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5   **Differential responses of captive southern hairy-nosed wombats (*Lasiorhinus latifrons)* to the**

6   **presence of faeces from different species and male and female conspecifics**

7

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14

15 **Abstract**

16 The southern hairy-nosed wombat (*Lasiorhinus latifrons*) appears to use scent marking, including

17 defaecation, for social communication in the wild. This premise assumes that the receiver wombat is

18 able to distinguish between faeces from different sources. To examine this theory, four types of faeces

19 (male wombat, female wombat, dingo and a plastic control) were placed into the enclosures of 12

20 captive wombats. Behaviour, inter-individual distance and enclosure use were recorded during the

21 period of placement, as well as the period before and the period after. When faeces were present, the

22 wombats used concealed locations more often than other periods (mean %: pre-treatment: 71.3,

23 treatment: 75.6, post-treatment: 72.7; $P < 0.05$). During the same period they also reduced grazing

24 (mean min/period: pre- treatment: 15.8, treatment: 6.9, post- treatment: 13.1; $P = 0.0002$) and walking

25　activity (mean min/period: pre- treatment: 85.2, treatment: 66.9, post- treatment: 78.2; P = 0.01),

26　indicating an increased perception of risk. Wombats approached the dingo faeces 5.6 times per

27　treatment period, which was greater than for the control (3.0; P = 0.004) or female wombat faeces

28　(3.7; P = 0.049). They also avoided other wombats most when male wombat faeces were present (8.3

29　retreats/period) compared to the control (4.5; P = 0.02), or female wombat (4.3; P = 0.01). There was a

30　residual effect of increased wombat avoidance the period after presentation of dingo faeces (9.6; P ≤

31　0.05). It is concluded that the southern hairy-nosed wombat can differentiate between faeces from

32　different species and sex of conspecifics, and that predator faeces and those from male conspecifics

33　increase wombat avoidance behaviour either during or after presentation.

34

35　**Key words**

36

37　Wombat, olfactory, faeces, scent, captivity, communication

38

39　**1.0 Introduction**

40

41　Scent marking is an energetically efficient method of advertising position, territory and reproductive

42　state (Brashares and Arcese, 1999). It is particularly effective when vision is restricted, such as in

43　burrows or at night (Arakawa et al., 2008; Monclús et al., 2009). Animal odours can facilitate

44　communication between conspecifics according to four different functions, scent matching,

45　reproductive signaling, temporal or spatial signaling and resource protection (Begg et al., 2003). Scent

46　matching allows a resident animal to distinguish other residents from intruders by recognizing their

47　scent, thereby reducing the need for territorial encounters (Gosling and McKay, 1990; Le Roux et al.,

48　2008; Luque-Larena et al., 2001). Male snow voles (*Chionomys nivalis*), for example, show less

49　aggression and more avoidance towards males that have been recognised by scent matching than for

50   those without matched scents (Luque-Larena et al., 2001). This function is particularly relevant to

51   species with overlapping boundaries, or those that operate within a hierarchical social system. Scent

52   marks may also advertise reproductive status and receptivity as they contain gonadal steroid

53   metabolites (Jannett, 1984; Ruibal et al., 2010; Swaisgood et al., 2000). Male captive pandas

54   (*Ailuropoda melanoleuca*), for example, vocalise, lick, investigate and scent mark more when exposed

55   to female faeces compared to male faeces, and they vocalise even more when the marker female is in

56   oestrus (Swaisgood et al., 2000). When scent marks are used for reproductive purposes, behavioural

57   differences should be evident between male and female markers and/or receivers (Begg et al., 2003),

58   and yearly patterns should be apparent for seasonal breeders (Pal, 2003). Scent marks may repel

59   neighbouring individuals allowing temporal and spatial relationships to be established without

60   physical or visual contact (Begg et al., 2003; Clapperton et al., 1989; Gosling and Roberts, 2001).

61   Free-ranging male dogs (*Canis familiaris*) mark close to boundaries shared with neighbours, while

62   females mark closer to nesting sites (Pal, 2003), indicating that scent marks are intended to deter

63   intruders. Scent marks around feeding sites may protect resources (Begg et al., 2003; Kruuk, 1992;

64   Miller et al., 2003). Golden lion tamarins (*Leontopithecus rosali*) and otters (*Lutra lutra*) both mark

65   feeding areas to reduce foraging competition. Otters also scent mark more during seasons when food is

66   scarce (Kruuk, 1992; Miller et al., 2003).

67

68   For prey species, scent marks may provide information about predation risk (Hayes et al., 2006).

69   Rodents (*Melomys cervinipes*, *Rattus fuscipes* and *Uromys caudimaculatus*) and cows (*Bos taurus*)

70   avoid feeding areas where there is evidence of predators (Hayes et al., 2006; Kluever et al., 2009).

