, 1982; Matthews et al., 1993). The fact that visual stimuli can be potent triggers for dustbathing behaviour, leads to the question posed by Beilharz and Zeeb (1981) nearly 20 years ago: "Is it possible to measure a 'basic' motivation for sand-bathing without showing the hen a sand-bath and thus raising its level of motivation?" The second factor that may have led to different conclusions from different studies is the type of substrate used during the test. It is known that type of substrate can affect the amount of dustbathing shown (Petherick and Duncan, 1989; van Liere et al., 1990) and that birds also consistently demonstrate preferences for different visual and textural qualities of dustbathing substrate (van Liere and Siard, 1991; Vestergaard and Hogan, 1992; Sanotra et al., 1995).

However, a wide variety of substrates have been used in dustbathing studies including, peat moss, sand and wood-shavings.

The performance of elements of vacuum dustbathing in the runway leads us to some interesting speculation about the role of vacuum dustbathing. The fact that two thirds of the instances of vacuum dustbathing occurred when hens were deprived of dustbathing and during trials when hens were near or at their maximum weight suggests that hens were highly motivated to dustbathe but that their attempts to gain access to dust were thwarted. Therefore, it might be argued that vacuum dustbathing was a result of frustration. On the other hand, 14 of 15 of the instances of vacuum activity occurred when hens had dust in or on their feathers and it became scattered on the floor of the runway. The appearance of 'vacuum dustbathing' may simply have indicated that contact with even a few particles of dust made the stimulus conditions strong enough to ''switch on'' dustbathing and its performance in the runway had nothing to do with feelings of frustration. Although the runway may appear to us to be sub-optimal conditions for dustbathing, for the hen, the behaviour may not have been performed in a 'vacuum' at all.

In conclusion, this study shows that, when deprived of the opportunity to dustbathe, most hens will work in order to gain access to a dry, dusty substrate that they can see. On gaining entry to the substrate, most hens will dustbathe. However, some non-deprived hens will also work in order to gain access to the substrate and when they have gained entry, they generally do not dustbathe. Overall, hens are not consistently more willing to work for substrate when deprived than when they have recently dustbathed. These results are very difficult to explain using a 'needs' model of motivation in which deprivation leads to a state of suffering. They are much more consistent with an 'opportunity' model of motivation in which performance of the behaviour, when the opportunity presents itself, leads to a state of pleasure.

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