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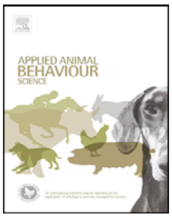

Stereotypies and environmental enrichment in captive southern hairy-nosed wombats, *Lasiorhinus latifrons*

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ABSTRACT

A captive colony of 12 (4♂, 8♀) wombats, *Lasiorhinus latifrons*, was used to investigate stereotypic behaviour in this species and determine the beneficial effects of enrichment on wombat behaviour and wellbeing. The wombats were housed in four groups of 1♂ and 2♀, each in a separate enclosure and subjected to two different treatments: (1) enrichment, where the animals received two types of enrichment along with a treatment diet and (2) no-enrichment, where the animals received no such enrichment and were fed the standard diet. Each treatment was implemented twice, for a period of 12 weeks, in a pseudo-random order. Wombat behaviour was remotely observed via digital video surveillance. Each wombat was observed for 12 × 24-h periods during each treatment rotation with behaviours (both major and minor) being recorded at 5-min intervals over each 24-h sampling period. Eight (67%) of the captive wombats displayed a singular stereotypy in the form of straight-line pacing, boundary pacing, figure-8 pacing or wall climbing. Mean daily time spent stereotyping was variable between individuals ($P < 0.01$) ranging from 61 to 129 min (4–9%), with a mean value of 86.9 ± 6.7 min ($6.0 \pm 0.5\%$). There was a significant ($P \leq 0.02$) increase in foraging (by 333%, from 7 to 30 min/day) and exploration (by 13%, from 70 to 79 min/day) in response to enrichment. However, enrichment had no effect ($P \geq 0.13$) on the time spent stereotyping or being inactive. Enrichment may have been unsuccessful at reducing stereotypic behaviour in the captive wombats due to the wrong type of enrichment being provided (i.e. the underlying problem motivating this behaviour may not have been addressed) or because the expression of this behaviour had become resistant to change, i.e. habit-like and/or perseverative. Although stereotyping and inactivity were not reduced by enrichment, it still resulted in improved welfare as the animals were given more stimulus diversity, had more choice in behaviour options, had more opportunity to interact with their environment and were able to express a larger amount of natural behaviour.

1. Introduction

Welfare is a concept that embraces both the physical as well as mental wellbeing of an animal; as such there is no single indicator that provides a complete understanding of an animal's state of welfare. Most indicators of poor wel-

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fare are related to the concept of stress. Stress is defined as a departure from the animal's usual state of equilibrium, i.e. the behavioural and physiological responses elicited when an animal perceives a threat to its homeostasis (Moberg, 2000). Poor welfare, therefore, is often associated with chronic, uncontrollable stress where the animal is unable to return to its preferred homeostatic set points (Swaisgood, 2007). Aspects of physiology and behaviour often associated with chronic stress include hyper-activity of the hypothalamic–pituitary–adrenal (HPA) axis, reduced longevity, delays or absence of breeding, immunosuppression, behavioural pathology (e.g. stereotypies and apathy), suppression of normal behaviours, misdirected behaviour and high levels of aggression and/or avoidance (Fraser and Broom, 1997; Carlstead and Shepherdson, 2000; Young, 2003). In contrast, good welfare is suggested by the absence of these signs, namely a diverse behavioural repertoire, expression of species-typical behaviours observed in the wild and baseline glucocorticoid secretion (Swaisgood, 2007).

Stereotypies are repetitive, unvarying and apparently functionless behaviour patterns, commonly suggested to indicate welfare problems (Mason et al., 2007). They have a high frequency of occurrence in zoo fauna but are rarely observed in free-ranging animals and are a sign of probable poor welfare because in captive animals they (1) are typically more time consuming and prevalent in conditions known to be aversive, (2) often demonstrably develop from thwarted attempts to perform specific motivated behaviours (i.e. frustration) and (3) may co-vary with other signs of stress and disturbance (Mason et al., 2007). Whilst stereotypies should always be taken seriously as a sign of potential poor welfare, they should never be used as a sole index of welfare. Stereotypies are nearly as often linked with good or neutral welfare as with poor welfare. In part, this is because circumstances that lead to stereotyping (e.g. frustration, boredom, lack of sensory stimulation, and stress) tend to be linked with poor welfare, whilst individual expression of stereotypies in aversive situations are often linked with improvements in welfare for that individual (Mason and Latham, 2004). Some stereotypies seem to have benefits, or are at least reinforcing; for example, repeated foraging-like behaviours (i.e. oral stereotypies) serve a coping function in many herbivores by minimizing the adverse effects associated with artificial diets (Terlouw et al., 1991). As stereotyping may be a means of coping with aversive situations, individual animals that perform stereotypies in suboptimal environments may well have better welfare than those that do not perform stereotypies within the same environments (Swaisgood and Shepherdson, 2005). Moreover, performance of stereotypies may not correspond to current wellbeing as stereotypies that have become centrally controlled (habit-like or perseverative) can be elicited by, or persist in, circumstances that improve welfare (Mason and Latham, 2004).

In an attempt to overcome the problem of stereotypies, many zoos are now improving the way they manage their captive animals by providing them with extra environmental stimuli. Environmental enrichment can be defined as a principle that seeks to enhance the quality of captive care by identifying and providing environmental stimuli necessary for optimal psychological and physiological wellbeing (Swaisgood and Shepherdson, 2005). It has become the method of choice for reducing stereotypic behaviour, but to date has had only partial success, with no study managing to abolish stereotypies in all its subjects. This suggests that the enrichments being used are not optimal or that by the time they are addressed, stereotypies have become highly resistant to change (Mason et al., 2007).

Wombats are large herbivorous marsupials that are nocturnal and semi-fossorial in nature (Gaughwin, 1981). A previous study examining the prevalence and cause of stereotypic behaviour in captive common wombats (*Vombatus ursinus*) revealed that this species is susceptible to the development of locomotor stereotypies and that frustration of the foraging motivational system is the underlying reason for their development (Hogan and Tribe, 2007). To date, stereotypic behaviour in southern hairy-nosed wombats (*Lasiorhinus latifrons*), a close relative of *V. ursinus*, has not been examined. A captive population of *L. latifrons*, housed at Rockhampton Zoo, was used in this study to further examine stereotypic behaviour in the Vombatidae. It was predicted that stereotypies in *L. latifrons* would (similar to *V. ursinus*) be locomotor in form, caused by frustration to foraging motivations and that enrichment could result in a reduction in stereotypic behaviour. Specific aims were to (1) define and measure the occurrence of stereotypic behaviour, (2) assess the behavioural responses to two types of enrichment and (3) to enhance the welfare of the captive wombats.

