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6 **The effect of group size on vigilance in a semi-solitary, fossorial marsupial (*Lasiorhinus latifrons*)**

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18 **ABSTRACT**

19

20 Prey species that congregate gain protection against predatory attacks and this advantage is often reflected  
21 by a reduction in vigilance behaviour by individuals in larger groups. Comparatively few studies have  
22 investigated vigilance in solitary animals, but those that have, found that vigilance increases as group size  
23 increases because of the threat posed by conspecifics and/or competition for resources. The southern hairy-  
24 nosed wombat (*Lasiorhinus latifrons*) is a large fossorial, nocturnal marsupial that is neither strictly solitary  
25 nor gregarious, sharing warren systems with multiple conspecifics. We investigated the effects of  
26 conspecific presence on vigilance behaviour in this semi-solitary species. We observed wild-born, adult *L.*  
27 *latifrons* wombats in three group sizes, (Large (1♂, 3♀), Medium (1♂, 2♀) and Small (1♂, 1♀) in a  
28 captive, naturalistic environment that allowed above-ground and den behaviour monitoring. Vigilance  
29 behaviours were performed less frequently by wombats in large groups (e.g. scanning, counts/day, Large:  
30 55, Medium: 69, Small: 115,  $P = 0.002$ ) and more frequently as the distance from their nearest conspecific  
31 increased ( $r_{64} = 0.30$ ,  $P = 0.016$ ). Vigilance within burrows was also affected by social influences, with  
32 solitary wombats significantly more vigilant than those denning with a conspecific (e.g. scanning:  
33 conspecific absent: 0.13 / 5 min, present: 0.03/ 5 min,  $P < 0.0001$ ). It is concluded that the presence of  
34 conspecifics reduces vigilance in *L. latifrons* wombats, even within burrows, and this may partially explain  
35 the occurrence of warren sharing in the wild.

36

37 **Key words: burrow, group size, marsupial, sociality, vigilance, wombat.**

38

39 **1.0 INTRODUCTION**

40 Group living has both advantages and disadvantages for the individual animal. Benefits include ready  
41 access to mates (Krause and Ruxton, 2002), co-operative defense (Furrer et al., 2011) and reduced energy  
42 expenditure for maintenance activities such as thermoregulation (McGowan et al., 2006; Schradin et al.,  
43 2006) or warren construction (Johnson, 1998; Walker et al., 2007). For prey species, feeding in groups is a  
44 protective strategy against attack by predators. When more animals are present, the individual risk of being  
45 targeted by a predator decreases ('dilution effect' hypothesis) and the probability that the group will detect

46 a predator increases ('many eyes' hypothesis) (Beauchamp, 2008; Caro, 2005; Estevez et al., 2007;  
47 Pulliam, 1973; Whitfield, 2003). Reflecting this change in predation risk, gregarious animals (e.g. Tibetan  
48 antelope, *Pantholops hodgsoni*) often reduce vigilance as group size increases (Lian et al., 2007). However,  
49 large congregations are also more detectable by predators than small ones ('attraction effect') (Hebblewhite  
50 and Pletscher, 2002), and gregarious animals have to compete with conspecifics for food or mating partners  
51 (Schoept and Schradin, 2012; Sugardjito et al., 1987). Therefore group size effects on vigilance may be  
52 amplified, tempered or reversed by variables other than predation, including intraspecific competition  
53 (Burger, 2003), food location efforts ('scrounging') (Beauchamp, 2001), or conspecific threat avoidance  
54 (Treves, 2000). Motivation for vigilance may be determined by the frequency of agonistic encounters,  
55 competition style (scramble / conflict), demand for mates, as well as external factors such as predation risk  
56 and forage availability (Arenz, 2003; Barboza, 2003; Estevez et al., 2007).

