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The Development of Stereotypic Behavior in Caged European Starlings, *Sturnus vulgaris*

ABSTRACT: *Stereotypic behavior in captive animals has been hypothesized to emerge from thwarted natural behavior patterns and is thought to be more common in captive-reared animals. However, data on the early stages of developing stereotypies are currently scarce. We compared the development of stereotypic route-tracing and somersaulting in hand-reared and wild-caught starlings placed in individual cages for the first time. We found that wild-caught birds were less active but showed more escape motivation and more evidence of route-tracing behavior. Furthermore, somersaulting was only observed in wild-caught birds. Development of somersaulting was predicted by subtle differences in behavior during the first few days in cages and developed in individuals with low levels of route-tracing behavior. Our data suggest a role for escape motivation in the development of starling stereotypies and additionally that route-tracing and somersaulting may represent alternative outlets for thwarted escape. In contrast to observations from mammals, our results show that stereotypies are more common in wild-caught starlings.* Dev Psychobiol 54: 773–784, 2012.

Keywords: *stereotypic behavior; abnormal repetitive behavior; starling; songbirds; early life development; captive breeding; route-tracing*

INTRODUCTION

Stereotypic behavior describes abnormal behavior patterns, such as pacing, jumping, and bar-gnawing, that are defined by their invariant, repetitive nature, and apparent lack of function (Mason, 1991; Ödberg, 1978). While it is now well-established that stereotypies in farm, zoo, and laboratory animals can be induced by poor captive husbandry, including housing in barren cages, and early maternal deprivation (Latham & Mason, 2008; Lewis, 2004; Mason, Clubb, Latham, & Vickery, 2007; Mason & Rushen, 2006; Meehan, Garner, & Mench, 2004), little is known about the early stages of their development (Mason, 1993).

There is accumulating evidence that stereotypic behavior patterns emerge from thwarted normal behavior. For example, in laboratory mice, stereotypic bar-gnawing, and jumping have been described to develop from escape-motivated behavior (mother seeking and exploration, respectively) during the first few days after weaning (Würbel & Stauffacher, 1997; Würbel, Stauffacher, & von Holst, 1996). Similarly, in caged wild-caught European starlings (*Sturnus vulgaris*), the somersaulting stereotypy has been proposed to develop from attempts to perform vertical escape flights that are prevented by the roof of the cage (Asher, Davies, Bertenshaw, Cox, & Bateson, 2009; Brilot, Asher, Feenders, & Bateson, 2009). In zoo carnivores, there is a suggestion that motivation to move might be important in the development of route-tracing stereotypies, because a comparative meta-analysis of zoo data showed that stereotypy levels (typically pacing or

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Manuscript Received: 27 August 2011
Manuscript Accepted: 31 October 2011
Correspondence to: Melissa Bateson
Contract grant sponsor: BBSRC
Contract grant number: BB/05623/1

DOI 10.1002/dev.20623 • © 2011 Wiley Periodicals, Inc.

route-tracing in these species) are predicted by a species' natural home range and daily travel distance (Clubb & Mason, 2007). However, despite these efforts to identify the motivational systems involved in the development of stereotypies and the behavior patterns from which they originate, little is currently known about the appearance of the very early stages of stereotypic behavior.

Stereotypies have been hypothesized to develop through a series of stages: first, during ritualization, the behavior becomes less variable; second, during emancipation, the behavioral sequence is elicited by progressively more environmental stimuli; third, during establishment, the sequence becomes more difficult to reverse; and finally, during escalation, the sequence takes up progressively more of the animal's time (Mason, 1993; Meehan et al., 2004). Although a variety of studies on mainly mammalian species have focused on the emancipation and establishment stages of development of stereotypic behavior (reviewed in Mason, 1993), more detailed data are required from longitudinal studies that include the very early stages of stereotypy development. Such data are needed to validate the descriptive model of stereotypy development outlined above and to identify the causes for the development of these abnormal behavior patterns. Understanding the early development of stereotypies is likely to be important in designing interventions to prevent abnormal behavior patterns becoming established as irreversible stereotypies.

One problem in this field of research is the heterogeneity within species in how individuals cope with captive environments. While some individuals develop high levels of stereotypic behavior, others behave apparently normally, meaning that large sample sizes are needed in order to study developing stereotypies. The acquisition of large datasets on behavior can be prohibitively time consuming if manual scoring of video data is involved. Technology for automated tracking of behavior provides an obvious solution to this problem, since it potentially allows collection of detailed, longitudinal data on many individuals simultaneously. Route-tracing stereotypies would appear to be particularly amenable to automated tracking since they involve clear changes in physical location within the cage that should be readily detectable. A major advantage of using changes in location to quantify stereotypic behavior is that continuous changes in the animals' behavior can be measured as routes become established, allowing the detection of subtle changes in behavior (Brilot et al., 2009).

The aim of the current study was to describe the development of stereotypic route-tracing behavior in European starlings placed in individual laboratory cages for the first time. We chose starlings as a model of a wild animal frequently held in captivity for research purposes (Asher & Bateson, 2008; Bateson & Feenders, 2010). Route-tracing is one of the most commonly reported stereotypies in passerine birds (Garner, Meehan, & Mench, 2003; Keiper, 1969), and has previously been described in starlings (Asher et al., 2009). Caged starlings are also known to develop stereotypic somersaulting (Asher et al., 2009; Brilot, Asher, & Bateson, 2010; Brilot et al., 2009). Specifically, we sought to (i) identify behavior patterns associated with the early development of route-tracing stereotypies and somersaulting; (ii) investigate the effect of early life experience on the development of stereotypies by comparing birds that had been reared in the laboratory by humans with birds reared in the wild by their parents; (iii) evaluate the reversibility of stereotypies by moving birds to large aviaries for a period before returning them to individual cages; (iv) investigate whether there is a positive correlation between the development of route-tracing and somersaulting stereotypies.

We measured the birds' movements in the cage using an automated tracking system that recorded the position of the bird within the cage continuously. From these data we extracted a variety of behavioral metrics that described general activity levels, space use within the cage and temporal patterning of space use (route-tracing). To measure temporal patterning of space use we used T-pattern analysis implemented in the software package Theme (Magnusson, 2000) to detect event sequences that are repeated more often than expected by chance, based on the observed frequency and timing of the events (Brilot et al., 2009; Magnusson, 2000). The advantage of T-pattern analysis over, for example, Markov chain analysis is that it is insensitive to distracting events: whereas the Markov chain algorithm is strictly based on the sequence of events (e.g., B follows A), the T-pattern algorithm analyses the event sequence based on the temporal distribution, ignoring events that are only occasionally inserted within the T-pattern (e.g., the sequence A—B produced within 2 s is identified as a T-pattern irrespective of an additional event occurring during these 2 s). Thus, with this algorithm even event sequences with some variability will be identified as T-patterns, making this technique very useful for quantifying the early, more variable stages in the development of route-tracing.