2. Methods

2.1. Animals and housing

Twelve (4♂, 8♀) sexually mature (>5 years) *L. latifrons* housed at Rockhampton Zoo's Research Centre (23°23′S, 150°29′E) were used in this study. The wombats were wild caught on Kooloola Station, Swan Reach, South Australia (34°55′S; 139°28′E) and transferred to Rockhampton Zoo in December 2001 (2♂, 4♀), July 2002 (2♂, 3♀) and September 2004 (1♀). Throughout the study, the animals were group housed (1♂:2♀) in four separate, adjacent enclosures (Fig. 1A). Each enclosure consisted of a temperature-controlled (air-conditioned) indoor area equipped with concrete sleeping dens and interrelated tunnels as well as an outdoor area with a soil and sand substrate, a digging chamber, a hollow log and trees (*Eucalyptus* spp.). Each outdoor area was partially vegetated with couch (*Cynodon dactylon*) and guinea grass (*Panicum maximum*) (Fig. 1B). Intrinsic differences in the physical topography of the outdoor areas included total area (E1, 248.8 m^2; E2, 249.5 m^2; E3, 180.2 m^2; E4, 162.5 m^2), slope (E1, 6°; E2 14°; E3, 17°; E4, 4°) and degree of grass coverage (E1, 38%; E2, 75%; E3, 47%; E4, 19%; Fig. 1B).

The standard (baseline) diet comprised one feed per day (17:00 h), consisting of (per animal) 300 g kangaroo pellets (Riverina Australia Pty Ltd., Brisbane, Australia), 150 g chopped carrots and 50 g of oaten hay chaff (Johnson and Sons, Kapunda, Australia). The daily ration for each group was placed (17:00 h) into a communal trough covered by

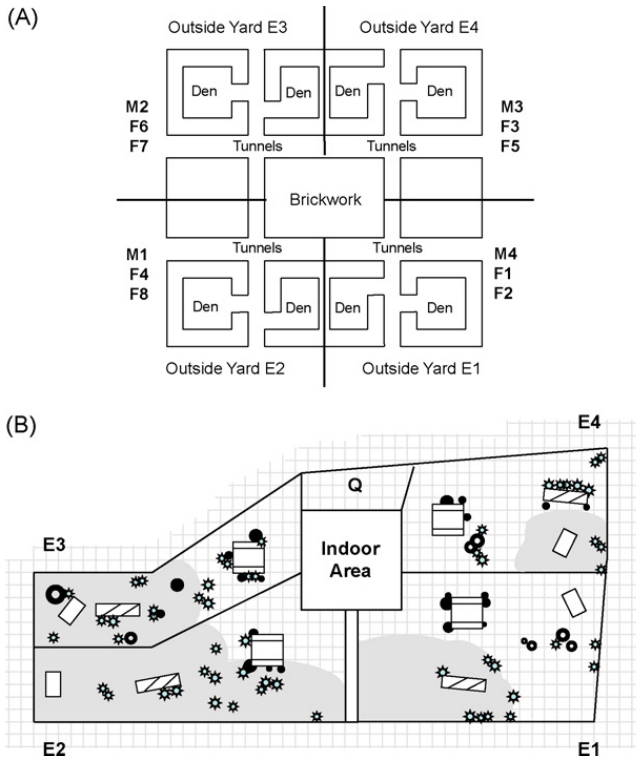

Fig. 1. Overhead schematic view of the (A) indoor enclosure area (enlargement) and (B) indoor and outdoor enclosure areas, at Rockhampton Zoo. Key: E = enclosure, M = male, F = female, (B) outdoor areas – shaded grey sections illustrate couch grass, *Cynodon dactylon* coverage. Key: ✲ guinea grass, *Panicum maximum*; ● rock/Boulder; ⭘ eucalyptus tree; ▭ feeding trough; ▧ hollow log; ☐ digging chamber; **Q** = quarantine area. Drawn to scale – 1 square: 1.0 m^2 area.

a feed-house designed to prevent local pest species from scavenging the wombat's feed and protect the food in wet weather. Surplus feed was removed daily at 07:00 h, with no food being available during the day. Water was available *ad libitum*.

To prevent over-feeding and weight gain, the standard diet was reduced during enrichment periods. On a daily basis the 'treatment diet' during enrichment consisted of (per animal) 100 g kangaroo pellets and 20 g of oaten hay chaff. During a 10-week preliminary enrichment program (September–November 2005) it had been found that the wombats consumed approximately 50% of the enrichment offered. The replacement value, based on energy (calories) rather than volume, of these consumed foods was then used to calculate the necessary reduction, in proportion of caloric contribution, of the standard diet so that an iso-energetic intake could be maintained over the entire experimental period. The wombats were weighed fortnightly, throughout the experimental period to ensure proper weight maintenance. Mean body weight of the male and female wombats was 27.7 ± 1.0 and 26.3 ± 1.4 kg, respectively and did not change significantly across the sampling period ($Z_{1,7} = 1.94$, $P = 0.23$).

Eleven animals remained clinically healthy throughout the experimental period. One male (M1) was quarantined for 3 weeks in September 2006 for treatment of an urinary tract infection; after which it made a full recovery and was re-introduced back into the captive population. During times of convalescence the standard diet was replaced with a recuperative diet, which consisted on a daily basis of (per animal) 300 g horse pellets (Ridley Agriproducts Pty Ltd., VIC, Australia), 150 g corn, 150 g sweet potato and 50 g of oaten hay chaff.

2.2. Experimental design

The four wombat groups were randomly allocated to one of two treatments: enrichment (treatment) and no-enrichment (baseline). The animals in the enrichment groups received two types of enrichment (feed and olfaction) along with the treatment diet, for 5 consecutive days a week for 12 weeks. The animals in the no-enrichment groups received no such enrichment and were fed the standard diet. The experiment had a repeated measures design so that each treatment was repeated twice in a pseudo-random order. In the first test period (1–12 weeks; February–April 2006) groups 1 and 2 (Fig. 1A) received enrichment, whilst groups 3 and 4 received no-enrichment. In the second test period (13–24 weeks; May–August 2006) groups 1 and 3 received enrichment, whilst groups 2 and 4 received no-enrichment. In the third test period (25–36 weeks; September–December 2006) groups 2 and 4 received enrichment, whilst groups 1 and 3 received no-enrichment, whilst in the fourth test period (37–48 weeks; January–March 2007) groups 3 and 4 received enrichment, whilst groups 1 and 2 received no-enrichment. Such a lengthy treatment period (12 weeks) was chosen because previous research has indicated that enrichments (1) that are in place for longer periods (i.e. months rather than weeks) reduce stereotypic behaviours to the greatest extent and (2) may initially be stressful, therefore taking time for subjects to find the enrichments enriching (Mason et al., 2007).

Feed enrichment was employed because it was predicted that stereotypies in *L. latifrons*, similar to *V. ursinus*, are feed motivated (and such as would be reduced by the provision of feed enrichment) and because this type of stimuli has been shown to promote a wider range of movement leading to improved activity, increase the time required to process and ingest food (i.e. increased foraging) and reduce the expression of certain forms of stereotyped behaviour (Newberry, 1995). Olfactory enrichment was implemented because this type of stimuli can easily integrated into zoo management programs and has been shown to stimulate naturalistic behaviour, enhance enclosure exploration and reduce inactivity (Clark and King, 2008; Wells, 2009). The study was approved by The University of Queensland's Animal Ethics Committee.

