

The effects of cage volume and cage shape on the condition and behaviour of captive European starlings (*Sturnus vulgaris*)

Lucy Asher^{*}, Gareth T.O. Davies, Catherine E. Bertenshaw, Michael A.A. Cox, Melissa Bateson

Epidemiology Division, The Royal Veterinary College, Northumberland Hall, Hawkshead Lane, North Mymms, Hertfordshire AL9 7AT, United Kingdom

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ABSTRACT

Cage size is widely recognised as an important determinant of captive animal welfare, but in contrast, cage shape has received far less attention. Husbandry recommendations for flying birds state that cages should be long in shape because this allows greater potential for flight. However, so far no studies have investigated the impact of cage shape on the behaviour or welfare of captive flying birds. We measured the effects of cage size and shape on the condition and behaviour of captive wild-caught European starlings (*Sturnus vulgaris*) using a 2×3 factorial design in which birds were individually housed for 1 week in cages of one of two volumes (either medium at 0.3 m^3 or large at 1 m^3), and one of three shapes (long with an aspect ratio (i.e. length/height) of 3.43), standard with an aspect ratio of 1.72 or tall with an aspect ratio of 0.86). We found effects of cage size and the interaction of cage size and shape on the behaviour and condition of birds. In interpreting the welfare implications of our results we focused on stereotypic behaviour as measured by incidence of somersaulting and a novel statistic that quantifies sequential dependencies in the birds' locations within the cage. The lowest measures of stereotypic behaviour were recorded in the large cages and the medium long cage. Cage shape was more important in determining the quantity of stereotypic behaviour in the medium cages than the large cages. Our findings support the recommendation that starlings be housed in long-shaped cages.

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1. Introduction

Much importance is placed on providing large enclosures for captive animals (Hediger, 1964; Sauer, 2004). Many studies have shown that enclosure size is an important factor in determining captive animal welfare. For example, laying hens housed in battery caging systems display more foot and claw damage, more broken bones, fewer intact feathers, increased fearfulness, and reduced performance of comfort behaviours compared with birds allowed more space (for a review see Appleby and Hughes, 1991). In general, birds housed in larger cages perform less abnormal behaviour (Keiper, 1969; Gebhardt-Henrich and

Steiger, 2006), display more natural behaviour (Draper and Bernstein, 1963) and show fewer physiological signs of stress (Manosevitz and Pryor, 1975; Kuhnen, 1999; Mitsushima et al., 2003). Perhaps most significantly, animals prefer larger cages when given a choice (Dawkins, 1978; Patterson-Kane et al., 2001; Sherwin, 2004). However, investigations into the effects of cage size are often confounded with changes in cage shape. Cages of similar volume but different shapes can vary dramatically in the types of behaviour that they allow or promote. For example, a cage of the same volume might allow a rat to stand upright or not (Buttner, 1993). Thus, it is plausible that cage shape may be equally, if not more, important for animal welfare than cage size *per se*.

To date, the little research exploring the shape of enclosures has focused on farm animals (Stricklin et al., 1979; Ramos et al., 1986; Wiegand et al., 1994; Sevi et al.,

^{*} Corresponding author.

E-mail address: lasher@rvc.ac.uk (L. Asher).

2001) and is therefore almost exclusively limited to the shape of two-dimensional spaces. Nicol (1987) systematically investigated the effects of both floor area and height of cages on the welfare of laying hens. She found that in taller cages birds behaved more naturally, performing more comfort behaviour and less cage pecking. However, there is good reason to believe that the shape of a cage could be even more significant in flying birds that can utilize a three-dimensional space.

Our aim in this paper is to explore the effects of cage size and cage shape on the behaviour of captive European starlings (*Sturnus vulgaris*). Starlings are one of the most common flying bird species used in biological research, and are typically caught from the wild as adults (Asher and Bateson, 2008). Husbandry recommendations of the Joint Working Group on Refinement (JWGR; Hawkins et al., 2001) suggest that a singly housed starling should have a minimum cage size of 1 m³ volume. It is also suggested that, “the greater the space for flight the better, so a long narrow aviary is preferable to a cubic aviary of equivalent volume” (p. S1: 122). Pending revisions to European legislation on laboratory animal husbandry (Directive 86/609) could make the above recommendations mandatory. However, neither of the above recommendations for cage size or shape are supported by any scientific evidence demonstrating that there are welfare benefits to starlings housed in cages of this size and shape.

In a recent review of research papers using captive starlings published between 2000 and 2004 we found that the median volume of cage space provided for a starling was only 0.13 m³ (inter-quartile range = 0.08–1.05 m³). For example, at Newcastle University our standard starling cages are 0.44-m high × 0.75-m wide × 0.45-m deep, giving a volume of only 0.15 m³ (e.g. Barnett et al., 2007; Bateson and Matheson, 2007; Matheson et al., 2008). Given this gap between current practice and recommended best practice, data relating to the optimum design of starling cages are currently urgently needed. It would be useful to explore whether changes to cage shape could be a refinement to current husbandry practices independent of increases in cage volume. There are often financial and space constraints on providing larger cages, however, altering cage shape could be implemented at much lower cost.

This study directly addresses the lack of evidence regarding appropriate cage dimensions for laboratory starlings, and is the first to systematically tease apart the effects of cage size and shape on the behaviour of a flying bird. Our specific aim was to determine which of these cage types results in the best welfare for captive starlings (as indicated through the measures of condition and behaviour).