Based on previous studies of stereotypic behavior in passerines we predicted that a proportion of the birds (between 10% and 40% based on previous studies; Asher et al., 2009; Brilot et al., 2009, 2010) would develop stereotypies when placed in individual cages. We made the following specific predictions about how the behavior of the birds would change: (i) inactive periods should decrease with increasing stereotypic route-tracing because the animal spends progressively more time performing the stereotypic behavior pattern; (ii) general space use should decrease with increasing stereotypic route-tracing because the animal concentrates on a restricted number of movement patterns with decreasing variability; (iii) the use of the cage walls should increase with increasing escape motivation (Maddocks, Goldsmith, & Cuthill, 2002) and hence development of the somersaulting stereotypy (Brilot et al., 2009); (iv) both the number of different T-patterns and the total number of T-patterns performed should increase as route-tracing stereotypies develop (Brilot et al., 2009).

METHODS

Animals

A total of 34 starlings were used, with 17 birds in both the hand-reared and the wild-caught group. All birds originated from the same population of starlings in North East England, were hatched in 2009 and were of a similar age (the short-breeding season of starlings in Northern England only allows for only one brood each spring). We took all possible steps to ensure that the birds were not closely related (i.e., not siblings). Birds for the hand-reared group were taken from nest boxes as nestlings (~10 days old), one chick per clutch, in spring 2009 and hand-reared in the laboratory (for further details of husbandry procedures see Feenders & Bateson, 2011). Once they became independent (~4 weeks old), they were transferred to an indoor aviary (215 × 340 × 220 cm^3 WDH), provided with environmental enrichment and food and water ad libitum (~19°C, 14L:10D). Birds for the wild-caught group were caught in the autumn of the same year (when they could still be clearly identified as that year's birds from their juvenile plumage) with a baited whoosh net and housed in a separate indoor aviary under identical housing conditions to the hand-reared group. The wild-caught birds originated from different clutches from the hand-reared birds (we know this because the remaining chicks from clutches used for taking the hand-reared nestlings were marked with metal rings), and were caught from a flock of several hundred birds making it unlikely that any two wild-caught birds came from the same clutch.

Experimental Cages/Procedures

For behavioral recording birds were transferred to individual test cages. In the test room, eight cages (100 × 45 × 45 cm^3 WDH) with transparent Plexiglas roofs were placed on two rows of shelves at 38 and 120 cm height. Each cage was fitted with an overhead surveillance camera (Atom, CSP Technology, Scunthorpe, UK) connected to an adjacent room for remote observation and recording. Four cages were environmentally enriched with a small hide, a probing tray (filled with small wood chips) and water bath, while the other four cages had empty tray and bath (the bath was filled twice a week for 1 hr to ensure good hygiene). The experimental set-up has been described in detail in Feenders & Bateson (2011).

We sequentially tested four replicate groups of eight birds, each group consisting of four hand-reared and four wild-caught birds. The birds were assigned to the cages in a counterbalanced fashion with respect to developmental history and enrichment condition. Different environmental enrichment conditions had initially been introduced into our design because enrichment has been shown to modify the affective state (anxiety) in starlings (Bateson & Matheson, 2007; Matheson, Asher, & Bateson, 2008; but see Brilot et al., 2010) which in turn might affect the development of stereotypy. However, the enrichments used in this study did not have any significant effect on fear or exploration in our experimental birds (Feenders & Bateson, 2011; Feenders, Klaus, & Bateson, 2011) and in a preliminary analysis of the current dataset, so for the remainder of the paper we pool the data from the two enrichment conditions.

In part 1 of the experiment, the birds were kept in cages for 14 days before being returned to their aviaries and the next group being moved in. During this part, the birds had access to food and water at all times while participating in some personality tests (Feenders et al., 2011).

Part 2 started 8–21 weeks later, a wide range because birds were shuffled between replicate groups so that they were tested in new group compositions. One group of eight birds was placed back into the cages for 32 days, but now at a different cage location, before being returned to the aviaries and the next group being moved in. While in the cages, the birds were food-deprived over night to participate in operant tasks in the morning (unpublished data).

One of our stated aims was to relate route-tracing stereotypy to other, previously described abnormal behavior such as somersaults and loops (Asher et al., 2009; Brilot et al., 2009). However, during parts 1 and 2 somersaulting was only observed once (in part 2). Although we cannot exclude the occasional occurrence of somersaulting at earlier stages of the experiment because we did not manually analyze all the videos, this rate of somersaulting was unexpectedly low. We hypothesized that the lack of somersaulting behavior might be due to the smooth Plexiglas cage ceiling interfering with the development of somersaulting. Thus, in an attempt to explore this possibility, in part 3 the birds were moved into cages with a wire-mesh ceiling (75 × 45 × 45 cm^3 WDH) comparable to those used in previous studies. No enrichment was provided in these cages and the birds were kept in them for 7 days. Three replicate groups had been in aviaries for 6–34 weeks after completion of part 2 and prior to starting part 3, while the last group (due to time constraints) was directly transferred from the test cages used in parts 1 and 2 to the wire-ceilinged cages. Figure 1 provides an overview of the experimental schedule experienced by the birds.

One wild-caught bird died during part 1 and was replaced for part 2; one hand-reared bird died after completion of part 1 and was replaced for part 2. Thus, a total of 4 birds did not

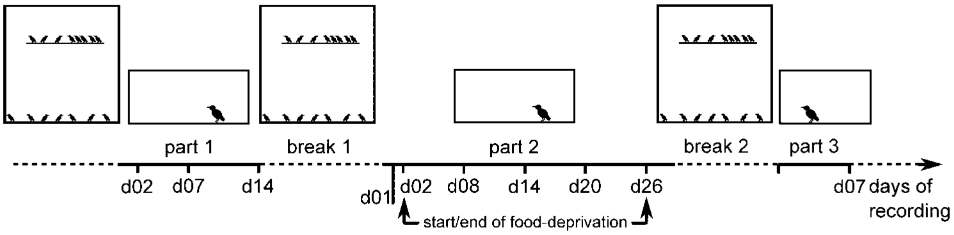

FIGURE 1 Experimental schedule showing the change between aviaries (large rectangles with multiple birds) and individual cages (smaller rectangles with one bird) in the three parts of the study. Birds in cages/aviaries are drawn approximately to scale; aviaries are not in scale to cages. Cage/aviary furnishing is not shown.

participate in all three parts of the experiment. Data from these 4 birds were excluded from the data analysis because of discontinuous data collection resulting in a final sample size of 15 hand-reared and 15 wild-caught birds.