71   Prey species may also use scent marks from co-habiting species to assess predation risk. Domestic

72   cows exposed to deer (*Odocoileus hemionus*) scents are less vigilant and eat more, indicating a

73   perceived reduction in predation risk (Kluever et al., 2009).

74

The southern hairy-nosed wombat (*Lasiorhinus latifrons*) is an Australian terrestrial marsupial that appears to use scent marks for social and reproductive signaling (Gaughwin, 1979; Taylor, 1993). Wombats often defaecate at their burrow entrance and on conspicuous objects such as rocks (Taylor, 1993) and males have been observed to display flehmann (Gaughwin, 1979). Wombats also rub their rumps on prominent objects such as burrow entrances, although this behaviour is not influenced by gender or breeding season and may, therefore, be performed more for grooming purposes rather than for scent marking (Walker et al., 2006). Studies into the function of olfactory communication in wombats may facilitate a better understanding of reproductive and social processes in wild populations, including the critically endangered Northern hairy-nosed wombat (*Lasiorhinus krefftii*). They may also assist in the management of captive populations. To determine if southern hairy-nosed wombats use scents such as faeces for social communication or predator avoidance, it is important to determine firstly whether they can distinguish between scents from different sources and secondly how the scents from different sources affect behaviour (Swaisgood et al., 2000). This study, therefore, aimed to quantify the level of differentiation and behavioural response of southern hairy-nosed wombats to faeces from conspecifics and a predator.

2.0 Materials and Methods

2.1 Study Animals

The study was conducted at the Rockhampton Botanic Gardens and Zoo (23° 22' S, 150° 30' E), Australia, using 12 adult southern hairy-nosed wombats housed in four groups of unrelated individuals each containing one male and two females. Eleven of these animals were wild caught prior to 2005 and the remaining one was born at the zoo in 2003. Accommodation for each wombat group was similar and included a temperature-controlled burrow system, a digging chamber, feeding house, native grass and a log (Hogan et al., 2009). The total area for each enclosure measured between 163

4

100 m^2 and 249 m^2 (Fig. 1). All wombats were fed carrots, chaff and macropod pellets (Riverina Australia

101 Pty Ltd., West End, Australia) daily and were weighed weekly. Each wombat wore a distinctive

102 reflective collar for identification on video. Ethics approval was obtained from the University of

103 Queensland Animal Ethics Committee (SAS/806/88).

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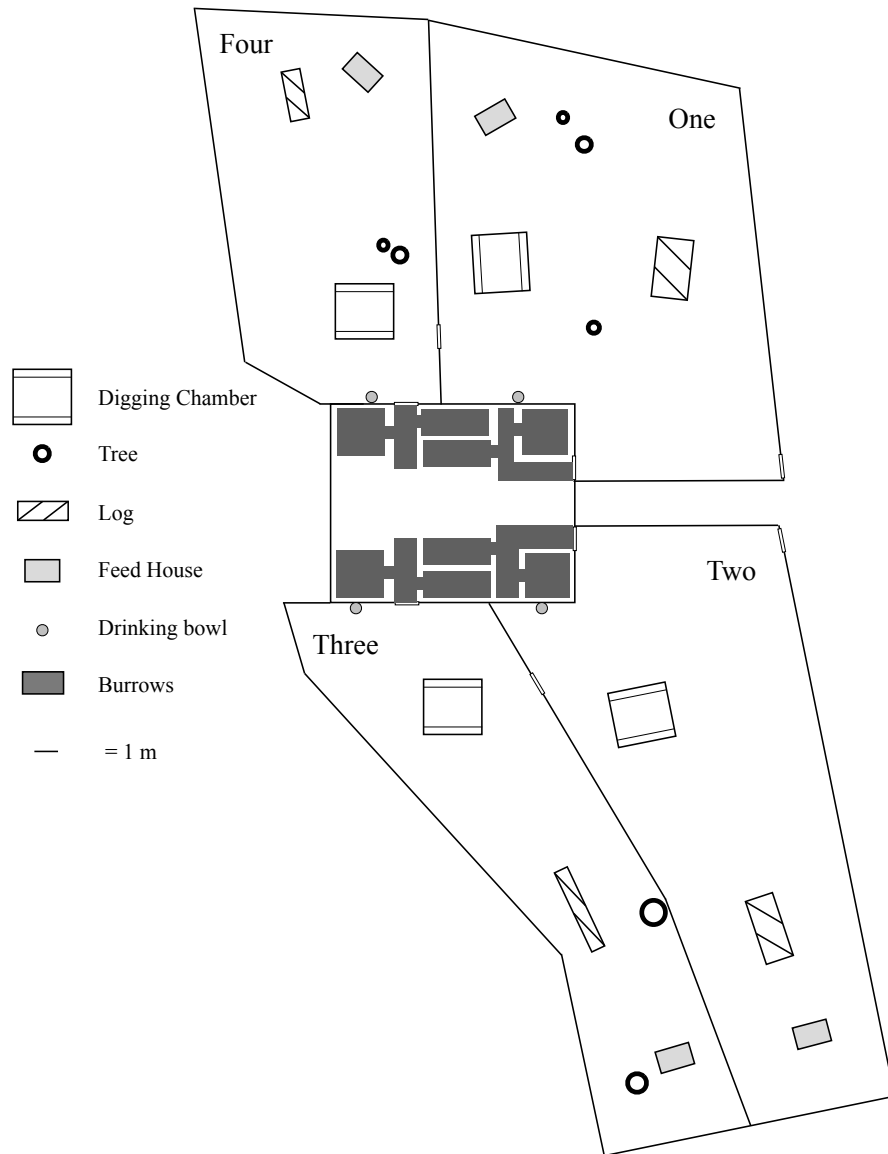
105