2. Methods

2.1. Experimental subjects

The subjects were 30 adult wild European starlings (*Sturnus vulgaris*), 15 males and 15 females, caught under licence from Natural England in the autumn. For 4 months prior to the experiment all birds were housed in a large indoor aviary (2.25-m high × 3.60-m wide × 2.40-m deep) furnished with two water baths, wood chippings covering the floor and a number of small dead pine trees. Birds were fed a diet of Purina

Wild Game Starter at *ad libitum*, supplemented with assorted fruit and mealworms (*Tenebrio* larvae) throughout the experimental period. Birds were kept under a 14:10 light:dark cycle, with light provided by Phillips Master bulbs of 50 Hz in strips across the top of the room. The aviary was air conditioned and varied in temperature between 17 and 21 °C.

This research adhered to the Association for the Study of Animal Behaviour’s guidelines for use of animals in research, and the experimental protocol was subject to internal ethical review. Following the experiment the birds were released to wild at the site of original capture upon the conclusion of the experiment.

2.2. Cage manipulation

Birds were randomly assigned to one of six cage types (Fig. 1): medium tall (0.88-m high × 0.76-m wide × 0.45-m deep), medium standard (0.55-m high × 0.95-m wide × 0.57-m deep), medium long (0.44-m high × 1.51-m wide × 0.45-m deep), large tall (1.32-m high × 1.13-m wide × 0.67-m deep), large standard (0.83-m high × 1.42-m wide × 0.85-m deep) or large long (0.66-m high × 2.26-m wide × 0.67-m deep). The two sizes, medium (0.3 m³) and large (1 m³), represent double the volume of current cages used at Newcastle University, and the minimum cage volume specified by the JWGR guidelines, respectively. The cage shapes were chosen based on manipulations of current cages used at Newcastle University and were double the length (long, front wall aspect ratio (width/height) = 3.43), double the height (tall, front wall aspect ratio = 0.86) or the same shape as our current cages (standard, front wall aspect ratio = 1.72). All cages were made of 1 cm square metal mesh and a solid papered base furnished with two natural branches one positioned 0.15 m from the roof and left wall and the other 0.15 m from the base and right wall of the cage, two water bottles, a water bath and a food bowl on the ground and a covering of bark chippings on the ground.

The six cages were arranged in a single room on shelves 0.7 m from the floor, with the back of each cage against a wall. Translucent white plastic covered the lateral sides of the cage to visually isolate adjacent birds and reduce any neighbour effects, but birds had visual access to birds on shelving opposite and acoustic contact with all birds.

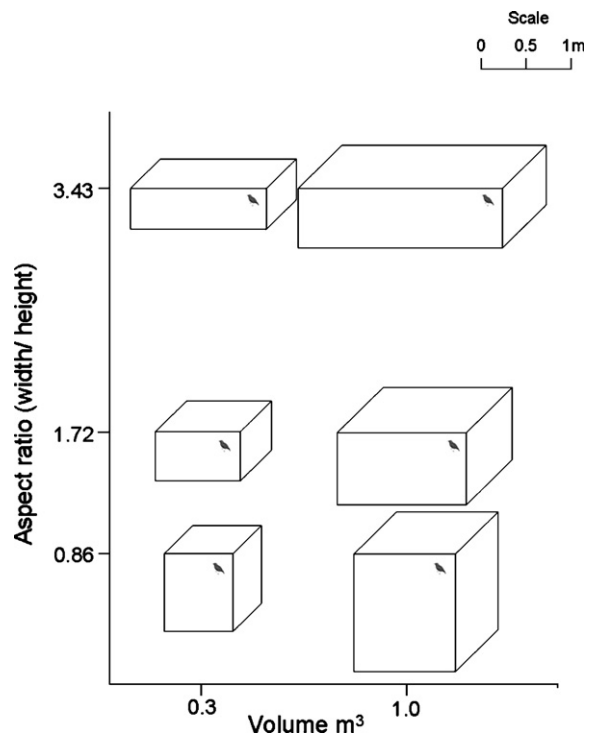


Fig. 1. A scale diagram showing the relative sizes and shapes of the six cage types used in the study.

2.3. Procedure

Individual birds were assigned to one of the six cage types for a total of 7 days. On the first day birds were caught by experienced handlers from the aviary, weighed, flight feathers condition scored from 1 (no damage to flight feathers) to 5 (no viable flight feathers), Biometrics Working Group (BWG) fat scores (an index between 1: no fat and 8: most fat) and European Science Foundation (ESF) pectoral muscle scores (an index between 0: no fat and 3: most fat) taken (for full description see Redfern and Clark, 2001) and then they were placed into the predetermined cage. Every morning at 09:00 the cages were cleaned, water changed and the remaining food left in the food bowl was weighed before the food bowl was replenished. Birds had a 4-day acclimation period, prior to being filmed for 20 min on days 5 and 6. Filming was divided into two time slots: half were made in the morning after cleaning (10:00) and the other half in the afternoon (16:00) and this was reversed the following day. On the morning of day 7 birds were removed from cages, re-weighed and feather, fat, and pectoral muscle scores taken.

We replicated this experiment over 5 weeks with six birds per week, to give a total of five birds per cage type. The position of the six cages within the room was changed for each replicate to reduce the impact of any positional effects on birds' behaviour.

2.4. Behavioural analysis

The time of arrival at one of nine locations within each cage was recorded to a resolution of one second. Locations were: the four cage walls (left, right, front and back), the cage top or ceiling, the ground, the two perches (left higher and right lower) and the air. Air was always recorded between movements to each location.