2.2.1. Enrichment items

The animals in the enrichment groups ($n = 2$) received four (three feed, one olfactory) enrichment items for 60 days, i.e. 5 consecutive days per week for 12 weeks. The feed enrichment items supplied to each group were (1) browse: one large eucalyptus branch, (2) grass: one large circular grass sward (*Cenchrus* spp., *Chloris* spp., *Austrostipa* spp.), inclusive of roots but free of soil, 120–150 cm in height by 100 cm in diameter and (3) buried food: 290–320 g sweet potato, 290–320 g carrot and 110–250 g corn. Buried food

Table 1
Behavioural categories analyzed for 12 captive *L. latifrons* at Rockhampton Zoo. Behaviours are sorted by category and behavioural units with associated definitions.

Behavioural category	Behavioural unit	Description of behaviour
1. Inactive	Sleeping	Lying with neck recumbent on the ground, ears relaxed, eyes closed
	Lying resting	Lying awake (ears up, eyes open) in sternal recumbency, whilst doing nothing else
	Sitting-at-rest	Sitting on hind quarters and front paws, whilst doing nothing else
	Sun-basking	Lying awake in direct sunlight, in lateral recumbency
2. Active	Courtship/mating	Appetitive sexual behaviour and copulation between male and female
	Digging	Kicking away of soil around objects, e.g. hollow logs and digging chambers
	Exploring	
	General	Investigation or examination of inedible objects
	Scent logs	Sniffing/investigation of scented logs provided for enrichment
	Trough feeding	Consumption of food items within the feeding-house
	Other foraging	
	Browse	Grazing of eucalyptus branches provided for enrichment
	Buried food	Excavation and consumption of food buried in pits for enrichment
	General	Grazing of natural foliage in enclosure, i.e. guinea and couch grass
	Sward	Grazing of grass swards provided for enrichment
	Grooming	Scratching of body part with hind limbs or rubbing against a stationary object
	Handling	Physical contact with human caretakers
	Stereotypic behaviour	Unvarying, repetitive behavioural patterns with no apparent purpose

Underlined behaviours are the main (or major) behaviours, whilst the italicized behaviours are the sub (or minor) behaviours associated with the main behaviour.

was concealed in 10 circular shallow pits (10 cm diameter × 15 cm deep) dug in the outdoor area of each enclosure. In order to maintain novelty, the physical location of the pits was changed fortnightly and buried food was allocated to each pit according to a randomized design. Delivery time for all feed enrichment was 17:00 h and any surplus was removed the following morning (06:00 h) prior to enclosure cleaning. Following collection, any remaining buried food was weighed in order to calculate actual intake and pit disturbance was recorded.

The olfactory enrichment item was the provision of scented logs. Odours were chosen for their safety and reported positive influence on the behaviour (exploration and activity) of other captive mammals (Powell, 1995; Ostrower and Brent, 2000) and included aniseed, peppermint, vanilla, lemon, coconut and rose (Queen Fine Foods Pty. Ltd., Annerley, Queensland, Australia). Odours were introduced on pre-cut logs, measuring 10 cm in diameter by 100 cm in length. The logs were cut from the trunk of a eucalyptus tree and all bark was stripped prior to scenting. Each log was scented with one odour by placing 20 drops (~5 cm apart) of the scent along its length. To ensure the scent was placed on all sides, the logs were rotated by 10–15° between the applications of each drop. Odours were introduced in pairs, with the animals being exposed to two different odours, on two separate logs. The logs remained in the enclosures for 5 consecutive days, being freshly scented each day (17:00 h), after which they were removed. Following a transitional period of 2 days with no logs, two new odours were introduced. Again these logs remained in the enclosures for 5 continuous days, were freshly scented each day and were then removed. This process continued throughout the 12-week enrichment period, with the wombats first being presented with aniseed and peppermint, followed by vanilla and lemon and then coconut and rose; with four repetitions of each pair. Every day during re-scenting the position of the logs was changed, with the distance between each log being at least 10 m.

2.3. Data collection: behaviour

A digital video surveillance system was used for the remote monitoring of wombat behaviour. The system's component parts, installation and modes of operation have been described previously (Hogan et al., 2009). In brief, multiple digital video recording cards (OzSpy, Gold Coast, Queensland, Australia) were installed onto a desktop computer (IBM Australia Limited, Queensland, Australia), equipped with Skyview Super Series surveillance software. This computer-based recording station was connected to 16 cameras, comprising eight weatherproof colour-bullet cameras with inbuilt infrared light emitting diodes (OzSpy, Gold Coast, Queensland, Australia) for recording within the sleeping dens and eight Sony day/night cameras with infrared lights (OzSpy, Gold Coast, Queensland, Australia) for monitoring the outside yards.

Approximately 1100 h of behavioural observations (1 × 24-h period/weeks for 48 weeks) were collected for each wombat with accurate animal identification being achieved using specially designed light reflective, patterned collars. Despite some initial evidence of minor discomfort (mild hair loss, scratching at collars, head shaking) shown by the wombats to the presence of the collars, the long-term effect of the collars was considered to be negligible as the collars did not apparently inhibit the animal's movement, caused no physical trauma or pain and were quickly adjusted to; collar scratching and head shaking disappeared 10–14 days after fitting. A habituation period of 1 month was allowed before any formal behavioural data were recorded. Behaviours were recorded using a combined continuous and 1–0 sampling method, at 5 min intervals ($n = 288$) over each 24-h sampling period (Altmann, 1973). The 'major behaviour' occupying the longest time within each 5-min interval (continuous sampling) and the occurrence of any 'minor behaviours' within each 5-min interval (1–0 sampling) were recorded. Each wombat was observed for 12 × 24-h periods during each treatment rotation.

2.4. Data analysis

Residual plots (e.g. normal probability plots, box and whisker plots, scatter plots and histograms) were used to test each data set for normal distribution. None were found to violate the homoscedasticity assumption and as such all data sets were analyzed in their original scale, i.e. no data transformations were necessary (SAS/STAT software, Version 8.2, 2001). The calculation of statistical tests was carried out using the statistical program Minitab (Version 15, 2007) and SAS (SAS®/STAT, Version 8.2, 2001). Significance levels for all tests were set at $P \leq 0.05$ and means are given with standard errors (SE) unless otherwise noted.

2.4.1. Organization of behavioural data

Major behaviour (Table 1) intervals were combined to determine the total time, in units of 5 min, over the 24-h cycle. Major behaviour mean daily totals for each individual were calculated by aggregating the data from each animal from all sampling days ($n = 48$). Treatment mean daily totals were calculated from an integration of data from six animals, for all sampling days ($n = 24$) of that treatment, i.e. behavioural data were subdivided into two categories (1) enrichment and (2) no-enrichment. Mean daily totals of the enriched animals ($n = 6$) in periods 1 (groups 1 and 2), 2 (groups 1 and 3), 3 (groups 2 and 4) and 4 (groups 3 and 4) were combined to form the category of 'enrichment', whilst the totals of the non-enriched animals ($n = 6$) in periods 1 (groups 3 and 4), 2 (groups 2 and 4), 3 (groups 1 and 3) and 4 (groups 1 and 2) were combined to form the category of 'no-enrichment'. For total time, mean daily totals were calculated from a combination of data from all animals, from all sampling days ($n = 48$).

For assessment purposes 'exploring' was the combined value of two sub-behaviours (general and towards scented logs), whilst 'other foraging' was the combined value of four sub-behaviours (general and towards browse, sward and buried food; Table 1). In addition to being analyzed individually, trough feeding and other foraging were also combined to form the category 'total foraging'. For activity assessment, the major behaviours were combined to form the categories of 'active' (courtship/mating, digging, exploring, feeding, foraging, grooming, handling and stereotypy) and 'inactive' (lying resting, sleeping, sitting-at-rest and sun-basking; Table 1).