Data Collection

For parts 1 and 2, the birds' behavior was recorded daily for 1 hr in the morning starting at 07:00 hr (when the lights went on). The videos were automatically analyzed using the tracking software EthoVision XT v5.1 (Noldus Information Technology, Wageningen, Netherlands). This software is based on a contrast-detection algorithm to record the position of the target object within a pre-defined area of the video footage. The dark starling was reliably detected on the light background of the cage (cage floors were lined with white paper; solid cage sides were also white). A sampling rate of 2.5 frames per second yielded accurate results optimized for time efficiency. At each sample, the bird's position was recorded, expressed as *x*–*y*-coordinates as well as a distinct cage location. For the latter, the top-view image of the cage was divided into 15 areas corresponding to defined cage locations (perch left/right, floor, tray, food, bath, side wall left/right, back wall, front wall left/right, corner at top front left/right, corner at top back left/right; Fig. 2A). For part 3, the birds were recorded for 30 min at 08:45 hr directly prior to husbandry. In order to allow for clear detection of somersaults, camcorders (Sony) were placed in front of the cages to obtain better viewing angles as compared to the top-view cameras used in the test cages; the first and last 5 min of the videos were analyzed using JWatcher v1.0 (http://www.jwatcher.ucla.edu) to record any occurrence of somersaulting, loops, falls, and back-flips (see Tab. 1 for description of behavior patterns). Birds that performed three or more of any of these behavior patterns were grouped as "somersaulting" (SOM) and all other birds as "normal" (NML). The top-view videos taken on d02 of part 1 were also manually scanned for any occurrence of somersaulting, loops, falls, and back-flips to obtain additional information on the emergence of those behavior patterns.

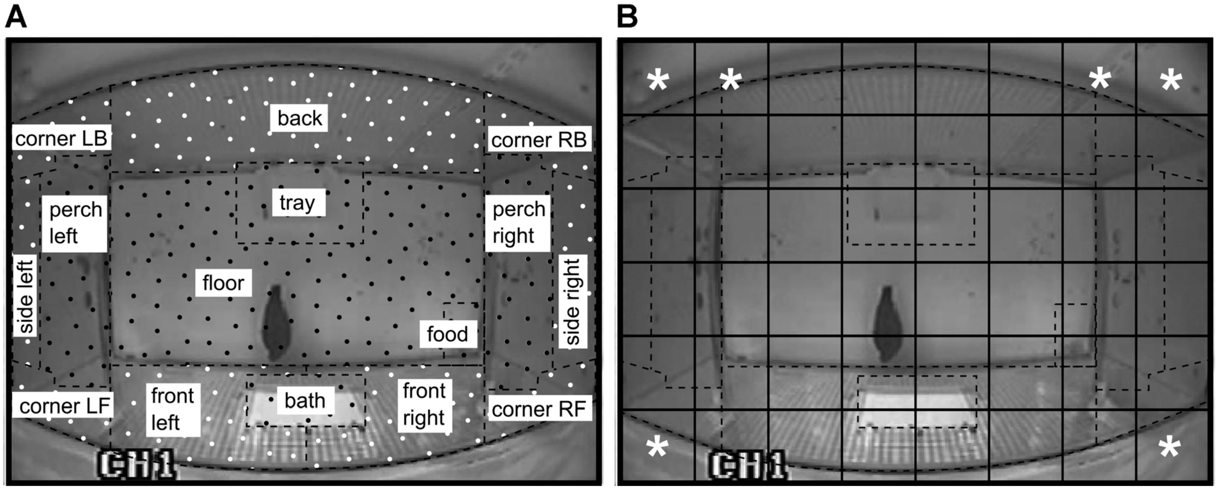

FIGURE 2 Experimental set-up showing the top-view of the video with the arrangement (A) of the 15 cage locations and (B) of the grid for space use calculations. White dotted areas in (A) indicate cage locations summarized as "cage walls." Asterisks in (B) mark grid cells hardly covered by the cage and thus not available to the bird as usable space.

Table 1. Description of the Abnormal Somersaulting Behavior Patterns

Behavior	Description
Somersault	Backward, aerial loop starting and ending on cage floor (never observed from anywhere else), with legs passing above the head
Loop	Similar to a somersault but with the bird very briefly clinging to the cage wall/ceiling or perch, usually up-side down with feet being highest; can be performed from floor (to ceiling, wall or perch) or perch (to ceiling)
Fall	"Falling" backwards off the perch
Back-flip	Rapid backward movement on the floor resembling a somersault without the actual loop-component (only observed in one bird)

General Activity and Use of Cage Walls

The bird's general activity was described by the total length of time the bird spent moving (>10 cm/s) within the observation time (3,600 s)—Tmove. In addition, the use of the cage walls (previously discussed as an indicator of escape attempts; Maddocks et al., 2002) was extracted from the tracking data: the total number of visits to the walls—Fwalls (for an illustration, see Fig. 2A).

Cells Visited

To provide a metric of how much of the available space within the cage a bird actually used, we divided the video image of the cage into a grid of 48 equally sized cells (8 × 6 array; Fig. 2B). The number of different grid cells visited by a bird was counted as our measure of space use (CellsVisited). Because the grid was applied to the full video image, with the cage interior covering most, but not all, of the video image, some marginal cells had very little overlap with the cage interior (approximately 6 cells; Fig. 2B). Thus, birds could actually make use of only 42 of the 48 grid cells, meaning that CellsVisited could theoretically take values between 1 and 42.

Temporal Pattern Analysis

The sequence of position changes (coded as distinct cage locations) was transferred from the EthoVision into the Theme software package (Noldus Information Technology, Wageningen, Netherlands). The algorithm of Theme detects T-patterns (temporal patterns), that is, recurring sequences of events with respect to their temporal distribution. The insensitivity to distracting events makes this algorithm well suited to detect "hidden" patterns (Magnusson, 2000). As discussed in Brilot et al. (2009), Theme has a battery of parameters to be set by the user. Based on our previous experience, we used the default settings except for the following parameters: "minimum pattern occurrences" (the threshold of occurrences a pattern has to reach in order to be counted as a pattern) was set to 3 (recommended as one default option by the Manual) because the algorithm does account for event frequency and we did not want to over-control for the bird's activity; the "significance level" (the acceptance threshold for the null hypothesis that a pattern could have occurred with a random distribution of the according events) was set to .0001 for a more conservative threshold on this large dataset (for a detailed discussion of this software and the parameters, please refer to Brilot et al., 2009). The following output metrics were used as potentially informative indicators of route-tracing intensity: the number of different T-patterns (PatDiff); and the total number of T-pattern occurrences (PatOcc).

Statistical Methods

Our dependent variables comprised the five metrics described above (Tmove, Fwalls, CellsVisited, PatDiff, PatOcc). These were extracted from days 02, 07, and 14 in part 1, and from days 01, 02, 08, 14, 20, and 26 in part 2. Day 01 of part 2 was used to compare with data collected in part 1 because all birds were provided with food on this first day of part 2 as on all days in part 1; in contrast, during the following days of part 2 the birds were without food in the morning, which could have potentially influenced their behavior and the data collected from this period is thus not directly comparable with data from part 1. The values for Tmove and Fwalls were expressed as a proportion of the observation period and of the total number of location changes, respectively. These proportions were arcsine square-root transformed and the values of PatDiff, PatOcc, and CellsVisited were log-transformed to normalize their distributions.