57

58 While conspecific effects on vigilance have been extensively tested in gregarious animals, species that  
59 operate within other social systems (e.g. solitary, semi-solitary, facultatively social) are underrepresented in  
60 the literature. Existing results indicate that solitary species should increase vigilance in the presence of  
61 conspecifics (e.g. *Sarcophilus harrisii*: Jones, 1998; *Dasyurus novemcinctus*: McDonough and Loughry,  
62 1995), while semi-solitary species display a more mixed response (e.g. *Thylogale thetis*: Blumstein et al.,  
63 2002; Pays et al., 2009). The propensity of a semi-solitary species to modulate group size vigilance patterns  
64 in a given direction is influenced by the conditions and situations that would normally encourage this  
65 species to aggregate or disperse. For example, the solitary forager, the yellow mongoose (*Cynictis*  
66 *penicillata*) increases vigilance when conspecifics are present if engaged in feeding behaviour (le Roux et  
67 al., 2009) but decreases vigilance when aggregating near sleeping burrows (Makenbach et al. 2013).

68 Studies of vigilance performed while grazing are important because they depict a trade-off of energy input  
69 with threat avoidance, however, it is clear that this alone cannot provide a full picture of how conspecifics  
70 influence vigilance behaviour, particularly for semi-social / semi-solitary animals, or those that are reliant  
71 on non-feeding behaviour (e.g. long resting periods or denning) to maintain energetic balance, such as the  
72 three wombat species (*Lasiorhinus latifrons*, *L. krefftii* and *Vombatus ursinus*: Evans et al., 2003).

73 Recently, the solitary common wombat (*V. ursinus*) was examined for social-vigilance patterns (Favreau et

74 al., 2009). It was found that during grazing bouts *V. ursinus* scan their environment more when in  
75 proximity to another wombat (Favreau et al., 2009), adhering to the pattern expected of a solitary species.  
76 The southern hairy-nosed wombat (*L. latifrons*) is less solitary than *V. ursinus*, and may share a warren  
77 system with multiple conspecifics (Walker et al., 2007), making it an interesting comparison species.  
78 Energetic conservation (e.g. low metabolic rate) is an important aspect of wombat biology (Evans et al.,  
79 2003). This is particularly true for *L. latifrons* because it survives within a semi-arid, resource-poor  
80 environment, which is likely to have contributed to the development of its social organization (Johnson et  
81 al., 2002). Similarly, warren-sharing is an adaptive strategy for reducing the energetic cost of digging and  
82 maintaining warrens (Johnson, 1998; Walker et al., 2007) but potentially also protects individuals against  
83 intruder conspecifics and predators, such as small dogs, which can enter the warren because of the large  
84 entrances (typically measuring up to 35 x 50 cm: Shimmin et al., 2002). Under-ground vigilance is yet to  
85 be examined in any species, but in *L. latifrons* may determine whether members of the species derive an  
86 anti-threat advantage from sharing warren systems. The use of this species as a research model also assists  
87 in understanding the relationship between nocturnality and vigilance, which is only beginning to be  
88 examined in the literature (Beauchamp 2007).

89

90 The aim of this experiment was to determine if semi-solitary species modulate vigilance with group size in  
91 a pattern more comparable to group-living or solitary animals. It can be hypothesized that animals which  
92 opportunistically congregate and separate do so to balance the same costs and benefits of group living that  
93 are experienced by social species. If this is true, it should follow that semi-solitary or facultatively social  
94 species will show group size vigilance patterns analogous to a social species, if observed in conditions in  
95 which aggregation is likely to have naturally occurred. We predict that when space and food availability are  
96 equal and abundant, our research model, *L. latifrons*, will be less vigilant in larger groups than in smaller  
97 groups (Prediction, P, 1), and when close to another group member (P2). We furthermore predict that this  
98 pattern of vigilance will be evident below-ground as well as above (P3), and during bouts of grazing (P4).  
99 Finally, we predict that vigilance will be positively correlated with the distance of the burrow entrance, if  
100 warrens act as sanctuaries from conflict or predation (P5).