Number of bouts and bout length for stereotypic, active and inactive behaviour also analyzed over a 24-h period. These behaviours each had to be expressed for ≥5 min to be classified as a bout and a break period (i.e. a period of a different behaviour) of ≥5 min had to occur for bouts to be considered as two separate events (Hogan and Tribe, 2007). Number of bouts was computed as a total count/day. Bout length (in units of 5 min) was calculated by dividing the daily total time by the number of bouts per day. Mean values for number of bouts and bout length were calculated for each individual by combining data from all sampling days ($n = 48$).

2.4.2. Analysis of stereotypic behaviour data

Preliminary analysis revealed that there was no significant period or treatment effect on stereotypic behaviour. For ease of analysis, the data sets were collapsed down to individual animals with the primary focus being on the effects over time. Thus, the initial analysis design of period by treatment was changed to individual subjects with 48 repeated measures. A range of covariant components were considered and using the AIC it was found that the compound symmetry (CS) model was the best fit. Ultimately, repeatedly measured stereotypic behaviour was assessed using a CS, mixed-model ANOVA with a REML estimation method with between animal ($n = 12$) and within animal effects being random factors and group ($n = 4$), sex ($n = 2$) and week ($n = 47$) effects being fixed factors (Wang and Goonewardene, 2004).

Spearman's rank correlations were used to detect the associations between stereotypies and nine other wombat behaviours. Grooming and handling behaviours were omitted from correlation analysis as grooming took up less than 0.1% of the animals' daily budget and the amount of handling was constant. Stereotyping was also not correlated against active behaviour as it was one of the behaviours included within this category. Stereotypic data were analyzed to determine the percentage of time spent ($X/12 \times 100$, with 12 being the number of intervals/h) in this behaviour, during each hour of the day. Data were divided into 24 × 1-h time increments, starting at 00:00 h and ending at 23:00 h; all samples between 00:00 and 00:59 were grouped into the 00:00 h time period. For every 1-h period, mean totals were calculated from an amalgamation of data from all 12 animals, from all sampling days.

Table 2
Mean (±SE, $n = 48$) daily stereotypic behaviour patterns of eight *L. latifrons* at Rockhampton Zoo.

ID	Group	Minimum daily total time (min)	Maximum daily total time (min)	Mean daily total time (min)	Mean daily no. of bouts	Mean daily bout length (min)	Type of stereotypy
M2	3	10.0	180.0	64.0 ± 5.7	5.6 ± 0.4	11.4 ± 0.5	Straight-line pacing
M4	1	0.0	175.0	83.8 ± 5.9	8.0 ± 0.5	10.3 ± 0.5	Straight-line pacing
F3	4	25.0	270.0	108.0 ± 7.7	9.3 ± 0.6	11.7 ± 0.4	Straight-line pacing
F4	2	0.0	170.0	76.3 ± 5.3	6.6 ± 0.5	11.8 ± 0.5	Straight-line pacing
F5	4	0.0	270.0	61.0 ± 9.1	4.5 ± 0.6	10.1 ± 1.2	Figure-8 pacing
F6	3	40.0	240.0	128.8 ± 7.1	11.1 ± 0.6	12.6 ± 1.1	Boundary pacing
F7	3	0.0	220.0	104.4 ± 7.6	10.1 ± 0.6	9.9 ± 0.5	Straight-line pacing
F8	2	5.0	145.0	68.8 ± 5.1	6.2 ± 0.4	11.3 ± 0.6	Wall climbing
Mean	1–4	0.0	270.0	86.9 ± 6.7	7.7 ± 0.5	11.1 ± 0.6	Straight-line pacing

2.4.3. Analysis of enrichment data

Mean daily total time spent interacting with each enrichment item was calculated for every individual, with variations in collective (i.e. total mean daily) interaction times being assessed using mixed-model ANOVA with a REML estimation method. Between group ($n = 4$) and between subject ($n = 12$) effects were random factors, whilst period ($n = 4$) and type of enrichment ($n = 4$) were fixed factors.

Daily percentages of pits discovered were calculated as $X/4 \times 100$ for potato, $X/4 \times 100$ for carrot and $X/2 \times 100$ for corn, with four and two being the number of pits per enclosure. Daily percentages consumed were calculated as [amount offered (g) − amount left (g)/amount offered (g)] × 100. Daily percentages of discovered food that was consumed were calculated as [(amount offered (g) − amount left (g)/amount offered (g))/($X/4$ or 2)] × 100. Total percentages were calculated by combining the mean daily percentages from all animals, from all sampling days. Differences in the total mean daily percentage of pits discovered, for each buried food ($n = 3$) was assessed using a CS, mixed-model ANOVA with a REML estimation method with pit content ($n = 3$) and trial week ($n = 12$) being fixed factors. Due to the inherent differences in the food items (i.e. unlike potato and carrot, corn was never 100% consumed as the 'cob' always remained) mixed-model ANOVA could only be used to compare the difference in the mean daily percentage of buried food consumed and discovered food that was consumed for sweet potato and carrot only. Superscripts (^{a,b,c}) indicating significant ($P < 0.05$) differences between compared means (daily percentages) are given with SED.

Due to the difference in number of items offered (e.g. one eucalyptus branch, one grass sward, 10 food pits and two scented logs per enclosure, per day) enrichment item preference testing (via a McNemar test) was restricted to browse versus sward only. Similarly, due to the odours being presented in static pairs, all preference testing (via a McNemar test) was restricted to within each pair.

3. Results

3.1. Stereotypic behaviour

Eight (2♂; 6♀) out of the 12 wombats displayed a singular stereotypic behaviour during the observational period. Four distinctive stereotypic patterns were identified: 'straight-line pacing', repetitive walking to and fro in a straight line, always conducted parallel to either a portion of enclosure fencing or an enclosure gate; 'boundary pacing', repeated walking along the entire perimeter of the enclosure; 'figure-8 pacing', repetitive walking along a track shaped like the number 8, always conducted in an unobstructed area of the enclosure; 'wall-climbing', repeated attempts to climb up a wall in one of the sleeping dens.

Table 2 shows the mean daily total time, number of bouts, bout length and pattern of stereotypic behaviour for each wombat ($n = 8$). Mean daily total time spent stereotyping was variable between individuals ($F_{3,8} = 15.84$, $P < 0.01$), ranging from 61 to 129 min, with a mean value of 86.9 ± 6.7 min. Mean percentage of daily total time spent stereotyping ranged from 4% to 9%, with a mean value of 6.0 ± 0.5%. No significant sex or group differences were found in the mean daily total time, number of bouts or bout length of stereotypic behaviour (Table 3). However, the mean daily total time, number of bouts and bout length of stereotypic behaviour did vary significantly according to week, season and sex by season (Table 3). Mean daily total time was increased for female wombats in winter and spring compared with summer and autumn, but there were no seasonal differences in the time spent stereotyping by male wombats. The seasonal difference in females was due to an increase in bout length in winter and bout number in both winter and spring. No significant treatment effects on mean daily total time stereotyping were detected (Table 3).