We used the spread of participation index (SPI) measure of space utilisation (Dickens, 1955, cited by Shepherdson et al., 1993) which is calculated by

$$S = \frac{M(n_b - n_a) + (F_a - F_b)}{2(N - M)} \quad (1)$$

where M is the mean frequency of observations in all enclosure locations, n_a is the number of locations with frequencies greater than M and n_b is the number of locations with frequencies less than M , F_a is the number of observations in locations with frequencies greater than M , F_b is the number of observations in locations with frequencies less than M , and N is the total number of observations. An S value of 1 denotes minimum space utilization (birds spending all time in one location) and 0 a maximum space utilization (time divided equally amongst all locations).

Sequential dependency was calculated using an adapted version of the chi-square test for first- against second-order dependency in sequences of acts (Haccou and Meelis, 1992) which examines the level of predictability in transitions between events. The transition probability of act YZ following act X , uses the chi-square test statistic:

$$C_Y = \sum_X \sum_Z \frac{(N_{XYZ} - N_{XY}P_{YZ})^2}{N_{XY}P_{YZ}} \quad (2)$$

where N is the number of occurrences of a particular transition, e.g. N_{XY} is the number of transitions of X to Y . C is calculated for all acts (A), summed and then compared to chi-square tables at the 95% level. C values exceeding critical were said to show some evidence of sequential dependency. C scores were normalised based on the degrees of freedom

using the calculation (Canal, 2005):

$$C = \frac{C_A - df}{\sqrt{2df}} \quad (3)$$

The degrees of freedom calculation was based on the transitions that occurred and was calculated by

$$df = \sum_A (m - k_A - 1)(m - l_A - 1) \quad (4)$$

where m is the total number of acts, k_A is the number of transitions towards A and l_A is the number of transitions from which A cannot occur.

We also scored videos by counting incidences of the abnormal repetitive behaviour somersaulting which has been previously noted in starlings (Greenwood et al., 2004; Smith et al., 2005). Somersaults were operationally defined as a movement where a bird's legs pass over its head.

2.5. Statistical analysis

The effects of size and shape of cage on condition scores (weight, feather, fat and pectoral muscle scores, and food displaced) were calculated using repeated measures general linear model GLM with one within-subject factor, time of measurement (day 1 measurement and day 7 measurement) and three between-subjects factors: cage size (medium/large), cage shape (tall/medium/long) and sex (male/female).

The frequency of visits to each location was entered into a principal components analysis (PCA). A GLM was used to analyse the principal components with eigen values exceeding one, and S space utilisation scores, total transition number, frequency of transitions to each of the nine locations and C sequential dependency scores (one mean score per bird). The model included the independent variables of cage size (medium/large) and shape (tall/medium/long), sex (male/female), week (1–5) and cage position (1–6), but non-significant factors were removed to simplify the model.

Although this study explicitly manipulated just two discrete aspects of cage design (size and shape) the six cage types varied continuously in a number of dimensions that could be important to starlings (see Table 1 for summary). Regression analyses were used to explore whether any of these dimensions was a good predictor of the dependent variables: condition and behaviour of the birds.

3. Results

3.1. Condition scores

Birds lost 6.09 ± 1.05 g (mean \pm standard error) of weight during the caging period ($F_{1,24} = 4.87$, $P = 0.037$). Fat or pectoral muscle scores did not change significantly during caging. Feather scores were affected by both cage size and cage shape reflected in a significant interaction between cage size and shape ($F_{2,24} = 4.04$, $P = 0.031$). Feather scores showed the greatest improvement in birds housed in the medium tall cages and the largest decline in birds housed in the large tall cages (Fig. 2A). There was less food left in the bowl in large cages ($F_{1,24} = 5.61$ $P = 0.029$, Fig. 2B). We intended to use this as a measure of food consumption, but

Table 1
Dimensions of the six cage types.

	Height (m)	Length (m)	Width (m)	Volume (m ³)	Wall area (m ²)	Ground area (m ²)	Periphery area (m ²)	Periphery: volume	Perch to perch distance (m)
Medium tall	0.88	0.76	0.45	0.33	2.13	0.34	2.81	9.37	0.74
Medium standard	0.55	0.95	0.57	0.33	1.67	0.54	2.76	9.18	0.69
Medium long	0.44	1.51	0.45	0.33	1.72	0.68	3.08	10.27	1.22
Large tall	1.32	1.13	0.67	1.00	4.75	0.76	6.26	6.26	1.32
Large standard	0.83	1.42	0.85	1.00	3.77	1.21	6.18	6.18	1.24
Large long	0.66	2.26	0.67	1.00	3.87	1.51	6.90	6.89	1.99