The independent variables that we explored in our analyses included: the origin of the birds, which was a between-subjects variable with two levels (hand-reared vs. wild-caught); the length of time that the birds had been in cages, which was a within subjects variable with three levels in part 1 (days 02, 07, and 14) and five levels in part 2 (days 02, 08, 14, 20, and 26). For the wild-caught birds only, we also explored the effects of whether or not the birds developed somersaulting in part 3. Because of the low sample size of group SOM ($N = 6$) and the heterogeneity of behavior patterns displayed in the birds, we did not include different stereotypy levels into the analyses but instead used the presence or absence of somersaulting behavior as a between-subjects categorical variable with two levels (SOM and NML). As stated above, previous data from this group of birds (Feenders & Bateson, 2011; Feenders et al., 2011) and preliminary analyses of the current dataset did not reveal any effect of current housing condition (enriched vs. non-enriched); thus, for simplicity and to maximize power, we decided to exclude this variable from all of the analyses reported in this paper.

All statistical analysis was conducted using SPSS 17.0 (IBM). To test for an overall effect of origin (hand-reared vs.

wild-caught) and time (days in cages), repeated-measures MANOVA was performed on the five behavioral metrics using the data from part 1 d02, 07, and 14 with origin as a between-subjects independent variable. Significant effects were further explored by running repeated-measures ANOVAs separately for each of the five metrics. A similar analysis was done on the data from part 2 d02, 07, 14, 20, and 26. The impact of the break in the aviary between parts 1 and 2 was examined using a repeated-measures MANOVA on all five metrics using the data from part 1 d14 and part 2 d01 with origin as a between-subjects independent variable. Data from the wild-caught birds only, were analyzed to identify predictors of somersaulting behavior. For this analysis, data from part 1 d02, 07, 14 were analyzed using a repeated-measures MANOVA with the occurrence of somersaulting behavior as a between-subjects variable and time as a within-subjects repeated measure. This MANOVA analysis was followed by forward stepwise discriminant function analyses, using either data from part 1 d02 or part 1 d14, with somersaulting occurrence as the grouping variable.

Since some ANOVA models showed a violation of sphericity (Mauchly's sphericity test, $p < .05$), we used the Greenhouse-Geisser correction for those cases. If the assumption of equal error variances was violated for testing the between-subjects effect (Levene's test, $p < .05$), we applied a non-parametric analysis implemented in the package "nparLD" of the R-project (http://www.r-project.org; using this non-parametric test did not change the significance of the results when compared to the parametric test). For the paired-samples comparison, if the normality assumption was not met (Shapiro–Wilk's test, $p < .05$) the non-parametric Wilcoxon Signed-Ranks Test was applied.

To explore correlations between metrics, the Pearson correlation was used. Where the assumption of normality was violated (Shapiro–Wilk's test, $p < .05$), the Spearman's rank correlation was used.

RESULTS

Change in Behavior Over Time

The repeated-measures MANOVA on data collected on days 02, 07, 14 in part 1 revealed a significant effect of time ($F_{2,27} = 13.777$, $p < .001$) and time × origin interaction (a larger increase in CellsVisited, PatDiff and PatOcc for hand-reared birds, in Tmove and Fwalls for wild-caught birds; $F_{2,27} = 7.648$, $p = .002$); there was no main effect of origin ($F_{1,28} = .005$, $p = .944$) because the groups differed in opposite directions for different metrics. Separate repeated-measures ANOVAs for each of the five metrics yielded a significant effect of time on each metric (increase over time; $p \leq .017$) and of origin as a main effect on all except PatDiff, with the hand-reared birds showing higher values than the wild-caught birds for Tmove and PatOcc, but lower values for CellsVisited and Fwalls ($p \leq .041$; for individual F- and p-values see Tab. 2). This shows that both groups changed their behavior over time, but the magnitude of the change depended on the birds' origin (Fig. 3A–E).

The repeated-measures MANOVA of data collected on days 02, 08, 14, 20, and 26 in part 2 revealed a significant effect of time ($F_{4,25} = 17.955$, $p < .001$), but not of the time × origin interaction ($F_{4,25} = 1.292$, $p = .300$) or origin as main effect ($F_{1,28} = 1.247$, $p = .274$). Separate repeated-measures ANOVAs for each of the five metrics yielded a significant effect (increase) of time on all except CellsVisited ($p \leq .012$), of time × origin interaction on PatDiff (hand-reared birds increased less than the wild-caught birds; $p = .026$) and of origin on Fwalls with the hand-reared

Table 2. Statistical Results From Separate Repeated-Measures GLMs (or Non-Parametric Equivalent) on the Five Behavior Metrics From Part 1 And Part 2, Including Time (Repeated Factor) and Origin (Hand-Reared vs. Wild-Caught)

Metric	Time	Time × Origin	Origin
Part 1 d02, 07, 14			
Tmove (time spent moving)	**8.633, .003**[a]	3.481, .059[a]	**4.577, .041**
PosVisited (diff. cells visited)	**4.358, .017**	2.298, .110	**5.393, .028**
Fwalls (visits to cage walls)	**6.143, .004**	.847, .434	**6.303, .018**
PatDiff (diff. T-patterns)	**4.834, .012**	.111, .895	1.140, .295
PatOcc (total T-pattern occur.)	**21.98, <.001**[b]	.49, .610[b]	**5.72, .017**[b]
Part 2 d02, 07, 14, 20, 26			
Tmove	**8.990, <.001**[a]	1.230, .303[a]	2.630, .116
PosVisited	2.337, .108[a]	1.520, .228[a]	.463, .502
Fwalls	**4.037, .012**[a]	.507, .665[a]	**7.948, .009**
PatDiff	**3.01, .030**[b]	**3.26, .022**[b]	.37, .544[b]
PatOcc	**10.14, <.001**[b]	1.34, .259[b]	.35, .553[b]

Each cell contains the F-ratio followed by the associated p-value (part 1: time, time × origin $df = 2.56$; part 2: time, time × origin $df = 4.112$; both parts: origin $df = 1.28$). Significant effects ($p < .05$) are highlighted in bold.

[a] Greenhouse-Geisser corrected values.

[b] Non-parametric test result.

