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Space allowance and the behaviour of captive southern hairy-nosed wombats (*Lasiorhinus latifrons*)

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Abstract

Captive southern hairy-nosed wombats (*Lasiorhinus latifrons*) often display indicators of sub-standard welfare, including aggression and stereotypical pacing. To determine if space availability influences the welfare of wombats, the behaviour of three groups of *L. latifrons* (n = 3) was studied in three different sized enclosures: small (S) (75.5 m^2; the minimum space requirement for three wombats in Queensland, Australia), medium (M) (151 m^2, twice the minimum space) and large (L) (224 m^2, three times the minimum space) in a Latin Square design. Compared to wombats in larger enclosures, those in the small enclosure were observed to display more biting (S: 1.96; M: 0.42; L: 0.28, SED ± 0.56 counts / day, P = 0.01), retreat from conspecifics (S: 15.0; M: 9.9; L: 7.1 SED ± 2.66 counts / day, P = 0.03), and visual scanning (S: 52.8; M: 33.9; L: 28.8, SED ± 4.62 counts / day, P < 0.001); they also spent more time fenceline digging, which may represent attempts to escape (S: 0.78; M: 0.16; L: 0.24, SED ± 0.07 min / m / day, P < 0.0001). Those in the largest enclosure showed less self-directed grooming behaviour than those in the two smaller enclosures (S: 23.80; M: 24.08; L: 14.42, SED ± 3.22 counts / day, P = 0.02). It is concluded that small

enclosure size had a negative impact on the behaviour of wombat, and as a consequence, current minimum space requirements for wombats in captivity should be reassessed.

Key Words

Wombat, captivity, enclosure, space allowance

1.0 Introduction

Animal welfare in zoological institutions is an important consideration for both zoo professionals and the public (Reade and Waran, 1986; Watters and Wielebnowski, 2009). Increasingly, it is recognized that inadequate attention to species requirements, or deficient facilities and zoo programs (e.g. enrichment, husbandry, veterinary) can result in poor welfare and reproductive success. The ability to survive and thrive in a captive environment varies greatly between species (Mason, 2010: Mason and Veasey, 2010; Müller et al., 2010). Potentially stressful stimuli may include human interaction, enforced social structure, novelty, proximity to predator or prey species, and husbandry among others (Dennis et al., 2008; Morgan and Tromborg, 2007).

Zoo enclosures often inadequately represent the wild environment, with both space and complexity greatly reduced. Small spaces restrict the number of resting and feeding locations, decrease opportunity for behavioural enrichment, and encourage confrontation by reducing inter-individual distance (DeVries et al., 2004; Eriksson et al., 2010). Display animals in small enclosures may also be less able to remove themselves from public view. Inadequate enclosure sizes for display animals have been linked to aggression (Li et al., 2007), stereotyped pacing (Brummer et al., 2010), and reduced breeding success (Metrione, 2011; Peng et al., 2007), as well as increased heart rates and high levels of adrenal hormones (Li et al., 2007; Marchant et al., 1997). In some social species (*Elaphurus davidianus, Equus przewalskii*) more agonistic and affiliative behaviour occurs when space availability is low (Hogan, et al., 1988; Li et al., 2007), while in solitary species such as tigers (*Panthera tigris*) more conspecific avoidance occurs in order to reduce both aggression and affiliation (Miller et al., 2010).

The southern hairy-nosed wombat (*Lasiorhinus latifrons*) is a fossorial, nocturnal marsupial, commonly maintained in captivity. Captive wombats experience several problems, including low breeding success, obesity, aggression and performance of stereotypies (Hogan and Tribe, 2007; Hogan et al., 2010, 2011a; Treby, 2005). These issues indicate that conditions in captivity may be inadequate and factors that influence welfare should be examined. Wild wombats have a core home range of two - four hectares and a maximum home range of 20 hectares (Evans, 2008; Walker at al., 2006; Wells, 1978). The minimum standard for exhibiting wombats in Australia requires only 45-50 m^2 / pair (Australasian Regional Association of Zoological Parks and Aquaria (ARAZPA), 2007; New South Wales Department of Primary Industries (NSW DPI), 2006). Despite strong evidence in other species that small enclosures can have negative consequences on behaviour and physiology, this issue has not been systematically investigated in wombats.