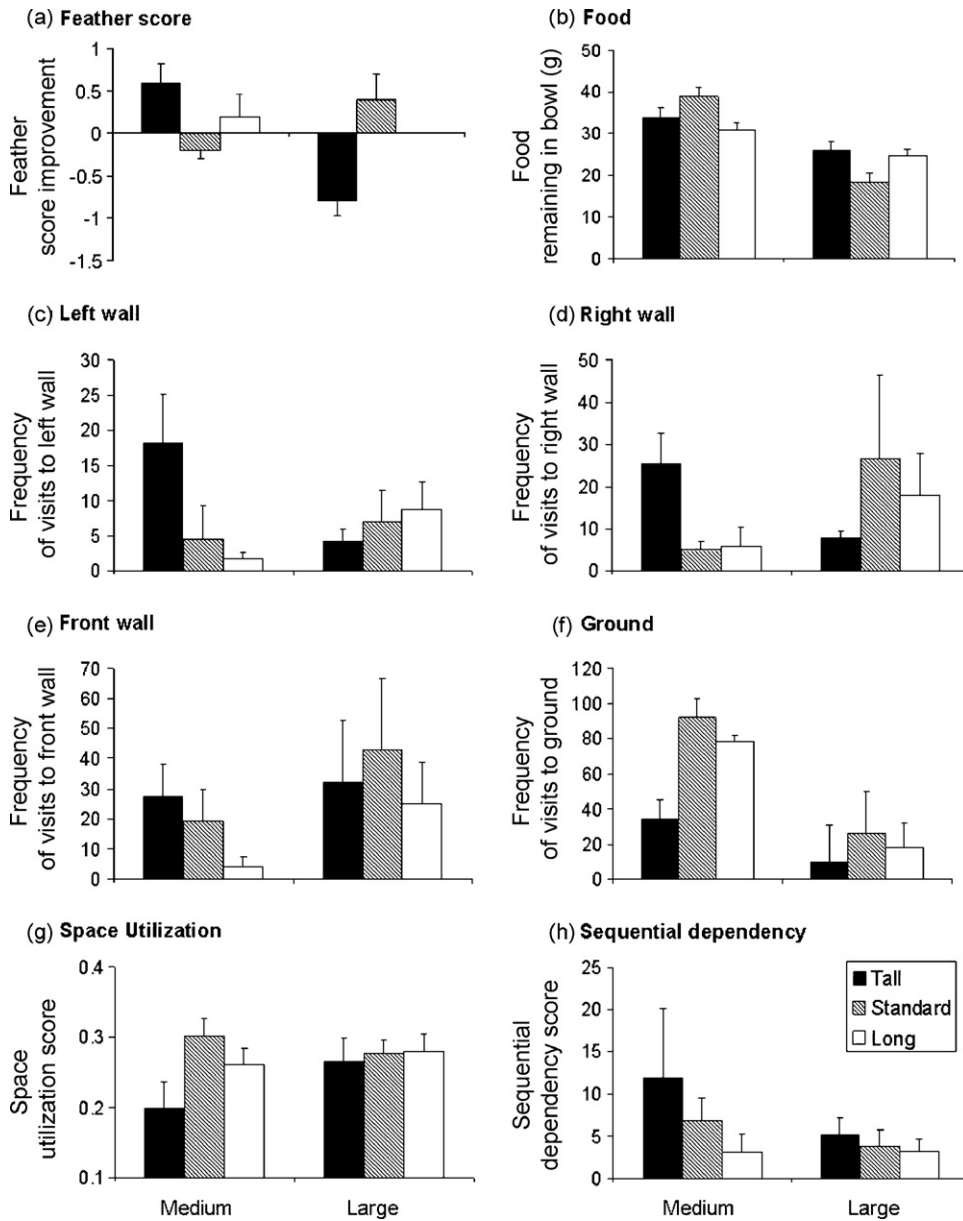


Fig. 2. Summary of main findings of differences between cage types. Mean (\pm S.E.) condition and behavioural scores for each cage type.

we could not calculate this due to a large amount of unrecoverable spillage caused by birds' probing behaviour. We therefore suggest that the lower amounts of food left in the bowl should be interpreted as evidence of increased foraging behaviour.

3.2. Behaviour

Birds performed a total of 178.51 ± 2.38 transitions (mean \pm S.E.) between locations per 20 min video recording. Males performed more transitions (220.03 ± 5.43 , mean \pm S.E.) than females (135.50 ± 4.09 , mean \pm S.E.) but neither cage size nor shape had an effect on the number of transitions performed.

A PCA of the frequency of transitions to the nine locations in the cage (the four cage walls, ceiling, ground, the high left perch, the low right perch and the air) reduced the data to three PCs with eigen values greater than one, that together explained 66.47% of the variance (Table 2). PC1 explained 36.52% of the variance and was positively associated with frequency of transitions to the right (coefficient 0.809), front (0.767), and left wall (0.568) in addition to the high left (0.568) and low right perch (0.654) and the air (0.630). PC1 was higher in male birds ($F_{1,24} = 5.60$, $P = 0.022$), and there was an interaction between sex and shape ($F_{2,24} = 3.69$, $P = 0.033$) with males having higher scores except in the long cages. There was also an interaction between size and shape ($F_{1,24} = 6.78$,

Table 2

Component matrix for principle components analysis on transitions to each location. Correlations $> |0.5|$ are asterisked.

	PC1	PC2	PC3
Right wall	0.809*	-0.135	-0.064
Left wall	0.568*	-0.069	-0.522*
Back wall	0.085	-0.602*	0.864*
Front wall	0.767*	-0.096	0.232
Ground	0.080	0.652*	0.354
Ceiling	0.095	0.648*	0.444
High left perch	0.568*	0.066	-0.139
Low right perch	0.654*	-0.168	0.081
Air	0.630*	0.217	-0.284

$P = 0.012$) with a higher PC1 scores in large cages except in tall cages where higher PC1 scores were found in the medium cages (Fig. 3a). PC2 explained 15.99% of the variance and was positively associated with transitions to the ground (coefficient 0.652) and ceiling (0.648) and