Correlation coefficients of stereotypic behaviour with nine other wombat behaviours are shown in Table 4. A significant negative relationship was detected between both sleeping and 'inactive behaviour' with stereotyping. Sleeping and inactive behaviour were both significantly and negatively correlated with stereotyping in all eight animals. Whilst a significant overall link did not exist between 'total foraging' and stereotyping, these two behaviours were significantly correlated in four out of the eight animals; negatively related in M2 and positively related in F5, F6 and F7. A significant overall association also did not exist between sitting-at-rest and stereotyping, but these two behaviours were significantly and positively correlated in three (M2, F4 and F6) of the eight animals. Lying resting and stereotyping were significantly correlated in two animals (negatively related in F5, positively related in M2), but no sig-

Table 3
Mixed-model ANOVA of captive *L. latifrons* ($n = 8$) stereotypic behaviour. Stereotypic behaviour has been analyzed according to mean (±SE) daily total time (min), number of bouts and bout length (min).

Variable	Sub-category	Mean daily total time (min)	Mean daily no. of bouts	Mean daily bout length (min)
Individual		$F_{3,8} = 15.84$, $P < 0.01$		
Treatment		$F_{1,30} = 0.02$, $P = 0.88$		
	Enrichment	57.6 ± 5.9		
	No-enrichment	86.2 ± 6.0		
Group		$F_{3,7} = 1.37$, $P = 0.33$	$F_{3,7} = 1.33$, $P = 0.34$	$F_{3,7} = 0.81$, $P = 0.53$
Sex		$F_{1,7} = 1..94$, $P = 0.21$	$F_{1,7} = 1.31$, $P = 0.29$	$F_{1,7} = 1.55$, $P = 0.25$
	M	73.9 ± 11.8		
	F	91.2 ± 11.9		
Week		$F_{47,466} = 3.80$, $P < 0.01$	$F_{47,466} = 1.80$, $P < 0.01$	$F_{47,466} = 1.48$, $P = 0.02$
Season		$F_{3,44} = 3.80$, $P = 0.02$	$F_{3,44} = 2.34$, $P = 0.09$	$F_{3,44} = 3.13$, $P = 0.04$
	Autumn	76.1^{b}	6.7^{b}	11.3^{ab}
	Winter	105.4^{a}	8.6^{a}	13.0^{a}
	Spring	86.1^{ab}	7.9^{ab}	10.5^{b}
	Summer	72.5^{b}	7.0^{b}	10.0^{b}
	SED	9.4	1.1	1.0
Sex by Season		$F_{3,510} = 6.57$, $P < 0.01$	$F_{3,510} = 5.76$, $P < 0.01$	$F_{3,510} = 10.39$, $P < 0.01$
	M Autumn	79.5^{a}	7.1^{a}	11.5^{a}
	M Winter	87.2^{a}	8.1^{a}	11.2^{a}
	M Spring	66.0^{a}	6.0^{a}	11.1^{a}
	M Summer	66.3^{a}	6.5^{a}	9.6^{a}
	SED	10.6	1.0	1.5
	F Autumn	72.8^{c}	6.3^{c}	11.1^{b}
	F Winter	123.6^{a}	9.1^{a}	14.8^{a}
	F Spring	106.1^{b}	9.9^{a}	9.8^{b}
	F Summer	78.7^{c}	7.5^{b}	10.5^{b}
	SED	9.8	0.8	1.1

For each comparison, different superscripts within the same column indicate significant differences.
M, male; F, female.

nificant overall link was detected between these two behaviours.

The mean (±SE) percentage of time the wombats spent stereotyping by hour is shown in Fig. 2. This behaviour showed bimodal peaks of expression over the night-time period, with peaks occurring in early evening (18:00–20:00 h) and early morning (01:00–04:00 h); peaks were dissimilar in size, with the second peak being larger than the first.

3.2. Behavioural response to enrichment

The mean (±SE) daily total time (min) spent in each of the wombat behaviours according to treatment are shown in Table 5. Mean daily total time spent foraging (other) and exploring were significantly greater during periods of enrichment, whilst mean daily total time spent trough feeding and sitting-at-rest was significantly less (Table 5). Specifically, mean daily total time spent foraging (other) and exploring increased by 333% (from 6.9 to 29.9 min) and 13% (from 69.9 to 78.8 min) during periods of enrichment, whilst trough feeding and sitting-at-rest decreased by 14% (from 79.9 to 70.2 min) and 17% (from 39.2 to 33.4 min). Despite the decrease in trough feeding times, mean daily total time spent foraging (total) still varied significantly between treatments (Table 5). There was no significant enrichment effect on the mean daily total time spent in the remaining 10 wombat behaviours (Table 5).

3.3. Interactions with enrichments

Fig. 3 shows the mean (±SE) daily total time spent interacting with the four enrichment items for each wombat ($n = 12$). Mean daily total interaction times with sward ($F_{3,8} = 3.75$, $P = 0.03$) and scented logs ($F_{3,8} = 4.29$, $P = 0.02$)

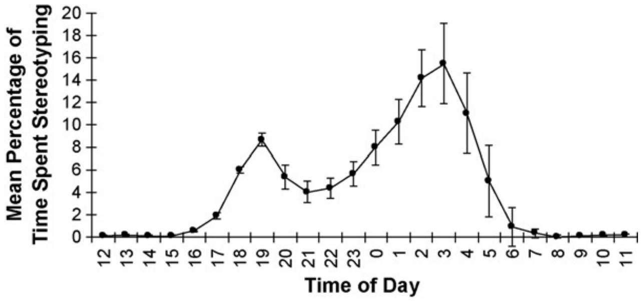

Fig. 2. Mean (±SE) percentage of time spent stereotyping, per hour, by eight *L. latifrons* at Rockhampton Zoo.

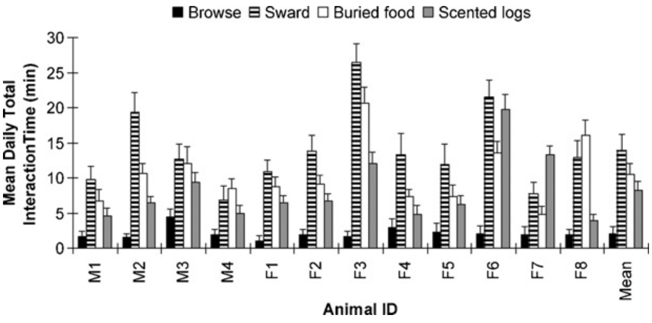

Fig. 3. Mean (±SE) daily total time (min) spent interacting with four different enrichment items by 12 *L. latifrons* at Rockhampton Zoo.

varied significantly between individuals, but no significant difference was found between individuals in the mean daily total interaction times with browse ($F_{3,8}=0.46$, $P=0.86$) or buried food ($F_{3,8}=0.22$, $P=0.88$) (Fig. 3). Scented logs were the only enrichment item that varied significantly in mean daily total interaction time (min) between groups (group 1, 6.0 ± 0.5^b; group 2, 4.4 ± 2.6^b; group 3, 13.2 ± 3.8^a; group 4, 9.2 ± 1.7^b; $F_{1,3}=9.13$, $P<0.01$) (Fig. 3). Total mean daily interaction time (min) was variable between enrichment items; sward (13.9 ± 0.9^a) had the highest interaction time, followed by buried food (10.5 ± 0.8^b), scented logs (8.2 ± 0.5^b) and browse (2.1 ± 0.4^c) ($F_{1,30}=9.13$, $P<0.01$). The collective mean total time spent interacting with all enrichment items was 34.7 ± 3.6 min/day.