The aim of this experiment was to determine how activity budgets and inter-individual distance are affected by space availability. Our hypothesis was that small enclosures increase the display of agonistic behaviour and other behavioural indicators of a low welfare state.

2.0 Materials and Methods

2.1 Study Animals

The study was conducted at the Wombat Research Centre, Rockhampton Botanic Gardens and Zoo (23^{o} 22’ S, 150^{o} 30’ E), Australia, using nine adult southern hairy-nosed wombats that were housed in three groups of one male and two females. Eight of the wombats were wild caught from Kooloola Station, Swan Reach, South Australia (34^{o} 55’ S, 139^{o} 28’ E) prior to 2005 and the remaining one was born at the Rockhampton zoo in 2003. While these wombats were located external to their natural range, this is nevertheless the case for many species in zoos. Therefore it was considered that experimental findings from this population would be relevant despite the departure from their natural climate. All wombats were fed carrots, chaff and macropod pellets (Riverina Australia Pty Ltd., West End, Australia) daily and were weighed weekly. Ethics approval was obtained from the University of Queensland Animal Ethics Committee (SAS/409/09/1).

2.2 Study Design

Three enclosure sizes were used as treatments in this study (Fig. 1): small (S) (75.5 m^2, 25.2 m^2 / wombat), medium (M) (151 m^2, 50.3 m^2 / wombat) and large (L) (224 m^2, 74.7 m^2 / wombat). The desired enclosure sizes were achieved by reducing the medium and small enclosures using wire mesh fencing attached to poles, and affixed to permanent underground mesh that prevented the wombats from digging out of the enclosures. The large enclosure was kept at its original full size. The smallest enclosure size used was the minimum standard for wombats in captive Queensland facilities (25 m^2/wombat, or 50 m^2/ pair; ARAZPA, 2007) although this differs slightly in other states (e.g. in NSW the standard is 45 m^2/pair with 9 m^2 for each additional wombat; NSW DPI, 2006). A three by three orthogonal, Latin Square design was used so that three groups completed one, 22-day period in each of the enclosure sizes, and a total of three, 22-day periods over the entire experiment. Twenty-two days was chosen as the treatment period firstly because, to the best of our knowledge, this allowed an adequate amount of time to pass (15 days) for habituation to the new enclosure size, to allow the animals to mark their enclosure and to minimise carry over effects. Previous research indicates that behavioural responses to unfamiliar wombat faeces appear to disappear within a day once faeces are removed (Descovich et al., 2012) and as the enclosures were cleaned daily it was unlikely that scents from previous enclosure inhabitants were still effective once observations began. Secondly, this allowed for three replications to be carried out, as the duration of time that the wombats could be exposed to varying treatments was restricted for animal ethics considerations. All groups had access to a pair of temperature-controlled dens linked by a tunnel. The outdoor area had a soil and sand substrate and was partially vegetated (35 – 40 %

coverage) with couch grass (*Cynodon dactylon*), guinea grass (*Panicum maximum*) and trees (*Eucalyptus spp.*). It included a digging chamber and a hollow log covered with dirt for digging. Each enclosure shared one boundary line with an adjacent group of wombats. Wombat groups were moved on the same day (day one) to their new enclosures with day 22 being the final day of each period. Behavioural observations were recorded on days 16, 18 and 20. Because of a temporary video failure on day 16 of the third period, behavioural observations for this period were taken from days 17, 18 and 20.

