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Strength of preference for dustbathing and foraging substrates in laying hens

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Abstract

The present experiment investigated the substrate preferences of laying hens, with particular respect to dustbathing and foraging behaviour, in order to guide decisions concerning which resources should be provided in laying hen housing systems to best enable the expression of these behaviours. The consumer demand approach was used to study the strength of preference. Individually-tested hens had to push a weighted door to enter one of four test pens containing either a wire floor, or sand, wood shavings or peat moss as substrate. The contents of the test pens were clearly visible from the central home pen. Twelve ISA-Brown hens, reared in battery cages, successfully learned to operate the push door. Most of these hens worked to get access to all the test pens. With respect to all visits to the test pens, the slopes of the demand curves for the numbers of entries to the test pens were steep and not significantly different. Furthermore, no differences were found in the maximum price paid for access to the various substrates or in the total expenditures. These findings indicate that the hens showed no preference for wire or any other substrate per se. However, when the hens showed dustbathing, almost all of them had worked for access to peat moss whereas only some had worked for sand or wood shavings. The slope of the demand curve for dustbathing in peat moss was relatively shallow and the maximum price paid and the total expenditure to take a dustbath in peat moss were significantly higher than those found for sand or wood shavings. With respect to foraging behaviour we found no clear substrate preference. We conclude that the value of a particular substrate varies according to its suitability for the expression of specific behaviours, and that there is a strong demand for peat moss for dustbathing.

Key words: consumer demand, dustbathing, foraging, substrate preference, laying hen

1. Introduction

An improved understanding of the behavioural requirements of laying hens can provide strong evidence for or against the inclusion of particular environmental resources in specific housing designs (e.g., Cooper and Albentosa, 2003). For example, since the provision of nest boxes (prior to start of lay) has a very high value for laying hens (Cooper and Appleby, 1996; Cooper and Appleby, 2003) these resources should be installed in the housing systems. It is generally accepted that alternative housing systems should provide opportunities for both dustbathing and foraging behaviours. Since cages with wire floors do not allow the full expression of dustbathing and foraging behaviour the incorporation of a suitable substrate in enriched cage systems is currently the subject of much discussion (Olsson and Keeling, 2002b; Cooper and Appleby, 2003; Appleby, 2004). It has also been suggested that a high incidence of aggressive pecking may occur if the type and amount of substrate provided in alternative systems is inadequate (Oden et al., 2002). Thus, with respect to laying hen welfare it is essential to determine which resources hens will work most for and which should therefore be provided in housing systems to allow the full expression of the above behaviours.

Dustbathing is a common behaviour in domestic fowl that apparently functions to remove feather lipids and to maintain plumage condition (Van Liere and Bokma, 1987). Using preference tests, it has been shown that laying hens chose sand or peat moss for dustbathing whereas woodshavings were not favoured (Van Liere and Siard, 1991; Van Liere and Wiepkema, 1992; Sanotra et al., 1995). However, the hens' choices seemed to be dependent on previous experience with a particular substrate, i.e. hens reared on sand preferred sand to peat moss for dustbathing (Van Liere and Siard, 1991).

Other studies measured the hens' motivation to enter areas containing substrates that could either be used for dustbathing or foraging. It was shown that hens readily chose a substrate that permitted either of these behaviours, but when asked to perform a task or to pay a price in order to obtain access to selected substrates they were either unwilling or unable to do so (Dawkins, 1981; Dawkins, 1983a). Hens worked more readily for access to food than a particular substrate (Dawkins, 1983a; Faure and Lagadic, 1994). It was also suggested that they did not use key-pecking as an operant task in order to gain access to a particular substrate (Dawkins and Beardsley, 1986; Lagadic and Faure, 1987; Faure, 1991), but this may have reflected an incompatibility of this task with the behaviour system of dustbathing (Dawkins and Beardsley, 1986). In contrast though, Matthews (Matthews et al., 1995) reported that hens would peck a key for access to a particular substrate and that the opportunity to perform either dustbathing or foraging was a highly important commodity. In addition, he suggested that the value of the different substrates varied with the type of activity performed, e.g., wood shavings were less valued for dustbathing than peat moss or sand but all three substrates were similarly valued for foraging behaviour (Matthews et al., 1995). Others have shown that hens will work for peat moss (Widowski and Duncan, 2000) or straw (Gunnarsson et al., 2000), but no dustbathing was observed in the latter substrate. This lack of a consensus of opinion concerning laying hens' preferences for various substrates hampers progress.

Consumer demand methods are considered useful for quantifying the value of activities or resources to an animal (e.g., Cooper and Appleby, 1995; Matthews et al., 1995; Cooper and Appleby, 1996; Cooper and Mason, 2000; Mason et al., 2001;

Olsson and Keeling, 2002a; Olsson et al., 2002; Cooper and Albentosa, 2003; Cooper, 2004). Animals can make cost-benefit trade-offs between paying the cost to use specific resources or spending their time using alternative resources and/or performing different activities (Cooper and Albentosa, 2003). Operant tasks that have been used in consumer demand studies of laying hens include: a weighted push door (Petherick and Rutter, 1990; Cooper and Appleby, 1995; Olsson and Keeling, 2002a; Olsson et al., 2002; Cooper and Appleby, 2003), key pecking (Dawkins, 1983a; Lagadic and Faure, 1987, 1988; Faure, 1991; Faure and Lagadic, 1994; Matthews et al., 1995; Gunnarsson et al., 2000), and pushing through narrow gaps (Cooper and Appleby, 1996). Of these, the more naturalistic operant task, such as the weighted push door, required the least pre-training and is considered the best (Cooper and Albentosa, 2003).

The consumer demand approach was used here to determine the preferences for dustbathing and foraging substrates in laying hens. Hens were asked to pay a cost (pushing a weighted door) to gain access to one of four different test pens containing either a wire floor or one of three different substrates (sand, wood shavings, or peat moss). Our study also tested Mathews's (1995) suggestion that the value of a substrate to a hen differs with the activity she wishes to perform. The substrates were chosen because previous studies suggested that they are attractive for dustbathing (peat moss or sand (Van Liere et al., 1990; Van Liere and Siard, 1991; Matthews et al., 1995)) or foraging (sand or wood shavings (Petherick and Duncan, 1989; Matthews et al., 1995)).

2. Materials and Methods

2.1 Animals and Housing

Forty beak-trimmed laying hens (ISA Brown) reared in battery cages were obtained from a commercial farm (Verbeek, Putten, The Netherlands) at 16 weeks of age. Upon arrival at the experimental farm, all birds were wing-tagged for identification purposes and housed in groups of four in pens (1.5 x 1.0 m), each with a wire floor and four laying nests. Sixteen test hens were subsequently tested in four batches (see below) of four birds. Three weeks before testing began all the hens were weighed (mean weight 1958 g), 4 birds were randomly chosen from four different pens and then individually housed in a pen (0.75 x 1.0 m) containing one of the three new test substrates (wood shavings, peat moss, or sand) and a laying nest. The substrate was changed at intervals of one week till they had experienced all three. In this way, hens were given the opportunity to habituate to individual housing and to each of the different substrates. The sequence of substrate exposure was randomised for each hen. Testing began immediately after this habituation period. Thus, the first batch of hens was tested at 21 weeks of age and the subsequent batches at 24, 27 and 30 weeks, respectively. All hens were in lay during testing. Food and water were supplied ad libitum, and the lights were on from 02.00 h – 18.00 h.