101

## 102 2.0 METHODS

103

### 104 2.1 Study Animals

105 This study was conducted at the Rockhampton Botanic Gardens and Zoo, Rockhampton, Australia (23° 22'  
106 S, 150° 30' E) using nine adult *L. latifrons* (3♂, 6♀) per experimental period. All but one wombat from  
107 this study were wild-caught as adults from Swan Reach, South Australia (34°55'S; 139°28'E) prior to 2005,  
108 with the remaining one born at the facility in 2003. Wombats were organized into three groups using a  
109 randomized blocked design: Large (1♂, 3♀), Medium (1♂, 2♀) and Small (1♂, 1♀). Groups were blocked  
110 to ensure that none contained multiple males as these could become aggressive towards each other and  
111 cause severe injury (ARAZPA, 2007), and wherever possible to avoid animals experiencing the same  
112 treatment or group members in consecutive experimental periods. All groups were given comparable  
113 facilities comprised of an interior section with two air-conditioned sleeping dens and an external pen  
114 containing a digging chamber, large log covered with dirt, feed-house and grassed areas. Carrots, chaff and  
115 macropod pellets (Riverina Australia Pty Ltd., West End, Australia) were provided each afternoon. Each  
116 wombat wore a collar with a distinctive reflective pattern (Titley Electronics, Ballina, Australia) for  
117 identification on video. Approval for this experiment was granted by the University of Queensland Animal  
118 Ethics Committee (SAS/288/09).

119

### 120 2.2 Study Design

121 Four consecutive experimental periods occurred in total, with each period comprised of one of each group  
122 size. New wombat groups were formed on day one of each experimental period and behavioural  
123 observations were then taken on day 7, 14 and 21 to account for possible changes over time. The size of the  
124 interior of the enclosures could not be altered, however, the external enclosures were adjusted for group  
125 size at 50 – 59 m<sup>2</sup> per individual, making the Large enclosure 224 m<sup>2</sup>, the Medium one 151 m<sup>2</sup> and the  
126 Small one 118 m<sup>2</sup>. The research facility was off-display to avoid interference by zoo patrons and the  
127 wombats were able to freely move between both sections of their enclosure. Not all animals experienced  
128 each treatment during the study, as more animals were needed for the Large group than for the Medium or  
129 Small. Also, three original participants (one from each group size) were removed during or after an

130 experimental period when it was considered that progression could result in poor welfare or injury from  
131 intra-specific aggression. In their place, a new wombat was substituted on commencement of the next  
132 experimental period.

133

134 For the purpose of this study, air smelling, scanning the environment and object smelling were collectively  
135 considered vigilance behaviour, as wombats use visual, auditory and olfactory cues to assess their  
136 environment and detect threat (Descovich et al., 2012a, b; Taggart et al., 2003). However, as vigilance is  
137 non-specific in the type of threat that it detects (e.g. predatory / conspecific), other relevant behaviours  
138 were recorded in order to identify the underlying motivation. Behaviour was monitored by one experienced  
139 observer via infra-red burrow cameras (Sony Model: N11368; Ozspy, Bundall, Australia), and external  
140 enclosure cameras (Sony Model: B480-312-TA; Ozspy, Bundall, Australia) with infrared (926 nM) lights  
141 (Hogan et al., 2009). As wombats are nocturnal, recording periods were confined to 16:00 – 06:55 h to  
142 encompass the active phase (Hogan et al., 2011b). An ethogram was adapted from Hogan et al. (2011a) to  
143 include behaviours of interest in this study, such as grazing, object and air smelling, and scanning (Table  
144 1). Major (long duration) behaviours were recorded at 5-min intervals and aggregated into minutes / day,  
145 and minor (short duration) behaviours were counted on each presentation and converted into count / day.  
146 Wombat locations in the external enclosure were recorded at five-minute intervals using a grid reference  
147 location with 1 m<sup>2</sup> cell size. Wombats inside a permanent structure were recorded as being in the larger or  
148 smaller of the two den chambers, or within the tunnel, digging chamber or feeding house.

149

**Table 1. Ethogram of *L. latifrons* behaviour with categorization for analysis**

Major	Category	Description	Minor	Category	Description
Dig	Dig	Digging in the outside area of the enclosure or digging chamber	Air smell	Air smell	Smelling of the air, usually accompanied by a head movement up and down
Explore	Explore	Investigating areas of the enclosure or inedible objects	Approach	Affiliation	Approaching another wombat
Feed	Feed	Eating within the feed house	Bite	Aggression	Bite or nip from one wombat to another
Graze	Graze	Grazing on grassed areas or grass clumps provided	Body rub	Groom	A body part rubbed against an inanimate object
Lie	Rest	Resting but awake in a lying position	Chase	Aggression	One wombat chasing another
Pace	Abnormal	Repetitive pacing, usually along the enclosure boundary	Follow	Affiliation	One wombat following another
Run	Locomotion	A fast gait using four limbs			
Sit	Rest	Resting but awake, sitting on the haunches with front paws on the ground and head down	Object smell	Object smell	Projecting the head towards an object and smelling
Sleep	Rest	Sleeping	Retreat	Avoidance	One wombat retreating from another
Stand	Rest	Standing on four feet	Roll		Rolling onto back briefly from a standing position. May repeat or wriggle whilst on the