106 *Fig. 1.Wombat enclosure design.*

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109 *2.2 Faeces treatments*

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111 Four faeces types were used as treatments in this study: natural predator, dingo (D); male wombat

112 (MW); female wombat (FW); and control (C). The predator scats were collected on a single occasion

113 from two adult dingoes (*Canis familiaris dingo*), one male and one female, at the Rockhampton

114 Botanic Gardens and Zoo. After collection they were evenly mixed and distributed into four 12 g

115 doses and frozen at -20 °C until required. Conspecific scats were collected weekly over 6 weeks from

116 two adult *L. latifrons* wombats (one male and one female) residing at a different institution to ensure

117 that the recipient animals were unfamiliar with the donor animals. Collection occurred outside of the

118 breeding season and the female wombat was determined to be anoestrous from faecal progesterone

119 metabolite concentrations (23.1, 24.8, 23.1, 24.8, 18.7, 26.9, 20.3 and 14.8 ng/g in weeks 1 – 6,

120 analysed by the method of Hogan et al., 2010). After collection, faeces were immediately frozen at -

121 20 °C. The MW and FW treatments were prepared by combining 2 g from each collection week for a

122 total of 12 g per treatment. Plastic, imitation canine faeces (Dog Dirt, Loftus, Taiwan) were used as a

123 control treatment. To avoid odour contamination, this was washed with the same detergent used to

124 clean the wombat food bowls (Goldie, Morrison C.Q., North Rockhampton, Australia) and rinsed

125 thoroughly with water.

126

127 Treatments were randomly assigned to the pre-established wombat groups using an orthogonal Latin

128 square design with four rotations. All groups had access to two dens, one of which was used for

129 sleeping. Each morning of the study the den floors were swept and faeces removed from the external

130 enclosure. Treatment faeces were placed onto the floor of the non-sleeping den for one night from the

131 beginning of the wombats' active phase (17:00 h) until morning husbandry (08:00 h), with an inter-

132 treatment interval of 1 week to ensure that any previous odours had dissipated (Clark and King, 2008).

133   Treatments were placed directly from the sample bag without contact with human skin to avoid

134   contamination.

135

136   *2.3 Behavioural Observation*

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138   Wombat behaviour was monitored via burrow cameras (Sony Model: N11368; Ozspy, Bundall,

139   Australia), external enclosure cameras (Sony Model: B480-312-TA; Ozspy, Bundall, Australia) and

140   custom-made infrared (926 nM) spotlights (Hogan et al., 2009). An ethogram adapted from Hogan

141   (2010) was used to record major behaviours at 5-min intervals and minor behaviours as counted events

142   (Table 1). Wombats are nocturnal therefore recording periods were defined as 17:00 – 16:55 to

143   identify effects occurring during exposure to the treatment and during the subsequent rest time, with

144   activity recorded over three of these 'periods': pre-treatment, treatment, and post-treatment. To

145   determine if faeces affected inter-individual distances or space use, the location of each wombat was

146   recorded at 5-min intervals. Wombats in the external enclosure were allocated a grid reference

147   location, while wombats situated inside the den system or another permanent structure, were allocated

148   a location code (e.g. digging chamber = DC). All locations within permanent structures were

149   categorized as 'concealed' locations. External locations were categorized as 'boundary' locations if

150   they were ≤ 2 m from the fence line, and 'central' locations if they were > 2 m from the fence line.