2.2. Test Arena

Figure 1 shows a schematic drawing of the test arena, which consisted of a home pen adjoined to four test pens. Four of these test arena's were available in two separate rooms (two arena's per room). From the home pen a hen could enter any of the test pens through a one-way vertically swinging, weighted door ('push door', one per test pen); this was based on those used in previous studies (Petherick and Rutter, 1990; Cooper and Appleby, 1995; Olsson and Keeling, 2002a; Olsson et al., 2002;

Cooper and Appleby, 2003). The bird could also make its way out of the test pen through an un-weighted exit door and either stay in the home pen or enter another test pen. The test pens had either a wire floor or a 5 cm layer of peat moss, sand or wood shavings as substrate. Water, food and a nest box were also available in the home pen (wire floor), and a filled food trough was available in all test pens. All walls were made of wire mesh and the push door consisted of regularly spaced steel bars. Thus, the contents of each of the test pens were clearly visible to a bird situated in the home pen. Weights were attached to the entry door via a pulley system. The dimensions of the push door are shown in Figure 2. When the entry door was un-weighted it could be opened with just a light force at shoulder height.

Because previous experiments showed that hens in isolation found it more difficult to learn the push door task (De Jong, unpublished results), companion hens (from the remaining group of 24) were housed in the testing rooms in such a way that at a companion was visible to the test hen at each corner of the test pen. The locations of the different substrates in the apparatus were changed after each complete test session.

2.3. Training and test protocol

The total test procedure for each hen lasted 21 days. Initially the push doors remained open for 48 h to facilitate exploration of the test pens. They were closed for the next 2 days but remained un-weighted (0 N). Thereafter, the following weights were attached to the doors for 48 h: days 5 & 6: 50 g (0.29 N), days 7 & 8: 100 g (0.59 N), days 9 &10: 150 g (0.88 N), days 11 & 12: 250 g (1.47 N), days 13 & 14: 500 g (2.94 N), days 15 & 16: 750 g (4.41 N), days 17 & 18: 1000 g (5.88 N), and days 19 & 20: 1250 g (7.35 N). Preliminary experiments had shown that this gradual increase in push door weights facilitated learning of the task (De Jong, unpublished results). Cameras were mounted above all test arenas, and the birds' behaviour was videotaped continuously using time-lapse recording.

2.4. Observations

We observed the behaviour of the hens during the light periods of two subsequent days on which the push doors were fitted with the following weights: 150 g, 250 g, 500 g, 750 g, 1000 g, and 1250 g. Initial analysis of the videotapes revealed that at between 0-100 g the hens were just beginning to learn the task whereas from 150 g onwards it seemed that they learned precisely how to push the door. We therefore focused our analysis on the behaviour of the hens exposed to doors weighted with 150 g or more. The locations of the hens and the accumulated times they spent in a particular test pen or in the home pen were scored continuously during the light period using the Observer software (version 4.1., Noldus, Wageningen, The Netherlands). The occurrence and duration of dustbathing was scored during three selected periods: 2-4 h (dawn), 9-13 h (midday) and 16-18 h (pre lights off). It has been previously suggested that dustbathing is most common around mid day (Vestergaard, 1982). A bout of dustbathing behaviour was considered to begin when a hen squatted down and performed vertical wing shaking, and the end of the bout was determined retrospectively as the start of an interval of 15 min or more that included no dustbathing behaviour. Bouts that were broken by shorter intervals were still considered as one uninterrupted dustbath (Van Liere et al., 1990). Foraging behaviour was scored using 0/1 sampling every 5 min during the same three observation periods described above. A pilot experiment had shown that foraging was most frequent in these periods (De Jong, unpublished observations) while it is also thought to be commonest just before lights off (Savory et al., 1978). Foraging behaviour was defined as pecking and scratching at the substrate, perhaps in an attempt to locate potential food sources (Cooper and Albentosa, 2003).

In addition to the slopes of the demand curves (price elasticity) (e.g., Cooper and Mason, 2000; Mason et al., 2001; Cooper, 2004) calculated from the (behavioural) observations, we scored the maximum weight a hen would push to access a test pen or to visit one expressly to perform dustbathing or foraging ('reservation price' (Cooper and Mason, 2000; Mason et al., 2001)). The 'total expenditure' per bird was defined as the sum of the number of visits per weight category x weight pushed per visit (Mason et al., 2001), and the consumption, i.e. the time spent dustbathing, as a percentage of the total time spent in a particular test pen (Cooper and Mason, 2000). Since foraging behaviour was measured as a binary variable within each 5-min interval, we defined foraging consumption as the frequency of foraging behaviour in a particular substrate divided by the total entries made into the pen containing that substrate.

2.5. Statistical Analysis

Four of the 16 hens were excluded from analysis because they failed to learn the push door task. Calculations were performed for the total number of visits to each of the test pens, as well the number of visits accompanied by dustbathing and foraging, respectively.

The time spent in a test pen was expressed as a fraction (percentage) of the observation period and then analysed using a logistic regression model. For the fractions (f) it was assumed that the variance was a multiple of the Bernoulli variance (overdispersed binomial model), i.e. $\mathrm{Var}(f) = \sigma^2 p(1\text{-}p)$, where p was the mean of f.

Effects, introduced on the logit scale, comprised a linear effect of weight with a separate intercept and slope for each chicken, i.e. $\log(p/(1-p)) = a + b$ * weight (with separate a and b for the chickens). The model, as an instance of a generalized linear model (GLM), was analysed by maximum quasi-likelihood (McCullagh and Nelder, 1989). Likewise, the frequency (c) of visits to a specific test pen was initially analysed with a log linear model, assuming over-dispersed Poisson data, also an example of a GLM. However, for uniformity of presentation, these analyses were subsequently replaced by ordinary regression analysis of log transformed data $\log(c+1)$ (see below). Average time per visit was analysed with an ordinary normal data regression model, comprising the aforementioned effects.

Additionally, separate regression analyses were performed per test pen per chicken for the frequency of visits, visits with dustbathing, and visits with foraging. Transformed counts $\log(c+1)$ were regressed on log-transformed weights, since these produced more stable estimates for the slopes than the aforementioned loglinear GLM. Hens that did not work for access to a particular test pen were excluded from this analysis. The estimated slope per chicken was saved. This rough-and-ready measure for overall trend (price elasticity) was subsequently analysed as a new response variable with a mixed analysis of variance model (Searle et al., 1992), comprising fixed effects for test pens and random animal effects.