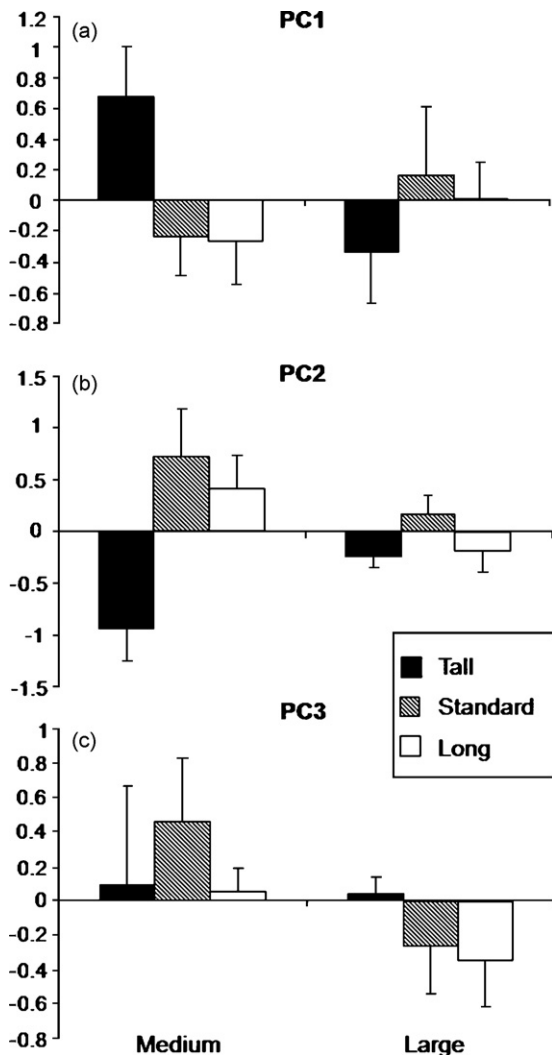


Fig. 3. Summary of principal component analyses containing visits to each location with coefficient matrix and mean and standard error scores for each cage type.

negatively associated with transitions to the back wall (-0.602). The shape of cages ($F_{2,24} = 5.51$, $P = 0.007$) and sex ($F_{1,24} = 7.99$, $P = 0.007$) affected PC2, with tall cages having the lowest PC2 scores and males producing higher PC2 scores (Fig. 3b). Finally PC3 explained 13.96% of the variance and was positively associated with transitions to the back wall (coefficient 0.864), and negatively associated with transitions to the left wall (-0.522). PC3 was affected by the interaction of bird sex, size and shape of the cage ($F_{2,24} = 3.72$, $P = 0.032$; Fig. 3c). In females the size of the cage affected the scores from long cages with larger cages having lower PC3 scores, in the males larger cages yielded higher PC3 scores for long and tall cages but this was reversed for standard cages.

Separate analysis of transitions to each location found significant effects for transitions to the right, front and left walls and ground. Males visited the right ($F_{2,24} = 6.33$, $P = 0.022$, Fig. 2D) and front ($F_{2,24} = 4.00$, $P = 0.030$, Fig. 2E) cage walls in larger cages more than females and less or the same amount of time as females in the medium sized cages. Both sexes displayed more transitions to left (Fig. 2C) and right (Fig. 2D) cage walls in large tall cages, and medium standard cages and fewer to the large long and large standard cages (interaction of cage size and shape, $F_{2,24} = 9.73$, $P = 0.008$ and $F_{2,24} = 4.23$, $P = 0.027$ respectively). Fewer transitions to the ground were made in larger cages ($F_{1,24} = 4.67$, $P = 0.041$, Fig. 2F).

The time budget of birds in different cage types is shown in Fig. 4. Space utilisation (a calculation based on the time budget) was highest in medium tall cages (S scores were lowest) and lowest in medium standard cages (interaction of cage size and shape, $F_{2,24} = 3.99$, $P = 0.037$, Fig. 2G).

Sequential dependency scores ranged from -1.32 to 43.95 . The mean across all recordings was 4.96 ± 0.93 (\pm S.E.). Thirty-seven recordings of 54 where it was possible to calculate the S scores, showed some evidence of sequential dependency when compared to appropriate value in chi-square tables. Within-individual variation (measured by the standard deviation of the two recordings) ranged between 0.17 and 21.43 ($X \pm$ S.E. = 3.64 ± 1.00) and was not affected by cage size or shape. Sequential dependency scores depended on both size and shape of cages ($F_{2,24} = 3.58$, $P = 0.042$) with medium tall cages having the highest scores and long cages and large standard cages having low scores (Fig. 2H). Only four birds (eight recordings) displayed the somersaulting stereotypy and this ranged from just one somersault to 310 viewed in one recording. The mean number of somersaults performed was 102.38 ± 35.58 (\pm S.E.). Somersaults were only performed in the medium cages and were performed in all cage shapes. Four out of four birds that performed somersaults also showed evidence of sequential dependency and a chi-square test ($\chi^2 = 5.870$, $df = 1$, $P = 0.015$) suggests that evidence for sequential dependency is associated with somersaulting behaviour. The data suggests a positive trend with suggestion of correlations within individuals, but more data would be required to confirm this.

Interestingly, no single cage feature (height, length, depth, ground area, wall area, periphery area, periphery to volume ratio, diagonal distance from perch to perch and