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152
153 *Table 1. Ethogram of recorded major and minor behaviour for the southern hairy-nosed wombat*
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Major Behaviour	Description	Minor Behaviour	Description
Digging	Digging with the front paws and pushing out dirt with the back feet	Affiliative behaviour	Non-aggressive social behaviour from one wombat to another
Exploring	Investigating or examining areas of the enclosure	Approach	Approaching another wombat
Feeding	Eating of prepared food in the feeding house	Approach treatment	Approaching the treatment area by entering the secondary den
Grazing	Grazing on grassed areas or provided grass clumps	Bite	Bite from one wombat to another
Laying Rest	Resting but awake in a lying position	Body Rubbing	A body part is rubbed against an inanimate object
Mating behaviour	Mating or courtship behaviour	Drinking	Drinking of water from a provided bowl
Pacing	Repetitive pacing, usually along the enclosure boundary	Following	Non-aggressive following of one wombat to another
Sleeping	Sleeping	Object smelling	Projecting the head towards an object and smelling
Sitting Alert	Resting but awake, sitting on the haunches with front paws on the ground. Head is up in an alert position.	Retreat	Retreating from another wombat
Sitting Rest	Resting but awake, sitting on the haunches with front paws on the ground and head down.	Rolling	Rolling onto the back briefly from a standing position. May repeat or wiggle whilst on the back.
Standing	Standing on four feet, head is level with the shoulders or in a down position	Scanning	Vigilance using side to side scanning head movements
Standing Alert	Standing on four feet, head is up in an alert position	Scratching	Vigorous back and forth motion of foot claws across an area of the body
Slow Walk	A slow gait using four limbs. Primary form of locomotion	Wombat Smelling	Projecting the head towards a conspecific and smelling
Wall Climbing	Climbing action repeatedly performed at the walls in a den		

155

156 *2.4 Statistical analysis*

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158 Behaviours with less than 20 (major) or 100 (minor) counts in total over the entire study were

159 discounted from analysis, as the data were noticeably bimodal and occurred in frequencies either under

160 or considerably over these designated thresholds. The data were analysed using SAS® (SAS Institute,

161   version 8.2, Lane Cove, Australia). Behavioural data were transformed (natural logarithmic

162   transformation + one) before analysis to achieve normality of residuals, following model fitting. To

163   determine the effects of period, sex and treatment, the transformed data were analysed using a linear

164   mixed model with a nested design for wombat within enclosure and a repeated measures design for the

165   periods of each treatment. Where a significant overall effect was apparent, back-transformed least

166   square means with 95% confidence intervals were calculated and protected *t*-tests (Howell, 2010)

167   conducted to determine if behaviour differed significantly between different periods of each treatment

168   and between treatments within the same period. Both transformed means with standard errors and

169   back-transformed means are reported.

170

171   Wombat location data were analysed using only data points encompassing the active phase (17:00 –

172   07:00 h, Hogan et al., 2011) to avoid long episodes in the same sleeping location influencing the data.

173   Inter-individual distances were calculated from the grid references for each pair combination within a

174   group (male - female 1; male – female 2; female 1 – female 2), unless there was a permanent structure

175   between the animals, in which case no record was taken. Inter-individual distance and the percentage

176   of time that pairs were separated by a permanent structure were analysed using the GLM procedure in

177   SAS® (SAS Institute, version 8.2, Lane Cove, Australia). Enclosure use was analysed using the

178   Genmod procedure in SAS® (SAS Institute, version 8.2, Lane Cove, Australia) with a binomial

179   distribution with a logit link to test initially for the use of concealed locations compared to

180   unconcealed, and subsequently, when the location was unconcealed, to test for the use of boundary

181   locations compared to central locations. Cohen's tests of standardized effect sizes are provided in

182   addition to the test statistics and probability values.

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184

3.0 Results

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187   *3.1 Behaviour*

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189   Faeces treatment significantly affected two behaviours: approach to the treatment area and retreating

190   from conspecifics (Fig. 2). During the treatment period, the wombats approached the treatment area

191   significantly more for treatment D compared to C (t_{88} = 3.0, P = 0.004, d = 1.25) or FW (t_{88} = 2.0, P =

192   0.049, d = 0.84) and retreated from conspecifics twice as often for treatment MW as for FW (t_{88} = 2.5,

193   P = 0.01, d = 1.18) or C (t_{88} = 2.3, P = 0.02, d = 1.09). Wombats receiving treatment D increased

194   retreating behaviour from the treatment to post-treatment period (t_{88} = 2.11, P = 0.04, d = 0.86), so that

195   retreat during the post-treatment period was more frequent for D than all other treatments (D vs. C: t_{88}

196   = 2.8, P = 0.007, d = 1.29; D vs. FW: t_{88} = 2.5, P = 0.01, d = 1.16; D vs. MW: t_{88} = 2.0, P = 0.05, d =

197   0.92). Pacing and investigatory behaviour, which are particularly important as behavioural indicators

198   of welfare in captive animals (Carlstead et al.,1993; Mallapur and Chellam, 2002) were unaffected by

199   treatment or period (Table 2).