A mixed analysis of variance model was used to analyse the maximum weight pushed and the total expenditure for each test pen (number of times an animal enters a test pen and expresses a particular type of behaviour multiplied by the weight pushed). This model comprised fixed effects for test pens and random animal effects. Effects across test pens were examined with the Wald test, and subsequently compared pairwise with Fisher's LSD method.

Finally, separate analyses were performed per weight applied, and test pens were compared with respect to the aforementioned response variables with a mixed analysis of variance model, comprising fixed effects for pens and random animal effects. For frequencies and fractions, these models were instances of generalized linear mixed models (GLMMs) and analysed accordingly (Engel and Keen, 1994; Keen and Engel, 2004).

All calculations were performed using the statistical software package GenStat (Committee Genstat, 2000).

3. Results

3.1. Total numbers of visits

Ten hens worked for access to peat moss, 10 for wood shavings, 9 for sand, and 11 for wire. The numbers of visits per test pen decreased with increasing door weight (Figure 3). For each weight, the number of visits to the home pen was significantly higher than that to the test pens (150 g: χ^2=23.74, 250 g: χ^2=23.45, 500 g: χ^2=22.48, 750 g: χ^2=36.20, 1000 g: χ^2=43.45, 1250 g: χ^2=90.10; $P<0.001$). At 750 and 1250 g the numbers of visits to peat moss and sand were significantly higher than those to the wire pen ($P<0.05$ for both substrates and weight categories; Figure 3). The slopes of the demand functions for the number of entries to the test pens were steep and not significantly different (Table 1; mean slope –1.18). Furthermore, no differences were found between the maximum weights pushed to enter the various test pens (Table 2) or the total expenditure per resource (Table 3).

With increasing door weight, the time spent in the home pen increased but the duration of visits to the test pens remained unchanged (Figure 4). Time spent in the home pen was significantly higher than in the test pens from 750 g onwards (750 g: χ^2=15.06, P<0.01;1000 g: χ^2=46.22, P<0.001; 1250 g: χ^2=113.89, P<0.001; Figure 4). The slopes of the curves of visit duration per test pen were not significantly different (data therefore not shown) and only slightly positive (mean slope 0.02), confirming the lack of change. Figure 5 shows the effect of door weight on the percentage of time spent in the home or test pens. Percentage time spent in the home pen increased while that in the test pens decreased with increasing door weight. Significant differences between the home pen and the test pens were found for several weight categories (Figure 6; 500 g: χ^2=13.20, P<0.01; 750 g: χ^2=15.26, P<0.01; 1000 g: χ^2=37.30, P<0.001; 1250 g: χ^2=54.99, P<0.001). The slopes of the curves of the percentage times spent in the various test pens were not significantly different (data not shown) and slightly negative (mean slope –0.02).

3.2. Visits with dustbathing

Nine hens worked for access to peat moss and subsequently showed dustbathing behaviour, whereas only 2 and 3 hens dustbathed after working for access to sand and wood shavings, respectively. We were not able to calculate demand functions for dustbathing in the two latter substrates because the numbers of entries were too low. The slope of the demand curve for dustbathing in peat moss was relatively shallow (Table 1), and the maximum weight the hens pushed to access peat moss was significantly higher than for sand or wood shavings (χ^2=7.66, P<0.05; Table 2). In addition, the total expenditure was greater for peat moss than sand or wood shavings (χ^2=9.83, P<0.01, Table 3). No hens showed dustbathing on wire.

Figure 6 shows the frequency of dustbathing per weight category for each substrate; this was significantly higher in peat moss than in sand or wood shavings at

150, 250, 500 and 750 g (χ^2=14.55, P=0.001, χ^2=12.53, P<0.01, χ^2=6.18, P<0.05, χ^2=12.38, P<0.01 respectively). Consumption of dustbathing was also higher in peat moss than sand or wood shavings at 150, 250 and 750 g (χ^2=14.17, P=0.001, χ^2=13.84, P=0.001, χ^2=10.98, P<0.01 respectively; Figure 7). There were no detectable effects of substrate type on the mean duration of dustbathing bouts.

3.3. Visits with foraging

The numbers of occasions on which hens performed foraging behaviour after working for access to peat moss, wood shavings, or sand, respectively were 10, 10 and 9. However, for 150, 250 and 750 g foraging was more frequently observed in sand than in the other substrate types (χ^2=6.00, P=0.05; χ^2=6.06, P<0.05; χ^2=5.11, P=0.08 respectively; Figure 8). Despite this, the slopes of the demand curves were steep and did not differ significantly between the substrates (Table 1; mean slope –0.98). Similarly, neither the maximum weight pushed to access a substrate to forage (Table 2) nor the total expenditure (Table 3) differed across substrates. The consumption of foraging in the different substrates was higher for sand than wood shavings only at 150 g (χ^2=5.91, P=0.05; data not shown).

4. Discussion

In the present experiment laying hens did not show a strong general preference for one or other of the substrates provided (peat moss, sand, wood shavings) or a preference for any of these substrates over a wire floor. However, the value of a particular substrate varied with the behaviour that was subsequently performed after the hen had worked for access to it, thus confirming previous suggestions (Matthews et al., 1995). Hens were much more likely to show dustbathing after gaining access to peat moss than to the other substrates, whereas no clear substrate preferences were observed for foraging.

With respect to dustbathing, all the measures used herein indicated that the strength of preference for peat moss was higher than for wood shavings or sand. Consistent with earlier findings (Matthews et al., 1995) the slope of the demand function for peat moss was inelastic. In addition, both the maximum price paid and the reservation price was higher for peat moss than sand or wood shavings. Our finding that the consumption of dustbathing in peat moss was significantly higher than in sand contrasts with an earlier report (Matthews et al., 1995) that peat moss and sand were both highly valued for the expression of this behaviour. However, in the latter experiment the hens only had access to one commodity at a time, whereas we used a closed economy setting offering four possibilities simultaneously. It is conceivable that sand could be the hens' second choice; for that reason it would be helpful to determine the relative values for peat moss and sand.

The present hens showed an inelastic demand for dustbathing in peat moss whereas the demand for access to the other substrates was elastic. This finding may be explained by the fact that hens made more visits to the test pens at the lower weights (less work) and that dustbathing was apparent on some of these visits. At higher weights they likely made cost-benefit trade-offs between paying the price and gaining the opportunity to perform the behaviour.

Although foraging behaviour was more frequently observed in sand than wood shavings or peat moss, there were no detectable substrate effects on the maximum price paid, the total expenditure, the slope of the demand curve, or consumption. These findings are consistent with a previous report (Matthews et al., 1995) and suggest that laying hens may not have a clear substrate preference for the expression of foraging behaviour.