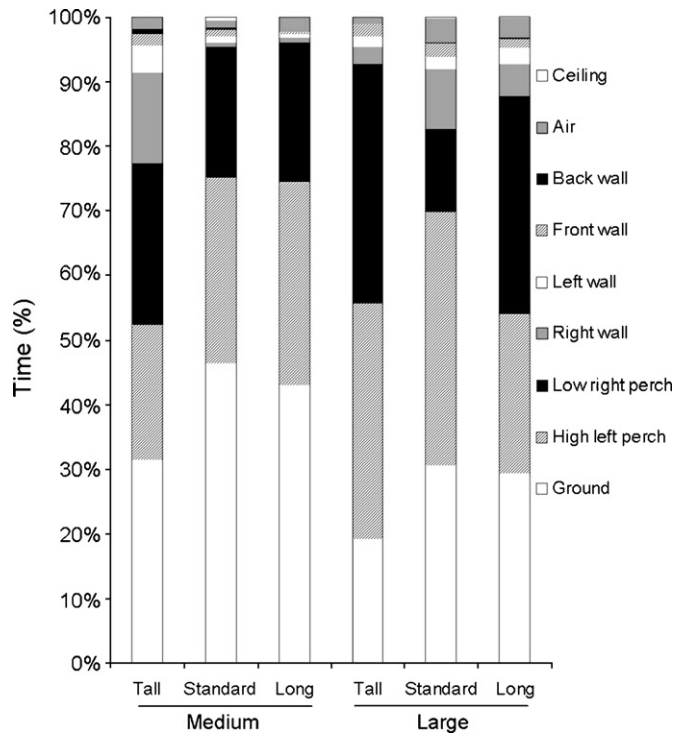


Fig. 4. Mean location time budget for each cage type.

the angle between the two perches) could predict the behaviour or condition of the starlings. Thus, no single continuously varying feature of the cage environment was responsible for differences observed in behaviour and condition.

A second principle component analysis containing all measures (condition and behavioural) revealed the most influential PC, accounting for 81.6% of the variance, was almost entirely dominated by the sequential dependency scores (covariance 0.953). This PCA was not further analysed to avoid replication of the sequential dependency score analysis.

4. Discussion

Cage size, and the interaction between cage size and shape, affected the condition and behaviour of captive starlings (see Table 3 for summary). This finding indicates

that shape is not a variable that can be independently manipulated to improve animal welfare and that the best shape of a cage may differ depending on the size of the cage. Furthermore, interactions between size and/or shape and sex indicate that the ideal cage could be different for male and female birds. The interactions between size and shape appear to be due to the presence of the tall cage shape. In general, the direction of the difference between medium and large cages is consistent for standard and long shapes but reversed in the tall shape. For instance, time spent on the walls is higher in the larger cages for the standard and long cages, but the opposite effect is found in the tall cages. Interactions could have resulted from the fewer transitions between locations observed in large tall cages.

Whilst some patterns of behaviour such as excessive inactivity and abnormal repetitive behaviour have been studied in relation to welfare, other elements of behaviour

Table 3
Summary of main effects of cage size and cage shape.

Variable	Cage size	Cage shape	Interaction cage size and cage shape
Feather score improvement			*
Food displaced	*		
Left wall			*
Right wall	*,a		**
Front wall	*,a		
Ground	*		
Space utilization scores			*
Sequential dependency scores			*

^a Interaction with sex.

* $P < 0.05$.

** $P < 0.01$.

are more difficult to interpret. If we consider time spent on cage walls as indicative of escape behaviour (as in Maddocks et al., 2002) and hence an inadequate environment, it could be argued that medium tall and large standard cages resulted in the worst welfare. This picture is, however, complicated by sex differences found in movement to cage walls. Due to the sex difference in the time spent on cage walls, particularly front walls (higher in males), suggests that this could be an aggressive behaviour. Alternatively it could be argued that males do not settle into captivity as well as females, if clinging to cage walls is indeed indicative of escape attempts. Time spent on the floor of the cage could be considered positive from a welfare perspective: birds that spend time on the ground are likely to be less fearful (Witter and Lee, 1995; Maddocks et al., 2002). However, we found birds visited the ground more frequently in medium-sized cages, and therefore, on this measure alone birds in medium-sized cages would be said to have better welfare. This conflicts with conclusions based on the usual interpretation of other welfare indices, such as time spent on cage walls and foraging behaviour. Whilst birds may have visited the floor more frequently they foraged less (more food remained in their food bowls). Two possible explanations for this are: (1) birds were more nervous when they came to the floor, and thus visited often but were less settled and foraged less; and (2) visits to the floor made up part of a route-tracing stereotypy.

Our first PCA conducted on transitions to the nine defined locations placed the locations into three distinct groupings (PCs1–3). The first principle component (PC1) showed a positive association with most of the locations, and thus could be indicative of general movement. The effects of sequential dependency and PC1 (related to transition number) on cage type are similar, which suggests birds with more repetitive sequences move around the cage more. If PC1 is related to stereotypy, then higher levels of PC1 indicate a poorer environment. Alternatively, if PC1 is related to more general movement this could be interpreted as either positive as regards welfare with the bird shows no signs of malaise, or negative, with the bird restless and making escape attempts (Maddocks et al., 2002). PC2 is related to movements to the ceiling which are also linked to escape behaviour. PC2 is also related to movements to the ground which, as discussed, could be interpreted as a positive or negative welfare indicator. There are lowest PC2 scores in the tall cages and the large long cage and greater in medium standard and long cages, where the distance between the ceiling and floor was less. Thus, the number of movements to the ground or ceiling might be related to distance between them. The last component from this analysis, PC3, covaries with movements to the back wall. The finding that PC3 scores are lower in the deeper cages suggests movement away from the exposed front of the cage to the back wall is more frequent in shallow cages.

Space utilisation was highest (scores lowest) in medium-tall cages, which also showed the best feather condition scores, but other measures of welfare suggest this was the worst cage for bird welfare. The main effects

on space utilisation are reversed in the scores of sequential dependency, suggesting that whilst birds are using more of the space they are provided with, their behaviour is more repetitive.