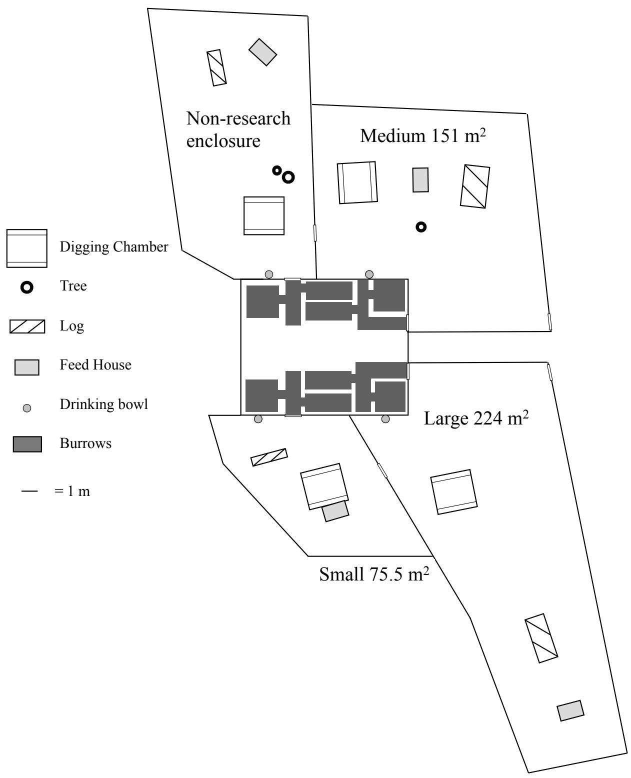

Fig. 1. Small, medium and large enclosures at the Wombat Research Centre, Rockhampton, QLD, Australia.

2.3 Behavioural Observation

Wombat behaviour in each den was monitored via a camera (Sony Model: N11368; Ozspy, Bundall, Australia), and the external enclosures were each monitored by two cameras (Sony Model: B480-312-TA; Ozspy, Bundall, Australia) with the aid of infrared (926 nM) spotlights (Hogan et al., 2009). Wombats wore collars (Titley Electronics, Ballina, Australia) that were uniquely patterned with IR reflective safety material (Protector Alsafe, Rockhampton, Australia) to allow individual identification on video. An ethogram was developed using behavioural categories from Hogan et al. (2011a) and adapted to include behaviour considered important for this study such as grazing, object smelling and visual scanning behaviour (Table 1). Major (long duration) behaviours were recorded at 5-min intervals and minor (short duration) behaviours were counted on each presentation. As wombats are nocturnal, behaviours were recorded during the active phase only (17:00 – 07:00 h, Hogan et al., 2011b). To record animal locations, wombats in the external part of the enclosure were allocated a position on a grid reference, while wombats inside the den system, digging chamber, feed house or log were allocated a location code.

Table 1. Recorded behaviour of southern hairy-nosed wombats.

Behaviour	Description
Major behaviour	
Dig chamber	Digging in the dirt chamber
Dig fenceline	Digging within 1m of the fenceline
Dig	Digging outside of permanent structures (includes fenceline digging)
Explore	Investigating areas of the enclosure or inedible objects
Feed	Eating within the feedhouse
Graze	Grazing on grassed areas or grass clumps provided
Lying Rest	Resting but awake in a lying position

Pace	Repetitive pacing, usually along the enclosure boundary
Sleep	Sleeping
Sitting rest	Resting but awake, sitting on the haunches with front paws on the ground and head down
Stand	Standing on four feet
Walk	A slow gait using four limbs; primary form of locomotion.
Wall climb	Climbing action repeatedly performed at the walls of a den.
Minor behaviour	
Approach	Approaching another wombat
Air smell	Smelling of the air, usually accompanied by a head movement up and down
Bite	Bite or nip from one wombat to another
Body rub	A body part rubbed against an inanimate object
Chase	One wombat chasing another
Enter	Entering the den system
Exit	Exiting the den system
Follow	One wombat following another
Object smell	Projecting the head towards an object and smelling
Retreat	One wombat retreating from another
Roll	Rolling onto back briefly from a standing position. May repeat or wriggle whilst on the back.
Scratch	Vigorous back and forth motion of foot claws across an area of the body
Visual scanning	Visual scanning using side to side head movements
Wombat smell	Projecting the head towards a conspecific and smelling