Some studies reported that hens have a clear preference for substrate over a wire floor (Dawkins, 1981; Dawkins, 1983b; Matthews et al., 1995) whereas others, including the present one, failed to find such a substrate preference (Dawkins and Beardsley, 1986; Lagadic and Faure, 1987; Faure, 1991). Although our hens were given the opportunity to become accustomed to the different substrate types before the experiment their preferences for wire or the various substrates were similar, irrespective of the behaviour they showed upon gaining access. This finding probably reflected the fact that the present birds had been reared on wire, because experience with a particular floor type is thought to affect subsequent preferences (Dawkins, 1983a). Alternatively, since the present experiment did not control for the value of the operant task itself or for that of occupying additional space or exploring the environment (Cooper, 2004) we cannot preclude the possibility that the hens simply worked for the latter 'rewards', especially when the weights of the push door were low.

The demand for food is often used as a yardstick for assessing the value of other resources because it is very inelastic (Cooper and Appleby, 2003). Other researchers have used a cut-off point (-1.0) to discriminate between inelastic necessities (shallower than –1.0) or elastic luxuries (steeper than –1.0) (Sherwin and Nicol, 1997; Gunnarsson et al., 2000) or to rank the slopes to produce a hierarchy of behavioural priorities (Mason et al., 2001). We did not assess the strength of preference for food here, but we can compare the present values with the demand for food reported elsewhere. For instance, an elasticity of demand for food of –0.88 has been reported (Matthews et al., 1995), indicating that the present demand for dustbathing in peat moss was very inelastic (e = -0.36). Ranking the slopes of the demand curves for foraging and dustbathing in peat also revealed the inelasticity of the demand for dustbathing in peat. Using e=1 as the cut-off point for essential resources or luxuries further confirmed that dustbathing in peat is a high priority for laying hens.

Comparing the maximum price paid (a robust measure of resource value (Cooper and Albentosa, 2003; Cooper, 2004)) for foraging or dustbathing should indicate if the performance of one or other of these behaviours is of higher or lower value for laying hens. However, our results suggest that hens were not willing to pay a higher price for dustbathing in peat moss than for foraging in any of the substrates.

Our expectation that hens would show longer visit durations, to allow greater interaction with the substrate (consumption), as the task became more demanding was not borne out. This may be because a full dustbath consists of a fixed repertoire of behavioural elements so, after a hen has performed completed it the motivation to perform another bout is probably very low (Vestergaard, 1982). On the other hand, there was a tendency towards greater consumption of foraging at higher weights.

5. Conclusion

The present results suggest that, in general, hens do not have a clear preference for substrate (peat moss, sand, wood shavings) over a wire floor. However, the value of a particular substrate varied with the behaviour performed. With respect to dustbathing, hens showed a clear preference for peat moss over sand and wood shavings, whereas there was no clear substrate effect on foraging behaviour. With respect to laying hen welfare the resource that provides for the greatest range of activities may be the best (Gunnarsson et al., 2000). The results of the present experiment suggest that the provision of peat moss may fulfil the need for both a dustbathing and a foraging substrate.

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References

Appleby, M.C., 2004. What causes crowding? Effects of space, facilities and group size on behaviour, with particular reference to furnished cages for hens. Animal Welfare 13, 313-320.

Committee Genstat., 2000. The guide to GenStat. Payne, R. W. (Ed) VSN International, Oxford.

Cooper, J., Appleby, M.C., 2003. The value of environmental resources to domestic hens: a comparison of the work-rate for food and for nests as a function of time. Animal Welfare 12, 39-52.

Cooper, J.J., Appleby, M.C., 1995. Comparison of demand for environmental resources in hens using a computer-controlled push-door. In: Rutter, S.M., Rushen, J., Randle, H.D., Eddison, J.C. (Eds) Proceedings of the 29th International Congress of the ISAE, Universities' Federation of Animal Welfare, Exeter, pp. 13-14.

Cooper, J.J., Appleby, M.C., 1996. Demand for nest boxes in laying hens. Behav. Proc. 36, 171-182.

Cooper, J.J., Mason, G.J., 2000. Increasing costs of access to resources cause re-scheduling of behaviour in American mink (mustela vision): implications for the assessment of behavioural priorities. Appl. Anim. Behav. Sci. 66, 135-151.

Cooper, J.J., Albentosa, M.J., 2003. Behavioural priorities of laying hens. Avian and Poultry Biol. Rev. 14, 127-149.

Cooper, J.J., 2004. Consumer demand under commercial husbandry conditions: practical advice on measuring behavioural priorities in captive animals. Animal Welfare 13, S47-56.

Dawkins, M., 1981. Priorities in the Cage Size and Flooring Preferences of Domestic Hens. Br. Poultry Sci. 22, 255-263.

Dawkins, M.S., 1983a. Battery hens name their price: consumer demand theory and the measurement of ethological needs. Anim. Behav. 31, 1195-1205.

Dawkins, M.S., 1983b. Cage Size and Flooring Preferences in Litter-Reared and Cage-Reared Hens. Br. Poultry Sci. 24, 177-182.

Dawkins, M.S., Beardsley, T., 1986. Reinforcing properties of access to litter in hens. Appl. Anim. Behav. Sci. 15, 351-364.

Engel, B., Keen, A., 1994. A simple approach for the analysis of generalized linear mixed models. Statistica Neerlandica 48, 1-22.

Faure, J.M., 1991. Rearing Conditions and Needs for Space and Litter in Laying Hens. Appl. Anim. Behav. Sci. 31, 111-117.

Faure, J.M., Lagadic, H., 1994. Elasticity of demand for food and sand in laying hens subjected to variable wind speed. Appl. Anim. Behav. Sci. 42, 49-59.

Gunnarsson, S., Matthews, L.R., Foster, T.M.,Temple, W., 2000. The demand for straw and feathers as litter substrates by laying hens. Appl. Anim. Behav. Sci. 65, 321-330.

Keen, A.,Engel, B., 2004. Procedure IRREML. In: Goedhart, P. W.Thissen, J. T. N. M. (Eds) Biometris GenStat procedure library 7th edition. http://www.biometris.nl/genstat

Lagadic, H., Faure, J.M., 1987. Preferences of Domestic Hens for Cage Size and Floor Types as Measured by Operant-Conditioning. Appl. Anim. Behav. Sci. 19, 147-155.

Lagadic, H., Faure, J.M., 1988. Operant-Conditioning and Use of Space by Caged Laying Hens. Behav. Proc. 16, 43-56.

Mason, G.J., Cooper, J., Clarebrough, C., 2001. Frustrations of fur-farmed mink. Nature 410, 35-36.

Matthews, L.R., Temple, W., Foster, T.M., Walker, A.W.,McAdie, T.M., 1995. Comparison of the demand for dustbathing substrates by layer hens. In: Rutter, S.M., Rushen, J., Randle, H.D., Eddison, J.C. (Eds), Proceedings of the 29th International Congress of the ISAE, Conference Universities' Federation of Animal Welfare, Exeter, pp 11-12.

McCullagh, P., Nelder, J.A., 1989. Generalized linear models. Chapman and Hall, London.

Oden, K., Keeling, L.J., Algers, B., 2002. Behaviour of laying hens in two types of aviary systems on 25 commercial farms in sweden. Br. Poultry Sci. 43, 169-181.