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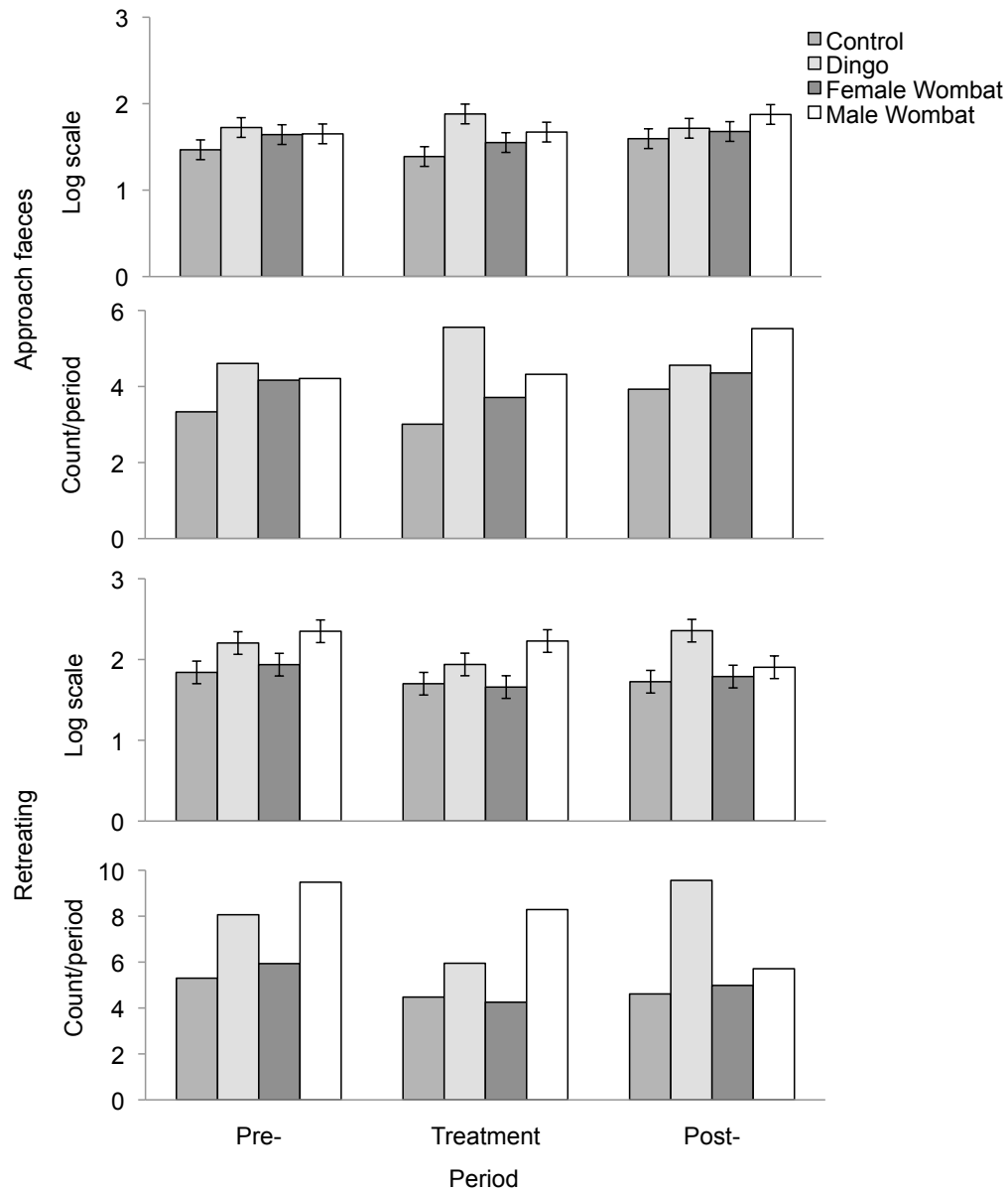
Fig. 2. The effect of faeces and period on approaching faeces treatments and retreating from conspecifics. Log transformed (natural log + 1) means with standard errors and backtransformed means are reported.

205

Table 2. Pacing (min/period) and smelling behaviour (count/period) [1] in the southern hairy-nosed wombat before (Pre-), during (Treatment) and after (Post-) exposure to faeces. Overall F statistic and P value are given.