					back.
			Rump	Avoidance	A firm, quick upward movement of the rump
			protect		caused by pushing up of the hind legs
Walk	Locomotion	A slow gait using four limbs; primary form of locomotion.	Scan	Scan	Visual or auditory scanning using side to side head movements
Wall climb	Abnormal	Repetitive wall climbing movement performed in the den	Scratch	Groom	Vigorous back and forth motion of foot claws across an area of the body
			Wombat smell	Affiliation	Projecting the head towards a conspecific and smelling

152

153 *2.3 Statistical analysis*

154 *2.3.1 General treatment of data*

155 Major behaviours that occurred less than 35 times over the entire study, and minor behaviours occurring  
156 less than once per day were excluded from analysis as the data were noticeably discontinuous and those  
157 that occurred in frequencies under these designated thresholds were rare.

158

159 *2.3.2 The effect of group size on vigilance and general behaviour (P1)*

160 Major and minor behaviour data were transformed by adding one and taking the natural logarithm to  
161 achieve normality of residuals and subsequently analysed using the Mixed Model Procedure in SAS®  
162 (SAS Institute, version 8.2, NC, USA) to determine the effects of group size on behaviour. Fixed effects  
163 were designated as Group Size, Experimental Period, Day, and Group Size x Day interaction. Random  
164 effects were designated as Experimental Period x Group Size interaction and Experimental Period x  
165 Individual nested within Group Size. Dependent variables were the log transformed behavioural variables  
166 (dig, explore, feed, graze, lying rest, pace, sleep, sitting rest, stand, walk, approach, bite, body rub, chase,  
167 follow, retreat, roll, scratch, wombat smell, air smell, object smell, scan). Transformed means with standard  
168 errors are reported throughout with backtransformed means also included for biological relevance. Where  
169 the Mixed Model showed a significant effect protected (post-hoc) t-tests were conducted.

170

171 *2.3.3 The relationship between vigilance levels and nearest neighbour distance (P2)*

172 Inter-individual distances for each pair combination within a group were calculated using a 3-step process.  
173 When both wombats were located within the same permanent structure (den A or B, digging chamber,  
174 feeding house or tunnel) their distance was considered to be 0 m. When only one wombat was within a  
175 permanent structure or both wombats were within different structures they were considered ‘separated’  
176 from each other, i.e. the distance was incalculable. When both wombats were in the external section of the  
177 enclosure, their distance was calculated using the grid reference system. The relationship between mean  
178 daily vigilance and nearest neighbor distance was quantified using partial correlations by carrying out a  
179 MANOVA in the GLM procedure of SAS® (SAS Institute, version 8.2, NC, USA). Effects allowed for in

180 the model were Group Size, Experimental Period, Day, Group Size x Day interaction, and Individual  
181 nested within Group Size.

182

#### 183 *2.3.4 The effect of conspecific presence/absence on vigilance behaviour within burrows (P3)*

184 The frequency of vigilance was recorded when the wombats were located in either Den A or B. The  
185 presence or absence of conspecifics was also noted using a binary coding (0 = no conspecific present, 1 =  
186 one or more conspecific present). The Mixed Model procedure in SAS® (SAS Institute, version 8.2, NC,  
187 USA) was used specifying vigilance behaviours as the dependent variables. Fixed effects were designated  
188 as Group Size, Experimental Period, Day, Group Size x Day interaction, Presence Of Conspecific, and  
189 Group Size x Presence of Conspecific interaction. Random effects were designated as Experimental Period  
190 x Group Size interaction and Experimental Period x Individual nested within Group Size.