Olsson, I.A.S., Keeling, L.J., 2002a. The push-door for measuring motivation in hens: Laying hens are motivated to perch at night. Animal Welfare 11, 11-19.

Olsson, I.A.S., Keeling, L.J., 2002b. No effect of social competition on sham dustbathing in furnished cages for laying hens. Acta Agriculturae Scandinavica Section a-Animal Science 52, 253-256.

Olsson, I.A.S., Keeling, L.J., McAdie, T.M., 2002. The push-door for measuring motivation in hens: An adaptation and a critical discussion of the method. Animal Welfare 11, 1-10.

Petherick, J.C., Duncan, I.J.H., 1989. Behaviour of young domestic fowl directed towards different substrates. Br. Poultry Sci. 30, 229-238.

Petherick, J.C., Rutter, S.M., 1990. Quantifying motivation using a computer-controlled push door. Appl. Anim. Behav. Sci. 27, 159-167.

Sanotra, G.S., Vestergaard, K.S., Agger, J.F., Lawson, L.G., 1995. The Relative Preferences for Feathers, Straw, Wood-Shavings and Sand for Dustbathing, Pecking and Scratching in Domestic Chicks. Appl. Anim. Behav. Sci. 43, 263-277.

Savory, C.J., Wood-Gush, D.G.M., Duncan, I.J.H., 1978. Feeding behaviour in a population of domestic fowls in the wild. Appl. Anim. Ethol. 4, 13-27.

Searle, S.R., Casella, G., McCulloch, C.E., 1992. Variance components. John Wiley, New York.

Sherwin, C.M., Nicol, C.J., 1997. Behavioural demand functions of caged laboratory mice for additional space. Anim. Behav. 53, 67-74.

Van Liere, D.W., Bokma, S., 1987. Short-term feather maintenance as a funciton of dustbathing in laying hens. Appl. Anim. Behav. Sci. 18, 197-204.

Van Liere, D.W., Kooijman, J., Wiepkema, P.R., 1990. Dustbathing behaviour of laying hens as related to quality of dustbathing material. Appl. Anim. Behav. Sci. 26, 127-141.

Van Liere, D.W., Siard, N., 1991. The experience with litter and subsequent selection of bathing substrates in laying hens. In: Appleby, M. C., Horrell, R. I., Petherick, J. C.Rutter, S. M. (Eds) Applied animal behaviour: past present and future. Potters Bar, Herts, UFAW, pp 132-133.

Van Liere, D.W., Wiepkema, P.R., 1992. Effects of long-term deprivation of sand on dustbathing behaviour in laying hens. Anim. Behav. 43, 549-558.

Vestergaard, K.S., 1982. Dust-bathing in the domestic fowl - diurnal rhythm and dust deprivation. Appl. Anim. Ethol. 8, 487-495.

Widowski, T.M., Duncan, I.J.H., 2000. Working for a dustbath: are hens increasing pleasure rather than reducing suffering? Appl. Anim. Behav. Sci. 68, 39-53.

Table 1. The means of the slopes of the demand functions ± SEM for each resource.

	Total number of visits	Visits with dustbathing	Visits with foraging
Peat moss	-0.97 ± 0.27 (n=10)	-0.36 ± 0.17 (n=9)	-0.72 ± 0.24 (n=10)
Wood shavings	-1.27 ± 0.21 (n=10)	*	-1.11 ± 0.21 (n=10)
Sand	-1.21 ± 0.22 (n=9)	*	-1.10 ± 0.25 (n=9)
Wire	-1.29 ± 0.15 (n=11)	**	**

* The slope could not be calculated because the behaviour was not shown sufficiently often. . **These behaviours were not observed on wire.

Table 2. Maximum prices paid (g) ± SEM to access a particular resource, or to make access followed by dustbathing or foraging behaviour.

	All entries	Dustbathing	Foraging
Peat moss	658 ± 137	604^{a} ± 145	637 ± 138
Wood shavings	608 ± 139	229^{b} ± 124	583 ± 132
Sand	638 ± 157	104^{b} ± 104	617 ± 160
Wire	542 ± 199	*	*

^{a,b} Different letters within a column indicate significant differences (P<0.05 at least)

*These behaviours were not observed on wire.

Table 3. Total expenditures (kg) ± SEM calculated for all entries to the resources, or for those followed by dustbathing or foraging behaviour.

	All entries	Dustbathing	Foraging
Peat moss	26.89 ± 8.0	3.88[a] ± 1.24	12.31 ± 3.68
Wood shavings	28.53 ± 6.82	0.86[b] ± 0.58	15.22 ± 4.18
Sand	43.78 ± 18.61	0.321[b] ± 0.17	29.39 ± 10.64
Wire	11.70 ± 3.33	*	*

[a.b] Different letters within a column indicate significant differences (P<0.05 at least).

*These behaviours were not observed on wire.

Figure captions

Figure 1. Diagrammatic representation of the test arena. Arrows within the pens indicate push doors; a dotted arrow means that the doors are unloaded whereas a full arrow indicates that weights were attached to the doors.

Figure 2. The dimensions of the push door.

Figure 3. The effects of door weight on the mean numbers of visits per hen per day to the un-weighted home pen and to the test pens. Different letters indicate significant differences per weight category ($P<0.05$ at least).

Figure 4. The mean duration of visits to the un-weighted home pen and to the test pens according to door weight. Different letters indicate significant differences per weight category ($P<0.05$ at least).