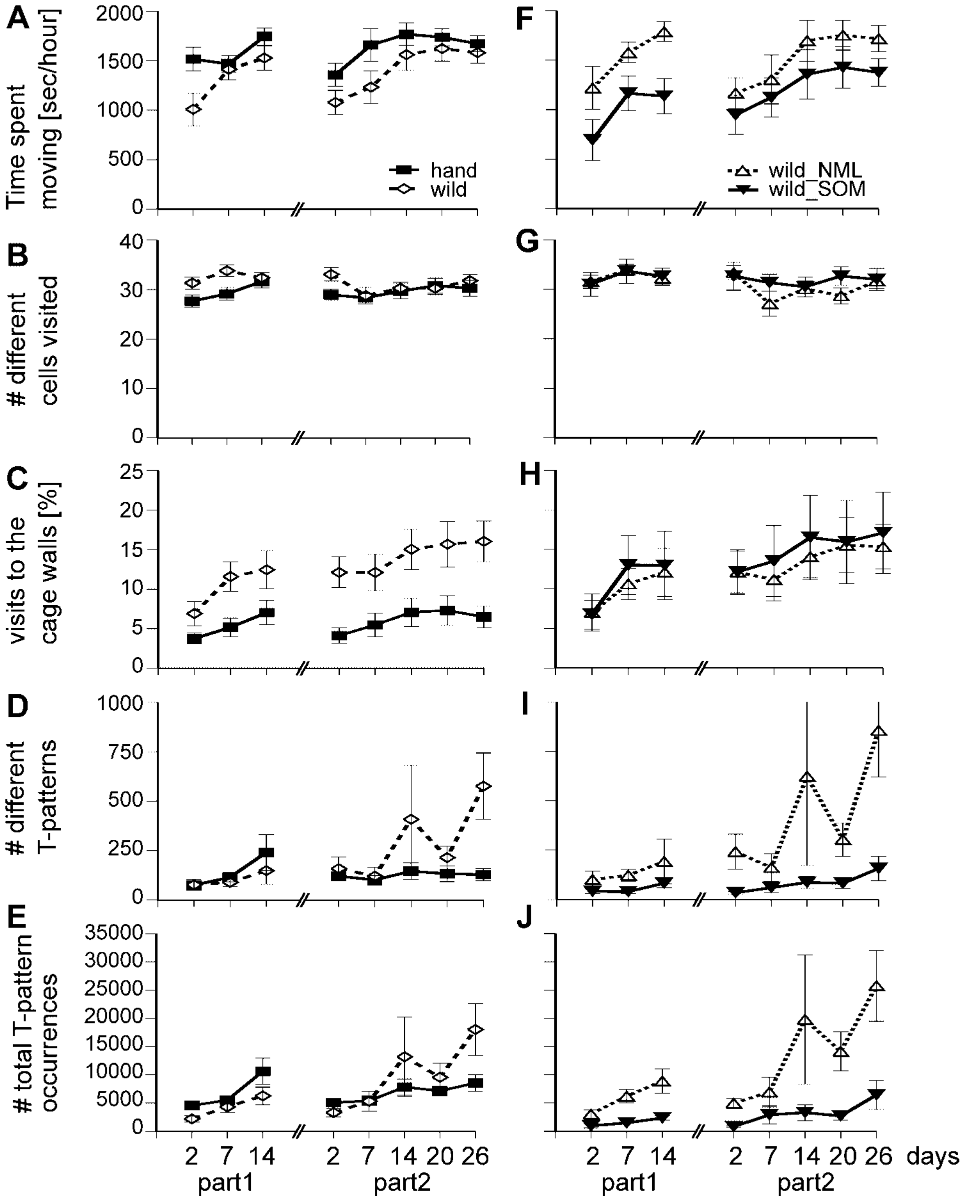

FIGURE 3 Change in behavior over time, comparing the effect of origin (A–E) and performance of somersaulting in wild-caught birds (F–J). (A,F) General activity, (B,G) space use, (C,H) use of cage walls, (D,E,I,J) route-tracing. hand = hand-reared birds, wild = wild-caught birds, NML = normal group, SOM = somersaulting group. Shown are means ± SEM.

birds showing lower values than wild-caught ones ($p = .009$; Tab. 2). This shows that both groups changed their behavior over time, with little effect of origin (Fig. 3F–J).

To examine whether Fwalls was driving T-pattern performance (by adding new cage locations to the repertoire), correlations were calculated. On part 1 d02, Fwalls was neither correlated with PatDiff (Spearman's rho = .171, $p = .367$) nor with PatOcc (Spearman's rho = −.344, $p = .064$). On part 1 d14, Fwalls was positively correlated with PatDiff (Pearson's $R = .665$, $p < .001$) and weakly positively with PatOcc (Pearson's $R = .365$, $p = .047$). On part 2 d26, Fwalls was positively correlated with PatDiff (Pearson's $R = .679$, $p < .001$) and with PatOcc (Pearson's $R = .494$, $p = .006$). Thus, the correlation of Fwalls with T-pattern performance increased over time.

Change in Behavior After Break in Aviary

When comparing data from part 1 d14 with part 2 d01, a repeated-measures MANOVA revealed a significant

Table 3. Statistical Results from Paired *t*-Tests Comparing Part 1 d14 With Part 2 d01

Tmove (Time Spent Moving)	PosVisited (Diff. Cells Visited)	Fwalls (Visits to Cage Walls)	PatDiff (Diff. T-Patterns)	PatOcc (Total T-Pattern Occurrences)
7.436, <.001	−1.842, .066[a]	**2.221, .034**	**4.160, <.001**	**7.349, <.001**

Each cell contains the relevant t_{29}- and p-values. Significant effects are highlighted in bold.

[a] Wilcoxon signed-rank test (t- and p-value, $N = 30$).

effect of time ($F_{1,28} = 47.572$, $p < .001$) but no time × origin interaction ($F_{1,28} = .009$, $p = .925$) or main effect of origin ($F_{1,28} = .220$, $p = .643$). Separate paired *t*-tests showed a significant change for all but CellsVisited ($p \leq .034$; Tab. 3), and this change was always due to a decrease (Fig. 4). Thus, both groups reduced levels of potentially stereotypic behavior after a break in the aviary.

Somersaulting Behavior

The analysis of video recordings showed no occurrence of somersaulting behavior (somersaults, loops, falls, or back-flips) on d02 in part 1; in part 3, a total of six birds performed such behavior (both during the first and the last 5 min of the observation period) and all these birds were from the wild-caught group (Fig. 5). Further analysis to identify predictors of this somersaulting behavior was done on data from the wild-caught birds only. A repeated-measures MANOVA of data collected on days 02, 07, 14 in part 1 resulted in a significant effect of time ($F_{2,12} = 19.942$, $p < .001$) and whether or not the bird developed somersaulting behavior ($F_{1,13} = 6.261$, $p = .026$), but not of the time × somersaulting interaction ($F_{2,12} = .875$, $p = .442$). Figure 3F–J indicates that most metrics increased over time, and that the SOM group had lower values than the NML group for Tmove, PatDiff, and PatOcc. Based on this main effect of somersaulting, a forward stepwise discriminant function analysis (DFA) was performed to extract those metrics that best describe the group difference. A DFA on data from d02 (part 1) resulted in a significant function ($p = .016$; Wilk's $\lambda = .626$) including PatOcc; this function classified a total of 86.7% of cases correctly (86.7% of cross-validated cases). When running the same analysis but instead on data from d14 (part 1), the resulting function ($p < .001$; Wilk's $\lambda = .198$) included PatOcc and PatDiff; this function classified a total of 100% of cases correctly (86.7% of cross-validated cases). These results show that the group difference between the SOM and NML birds was mainly driven by differing use of T-patterns. This conclusion is supported by separate repeated-measures ANOVAs showing a main effect of somersaulting behavior on PatDiff and PatOcc ($p \leq .019$; Tab. 4, Fig. 3F–J) with the SOM group exhibiting lower values than the NML group.