2.4 Statistical analysis

The three days of observations per treatment were aggregated for each individual. Major behaviours were collated as min per day and minor behaviours as counts per day. One behaviour, fenceline digging, was controlled for the availability of fenceline, as this differed between enclosure sizes. Therefore, fenceline digging was also analysed as min / m / day. A three by three Latin Square design was used, which gives limited statistical power but, when combined with observations on individuals, allows the origin of behavioural variance to be determined. A mixed model procedure in SAS (SAS Institute, version 8.2, Lane Cove, Australia) was performed on the data to determine the group contribution to variance. Out of 27 behaviour variables, only five were demonstrated to have any group contribution to the variance (lying rest, digging, following, object smelling and visual scanning). In the remaining behaviours, there was no evidence of group contribution. Given the lack of group contribution and the solitary nature of this species (Walker et al., 2007) we considered it valid to regard the animals as independent of each other. Therefore analysis of behavioural activity data was undertaken using the GLM procedure in SAS (SAS Institute, version 8.2, Lane Cove, Australia) regarding each individual x period combination as a unit. Residual plots (normal probability plot, box and whisker plot, scatterplot and histogram) were used to test data sets for normal distribution and it was determined that no transformations were necessary. Where a significant overall effect was apparent, protected *t* tests were conducted to determine if differences between treatments were significant.

Inter-individual distances were calculated from the grid references for each possible pair combination within a group (male - female 1; male – female 2; female 1 – female 2), unless there was a permanent structure between the animals. In this case they were considered as separated from each other. Both the mean inter-individual distance and the frequency of records when they were separated were analysed using the Mixed Model procedure in SAS® (SAS Institute, version 8.2, Lane Cove, Australia).

3.0 Results

3.1 Activity

As enclosure size decreased, less grazing was observed, and biting, retreating, visual scanning, standing and approaching conspecifics increased (Table 2). Wombats in the smallest enclosure dug significantly more along the fenceline than those in the other enclosures, while those in the medium enclosure dug the most overall. Other behaviours that were significantly less frequent in the largest enclosure than in the small or medium size enclosure were self-grooming by scratching, lying resting and approaching conspecifics.

Table 2. Behaviour of southern hairy-nosed wombats housed in small, medium and large enclosures observed during a 13 h recording 'day' (17:00 – 7:00 h)[1].

	Small	**Medium**	**Large**	**SED**	**P value, df = 2,26**
Dig chamber (min/day)	15.93	22.41	17.96	5.22	F = 0.81, P = 0.47
Dig (min/day)	30.74 ^{a}	45.37 ^{b}	27.04 ^{a}	6.11	F = 5.03, P = 0.02
Fenceline Dig (min/day)	15.74 ^{a}	4.81 ^{c}	9.26 ^{b}	1.99	F = 15.43, P = 0.0003
Fenceline Dig (min/m/day)	0.78 ^{a}	0.16 ^{b}	0.24 ^{b}	0.07	F = 25.65, P < 0.0001
Explore (min/day)	9.26	11.85	12.78	2.83	F = 0.83, P = 0.46
Feed (min/day)	47.78	54.07	44.63	5.01	F = 1.84, P = 0.19
Graze (min/day)	15.55 ^{a}	23.52 ^{b}	26.85 ^{b}	3.39	F = 5.87, P = 0.01
Lying Rest (min/day)	29.44 ^{a}	30.00 ^{a}	15.19 ^{b}	4.90	F = 5.86, P = 0.01
Pace (min/day)	27.41	9.81	4.81	13.33	F = 1.59, P = 0.24

[1] F statistics and P values for the effect of size on behaviour are given (GLM procedure in SAS), and where overall significance exists, pair-wise comparisons using protected t-tests are indicated by superscript.