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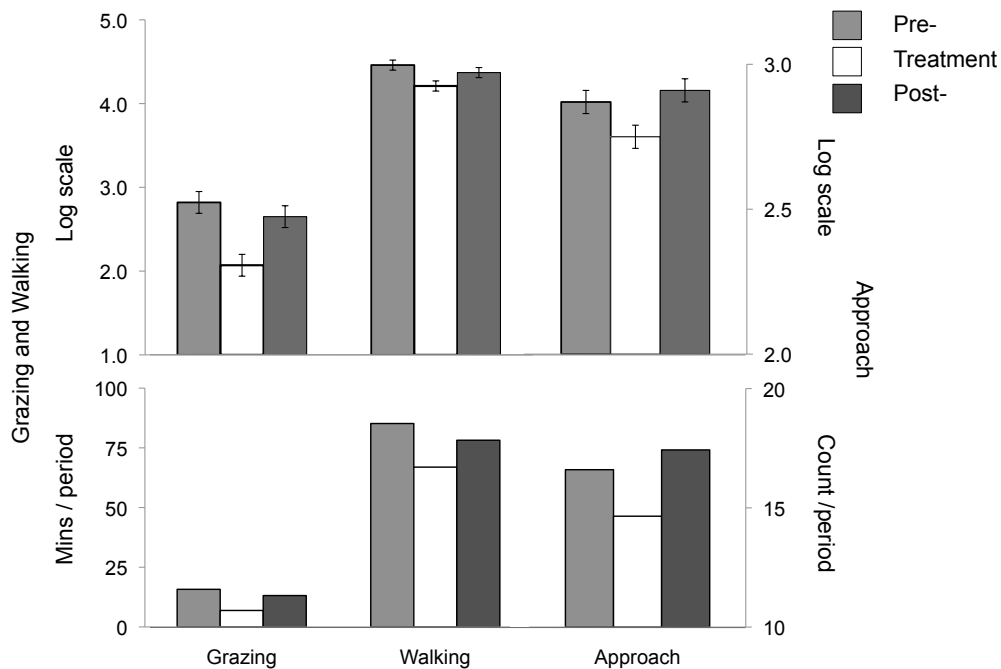| Behaviour	Period	Mean (Backtransformed mean; *d*)				
		Control	Dingo	Female Wombat	Male Wombat	SEM
Pacing	Pre-	2.14 (7.5)	2.42 (10.3; 0.43)	2.63 (12.9; 0.75)	2.11 (7.3; -0.05)	0.19
$F_{6,88} = 0.9$,	Treatment	2.34 (9.4)	2.03 (6.6; -0.48)	2.44 (10.4; 0.15)	1.99 (6.3; -0.54)	0.19
$P = 0.46$	Post-	2.38 (9.8)	2.14 (7.4; -0.37)	2.24 (8.4; -0.21)	2.27 (8.7; -0.17)	0.19
Smelling	Pre-	2.53 (11.6)	2.38 (9.8; -0.28)	2.44 (10.5; -0.17)	2.49 (11.1; -0.08)	0.15
$F_{6,88} = 0.66$,	Treatment	2.62 (12.7)	2.60 (12.4; -0.04)	2.67 (13.4; 0.09)	2.31 (9.0; -0.59)	0.15
$P = 0.68$	Post-	2.63 (13.0)	2.84 (16.1; 0.40)	2.61 (12.6; -0.04)	2.57 (12.1; -0.11)	0.15

210

[1] Transformed means (natural log + 1) and SEM are given. Backtransformed means and standardised effect sizes (*d*) comparing experimental to control treatments within the same period are also provided in brackets.

212 Period effects were evident in three behaviours regardless of the treatment type. These were grazing

213 ($F_{2,88} = 9.47$, P = 0.0002), walking ($F_{2,88} = 4.44$, P = 0.01), and approaching another wombat ($F_{2,88} =$

214 3.76, P = 0.03) (Fig. 3). These behaviours occurred less during the treatment period than the pre-

215 treatment (graze: $t_{88} = 4.15$, P = 0.0001, d = -0.85; walk: $t_{88} = 2.94$, P = 0.004, d = -0.60; approach: t_{88}

216 = 1.91, P = 0.06, d = -0.39) or post-treatment periods (graze: $t_{88} = 3.21$, P = 0.002, d = -0.66; walk: t_{88}

217 = 1.89, P = 0.06, d = -0.39; approach: $t_{88} = 2.66$, P = 0.009, d = -0.54), although the contrasts for

218 walking and approaching with the subsequent and previous periods, respectively, were only significant

219 at P = 0.06. Male and female wombats did not differ in their response to the treatments presented in

220 this experiment with no behaviour reaching significance for sex x treatment effects (P > 0.05).