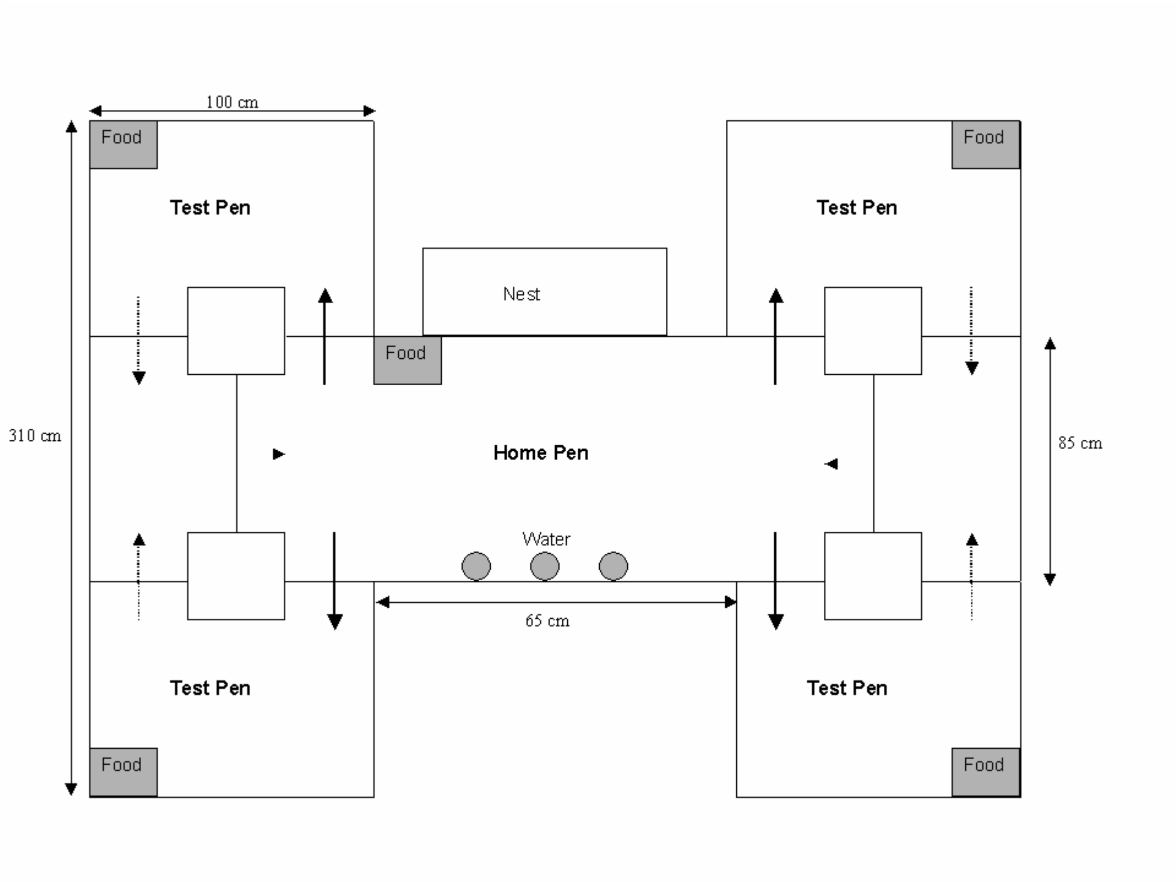
Figure 5. The effects of door weight on the percentages of time spent in the un-weighted home pen and in each test pen. Different letters indicate significant differences per weight category ($P<0.05$ at least)

Figure 6.The effects of door weight on the mean frequency of dustbathing per hen per day for each substrate. Different letters indicate significant differences per weight category ($P<0.05$ at least).

Figure 7. The effects of door weight on the time spent dustbathing as a percentage of the time spent in a particular substrate (consumption). Different letters indicate significant differences per weight category ($P<0.05$ at least).

Figure 8. The effects of door weight on the frequency of foraging behaviour in the particular substrates. Different letters indicate significant differences between the substrates ($P<0.05$ at least).

Figure 1.



100 cm
Food
Test Pen
Food
Test Pen
Nest
Food
310 cm
Home Pen
85 cm
Water
65 cm
Test Pen
Test Pen
Food
Food

Figure 2.

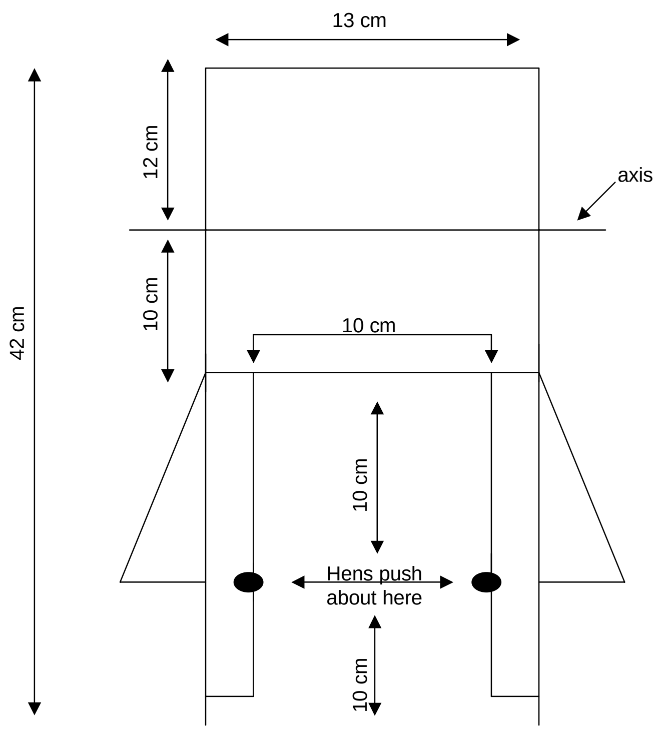
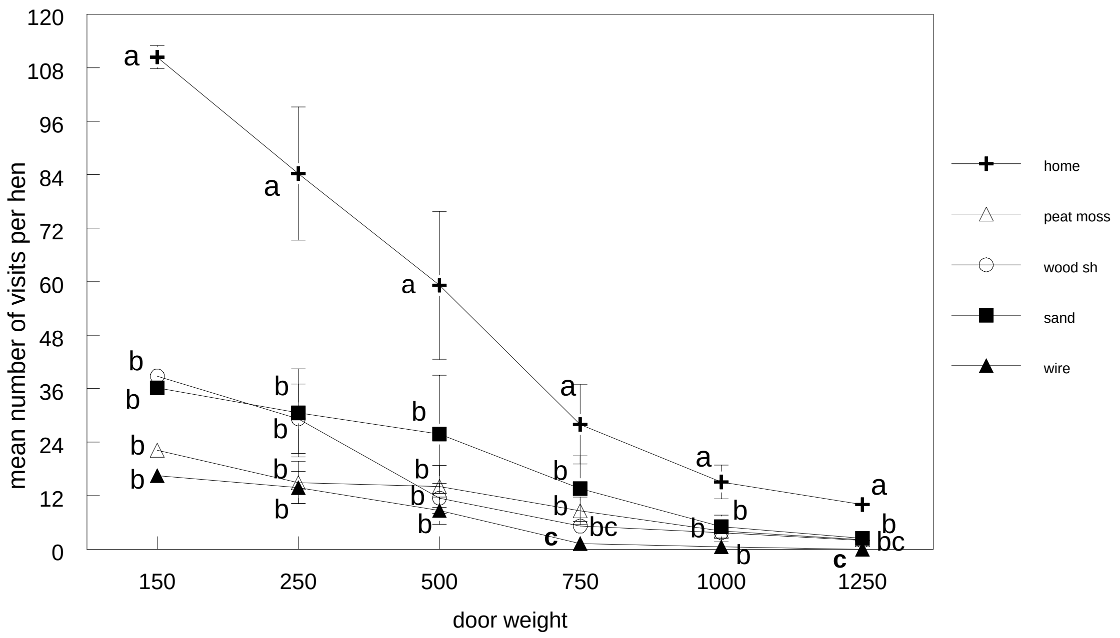
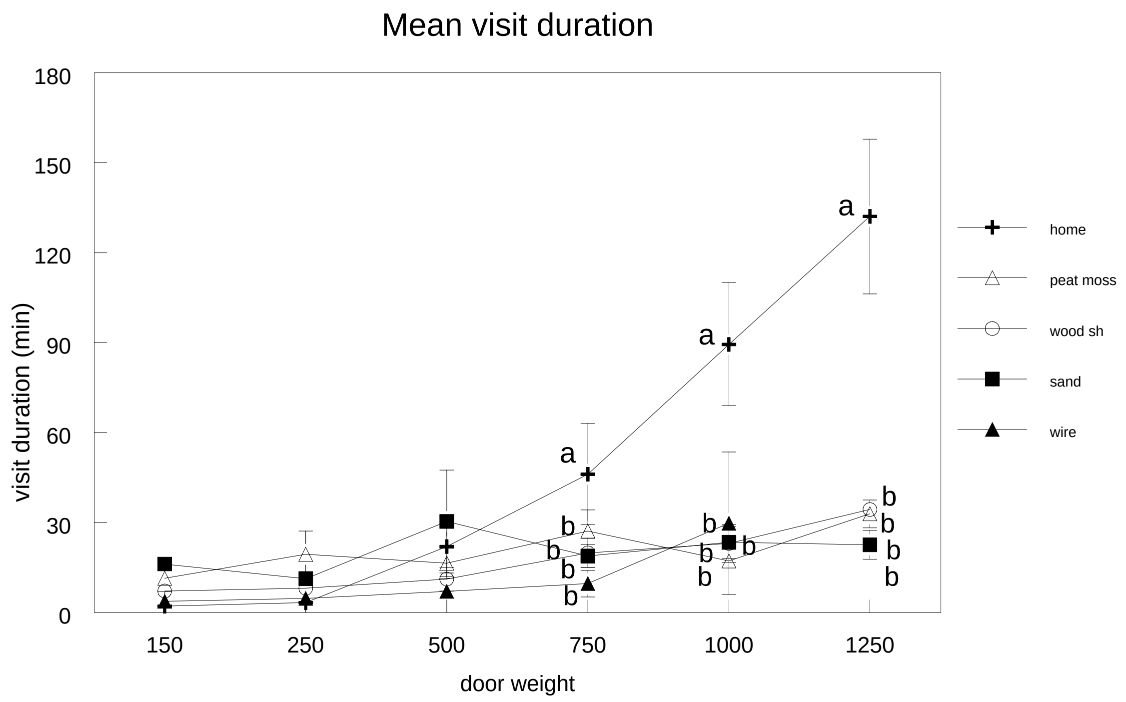