Sleep (min/day)	528.15	503.33	550.93	23.92	F = 1.98, P = 0.17
Sitting Rest (min/day)	29.81	29.81	24.63	5.08	F = 0.69, P = 0.52
Stand (min/day)	53.15 ^{a}	36.30 ^{b}	31.30 ^{b}	5.75	F = 7.92, P = 0.005
Walk (min/day)	37.04	40.93	47.96	6.81	F = 1.32, P = 0.30
Wall Climb (min/day)	3.33	3.89	1.30	3.02	F = 0.41, P = 0.67
Approach (count/day)	19.70 ^{a}	17.30 ^{a}	10.78 ^{b}	2.36	F = 7.66, P = 0.006
Air Smell (count/day)	14.19	12.52	8.48	2.95	F = 1.98, P = 0.18
Bite (count/day)	2.00 ^{a}	0.44 ^{b}	0.33 ^{b}	0.52	F = 6.40, P = 0.01
Body Rub (count/day)	2.30	3.07	2.19	0.68	F = 1.03, P = 0.38
Chase (count/day)	0.78	0.41	0.22	0.34	F = 1.36, P = 0.29
Enter (count/day)	10.07	15.96	14.33	2.40	F = 3.20, P = 0.07
Exit (count/day)	9.89	15.44	14.04	2.49	F = 2.69, P = 0.10
Follow (count/day)	1.11	0.59	2.44	1.32	F = 1.05, P = 0.38
Object Smell (count/day)	50.81	55.00	48.52	5.96	F = 0.61, P = 0.56
Retreat (count/day)	14.93 ^{a}	10.00 ^{ab}	7.11 ^{b}	2.62	F = 4.53, P = 0.03
Roll (count/day)	1.07	0.74	0.30	0.63	F = 0.77, P = 0.48
Scratch (count/day)	23.81 ^{a}	24.19 ^{a}	14.48 ^{b}	3.24	F = 5.75, P = 0.02
Visual scan (count/day)	52.81 ^{a}	33.85 ^{b}	28.81 ^{b}	4.68	F = 14.61, P = 0.0004
Wombat Smell (count/day)	1.26	0.81	1.48	0.75	F = 0.41, P = 0.67

3.2 Inter-individual distance

Inter-individual distance (m) was unaffected by space availability (S: 1.17; M: 1.31; L: 2.31, SED = 0.57) ($F_{2,2}$ = 2.48, P = 0.29). Similarly, the frequency (% of time) that individuals were observed out of range of each other was not affected by space availability (S: 64.46; M: 69.55; L: 73.13, SED = 4.10) ($F_{2,2}$ = 2.26, P = 0.31).

4.0 Discussion

It is evident from this study that space availability in captivity had a significant impact on the behaviour of southern hairy-nosed wombats; negative effects becoming increasingly apparent as space availability decreased. Wombats in the smallest enclosure approached each other more, which is likely to be a direct result of the reduced space. In the same enclosure, behaviour indicative of social conflict (biting, retreating and visual scanning, potentially for vigilance) was most frequent; a result that concurs with previous studies using captive deer (*Elaphurus davidianus)* and tigers (*Panthera tigris*) (Li et al., 2007; Miller et al., 2010). Standing behaviour was also highest in the small enclosure and as a stationary alert behaviour, was likely influenced by the frequency of visual scanning and social conflict. The results suggest that enclosure size affected group harmony, and in other species this has been demonstrated to interfere with welfare and successful breeding (Honess and Marin, 2006).

Digging behaviour occurred more in the medium sized enclosure than either the large or small. As wombats dig for a variety of reasons (e.g. thermoregulation, protection, escape) (Finlayson et al., 2005; Shimmin et al., 2002; Triggs, 2009), this result is difficult to interpret. It is probable that either this is a spurious result or that moderate spatial stress exerted by the medium enclosure size encouraged generalised digging behaviour. It is possible that this result occurred because of particular, undetected qualities found in this specific enclosure. Soil structure, for example, is known to affect burrowing behaviour (Walker et al., 2007) and the animals in this enclosure appeared to dig mostly around the loose soil surrounding the permanent log. However, it is considered by the authors to be unlikely as unpublished data from other studies, including Descovich et al. (2012), using the same enclosures found no differences for digging behaviour. While Descovich et al. (2012) used the same enclosures at their full sizes, the current study and a subsequent one (Descovich et al. unpublished results) reduced the area of the medium and small enclosures. Only the current study recorded a difference in digging behaviour between enclosures. More importantly, digging can also be a method of escape as wombats are powerful diggers and captive enclosures must be secured by wire underneath the ground to prevent this (ARAZPA, 2007). Digging along the fence line is most likely to be representative of escape attempts (Day and MacGibbon, 2007). Fence line digging behaviour was significantly greater in the smallest enclosure compared to the other enclosure sizes. This suggests that the wombats are more motivated to escape the enclosure when the space availability is low.