221

222

223 *Fig. 3. Wombat behaviour (grazing, walking and approaching a group member) during pre-treatment,*

224 *treatment and post-treatment periods. Log transformed (natural log + 1) means with standard errors*

225 *and backtransformed means are reported.*

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226

227 *3.2 Inter-animal spacing and enclosure use*

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229 Neither treatment nor period affected the distance between wombat pairs, or the frequency of

230 separation of these pairs by permanent enclosure structures (Table 3). However, wombats used

231 concealed locations more often during the treatment period (75.6 ± 1.7 % of time) compared to the

232 pre-treatment (71.3 ± 1.7 %) (χ^2_1 = 9.98, P = 0.002) or post-treatment period (72.7 ± 1.7 %) (χ^2_1 =

233 4.58, P = 0.03) and this occurred irrespective of faeces type (Table 3). Patterns of use within the

234 external section of the enclosure did not change due to treatment (χ^2_6 = 3.89, P = 0.69) or period (χ^2_1

235 = 1.42, P = 0.49) (Table 3).

236

Table 3. Measures of animal spacing (i and ii) and enclosure use (iii and iv)[2] for the southern hairy-nosed wombat before (pre-), during (treatment)
and after (post-) exposure to faeces.

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	Period	i) Inter-individual distance (m)	ii) Occurrence of separated pairs (%)	iii) Concealed locations (logit scale)	iv) Boundary locations (logit scale)
Control	Pre-	2.9	43.8	1.13 (75.5)	0.60 (64.5)
	Treatment	2.2	42.7	1.21 (76.9)	0.60 (64.5)
	Post-	3.5	40.9	0.94 (71.8)	0.84 (69.9)
Dingo	Pre-	4.1 (1.02)	46.6 (0.71)	0.80 (68.9; -0.99)	0.56 (63.7; -0.02)
	Treatment	2.6 (0.34)	42.3 (-0.10)	1.09 (74.8; -0.31)	0.58 (64.2; -0.01)
	Post-	3.2 (-0.25)	42.6 (0.43)	0.96 (0.72; 0.04)	0.79 (68.7; -0.02)
Female Wombat	Pre-	2.7 (-0.17)	46.4 (0.66)	0.86 (70.3; -0.72)	0.52 (62.6; -0.03)
	Treatment	2.8 (0.51)	45.9 (0.81)	1.22 (77.1; 0.07)	0.55 (63.3; -0.01)
	Post-	2.0 (-1.27)	46.0 (1.3)	1.26 (7.79; 0.93)	0.41 (60.1; -0.16)
Male Wombat	Pre-	3.3 (0.34)	42.4 (-0.36)	1.07 (74.4; -0.22)	0.72 (67.3; 0.04)
	Treatment	2.5 (0.25)	41.6 (-0.28)	1.26 (76.5; 0.09)	0.74 (67.7; 0.05)
	Post-	3.2 (-0.25)	45.9 (1.27)	0.99 (72.9; 0.10)	0.74 (67.8; -0.03)
SE		0.6	2.0	0.1	0.1
Period effect		$F_{2,24} = 1.53$, P = 0.24	$F_{2,24} = 0.78$, P = 0.47	$\chi^2_2 = 10.40$, P = 0.006	$\chi^2_2 = 1.42$, P = 0.49
Treatment x Period Effect		$F_{6,24} = 0.83$, P = 0.56	$F_{6,24} = 0.91$, P = 0.50	$\chi^2_6 = 10.28$, P = 0.11	$\chi^2_6 = 3.89$, P = 0.69

241

242

[2] Means and SE are given, with backtransformed means (%) also provided for iii) and iv). F and P values are given for period and treatment x period effects with P < 0.05 considered significant. Standardised effect sizes (*d*) comparing experimental to control treatments within the same period are provided in brackets beside the mean for i) and ii). Approximations of the standard effect size (*d*) comparing experimental to control treatments within the same period have been calculated using data from a Mixed Model in SAS® (SAS Institute, version 8.2, Lane Cove, Australia) and are presented after the backtransformed means for iii) and iv).

243   **4.0 Discussion**

244

245   It is evident from the results of this study that wombats are able to differentiate between faeces from

246   different species, and between sexes of conspecific donors. Studies in other herbivorous species such

247   as Australian rodents (*Melomys cervinipes, Rattus fuscipes, Uromys caudimaculatus*) and cattle

248   showed comparable differentiation between species (Hayes et al., 2006; Kluever et al., 2009). Giant

249   pandas have been observed to similarly discriminate between male and female odours (Swaisgood et

250   al., 2000), although females in oestrus were not included in our study design.