DISCUSSION

Extracting and analyzing five behavioral metrics that characterize different aspects of movement within the cage, we found that the movement patterns of caged starlings changed over time and were partly re-set after a break in aviaries. The origin of the birds had a significant impact on these behavioral changes, with the wild-caught birds showing an overall higher use of cage walls. Furthermore, somersaulting and its precursors were only observed in wild-caught birds, and whether a given wild-caught bird subsequently developed these abnormal behavior patterns could be predicted from subtle differences in the spatial patterning of its behavior (T-pattern metrics) during its first few days in a cage. We discuss these findings in more detail in the following paragraphs.

General Activity—Time Spent Moving

During both spells in cages (parts 1 and 2), the birds increased their activity over time. This may be due to an initial escape motivation (e.g., jumps to the cage walls, see next section) that was driving the birds to move around the cage, a behavior that became more ritualized and emancipated over time. The break in the aviary seemed to reset this behavior—expressed in the prominent drop in Tmove between the last day of part 1 and the first days of part 2 (Fig. 4A)—indicating that it had not crystallized as a full stereotypy (neither established nor escalated). Alternatively, elevated activity levels may be motivated by food anticipatory behavior (e.g., Hansen & Jeppesen, 2006; Mistlberger, 1994; Spruijt, van den Bos, & Pijlman, 2001), but in the current study this would only apply to part 2 where food deprivation over night was followed by operant testing with food rewards in the morning. As our data showed an increase in activity over the first 2 weeks in both parts of the study, with the recording scheduled 4–5 hr before husbandry (and fresh food supplies), this explanation seems unlikely. Instead, as argued initially, the

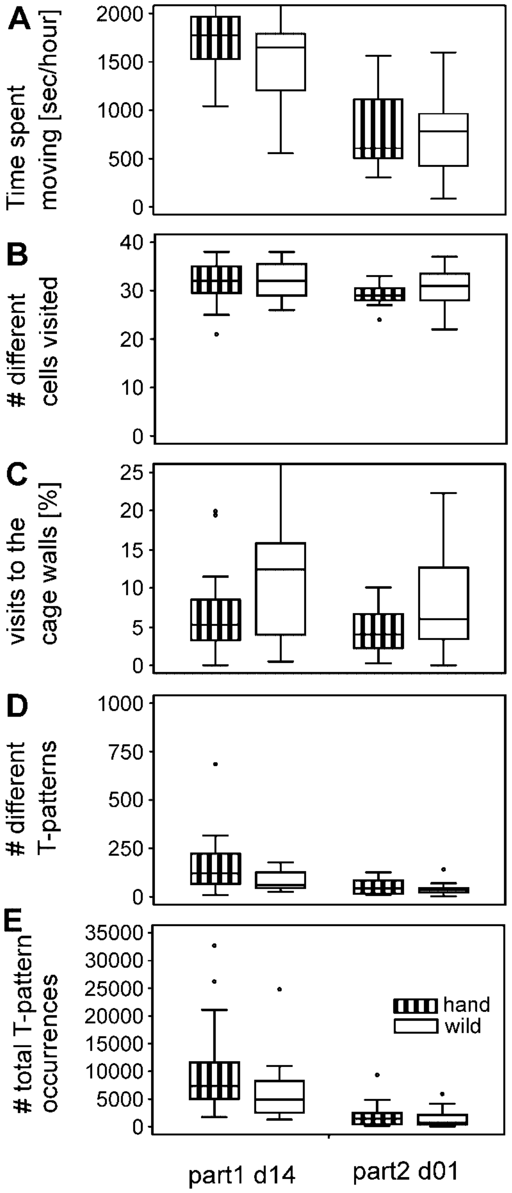

FIGURE 4 Change in behavior following aviary break (last day of part 1, first day of part 2), comparing the effect of origin. (A) General activity, (B) space use, (C) use of cage walls, (D, E) route-tracing. Striped boxes represent hand-reared (hand), white boxes wild-caught (wild) birds, whiskers indicate 1.5 IQR, dots represent outliers.

birds most likely developed very high activity levels, potentially some form of abnormal hyperactivity, as a reaction to the caged environment. We need to emphasize, though, that we cannot distinguish between different motivations for "activity" in this analysis, as we only measured the time the bird spent moving irrespective of the type of movement (e.g., regular exploration vs. route-tracing). Thus, it is important to examine other behavioral measures that are better suited as indicators of escape motivation or stereotypy, as discussed in the following section.

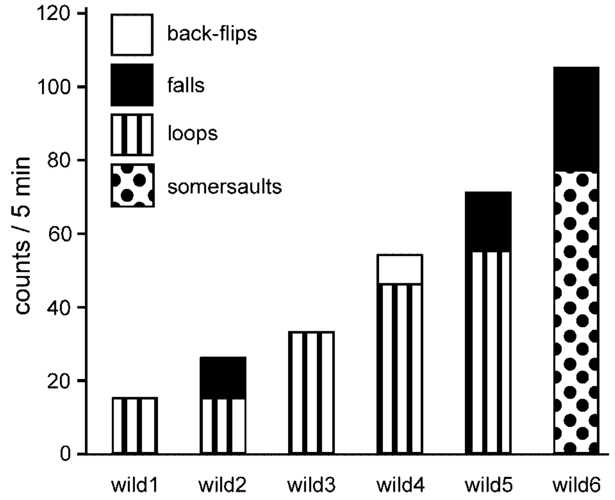

FIGURE 5 Occurrence of four different abnormal repetitive behavior patterns in six wild-caught birds (wild 1–6). Shown are the absolute numbers of events recorded during the first 5-min period in part 3 of the study.

Use of Cage Walls and Repetitive Patterns

The use of cage walls has been suggested as a measure of escape motivation in caged starlings (Feenders & Bateson, 2011; Maddocks et al., 2002). In our hand-reared birds it increased over time, starting at comparable levels in both parts 1 and 2; the wild-caught birds exhibited higher use of cage walls throughout and showed a steep increase after the aviary break to reach the high levels measured at the end of part 1 within <48 hr (Figs. 3C and 4C). It seems that for the wild-caught birds the routes incorporating the cage walls had reached more established (possibly irreversible) levels. The hypothesis that the use of cage walls could lead to an increase in T-pattern formation is supported by the finding that those measures showed an increase in correlation over time: on d02 (part 1) the use of cage walls was not correlated with T-pattern metrics, on d14 (part 1) it was strongly correlated with the number of different patterns but only weakly with total pattern occurrences, while on d26 (part 2) correlations were strong with both T-pattern numbers and occurrences. This suggests that, initially, incorporating the cage walls as new locations resulted mainly in an increase in the number of different T-patterns, and during later stages, these T-patterns were performed more frequently, leading also to an increase of T-pattern occurrences. In conclusion, we hypothesize that the birds' jumps to the cage walls were initially escape motivated but, over

Table 4. Statistical Results From Repeated-Measures GLMs From Part 1 of the Wild-Caught Group, Including Time (Repeated Factor) and somersaulting (NML vs. SOM)

Metric	Time	Time × somersaulting	somersaulting
Tmove (time spent moving)	**8.071, .009**[a]	.360, .603[a]	**9.610, .008**
PosVisited (diff. cells visited)	2.058, .148	.159, .854	.025, .877
Fwalls (visits to cage walls)	**4.174, .027**	.038, .963	.023, .883
PatDiff (diff. T-patterns)	1.576, .226	.151, .435	**7.184, .019**
PatOcc (total T-pattern occur.)	**11.907, <.001**	.416, .664	**25.601, <.001**

Each cell contains the F-ratio followed by the associated p-value (time, time × somersaulting $df = 2.26$; origin $df = 1.13$). Significant effects ($p < .05$) are highlighted in bold.