Figure 3.



mean number of visits per hen
door weight
0
12
24
36
48
60
72
84
96
108
120
150
250
500
750
1000
1250
home
peat moss
wood sh
sand
wire

Figure 4.



Mean visit duration
visit duration (min)
180
150
120
90
60
30
0
150
250
500
750
1000
1250
door weight
home
peat moss
wood sh
sand
wire
a
a
a
b
b
b
b
b
b
b
b
b
b
b
b
b

Figure 5.

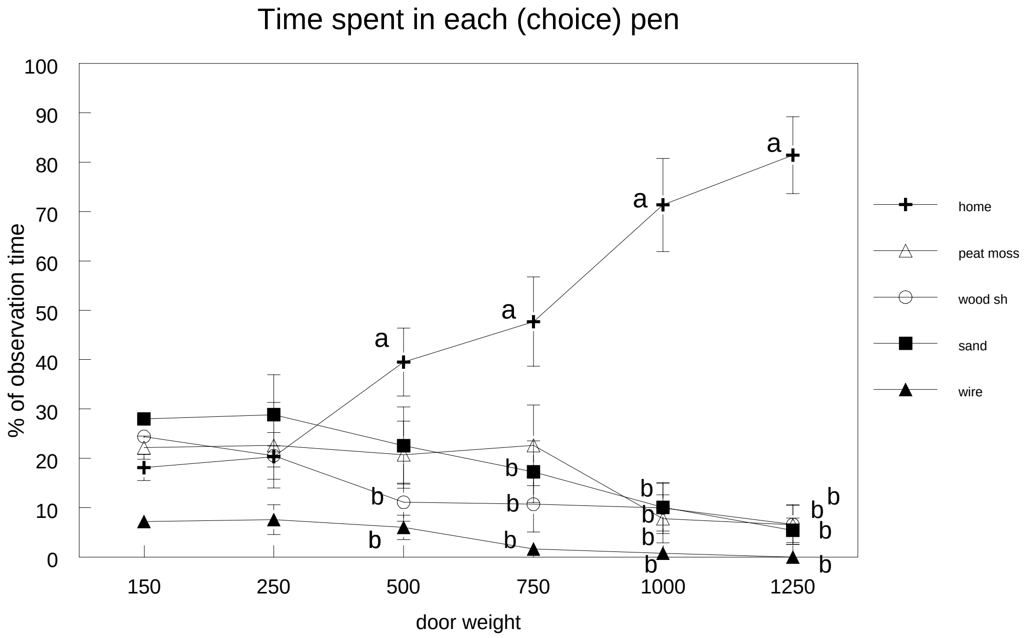

Time spent in each (choice) pen
% of observation time
100
90
80
70
60
50
40
30
20
10
0
150
250
500
750
1000
1250
door weight
home
peat moss
wood sh
sand
wire
a
a
a
a
a
b
b
b
b
b
b
b
b
b
b
b
b
b

Figure 6.