Sward, buried food and browse mean daily interaction times (min) accounted for 52.5%, 39.6% and 7.9% of the increase in the mean daily total time spent foraging (other) during periods of enrichment, respectively. Scented logs mean daily interaction times (min) accounted for 100% of the increase in mean daily total time spent exploring during periods of enrichment. Total interaction rates (i.e. $X/480$, where X is a total count of times interacted with and 480 is the number of times offered) was variable between enrichment items being 46.6% for browse, 90.8% for sward, 100.0% for buried food and 83.8% for scented logs. Browse and sward were not interacted with equally ($x^2=176$, $P<0.01$, and $n=480$); the animals selected sward over browse in 232 cases (offerings), browse over sward in 21 cases and showed no preference (i.e. interacted with both or neither) in 227 cases.

Total mean daily percentage of pits discovered was variable between the three buried foods, with corn (62.7 ± 2.6%^{a}) having the highest rate of discovery, followed by sweet potato (45.9 ± 1.9%^{b}) and then carrot (41.4 ± 1.7%^{c}) ($F_{2,14}=81.78$, $P<0.01$). Corn was the only buried food to show a significant variation ($F_{11,77}=2.50$, $P=0.02$) in discovery rate over time, increasing over the 12-week enrichment period. Total mean daily percentage of buried food consumed was not variable ($F_{1,14}=1.58$, $P=0.17$) between sweet potato (26.7 ± 0.6%) and carrot (24.1 ± 0.7%). Similarly, total mean daily percentage of discovered food that was consumed was not variable ($F_{1,14}=0.34$, $P=0.79$) between sweet potato (58.7 ± 1.2%) and carrot (58.5 ± 1.0%). The total mean daily percentage of corn consumed and of discovered corn that was consumed were 46.2 ± 1.2% and 74.8 ± 1.5%, respectively.

Total individual scent interaction rates (i.e. $X/160$, where X is a total count of times interacted with and 160 is the number of times the scent was offered) were 66% for aniseed, 61% for coconut, 56% for lemon, 52% for peppermint, 46% for vanilla and 33% for rose. Aniseed and peppermint (1st odour pair) were not interacted with equally ($x^2=5.57$, $P=0.02$, and $n=160$); the animals selected aniseed over peppermint in 59 cases (offerings), peppermint over aniseed in 36 cases and showed no preference in 65 cases. Similarly, coconut and rose (3rd odour pair) were not interacted with equally ($x^2=19.9$, $P<0.01$, and $n=160$); the animals selected coconut over rose in 68 cases, rose over coconut in 25 cases and showed no preference in 67 cases. In contrast, vanilla and lemon (2nd odour pair)

Table 4
Associations (Spearman's correlation coefficients) of stereotypic behaviour with other 9 other wombat behaviours.

Variable	M2	M4	F3	F4	F5	F6	F7	F8	Overall
Courtship/mating	NS	$r=-0.33$, $P=0.02$						NS	NS
Digging	NS	NS	NS	NS	NS	NS	NS	NS	NS
Exploring	NS	$r=0.34$, $P=0.01$	NS	NS	NS	$r=0.28$, $P=0.05$	NS	NS	NS
Total foraging	$r=-0.29$, $P=0.05$	NS	$r=0.31$, $P=0.03$	NS	NS	$r=0.46$, $P<0.01$	$r=0.31$, $P=0.03$	NS	NS
Lying resting	$r=0.38$, $P<0.01$	NS	NS	NS	$r=-0.34$, $P=0.02$	NS	NS	NS	NS
Sitting-at-rest	$r=0.54$, $P<0.01$	NS	NS	$r=0.30$, $P=0.04$	NS	$r=0.40$, $P<0.01$	NS	NS	NS
Sleeping	$r=-0.61$, $P<0.01$	$r=-0.56$, $P<0.01$	$r=-0.53$, $P<0.01$	$r=-0.49$, $P<0.01$	$r=-0.62$, $P<0.01$	$r=-0.61$, $P<0.01$	$r=-0.61$, $P<0.01$	$r=-0.39$, $P<0.01$	$r=-0.83$, $P<0.01$
Sun-basking	NS	NS	NS	NS	NS	$r=0.29$ $P=0.04$	NS	NS	NS
Inactive	$r=-0.51$, $P<0.01$	$r=-0.61$, $P<0.01$	$r=-0.72$, $P<0.01$	$r=-0.75$, $P<0.01$	$r=-0.66$, $P<0.01$	$r=-0.80$, $P<0.01$	$r=-0.70$, $P<0.01$	$r=-0.45$, $P<0.01$	$r=-0.77$, $P<0.01$

NS, not significant and $P>0.05$.

Table 5
Mean (±SE) daily total time (min) spent in 15 behaviours, by 12 *L. latifrons*, during periods of enrichment and no-enrichment.

Behaviour	Enrichment	No-enrichment	SED	Mixed-model ANOVA
Courtship/Mating	1.3	1.3	0.9	$F_{1,30} = 0.01$, $P = 0.93$
Digging	26.4	24.0	3.8	$F_{1,30} = 0.41$, $P = 0.53$
Exploring	78.8	69.9	3.6	$F_{1,30} = 6.62$, $P = 0.02$
Trough Feeding	70.2	79.9	3.6	$F_{1,30} = 13.42$, $P < 0.01$
Other Foraging	29.9	6.9	5.0	$F_{1,30} = 100.55$, $P < 0.01$
Total Foraging	99.7	85.0	4.0	$F_{1,30} = 7.30$, $P = 0.01$
Grooming	2.9	3.5	0.3	$F_{1,30} = 3.42$, $P = 0.07$
Handling	5.8	5.8	0.3	$F_{1,30} < 0.01$, $P = 1.00$
Lying Resting	124.2	130.8	5.4	$F_{1,30} = 1.50$, $P = 0.23$
Sitting-at-rest	33.4	39.2	2.1	$F_{1,30} = 7.67$, $P = 0.01$
Sleeping	1006.4	1006.4	9.8	$F_{1,30} = 0.01$, $P = 0.94$
Stereotypic Behaviour	87.6	86.2	8.5	$F_{1,30} = 0.02$, $P = 0.87$
Sun-basking	5.2	3.6	0.9	$F_{1,30} = 3.38$, $P = 0.07$
Total Active Behaviour	264.0	260.3	22.5	$F_{1,30} = 0.13$, $P = 0.72$
Total Inactive Behaviour	1176.1	1179.8	22.3	$F_{1,30} = 0.13$, $P = 0.72$

Numerical values represent mean total daily time spent (in minutes).

were interacted with equally ($x^2 = 2.41$, $P = 0.12$, and $n = 160$).