Treatment differences in the sequential dependency scores were similar to those found in the time spent on cage walls. This is consistent with cage walls making up part of a route-tracing pattern. Sequential dependency also emerged as the most important factor in the final PCA of all measures taken, and therefore explains most of the variance in the data. Sequential dependency scores are measuring an element of the behaviour that simpler analyses are not. Furthermore, sequential dependency shows a positive trend with an established stereotypy measure, counting somersaults. Few instances of somersaulting behaviour were observed, but where they were observed it was always in the smaller (i.e. medium) sized cages. A different form of stereotypy may have developed in the large cages (which would have been reflected in the sequential dependency scores), and somersaults may have developed in large cages over a longer period of time, but this study would suggest that larger cages at least buffer against development of the somersaulting stereotypy.

Although there are no simple patterns in the behavioural and condition measures we took, many of the measures can be related to repetitive or stereotypic behaviour. The sequential dependency scores accounted for the most variation in the PCA; the number of movements to the floor and the cage walls is consistent with route-tracing stereotypes; and the sequential dependency score is partially validated as a measure of stereotypic behaviour through the positive relationship with the number of somersaults performed. Stereotypic behaviour is believed to be caused by inadequate captive environments (Mason and Rushen, 2006) and captive environments which lead to stereotypic behaviour are considered to be unacceptable according to European legislation regarding laboratory animal housing (Appendix A of ETS 123). If we assume that sequential dependency scores are a measure of stereotypic behaviour and that stereotypic behaviour is indicative of poor housing then our analysis shows that medium tall cages were least conducive to good welfare for starlings whereas standard large and medium and large long cages were the most conducive. Therefore, based on the results from this experiment long cages are associated with better welfare, and cage shape emerges as particularly important in the smaller (i.e. medium) cages. Therefore, our results are in agreement with JWGR guidelines suggesting that starlings should be housed in long cages (Hawkins et al., 2001).

In this experiment birds were singly housed in cages for 7 days, environmental enrichment was kept constant between the cage types and all birds were wild-caught. Social housing (Paulus et al., 1998; Meehan et al., 2003), time in environment (Meehan et al., 2004; Hadley et al., 2006), environmental enrichment (Ödberg, 1987; Lewis et al., 2006) and developmental history (Cooper and Nicol, 1996; Schmid et al., 2006), have all been suggested as causal factors in the development, and reversibility of stereotypic behaviour. Thus, with regard to external

validity, effects found in this experiment only apply to wild-caught starlings individually caged for short periods with the enrichments of natural branches, bark trays and water baths. Any or all of the factors mentioned above could interact with cage size and shape in unpredictable ways, for instance a large long cage might be the better cage with appropriate enrichment but the larger space could increase stress and lead to more stereotypic behaviour if enrichment was not provided (see also Asher et al., in preparation). Therefore, there may not be a definitive recommendation on the most suitable cage shape for starlings as it may be contingent on other factors within the captive environment.

5. Conclusions

Cage size and the interaction between cage size and shape affected the condition and behaviour of captive starlings. It is difficult to interpret the welfare implications of many of the measures that were affected by cage size and shape. However, stereotypic behaviour (measured by somersaulting and sequential dependency in location), which is widely cited as an indicator of inadequate environments, differed with cage type. Overall, the lowest measures of stereotypy were recorded in large cages. However, the long medium cage had equally low levels. Cage shape was more important in determining the quantity of stereotypic behaviour in the medium cages than the large cages. Our results support the use of long cages for housing captive starlings.

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References

Asher, L., Bateson, M., 2008. Use and husbandry of captive European starlings (*Sturnus vulgaris*) in scientific research: a review of current practice. *Lab. Anim.* 42, 111–126.

Appleby, M.C., Hughes, B.O., 1991. Welfare of laying hens in cages and alternative systems: environmental, physical and behavioral aspects. *World Poultry Sci. J.* 47, 109–128.

Barnett, C.A., Bateson, M., Rowe, C., 2007. State-dependent decision making: educated predators strategically trade off the costs and benefits of consuming aposematic prey. *Behav. Ecol.* 18, 645–651.

Bateson, M., Matheson, S.M., 2007. Performance on a categorisation task suggests that removal of environmental enrichment induces 'pessimism' in captive European starlings (*Sturnus vulgaris*). *Anim. Welf.* 16, S33–36.

Buttner, D., 1993. Upright standing in the laboratory rat: time expenditure and its relation to locomotor activity. *J. Exp. Anim. Sci.* 36, 19–26.

Canal, L., 2005. A normal approximation for the chi-square distribution. *Comput. Stat. Data An.* 48, 803–808.

Cooper, J.J., Nicol, C.J., 1996. Stereotypic behaviour in wild caught and laboratory bred bank voles (*Clethrionomys glareolus*). *Anim. Welf.* 5, 245–257.

Dawkins, M., 1978. Welfare and structure of a battery cage—size and cage floor preferences in domestic hens. *Br. Vet. J.* 134, 469–475.

Draper, W.A., Bernstein, I.S., 1963. Stereotyped behavior and cage size. *Percept. Motor Skill.* 16, 231–234.

Gebhardt-Henrich, S.G., Steiger, A., 2006. Effects of aviary and box sizes on body mass and behaviour of domesticated budgerigars (*Melopsittacus undulatus*). *Anim. Welf.* 15, 353–358.

Greenwood, V.J., Smith, E.L., Goldsmith, A.R., Cuthill, I.C., Crisp, L.H., Walter-Swan, M.B., Bennett, A.T.D., 2004. Does the flicker frequency of fluorescent lighting affect the welfare of captive European starlings? *Appl. Anim. Behav. Sci.* 86, 145–159.

Haccou, P., Meelis, E., 1992. *Statistical Analysis of Behavioural Data: An Approach Based on Time-structured Models*. Oxford University Press, Oxford.