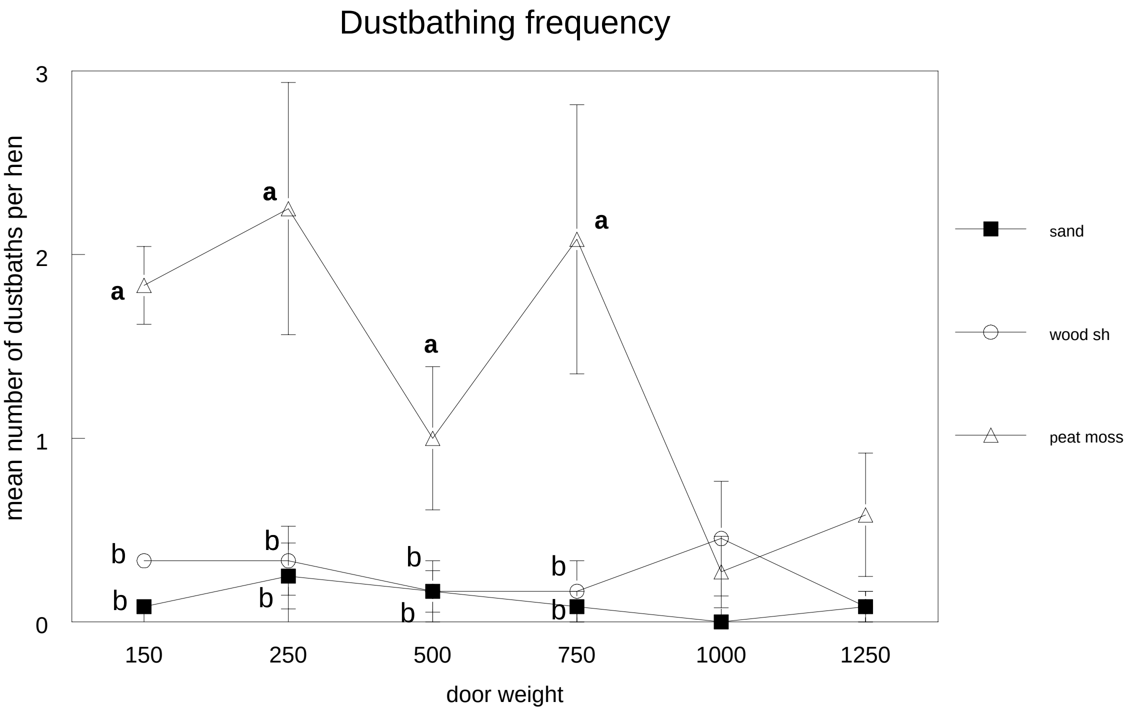

Dustbathing frequency
mean number of dustbaths per hen
0
1
2
3
150
250
500
750
1000
1250
door weight
a
a
a
a
a
b
b
b
b
b
b
b
b
sand
wood sh
peat moss

Figure 7.

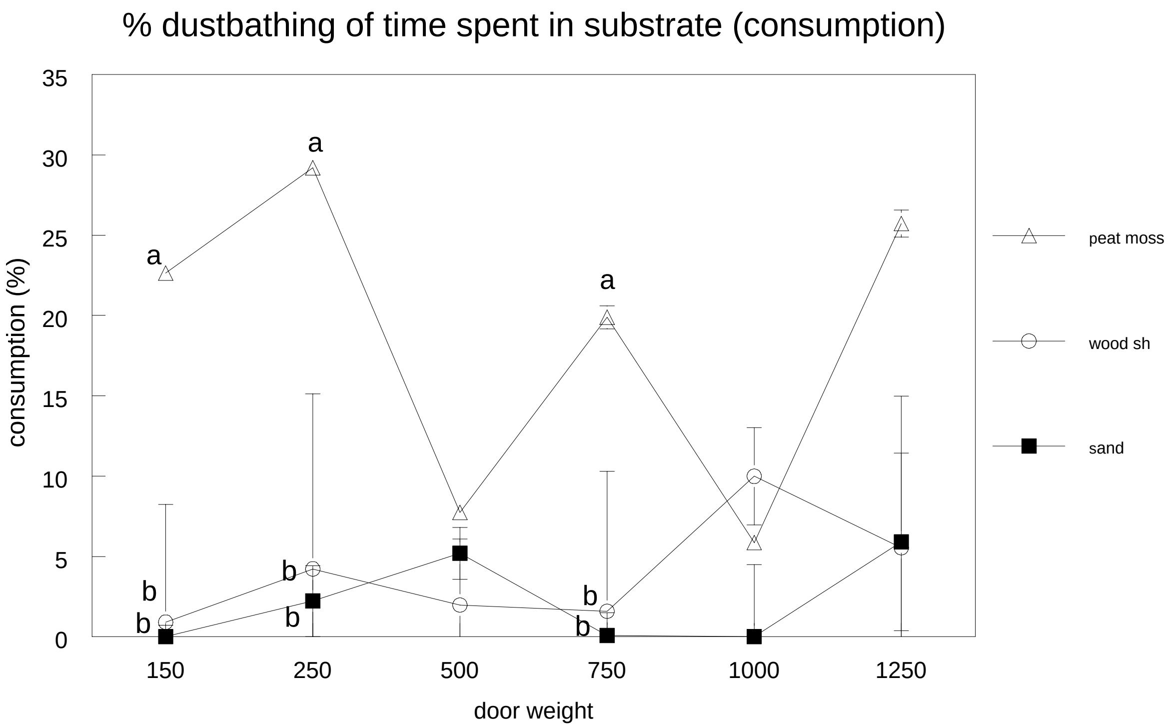
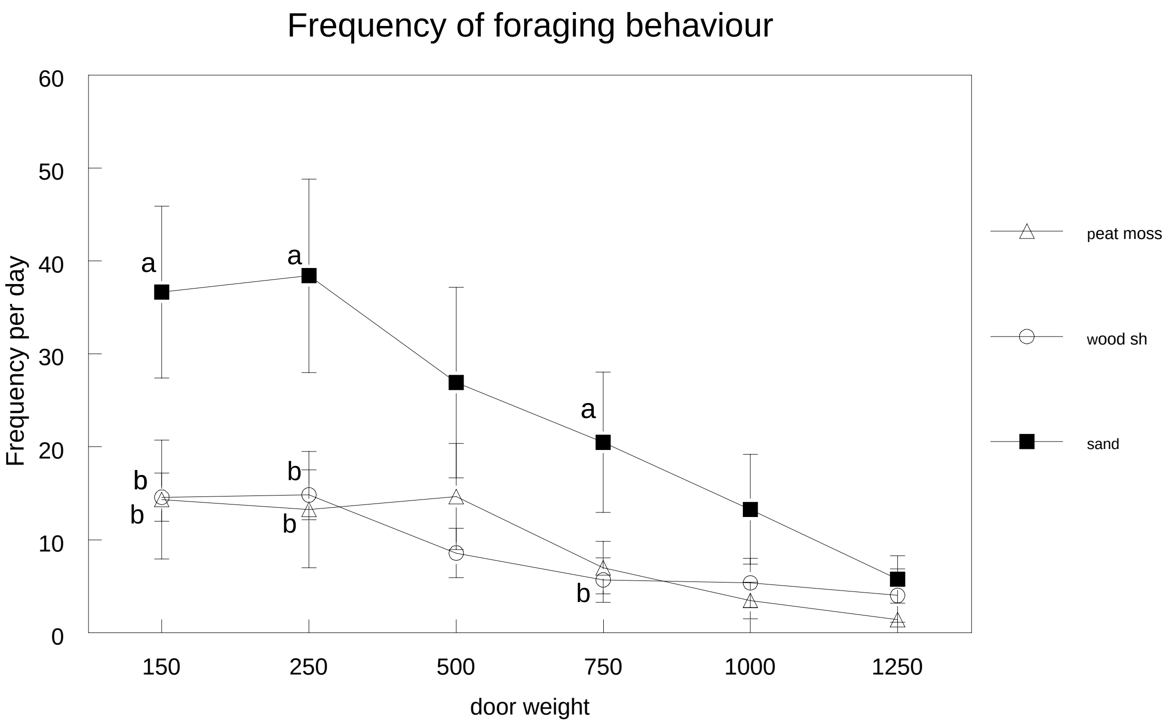

% dustbathing of time spent in substrate (consumption)
consumption (%)
35
30
25
20
15
10
5
0
150
250
500
750
1000
1250
door weight
a
a
a
b
b
b
b
b
b
peat moss
wood sh
sand

Figure 8.



Frequency of foraging behaviour
Frequency per day
60
50
40
30
20
10
0
a
a
a
b
b
b
b
b
150
250
500
750
1000
1250
door weight
peat moss
wood sh
sand