Stereotypical pacing is an important behavioural indicator of stress in many species including wombats (Hogan et al., 2010), yet this remained unaffected by space availability. Wombats were housed in each enclosure for only 3 weeks, and this time-frame may not be long enough to induce changes in stereotypy presentation as other research indicates that it may be more commonly a result of chronic stress (McBride and Hemmings, 2009). An alternative possibility is that poor welfare caused by spatial constraints does not manifest as stereotypical pacing in wombats, despite these patterns being evident in other species such as coyotes (*Canis latrans*) (Brummer et al., 2010).

Wombats in the largest enclosure scratched significantly less than those in the medium or small enclosures. Along with rump rubbing, scratching is one of two main self-grooming behaviours for wombats (Hogan et al., 2011a) and has not previously been associated with welfare. In other species such as primates and birds, self-directed grooming is a well-established indicator of underlying anxiety (Carder and Semple, 2008; Daniel et al., 2008; van Zeeland et al., 2009). Therefore, a possible but tentative explanation could be that grooming in wombats indicates anxiety when considered in combination with the social conflict and escape behaviour observed in the current study. Alternatively, within-group aggression manifests as biting behaviour, which can result in (mostly superficial) damage to the skin and therefore scratching may be a direct result of discomfort from the healing of bite marks.

The smallest enclosure size used in this experiment was the current minimum standard per wombat for Queensland zoos (ARAZPA, 2007), and is slightly larger per group of three wombats compared to other states (e.g. NSW DPI, 2006). No negative behavioural effects were apparent in this study when the enclosure size was increased. The higher frequency of social conflict, self-directed behaviour, and escape digging by wombats housed in the smallest enclosure suggest that the minimum space standard is insufficient and requires revision. In captivity, this species shows clear indications of sub-standard welfare including low breeding rates. This study therefore indicates that welfare is likely to improve with enclosure size and addressing this issue may help to improve the ability of the species to breed in captivity. It is recommended that future research include longitudinal studies on the effect of enclosure size on reproductive performance and breeding outcomes.

This study has some limitations that should be acknowledged, as well as scope for future research Firstly, only one enclosure was used for each treatment type. Ideally, this would have been replicated to include three enclosures for each treatment type. Although it was theoretically possible that this could be achieved by manipulating the size of each enclosure, this was not possible due to permanent fencing and the small size of some enclosures. Thus, enclosure sizes could be reduced with temporary fencing but not enlarged. This study was conducted in the world's largest captive wombat facility with its four enclosures. No other existing facility could provide better experimental outcomes and the necessity for concrete, air-conditioned denning structures in captive enclosures make them costly to build. A second limitation already mentioned is the duration of the experiment. Future research that could incorporate longer treatment periods to assess the effects on welfare and breeding would be valuable in light of captive welfare issues for this species (Hogan and Tribe, 2007; Hogan et al., 2010, 2011a; Treby, 2005), and its value as an analogue species for the critically endangered *L. krefftii* wombat (Horsup, 2004). Thirdly, we expect carry over effects in this study to be minimal because of the 15-day period that elapsed prior to observations being recorded, allowing the wombats time to habituate and mark their surroundings. A future study, however, could quantify the duration of carry over effects for this species using a larger Latin Square design that allows more repeated crossover of treatments. We expect that, notwithstanding long-term effects on health or breeding, the effects of space allowance on behaviour were accurately identified by this experiment.

In conclusion, space availability is an important factor for captive southern hairy-nosed wombats. As enclosure size decreased, social conflict, escape behaviour and self-directed grooming increased. Stereotypical pacing was unaffected over the time period used. There were no negative effects of a large enclosure recorded. Increasing enclosure size may be an effective but simple way of improving the welfare of captive wombats.

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