191

#### 192 *2.3.5 The effect of group size on vigilance behaviour during grazing (P4)*

193 Vigilance while grazing was isolated by counting the occurrence of vigilance (scanning, air smelling and  
194 object smelling) in the five minutes prior to and after grazing behaviour was observed. Mean vigilance  
195 counts were calculated per grazing event, for each animal per day. This was analysed using the Mixed  
196 Model Procedure in SAS® (SAS Institute, version 8.2, NC, USA). Fixed effects were designated as Group  
197 Size, Experimental Period, Day, and Group Size x Day interaction. Random effects were designated as  
198 Experimental Period x Group Size interaction and Experimental Period x Individual nested within Group  
199 Size. Dependent variables were the vigilance behavioural variables, weighted for the number of grazing  
200 events.

201

#### 202 *2.3.6 The relationship between vigilance and the proximity from the burrow entrance (P5)*

203 The distance of individuals from their nearest burrow entrance was calculated for animals in the external  
204 section of the enclosure using their grid reference location recorded at 5-minute intervals. Similar to the  
205 process outlined in 2.3.3, the relationship between mean daily Vigilance and the proximity of the burrow  
206 entrance was quantified using partial correlations by carrying out a MANOVA in the GLM procedure in

207 SAS® (SAS Institute, version 8.2, NC, USA). Effects allowed for in the model were Group Size,  
208 Experimental Period, Day, Group Size x Day interaction, and Individual nested within Group Size.

209

### 210 **3.0 RESULTS**

#### 211 *3.1 The effect of group size on vigilance and general behaviour (P1)*

212 All vigilance behaviours were affected by group size (Table 2). Scanning and air smelling occurred more  
213 frequently in the Small group compared to the Large ( $t_6 = 6.42, P = 0.001$  and  $t_6 = 5.41, P = 0.002$ ,  
214 respectively) or Medium group ( $t_6 = 4.20, P = 0.006$  and  $t_6 = 3.27, P = 0.017$ ). Similarly, object smelling  
215 was observed less in the large group than either the Small ( $t_6 = 4.14, P = 0.006$ ) or Medium groups ( $t_6 =$   
216  $3.40, P = 0.015$ ). Only one other behaviour, locomotion, was affected by group size, occurring most  
217 frequently in the largest group, and significantly more than in the Small ( $t_6 = 3.95, P = 0.008$ ) or Medium  
218 sized groups ( $t_6 = 2.67, P = 0.04$ ). Aggression and avoidance between conspecifics occurred at similar  
219 frequencies for each group size (Table 2).

220

221 **Table 2. Log means and pooled SED for vigilance behaviour and general activity of *L. latifrons* in Small, Medium and Large groups, with back-**  
 222 **transformed means provided in brackets as counts/day for vigilance and minor behaviours and minutes/day for major behaviours. Day = 15 hour**  
 223 **observation day over active period. Where behaviour is affected by group size, groupings are indicated with superscript.**  
 224

<b>Vigilance behaviour [Log (count / day)]</b>	<b>Small</b>	<b>Medium</b>	<b>Large</b>	<b>Pooled SED</b>	<b>F statistic, P value</b>
Air smell	3.54 <sup>a</sup> (33.57)	3.06 <sup>ab</sup> (20.29)	2.78 <sup>b</sup> (15.19)	0.14	F <sub>2,6</sub> = 14.65, P = 0.005
Object smell	4.84 <sup>a</sup> (125.22)	4.69 <sup>a</sup> (107.82)	4.27 <sup>b</sup> (70.69)	0.14	F <sub>2,6</sub> = 10.46, P = 0.01
Scan	4.76 <sup>a</sup> (115.41)	4.25 <sup>b</sup> (69.13)	4.02 <sup>b</sup> (54.68)	0.11	F <sub>2,6</sub> = 20.70, P = 0.002
<b>Major behaviour [Log (min / day)]</b>					
Abnormal	0.71 (5.15)	1.23 (12.08)	1.69 (22.07)	0.44	F <sub>2,6</sub> = 2.48, P = 0.16
Dig	2.87 (82.80)	2.97 (91.99)	3.12 (107.85)	0.22	F <sub>2,6</sub> = 0.70, P = 0.53
Explore	1.48 (16.99)	1.56 (18.90)	1.51 (17.66)	0.18	F <sub>2,6</sub> = 0.10, P = 0.91
Feed	2.29 (44.56)	2.49 (55.19)	2.41 (50.61)	0.11	F <sub>2,6</sub> = 1.30, P = 0.34
Graze	1.55 (18.67)	1.83 (26.17)	1.67 (21.66)	0.20	F <sub>2,6</sub> = 0.90, P = 0.46
Locomotion	2.74 <sup>a</sup> (72.16)	2.92 <sup>b</sup> (87.23)	3.24 <sup>b</sup> (122.24)	0.13	F <sub>2,6</sub> = 8.35, P = 0.02
Rest	4.69 (540.60)	4.58 (483.10)	4.28 (357.80)	0.22	F <sub>2,6</sub> = 1.89, P = 0.23