[a] Greenhouse-Geisser corrected values.

time, became emancipated, and established as repetitive routes.

Space Use

The number of cells visited (note that this is independent of the visit frequency) changed over time in part 1 but not in part 2. In a similar fashion, this metric was affected by origin in part 1 but not in part 2. Following up our hypothesis on the increased use of cage walls, it seems most likely that during part 1 the birds, and specifically the wild-caught birds, started to use the cage walls at various locations (e.g., front left, front right, back), resulting in an increased number of cells visited. In part 2, in contrast, the birds had more established movement patterns, visiting the same cells consistently. It is also noteworthy that the birds used the majority of the available grid cells—on average 30 of the 42 cells. This shows that despite the differences in activity levels between groups, both hand-reared and wild-caught birds were using the majority of the space available to them.

Development of Somersaulting Behavior

In part 3 of the present study, somersaulting behavior (comprising somersaults, loops, falls, and back-flips) occurred in six birds within 1 week of the birds being placed in wire-ceilinged cages. Although the scoring for somersaulting was done on birds that had experienced different repetitions of caged housing and differing durations in the aviary prior to testing, measures taken in part 1 already segregated birds that developed somersaulting from those that did not although none of the birds (or any of the other birds) performed this behavior from the very beginning (i.e., day 02 part 1). We do not know when these behavior patterns emerged, because we did not measure the occurrence of somersaulting at any other stage during the caged housing as our aim was to characterize the change in behavior by time-efficient automated techniques. Nevertheless, we know from previous studies that starlings sometimes perform somersaults after 1 week in cages (Asher et al., 2009; Brilot et al., 2009). Furthermore, as can be seen from the graphs, changes in various behavioral measures happened mainly during the first 2 weeks in cages (in both part 1 and 2) after which time the measures reached more stable levels. Based on these results, we argue that for starlings the birds' behavioral response to being confined in a cage occurs rapidly, within the first 2 weeks. Previous studies have reported longer delays in the onset of stereotypy in a range of other species, for example, 2 weeks or more in deer mice (Powell, Newman, Pendergast, & Lewis, 1999), about 3 weeks in domestic mice (Würbel, Chapman, & Rutland, 1998; Würbel et al., 1996), and 4 weeks in young parrots (Meehan et al., 2004), but these studies mainly considered the onset of stereotypic behavior directly after weaning. In our study, however, we observed animals that had reached independence several months before being tested (c.f. Meehan et al.'s (2004) study of 4-month-old parrots). It is possible that wild passerine birds, or specifically starlings, quickly habituate to captive environments by forming certain fixed behavior patterns that may develop into stereotypies. This emphasizes the importance of the housing quality during the first days in cages.

Interestingly, within the wild-caught birds those that exhibited somersaulting in part 3 showed consistently lower activity (Tmove) and lower numbers of T-patterns (PatDiff and PatOcc) in parts 1 and 2 when compared to the non-somersaulting birds. It seems that these birds, instead of increasing their activity in terms of distance covered and route-tracing, performed thwarted escape attempts on the spot such as head-tilting and unbalancing that developed into falls, loops, and somersaults (Brilot et al., 2009).

Escape Motivation

Combining the results from the current study with those of a previous study in which we compared the reaction of hand-reared and wild-caught starlings to a novel environment reveals an interesting picture: wild-caught starlings had shorter latencies to start moving in a novel environment test than hand-reared birds (Feenders et al., 2011), and were also more likely to develop somersaulting than hand-reared birds (present study). This is in line with a finding from Cooper and colleagues (Cooper, Ödberg, & Nicol, 1996), who tested the reaction of bank voles (*Clethrionomys glareolus*) to a sudden rattle and found voles that stereotyped to have shorter latencies to move after the rattle. These authors argued that the voles with shorter latency to move either experienced the stimulus as more aversive or had higher escape motivation than the individuals with longer latencies. Based on this discussion we suggest that the wild-caught birds in our own studies were more prone to develop somersaulting because they had higher escape motivation (short latency to move, higher use of cage walls) in a small confined space.

The Impact of Origin

Previous studies have suggested that captive-bred animals exhibit a stronger tendency to develop stereotypies than their wild-caught conspecifics (Mason & Rushen, 2006). A recent experimental study on African striped mice (*Rhabdomys*; Jones, Mason, & Pillay, 2011) provides further evidence by showing that captive-bred mice were more stereotypic than mice caught from the wild (although, when mice were caught as juveniles, stereotypy levels were much higher and reached levels of captive-bred mice). However, the wild-caught mice were less active and more fearful than the captive-bred mice, a behavior that, according to the authors, may indicate depression-related apathy. In our study, wild-caught birds were also less active than the hand-reared birds, at least in part 1, suggesting that the wild-caught birds were more fearful in the captive environment. However, our data do not support the previous finding that captive-bred animals are more prone to develop stereotypies. Our wild-caught birds showed higher use of cage walls and developed higher numbers of T-patterns indicating more route-tracing. This is in line with a previous study in blue jays (*Cyanocitta cristata)* reporting more route-tracing stereotypies in wild-caught as compared to hand-reared birds (Keiper, 1969). Furthermore, we exclusively recorded somersaults, falls, loops, and back-flips in the wild-caught birds. Moreover, the hypothesis that high activity levels are related to stereotypic behavior (Garner & Mason, 2002; Jones et al., 2011) is not supported by our results because we found that hand-reared birds were more active but engaged less in both somersaulting and route-tracing stereotypies. This discrepancy between the mainly mammalian-based results and our results from starlings may reflect species-specific responses to captive environments. Further research is needed to elucidate in more detail what factors trigger the development of stereotypies. Automated tracking techniques, as used in our study, are useful tools to collect detailed, longitudinal data on a variety of species under different rearing and housing regimes; only such a comparative approach will provide the data to allow the discrimination of species-specific from common features of stereotypic behavior.

In conclusion, we have shown that automated tracking techniques are time efficient tools to describe movement patterns characterizing starlings with different upbringing. Distinctly stereotypic behavior was only observed in some of the wild-caught birds, and interestingly these individuals could already be distinguished from features of the their behavior during the first days of caged housing. Our data suggest a role for escape motivation in the development of starling stereotypies and additionally that route-tracing and somersaulting may represent alternative outlets for thwarted escape.