Hadley, C., Hadley, B., Ephraim, S., Yang, M., Lewis, M.H., 2006. Spontaneous stereotypy and environmental enrichment in deer mice (*Peromyscus maniculatus*): reversibility of experience. *Appl. Anim. Behav. Sci.* 97, 312–322.

Hawkins, P., Morton, D.B., Cameron, D., Cuthill, I., Francis, R., Freire, R., Gosler, A., Healy, S., Hudson, A., Inglis, I., Kirkwood, J., Lawton, M., Monaghan, P., Sherwin, C., Townsend, P., 2001. Laboratory birds: refinements in husbandry and procedures. *Lab. Anim.* 35, S120–126.

Hediger, H., 1964. *Wild Animals in Captivity*. Dover Publications, New York.

Keiper, R.R., 1969. Causal factors of stereotypies in caged birds. *Anim. Behav.* 17, 114.

Kuhnen, G., 1999. The effect of cage size and enrichment on core temperature and febrile response of the golden hamster. *Lab. Anim.* 33, 221–227.

Lewis, M.H., Presti, M.F., Lewis, J.B., Turner, C.A., 2006. The neurobiology of stereotypy I: environmental complexity. In: Mason, G., Rushen, J. (Eds.), *Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare*. second ed. CABI, Wallingford.

Maddocks, S.A., Goldsmith, A.R., Cuthill, I.C., 2002. Behavioural and physiological effects of absence of ultraviolet wavelengths on European starlings *Sturnus vulgaris*. *J. Avian Biol.* 33, 103–106.

Manosevitz, M., Pryor, J.B., 1975. Cage size as a factor in environmental enrichment. *J. Comput. Physiol. Psychol.* 89, 648–654.

Mason, G., Rushen, J., 2006. *Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare*, second ed. CABI, Wallingford.

Matheson, S.M., Asher, L., Bateson, M., 2008. Larger, enriched cages are associated with 'optimistic' response biases in captive European starlings (*Sturnus vulgaris*). *Appl. Anim. Behav. Sci.* 109, 374–383.

Meehan, C.L., Garner, J.P., Mench, J.A., 2003. Isosexual pair housing improves the welfare of young Amazon parrots. *Appl. Anim. Behav. Sci.* 81, 73–88.

Meehan, C.L., Garner, J.P., Mench, J.A., 2004. Environmental enrichment and development of cage stereotypy in Orange-winged Amazon parrots (*Amazona amazonica*). *Dev. Psychobiol.* 44, 209–218.

Mitsushima, D., Funabashi, T., Shinohara, K., Kimura, F., 2003. Rats living in small cages respond to restraint stress with adrenocortical corticosterone release but not with hippocampal acetylcholine release. *Psychoneuroendocrinology* 28, 574–583.

Nicol, C.J., 1987. Effect of cage height and area on the behavior of hens housed in battery cages. *Br. Poultry Sci.* 28, 327–335.

Ödberg, F.O., 1987. The influence of cage size and environmental enrichment on the development of stereotypes in bank voles (*Clethrionomys glareolus*). *Behav. Process.* 14, 155–173.

Patterson-Kane, E.C., Harper, D.N., Hunt, M., 2001. The cage preferences of laboratory rats. *Lab. Anim.* 35, 74–79.

Paulus, M.P., Bakshi, V.P., Geyer, M.A., 1998. Isolation rearing affects sequential organization of motor behavior in post-pubertal but not pre-pubertal Lister and Sprague-Dawley rats. *Behav. Brain Res.* 94, 271–280.

Ramos, N.C., Anderson, K.E., Adams, A.W., 1986. Effects of type of cage partition, cage shape, and bird density on productivity and well-being of layers. *Poultry Sci.* 65, 2023–2028.

Redfern, C.P.F., Clark, J.A., 2001. *Ringers' Manual*. British Trust for Ornithology, Thetford.

Sauer, U.G., 2004. The revision of European housing guidelines for laboratory animals: expectations from the point of animal welfare. *ATLA* 32, 187–190.

Schmid, R., Doherr, M.G., Steiger, A., 2006. The influence of breeding method on the behaviour of adult African grey parrots (*Psittacus erithacus*). *Appl. Anim. Behav. Sci.* 98, 293–307.

Sevi, A., Muscio, A., Dantone, D., Iascone, V., D'Emilio, F., 2001. Paddock shape effects on grazing behavior and efficiency in sheep. *J. Range Manag.* 54, 122–125.

Shepherdson, D.J., Carlstead, K., Mellen, J., Seidensticker, J., 1993. The influence of food presentation on the behavior of small cats in confined environments. *Zoo Biol.* 12, 203–216.

Sherwin, C.M., 2004. The motivation of group-housed laboratory mice, *Mus musculus*, for additional space. *Anim. Behav.* 67, 711–717.

- Smith, E.L., Evans, J.E., Parraga, C.A., 2005. Myoclonus induced by cathode ray tube screens and low-frequency lighting in the European starling (*Sturnus vulgaris*). *Vet. Rec.* 157, 148–150.
- Stricklin, W.R., Graves, H.B., Wilson, L.L., 1979. Some theoretical and observed relationships of fixed and portable spacing behavior of animals. *Appl. Anim. Ethol.* 5, 201–214.
- Wiegand, R.M., Gonyou, H.W., Curtis, S.E., 1994. Pen shape and size—effects on pig behavior and performance. *Appl. Anim. Behav. Sci.* 39, 49–61.
- Witter, M.S., Lee, S.J., 1995. Habitat structure, stress and plumage development. *Proc. R. Soc. Lond. Ser. B: Biol. Sci.* 261, 303–308.