<b>Minor behaviour [Log (count / day)]</b>					
Aggression	0.48 (0.62)	1.15 (2.17)	1.15 (2.14)	0.42	$F_{2,6} = 1.42, P = 0.31$
Groom	3.14 (22.17)	2.55 (11.79)	2.72 (14.26)	0.24	$F_{2,6} = 2.79, P = 0.14$
Avoidance	2.18 (7.82)	2.48 (10.92)	2.76 (14.87)	0.39	$F_{2,6} = 1.16, P = 0.37$
Affiliation	3.17 (22.79)	3.10 (21.16)	3.19 (23.36)	0.24	$F_{2,6} = 0.10, P = 0.91$
Roll	0.86 (1.36)	0.55 (0.73)	0.92 (1.50)	0.22	$F_{2,6} = 1.71, P = 0.26$

225 3.2 The relationship between vigilance levels and nearest neighbour distance (P2)

226 There were positive correlations between nearest neighbor distance and two vigilance behaviours  
227 (scanning:  $r_{64} = 0.30$ ,  $P = 0.016$ ; object smelling:  $r_{64} = 0.42$ ,  $P = 0.0005$ ). Air smelling was not significantly  
228 affected by nearest neighbour distance ( $r_{64} = 0.21$ ,  $P = 0.099$ ).

229

230 3.3 The effect of group size and conspecific presence on vigilance behaviour within burrows (P3)

231 The amount of vigilance performed while inside the dens was unrelated to group size (air smelling:  $F_{2,6} =$   
232  $0.16$ ,  $P = 0.86$ , object smelling:  $F_{2,6} = 1.30$ ,  $P = 0.34$ , scanning:  $F_{2,6} = 0.44$ ,  $P = 0.66$ ) or the interaction  
233 between group size and the presence of a conspecific (air smelling:  $F_{2,127} = 0.08$ ,  $P = 0.45$ , object smelling:  
234  $F_{2,127} = 0.67$ ,  $P = 0.51$ , scanning:  $F_{2,127} = 1.11$ ,  $P = 0.33$ ). However, there was a significant relationship  
235 between the frequency of vigilance and the presence or absence of a conspecific. Wombats were  
236 significantly less vigilant when they were in the company of another wombat, compared to when they were  
237 alone (Table 3).

238

239 **Table 3. Mean (count / 5 min observation interval) and pooled SED for vigilance behaviours of *L.***  
240 ***latifrons* whilst in the burrow, in the presence or absence of a conspecific.**

241

Behaviour (count / 5 min interval)	Present	Absent	Pooled SED	F statistic, P value
Air smell	0.007	0.045	0.009	$F_{1,127} = 17.31$ , $P < 0.0001$
Object smell	0.06	0.257	0.04	$F_{1,127} = 22.73$ , $P < 0.0001$
Scan	0.03	0.13	0.025	$F_{1,127} = 5.79$ , $P < 0.0001$

242

243

244 3.4 The effect of group size on vigilance behaviour during grazing (P4)

245 Vigilance behaviour while grazing was affected by group size in a pattern similar to that recorded over the  
246 entire observation period (Table 4). Air smelling occurred more frequently in the Small group compared to  
247 the Large or Medium group ( $t_6 = 7.19$ ,  $P = 0.0004$  and  $t_6 = 5.94$ ,  $P = 0.001$ , respectively). Object smelling

248 was significantly different between all group sizes (Large vs. Small:  $t_6 = 4.86$ ,  $P = 0.003$ ; Large vs.  
 249 Medium:  $t_6 = 2.47$ ,  $P = 0.048$ ; Medium vs. Small:  $t_6 = 2.48$ ,  $P = 0.048$ ), and scanning occurred less in the  
 250 Large group compared to either the Small ( $t_6 = 4.07$ ,  $P = 0.007$ ) or Medium group ( $t_6 = 2.58$ ,  $P = 0.04$ ).