NOTES

This work was supported by a BBSRC grant to MB (Ref: BB/05623/1). We thank Martin Hughes for helping us to obtain the starling chicks; the Northumbrian farmers for allowing us to hang nest boxes on their properties; our colleagues for their help with hand-rearing the chicks; Michelle Waddle and Rachel Kendal for animal care; Charles Gray for building the cages; and Christoph Feenders for the computer script to analyze space use.

REFERENCES

Asher, L., & Bateson, M. (2008). Use and husbandry of captive European starlings (*Sturnus vulgaris*) in scientific research: A review of current practice. Laboratory Animals, 42(2), 111–126.

Asher, L., Davies, G. T. O., Bertenshaw, C. E., Cox, M. A. A., & Bateson, M. (2009). The effects of cage volume and cage shape on the condition and behaviour of captive European starlings (*Sturnus vulgaris*). Applied Animal Behaviour Science, 116(2–4), 286–294.

Bateson, M., & Feenders, G. (2010). The use of passerine bird species in laboratory research: Implications of basic biology for husbandry and welfare. ILAR Journal, 51(4), 394–408.

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*). Animal Welfare, 16, 33–36.

Brilot, B. O., Asher, L., & Bateson, M. (2010). Stereotyping starlings are more ‘‘pessimistic. Animal Cognition, 13(5), 721–731.

Brilot, B. O., Asher, L., Feenders, G., & Bateson, M. (2009). Quantification of abnormal repetitive behaviour in captive European starlings (*Sturnus vulgaris*). Behavioural Processes, 82(3), 256–264.

Clubb, R., & Mason, G. J. (2007). Natural behavioural biology as a risk factor in carnivore welfare: How analysing species differences could help zoos improve enclosures. Applied Animal Behaviour Science, 102(3–4), 303–328.

Cooper, J. J., Ödberg, F., & Nicol, C. J. (1996). Limitations on the effectiveness of environmental improvement in reducing stereotypic behaviour in bank voles (*Clethrionomys glareolus*). Applied Animal Behaviour Science, 48(3–4), 237–248.

Feenders, G., & Bateson, M. (2011). Hand-rearing reduces fear of humans in european starlings, *Sturnus vulgaris*. PLoS ONE, 6(2), e17466.

Feenders, G., Klaus, K., & Bateson, M. (2011). Fear and exploration in European starlings (*Sturnus vulgaris*): A comparison of hand-reared and wild-caught birds. PLoS ONE, 6(4), e19074.

Garner, J. P., & Mason, G. J. (2002). Evidence for a relationship between cage stereotypies and behavioural disinhibition in laboratory rodents. Behavioural Brain Research, 136(1), 83–92.

Garner, J. P., Meehan, C. L., & Mench, J. A. (2003). Stereotypies in caged parrots, schizophrenia and autism: Evidence for a common mechanism. Behavioural Brain Research, 145(1–2), 125–134.

Hansen, S. W., & Jeppesen, L. L. (2006). Temperament, stereotypies and anticipatory behaviour as measures of welfare in mink. Applied Animal Behaviour Science, 99(1–2), 172–182.

Jones, M. A., Mason, G. J., & Pillay, N. (2011). Correlates of birth origin effects on the development of stereotypic behaviour in striped mice, *Rhabdomys*. Animal Behaviour, 82(1), 149–159.

Keiper, R. R. (1969). Causal factors of stereotypies in caged birds. Animal Behaviour, 17(1), 114–119.

Latham, N. R., & Mason, G. J. (2008). Maternal deprivation and the development of stereotypic behaviour. Applied Animal Behaviour Science, 110(1–2), 84–108.

Lewis, M. H. (2004). Environmental complexity and central nervous system development and function. Mental Retardation and Developmental Disabilities Research Reviews, 10(2), 91–95.

Maddocks, S. A., Goldsmith, A. R., & Cuthill, I. C. (2002). Behavioural and physiological effects of absence of ultraviolet wavelengths on European starlings *Sturnus vulgaris*. Journal of Avian Biology, 33(1), 103–106.

Magnusson, M. S. (2000). Discovering hidden time patterns in behavior: T-patterns and their detection. Behavior Research Methods Instruments & Computers, 32(1), 93–110.

Mason, G. J. (1991). Stereotypies—A critical-review. Animal Behaviour, 41(6), 1015–1037.

Mason, G. J. (1993). Age and context affect the stereotypies of caged mink. Behaviour, 127, 191–229.

Mason, G. J., Clubb, R., Latham, N., & Vickery, S. (2007). Why and how should we use environmental enrichment to tackle stereotypic behaviour? Applied Animal Behaviour Science, 102(3–4), 163–188.

Mason, G. J., & Rushen, J. (2006). Stereotypic animal behaviour: Fundamentals and application to welfare. Wallingford (UK): CABI.

Matheson, S. M., Asher, L., & Bateson, M. (2008). Larger, enriched cages are associated with ‘‘optimistic’’ response biases in captive European starlings (*Sturnus vulgaris*). Applied Animal Behaviour Science, 109, 374–383.

Meehan, C. L., Garner, J. P., & Mench, J. A. (2004). Environmental enrichment and development of cage stereotypy in Orange-winged Amazon parrots (*Amazona amazonica*). Developmental Psychobiology, 44(4), 209–218.

Mistlberger, R. E. (1994). Circadian food-anticipatory activity: Formal models and physiological mechanisms. Neuroscience & Biobehavioral Reviews, 18(2), 171–195.

Ödberg, F. (1978). Abnormal behaviours: Stereotypies. Proceedings of the first world congress on ethology applied to zootechnics (pp. 475–480). Madrid: Industrias Graficas Espana.

Powell, S. B., Newman, H. A., Pendergast, J. F., & Lewis, M. H. (1999). A rodent model of spontaneous stereotypy: Initial characterization of developmental, environmental, and neurobiological factors. Physiology & Behavior, 66(2), 355–363.

Spruijt, B. M., van den Bos, R., & Pijlman, F. T. A. (2001). A concept of welfare based on reward evaluating mechanisms in the brain: Anticipatory behaviour as an indicator for the state of reward systems. Applied Animal Behaviour Science, 72(2), 145–171.

Würbel, H., Chapman, R., & Rutland, C. (1998). Effect of feed and environmental enrichment on development of stereotypic wire-gnawing in laboratory mice. Applied Animal Behaviour Science, 60(1), 69–81.

Würbel, H., & Stauffacher, M. (1997). Age and weight at weaning affect corticosterone level and development of stereotypies in ICR-mice. Animal Behaviour, 53, 891–900.

Würbel, H., Stauffacher, M., & von Holst, D. (1996). Stereotypies in laboratory mice—Quantitative and qualitative description of the ontogeny of ‘wire-gnawing’ and ‘jumping’ in Zur:ICR and Zur:ICR nu. Ethology, 102(5), 371–385.