4. Discussion

This study found that there was a high incidence of stereotypic behaviour in the captive *L. latifrons* and that enrichment successfully increased foraging and exploration, but had no discernable effect on time spent stereotyping or inactive. The type and incidence of stereotypic behaviour in the *L. latifrons* were similar to those reported for captive *V. ursinus* (Hogan and Tribe, 2007). Firstly, the stereotypies were locomotor in form, with straight-line pacing being the most common. Secondly, there was a prevalence of stereotypies in the *L. latifrons* colony of 67%, a rate comparable to that reported for the Australian *ex situ* population of *V. ursinus* (Hogan and Tribe, 2007). Alternatively, the duration and cause of stereotypic behaviour in the *L. latifrons* were different to those reported for *V. ursinus* (Hogan and Tribe, 2007). Captive *V. ursinus* exhibit stereotypies for a mean of 15.5 ± 4.3% each day, whereas the *L. latifrons* in this study had a mean daily value of only 6.0 ± 0.5%. It is possible that daily duration of stereotypic behaviour in the *L. latifrons* was less because their captive environments were better, i.e. they had access to spatially larger enclosures, complex artificial burrows and purpose-build digging chambers. The motivational trigger of stereotypies in *V. ursinus* was found to be foraging related, i.e. a strong, negative correlation ($r = -0.99$) was discovered between foraging and stereotyping times (Hogan and Tribe, 2007). In contrast, only 50% of the stereotypic animals in this study had a significant correlation between time spent foraging (total) and stereotyping and the nature of this correlation was inconsistent (negatively correlated in one animal and positively correlated in three). Therefore, unlike *V. ursinus* stereotyping in *L. latifrons* may not be foraging related.

We hypothesized, based on previous wombat research, that frustration of foraging related motivations would be the cause for stereotypic behaviour in *L. latifrons*. In captivity, wombat diets are more spatially and temporally concentrated (i.e. present fewer variables) and this reduces time spent in foraging related activities. Studies with captive *V. ursinus* and *L. latifrons* (Hogan and Tribe, 2007; Hogan et al., 2009) have found that they only spend 7–10% of their daily budget foraging, whereas wombats living in the wild spend 19–29% of their daily time foraging (Brown and Young, 1979). If frustration of foraging related motivations was not the primary cause of stereotyping in the *L. latifrons*, then this would explain why the enrichment used in this study had no discernable effect on time spent stereotyping. Captive animals typically perform stereotypic behaviour for the following reasons (1) frustration of highly motivated behaviours, (2) boredom, (3) lack of sensory stimulation, (4) stress, (5) coping mechanisms to deal with stressors and (6) environmental channelling (Swaisgood, 2007). Given that all the stereotypic patterns in this study were locomotor in form, a lack of space may have been a causal factor for stereotyping in the *L. latifrons*. The observed ‘boundary pacing’ stereotypy may have derived from the natural patrolling of territory, which has become stereotyped because of the limited space available (Rushen et al., 1993). The observed ‘wall-climbing’ stereotypy may be the remnant behavioural pattern of previous escape trials; with the need to escape being motivated by a desire for more space or control (Rushen et al., 1993). Previous research has suggested that enclosures of up to 400 m^2 may be necessary to alleviate movement restraint and reduce pacing in wombats (Booth, 1999).

Environmental under-stimulation may have also been a cause of stereotypies in the *L. latifrons*. It is difficult to design complex environments for captive wombats due to their destructive digging habits (Jackson, 2003). Captive *L. latifrons* are less active than their wild counterparts (19% vs. 26%), with low stimulus diversity within their captive environment being the main reason for the reduced activity (Hogan et al., 2009). Low complexity means that the animals have limited opportunities to purposefully interact with their environment and as such may express stereotypic behaviour in an attempt to increase sensory input (Wemelsfelder, 1993).

Further research is required to adequately understand the functional basis and motivation of stereotypies in *L. latifrons*. Enrichment may not have an effect on stereotypic behaviour because this behaviour has become hard-wired through years of deprivation. With repetition, stereotypic behaviour may shift into a form of automatic processing known as central control; such centrally controlled stereotypies are performed in a more diverse set of situations and are hard to interrupt or modulate by changes to the environment (Mason and Latham, 2004). In addition, some stereotypic animals show reduced behavioural diversity and interaction with environmental stimuli (Wemelsfelder, 1993). In these animals, stereotypies persist or may increase following environmental enrichment due to the animals' inability to respond to changing environmental stimuli (Wemelsfelder, 1993).

The feed enrichment was designed to increase food searching (e.g. by hiding of foods), handling and consumption times (e.g. by provision of sward and browse). Feed enrichment has been successfully used before to promote more species-specific foraging behaviour (Stoinski et al., 2000; Baxter and Plowman, 2001; Swaisgood et al., 2001). In this study feed enrichment increased daily time spent foraging by 333%. Additionally, we observed that feed enrichment allowed the wombats to engage in a wider range of naturalistic foraging behaviours, e.g. the stripping of leaves, branches and bark of browse, splitting up and selective grazing of sward and olfaction to locate and dig up buried food. These results constituted a positive improvement in welfare; first, because there was an increase in species-typical behaviour and second, because the animals were encouraged to use that part of their behavioural repertoire devoted to the searching for and processing of food (usually captive feeding for wombats only involves consumptive behaviour).

The olfactory enrichment was designed to increase enclosure exploration time by providing scented logs. Olfactory stimulation has been shown to positively influence the exploratory behaviour of many species and is now considered to be a useful form of enrichment (Pearson, 2002; Wells and Egli, 2004; Graham et al., 2005; Wells et al., 2007). In this study the odour-impregnated logs resulted in a 13% increase in daily exploration time, with odour interaction rates varying from 33% to 66%. This result also constituted an improvement in welfare as (1) natural exploring behaviour was enhanced, (2) the animals were provided with more opportunities to interact with their environment and (3) the animals were able to choose which scents they preferred to interact with.

Several studies have shown that environmental enrichment can result in a reduction in inactivity in captive animals (Swaisgood et al., 2001; Cummings et al., 2007; Skibiel et al., 2007). In this study, however, enrichment had no discernable effect on the wombats' time spent inactive. The reasons for the lack of a discernable difference in inactivity between treatments are unknown. It is possible that enrichment did not have a strong enough impact to cause an alteration in overall activity/inactivity levels, but this is doubtful. *L. latifrons* as a species is very energy conservative and it spends more time inactive than most other arid-dwelling species (Evans, 2000, 2008). Therefore, the observed 17% decrease in sitting-at-rest (an inactive behaviour), coupled with the major increase in foraging and exploratory behaviour (both active behaviours) during periods of enrichment, should have resulted in a detectable change to overall activity/inactivity.

5. Conclusions

Captive *L. latifrons* are susceptible to the development of stereotypies and this behaviour is most likely caused by an environmental deficit, such as a lack of space and/or stimulation, rather than by the frustration of foraging related motivations. A better understanding the functional basis and motivation of stereotypies in *L. latifrons* is crucial, as this understanding will facilitate the development of new management practices to improve welfare. The enrichment used in this study resulted in a significant increase in foraging and exploration, but did not reduce time spent stereotyping or inactive. Despite the fact that stereotypies and inactivity were not reduced by enrichment, animal welfare was still enhanced. Enrichment resulted in (1) sizeable increases in the expression of natural wombat-specific behaviour, (2) an enhancement in foraging-related behaviour diversity, (3) greater opportunities for animals to choose between various behavioural options, and (4) elevated environmental stimulation. Future directions with wombat enrichment must involve finding new ways to enrich this animal's life within captivity, e.g. employ techniques that increase reproductive success, reduce stereotypies, lower corticosteroid production, increase activity and/or promote more natural/normal behaviour.