251

252 **Table 4. Mean (count / 5 min grazing interval) and pooled SED for vigilance behaviours during**  
 253 **grazing for *L. latifrons* in Small, Medium and Large groups. Groupings as determined by post-hoc**  
 254 **tests are indicated by superscript letters.**

255

Behaviour (count / 5 min grazing interval)	Small	Medium	Large	Pooled SED	F statistic, P value
Air smell	1.24 <sup>a</sup>	0.50 <sup>b</sup>	0.37 <sup>b</sup>	0.12	$F_{2,6} = 27.46$ , $P = 0.01$
Object smell	4.07 <sup>a</sup>	2.74 <sup>b</sup>	1.46 <sup>c</sup>	0.53	$F_{2,6} = 8.57$ , $P = 0.008$
Scan	2.64 <sup>a</sup>	2.07 <sup>ab</sup>	1.23 <sup>b</sup>	0.34	$F_{2,6} = 20.70$ , $P = 0.002$

256

257

### 258 3.5 The relationship between vigilance and the proximity of the burrow entrance (P5)

259 There was no significant relationship between vigilance behaviour and the proximity of the burrow  
 260 entrance for any vigilance variable – air smelling ( $r_{64} = 0.13$ ,  $P = 0.296$ ), scanning ( $r_{64} = -0.10$ ,  $P = 0.41$ )  
 261 and object smelling ( $r_{64} = -0.22$ ,  $P = 0.083$ ).

262

## 263 4.0 DISCUSSION

264 Our study demonstrates that *L. latifrons* modifies levels of vigilance in response to social influences.  
 265 Vigilance behaviour was performed less by wombats placed in larger groups (P1), and when conspecifics  
 266 were closer in proximity (P2). Social influences on vigilance while engaged in grazing activities were  
 267 similar to those recorded over the entire observation period (P4), and, for the first time, were documented  
 268 within the warren system (P3). Social conflict (aggression and avoidance) was not affected by group size.

269



270 Vigilance behaviour can be motivated by threat-avoidance (e.g. predator or conspecific evasion) and/or  
271 resource-management (e.g. identification of and competition for food sources) (Beauchamp, 2008). In  
272 many species, anti-predator vigilance decreases when conspecifics are present, or closer in proximity  
273 (Hebblewhite and Pletscher, 2002). While this pattern is well documented in social animals (e.g. Li and  
274 Jiang, 2008; Lian et al., 2007), it is rarely observed or is reversed in solitary animals or species for whom  
275 conspecifics may also pose a significant threat to safety (Burger and Gochfeld, 1994; Cameron and Du  
276 Toit, 2005; Favreau et al., 2009; Le Roux et al., 2009). Species that are vigilant to mitigate competition-  
277 related conflict or to scrounge and locate food would be expected to increase vigilance in the close  
278 presence of conspecifics (Beauchamp, 2009). However, those affected by scramble competition may  
279 prioritise foraging over vigilance in order to compete for an adequate share of finite resources (Beauchamp  
280 and Ruxton, 2003). Scramble competition therefore encourages a group size vigilance pattern similar to  
281 anti-predatory behaviour with a reduction of vigilance in larger groups. It is proposed, for four reasons, that  
282 adjustments to vigilance levels made by *L. latifrons* in response to social influences are primarily an anti-  
283 threat strategy, and that if scramble competition is present, it is a minor influence on behaviour. Firstly,  
284 individuals affected by scramble competition in larger groups should increase or improve feeding  
285 behaviour to remain competitive (Grand and Dill, 1999), however neither feeding nor grazing was affected  
286 by group size in this population. Secondly, this group size vigilance pattern occurred not only while  
287 grazing, but over the entire active period, of which grazing only contributed a small proportion (2.5 % of  
288 the time), as well as in the warren where feeding does not generally occur. Thirdly, the wombats rarely  
289 grazed simultaneously despite the space allowance that was adjusted for group size, and finally, our  
290 hypothesis is supported by observed changes in locomotion, with those in the largest group moving more  
291 than those in the smallest. Walking is the primary form of locomotion for wombats, and a previous study in  
292 the same population (Descovich et al., 2012a) demonstrated that walking decreases when there is evidence  
293 of a threat (e.g. unfamiliar faeces). It is, therefore, likely that locomotion fluctuates with perceived level of  
294 danger.