251

252   The avoidance of conspecifics that occurred when male wombat faeces were presented suggests that

253   they induced a fear of a novel and potentially aggressive male animal. Wombats have poor eyesight

254   (Triggs, 2009) and, therefore, precautionary behaviour such as retreat from familiar animals would

255   provide protection when a threat has been detected through olfactory communication. This suggests

256   that an initial threat may have been perceived in response to the sight of another wombat, before

257   confirmation could be obtained that this was a familiar group member, and not the animal that had

258   produced the faeces. A similar process of conspecific recognition has been demonstrated in sheep

259   (Alexander and Shillito, 1977) where initial visual and olfactory detection is followed by confirmation

260   of identity using olfaction when sufficiently close. The avoidance of conspecifics in the period

261   following presentation of dingo faeces suggests a delayed reaction. The dingo faeces were most often

262   approached during the period of presentation, which may have been because of the novelty of the

263   species information provided and the need for confirmation. It is conceivable that the wombats

264   recognized the faeces came from a predator, which then had the residual effect of triggering a retreat

265   response from any animals in the enclosure.

266

267   The presence of faeces did not promote exploratory behaviour of the enclosure environment or reduce

268   the incidence of stereotypical pacing. Abnormal behaviour may occur because of under-stimulating

269   conditions such as small enclosure sizes (Brummer et al., 2010) or concentrated diets that reduce

270   natural feeding behaviour (Hogan and Tribe, 2007). However, as investigatory behaviour of the

271   environment was not increased by the presence of faeces and grazing behaviour decreased, any

272   stimulation provided by the faeces was not sufficient to offset the time involved in abnormal

273   behaviour. This result suggests that the use of faeces in wombat enrichment programs would be of

274   little benefit in improving animal welfare indicators. However, as captive wombats generally exhibit

275   poor breeding rates and high levels of stereotypical pacing, further research into the benefits of

276   olfactory enrichment is warranted.

277

278   Large changes in behaviour occurred with the presentation of faeces regardless of the type. Hiding

279   behaviour increased during the treatment period. Wombats are fossorial and rely on their burrow

280   systems for protection from predators (Triggs, 2009). An increase in the use of burrows and other

281   concealed locations in this study suggests that the wombats perceived an increased risk of threat

282   during the treatment period, irrespective of the faeces type. Walking and grazing decreased when

283   faeces were present and this was most likely a direct result of increased hiding behavior, as both

284   behaviours are primarily performed in the external enclosure. This also explains why the wombats

285   were less likely to approach each other during treatment periods compared to other periods. The

286   control treatment in this experiment elicited the same reaction in hiding, grazing and walking

287   behaviour as other treatments. This cannot be attributed to human interference, as the level of human

288   presence was comparable across all periods. This suggests that either the wombats used visual

289   information to recognize the control as faeces or responded due to neophobia because of the novelty of

290   the stimulus. It is conceivable that the wombats used prior experience to associate the shape of the

291   plastic control with faeces, as fox and cat scats are occasionally found in the enclosures (Descovich,

292   pers. obs.). In dairy cows, however, research with artificial faeces has demonstrated that it is the smell

293   and not the sight that elicits an avoidance response (Marten and Donker, 1966). The phenomenon of

294   neophobia in response to novel stimuli is well established in captive species (Biondi et al., 2010; Fox

295   and Millam, 2007; Greenberg, 2003). Neophobia may also affect feeding behaviour as seen in this

296   population, although prior studies have only measured this when the food source and novel item are in

297   close proximity (Apfelbeck and Raess, 2008). Of the two possible explanations described, neophobia

298   is most likely to influence the behavioural changes observed in wombats.

299

300   Inter-animal distance was unaffected by the presence or absence of the different types of faeces.

301   Wombats in the wild are mostly solitary (Walker et al., 2007). Therefore, inter-individual distance

302   may not accurately reflect a response to threat in this species, because unlike herding animals

303   (Childress and Lung, 2003; Liley and Creel, 2008), wombats may not anticipate any protective

304   advantage from close conspecific proximity.

305

306   A proposed function of social communication through faeces is for reproductive synchronization and

307   this would be indicated when the recipient animals respond differently according to their sex. No sex

308   differences were found in any behavioural response to faeces treatment. Potentially, this is because the

309   influence of breeding season and oestrous cycle were controlled through the use of faeces from

310   animals in a non-reproductive phase. Future research could include faeces sampled across different

311   stages of the oestrous cycle and breeding season to determine the function of scats in reproductive

312   signaling.

313

314   In conclusion, the wombats in this study were clearly able to differentiate between faeces originating

315   from a predator, male and female conspecifics, and a plastic control. While the wombats were most

316   affected by faeces representing the largest threats (dingo and male conspecific) all treatments triggered

317   an increase in protective, hiding behaviour and a decrease in grazing and locomotion. This study

318   demonstrates that faeces are an important biological signal for wombats and further study on the

319   information gained by this species through exposure to faeces is recommended.

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