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References

Altmann, J., 1973. Observational Study of Behaviour: Sampling Methods. University of Chicago, Chicago.

Baxter, E., Plowman, A.B., 2001. The effect of increasing dietary fibre on feeding, rumination and oral stereotypies in captive giraffes (*Giraffa camelopardalis*). Anim. Welf. 10, 281–290.

Booth, R., 1999. Wombats: Care and Treatment of Sick, Injured and Orphaned Animals, Wildlife in Australia – Healthcare and Management, Post-Graduate Foundation in Veterinary Science. University of Sydney, pp. 1–10.

Brown, G.D., Young, G., 1979. Wombats – amiable native lawnmowers. Aust. Nat. Hist. 20, 279–285.

Carlstead, K., Shepherdson, D., 2000. Alleviating stress in zoo animals with environmental enrichment. In: Moberg, G.P., Mench, J.A. (Eds.), The Biology of Animal Stress. CAB International Publishing, United Kingdom, pp. 337–349.

Clark, F., King, A.J., 2008. A critical review of zoo based olfactory enrichment. In: Hurst, J.L., Beynon, K.J., Roberts, S.C., Wyatt, T.D. (Eds.), Chemical Signs in Vertebrates, 11. Springer, New York, USA, pp. 298–391.

Cummings, D., Brown, J.L., Rodden, M.D., Songsasen, N., 2007. Behavioural and physiologic responses to environmental enrichment in the Maned wolf (*Chrysocyon brachyurus*). Zoo Biol. 26, 331–343.

Evans, M.C., 2000. Ecological Energetics of Wombats. University of New England, Cairns, p. 284.

Evans, M.C., 2008. Home range, burrow-use and activity patterns in common wombats (*Vombatus ursinus*). Wildl. Res. 35, 455–462.

Fraser, A.F., Broom, D.M., 1997. Farm Animal Behaviour and Welfare. CAB International Publishing, United Kingdom.

Gaughwin, M.D., 1981. Socio-Ecology of the Hairy-Nosed Wombat (*Lasiorhinus latifrons*) in the Blanche Town Region of South Australia. University of Adelaide, Adelaide, South Australia, p. 141.

Graham, L., Wells, D.L., Hepper, P.G., 2005. The Influence of Olfactory Stimulation on the Behaviour of Dogs Housed in a Rescue Shelter. Appl. Anim. Behav. Sci. 91, 143–153.

Hogan, L.A., Phillips, C.J.C., Lisle, A., Horsup, A.B., Janssen, T., Johnston, S.D., 2009. Remote monitoring of the behaviour and activity of captive southern hairy-nosed wombats (*Lasiorhinus latifrons*). Aust. Mammal. 31, 123–135.

Hogan, L.A., Tribe, A., 2007. Prevalence and cause of stereotypic behaviour in common wombats (*Vombatus ursinus*) residing in Australian zoos. Appl. Anim. Behav. Sci. 105, 180–191.

Jackson, S., 2003. Wombats, Australian Mammals – Biology and Captive Management. CSIRO Publishing, Collingwood, Victoria, Australia, pp. 183–203.

Mason, G., Clubb, R., Latham, N., Vickery, S., 2007. Why and how should we use environmental enrichment to tackle stereotypic behaviour? Appl. Anim. Behav. Sci. 102, 163–188.

Mason, G.J., Latham, N.R., 2004. Can't stop, won't stop: is stereotypy a reliable animal welfare indicator? Anim. Welf. 13, 57–69.

Moberg, G.P., 2000. Biological response to stress: implications for animal welfare. In: Moberg, G.P., Mench, J.A. (Eds.), The Biology of Animal Stress: Basic Principles and Implications for Animal Welfare. CAB International Publishing, United Kingdom, pp. 1–20.

Newberry, R.C., 1995. Increasing the biological relevance of captive environments. Appl. Anim. Behav. Sci. 44, 229–243.

Ostrower, S., Brent, L., 2000. Olfactory enrichment for captive chimpanzees: responses to different odours. Lab Primate 36, 8–12.

Pearson, J., 2002. On a role: novel objects and scent enrichment for Asiatic lions. Shape Enrich. 11, 7–10.

Powell, D.M., 1995. Preliminary evaluation of environmental enrichment techniques for African lions (*Panthera leo*). Anim. Welf. 4, 361–370.

Rushen, J., Lawrence, E.M., Terlouw, F., 1993. The motivational basis of stereotypies. In: Lawrence, A.B., Rushen, J. (Eds.), Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare. CAB International Publishing, United Kingdom, pp. 41–64.

Skibiel, A.L., Trevino, H.S., Naugher, K., 2007. Comparison for several types of enrichment for captive felids. Zoo Biol. 26, 371–381.

Stoinski, T.S., Daniel, E., Maple, T.L., 2000. A preliminary study of the behavioural effects of feeding enrichment on African elephants. Zoo Biol. 19, 485–493.

Swaisgood, R.R., 2007. Current status and future directions of applied behavioral research for animal welfare and conservation. Appl. Anim. Behav. Sci. 102, 139–162.

Swaisgood, R.R., Shepherdson, D.J., 2005. Scientific approaches to enrichment and stereotypies in zoo animals: what's been done and where should we go next? Zoo Biol. 24, 499–518.

Swaisgood, R.R., White, A.M., Zhou, X., Zhang, H., Zhang, G., Wei, R., Hare, V.J., Tepper, E.M., Lindburg, D.G., 2001. A quantitative assessment of the efficacy of an environmental enrichment program for giant pandas. Anim. Behav. 61, 447–457.

Terlouw, E.M.C., Lawrence, A.B., Illius, A.W., 1991. Influences of feeding level and physical restriction on development of stereotypies in sows. Anim. Behav. 42, 981–991.

Wang, Z., Goonewardene, L.A., 2004. The use of MIXED models in the analysis of animal experiments with repeated measures data. Can. J. Anim. Sci. 84, 1–10.

Wells, D.L., 2009. Sensory stimulation as environmental enrichment for captive animals: a review. Appl. Anim. Behav. Sci. 118, 1–11.

Wells, D.L., Egli, J.M., 2004. The influence of olfactory enrichment on the behaviour of captive black-footed cats, *Felis nigripes*. Appl. Anim. Behav. Sci. 85, 107–119.

Wells, D.L., Hepper, P.G., Coleman, D., Challis, M.G., 2007. A note on the effect of olfactory stimulation on the behaviour and welfare of zoo-house gorillas. Appl. Anim. Behav. Sci. 106, 155–160.

Wemelsfelder, F., 1993. The concept of animal boredom and its relationships to stereotyped behaviour. In: Lawrence, A.B., Rushen, J. (Eds.), Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare. CAB International Publishing, United Kingdom, pp. 65–98.

Young, R.T., 2003. Environmental Enrichment for Captive Animals. Blackwell Publishing, Great Britain.