295

296 Vigilance behaviour has been examined previously in only one wombat species – *V. ursinus* (Favreau et al.,  
297 2009). This species increased vigilance when conspecifics grazed nearby, thus conforming to the expected

298 pattern for solitary species, and conflicting with the current pattern for *L. latifrons*. While *L. latifrons* is  
299 more social than *V. ursinus*, the distinction between the two lies largely in denning behaviour (Taylor,  
300 1993; Walker et al., 2006) as wild *V. ursinus* infrequently share warrens and *L. latifrons* may share warren  
301 systems with up to 9 other wombats in a single night (Walker et al., 2006); in other respects, the behaviour  
302 of *L. latifrons* is not gregarious. It is known that warren sharing in *L. latifrons* reduces the energetic cost of  
303 digging and maintaining warren systems (Walker et al., 2006), but as for other species, denning behaviour  
304 also is a feasible protective measure against predators (Predavec and Krebs, 2000) and to our knowledge  
305 this study is the first to examine social effects on underground vigilance for any burrowing species. The  
306 placement of wombats in different group sizes did not affect how vigilant they were in the den system,  
307 however wombats denning by themselves were more vigilant than those that were sharing a burrow. While  
308 denning congregations in wombats and other species are recognized as strategies for thermoregulation  
309 (Shimmin et al., 2002) and energetic conservation (Walker et al., 2007), our study is the first to suggest that  
310 denning in congregations may also serve an anti-threat purpose, either from intruder wombats or predators.  
311 *L. latifrons* wombats burrow-share more frequently than *V. ursinus*, which are rarely found in the same  
312 warren system (Favreau et al., 2009) at the same time, and therefore it is possible that *L. latifrons* are more  
313 susceptible to, or aware of, attack risk and recognize the protective advantage of denning in a group.

314

315 An alternative explanation for the divergence in results between the two species may be due to uncontrolled  
316 factors such as resource competition or population abundance. In our study, the availability of food and  
317 space was controlled for the number of wombats in each group but this is more difficult to achieve in the  
318 wild environment. The relationship between forage availability and vigilance is complex and, because of  
319 the influence of underlying motivations, it can occur in either a positive or negative direction, or may be  
320 entirely absent (Beauchamp, 2009). Species that are usually solitary because of environmental limitations  
321 may congregate when food is abundant and this can lead to aggressive encounters (Knott, 1998). This has  
322 important methodological implications for vigilance studies, as seasonal differences in forage availability  
323 may be a key ecological variable to incorporate into study design (Beauchamp, 2009). Interesting avenues  
324 for future research in wombat species should include vigilance patterns under varying resource pressures,  
325 especially seasonal fluctuations, as well as circadian patterns and predation risk levels.

326

327 Our study indicated that *L. latifrons* were not more or less vigilant as distance from the warren increased,  
328 contrary to our expectation (P5). This also contrasts with the result found in Favreau et al.'s (2009) study of  
329 a negative relationship between distance to cover and vigilance. The lack of a relationship in our study may  
330 indicate that larger distances are needed to induce changes in vigilance as a response to the proximity of the  
331 warren.

332

333 In conclusion, this study of social influences on vigilance and general activity in *L. latifrons* wombats in  
334 different group sizes demonstrated patterns more commonly observed in social species. Vigilance  
335 decreased as group size increased, and this pattern was apparent over the entire active period, as well as in  
336 the burrows. Vigilance decreased when conspecifics were closer in proximity. Other behaviour was largely  
337 unaffected by group size, with the exception of walking, which was performed most frequently by animals  
338 in the largest group. It is concluded that *L. latifrons* modify anti-threat behaviour with social context and  
339 perceive a protective advantage from the presence of conspecifics, even within the burrow system.

340 Furthermore, the hypothesis that semi-solitary species will reduce vigilance in larger groups if observed in  
341 conditions under which aggregation is likely to have occurred is supported by these results, however further  
342 research is needed to determine if this is supported under a variety of environmental or external conditions.

343

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352

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