

\*This is an “accepted manuscript” version of an article published in Behavioural Processes, Vol 100 (2013) pp 208-213.

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The final, published version is available at: <https://doi.org/10.1016/j.beproc.2013.09.015>

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

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## ABSTRACT

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

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

## 1.0 INTRODUCTION

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

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

60

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

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

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

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

92

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

## 104 2.0 METHODS

105

### 106 2.1 Study Animals

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

121

### 122 2.2 Study Design

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

133 intra-specific aggression. In their place, a new wombat was substituted on commencement of the next  
134 experimental period.  
135  
136 For the purpose of this study, air smelling, scanning the environment and object smelling were collectively  
137 considered vigilance behaviour, as wombats use visual, auditory and olfactory cues to assess their  
138 environment and detect threat (Descovich et al., 2012a, b; Taggart et al., 2003). However, as vigilance is  
139 non-specific in the type of threat that it detects (e.g. predatory / conspecific), other relevant behaviours  
140 were recorded in order to identify the underlying motivation. Behaviour was monitored by one experienced  
141 observer via infra-red burrow cameras (Sony Model: N11368; Ozspy, Bundall, Australia), and external  
142 enclosure cameras (Sony Model: B480-312-TA; Ozspy, Bundall, Australia) with infrared (926 nm) lights  
143 (Hogan et al., 2009). As wombats are nocturnal, recording periods were confined to 16:00 – 06:55 h to  
144 encompass the active phase (Hogan et al., 2011b). An ethogram was adapted from Hogan et al. (2011a) to  
145 include behaviours of interest in this study, such as grazing, object and air smelling, and scanning (Table  
146 1). Major (long duration) behaviours were recorded at 5-min intervals and aggregated into minutes / day,  
147 and minor (short duration) behaviours were counted on each presentation and converted into count / day.  
148 Wombat locations in the external enclosure were recorded at five-minute intervals using a grid reference  
149 location with 1 m<sup>2</sup> cell size. Wombats inside a permanent structure were recorded as being in the larger or  
150 smaller of the two den chambers, or within the tunnel, digging chamber or feeding house.  
151

152

153

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 protect	Avoidance	A firm, quick upward movement of the rump 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



154

## 155 2.3 Statistical analysis

### 156 2.3.1 General treatment of data

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

160

### 161 2.3.2 The effect of group size on vigilance and general behaviour (P1)

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

172

### 173 2.3.3 The relationship between vigilance levels and nearest neighbour distance (P2)

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

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

184

#### 185 *2.3.4 The effect of conspecific presence/absence on vigilance behaviour within burrows (P3)*

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

193

#### 194 *2.3.5 The effect of group size on vigilance behaviour during grazing (P4)*

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

203

#### 204 *2.3.6 The relationship between vigilance and the proximity from the burrow entrance (P5)*

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

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

211

## 212 **3.0 RESULTS**

### 213 *3.1 The effect of group size on vigilance and general behaviour (P1)*

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

222

223 **Table 2. Log means and pooled SED for vigilance behaviour and general activity of *L. latifrons* in Small, Medium and Large groups, with back-**  
224 **transformed means provided in brackets as counts/day for vigilance and minor behaviours and minutes/day for major behaviours. Day = 15 hour**  
225 **observation day over active period. Where behaviour is affected by group size, groupings are indicated with superscript.**  
226

<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	$F_{2,6} = 1.71, P = 0.26$

227 3.2 The relationship between vigilance levels and nearest neighbour distance (P2)

228 There were positive correlations between nearest neighbor distance and two vigilance behaviours

229 (scanning:  $r_{64} = 0.30$ ,  $P = 0.016$ ; object smelling:  $r_{64} = 0.42$ ,  $P = 0.0005$ ). Air smelling was not significantly

230 affected by nearest neighbour distance ( $r_{64} = 0.21$ ,  $P = 0.099$ ).

231

### 232 3.3 The effect of group size and conspecific presence on vigilance behaviour within burrows (P3)

233 The amount of vigilance performed while inside the dens was unrelated to group size (air smelling:  $F_{2,6} =$

234  $0.16$ ,  $P = 0.86$ , object smelling:  $F_{2,6} = 1.30$ ,  $P = 0.34$ , scanning:  $F_{2,6} = 0.44$ ,  $P = 0.66$ ) or the interaction

235 between group size and the presence of a conspecific (air smelling:  $F_{2,127} = 0.08$ ,  $P = 0.45$ , object smelling:

236  $F_{2,127} = 0.67$ ,  $P = 0.51$ , scanning:  $F_{2,127} = 1.11$ ,  $P = 0.33$ ). However, there was a significant relationship

237 between the frequency of vigilance and the presence or absence of a conspecific. Wombats were

238 significantly less vigilant when they were in the company of another wombat, compared to when they were

239 alone (Table 3).

240

241 **Table 3. Mean (count / 5 min observation interval) and pooled SED for vigilance behaviours of *L.***

242 ***latifrons* whilst in the burrow, in the presence or absence of a conspecific.**

243

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	$F_{1,127} = 5.79$ , $P < 0.0001$

244

245

### 246 3.4 The effect of group size on vigilance behaviour during grazing (P4)

247 Vigilance behaviour while grazing was affected by group size in a pattern similar to that recorded over the

248 entire observation period (Table 4). Air smelling occurred more frequently in the Small group compared to

249 the Large or Medium group ( $t_6 = 7.19$ ,  $P = 0.0004$  and  $t_6 = 5.94$ ,  $P = 0.001$ , respectively). Object smelling

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

253

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

257

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	$F_{2,6} = 20.70$ , $P = 0.002$

258

259

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

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

264

## 265 4.0 DISCUSSION

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

271

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

297

298 Vigilance behaviour has been examined previously in only one wombat species – *V. ursinus* (Favreau et al.,  
299 2009). This species increased vigilance when conspecifics grazed nearby, thus conforming to the expected



300 pattern for solitary species, and conflicting with the current pattern for *L. latifrons*. While *L. latifrons* is  
301 more social than *V. ursinus*, the distinction between the two lies largely in denning behaviour (Taylor,  
302 1993; Walker et al., 2006) as wild *V. ursinus* infrequently share warrens and *L. latifrons* may share warren  
303 systems with up to 9 other wombats in a single night (Walker et al., 2006); in other respects, the behaviour  
304 of *L. latifrons* is not gregarious. It is known that warren sharing in *L. latifrons* reduces the energetic cost of  
305 digging and maintaining warren systems (Walker et al., 2006), but as for other species, denning behaviour  
306 also is a feasible protective measure against predators (Predavec and Krebs, 2000) and to our knowledge  
307 this study is the first to examine social effects on underground vigilance for any burrowing species. The  
308 placement of wombats in different group sizes did not affect how vigilant they were in the den system,  
309 however wombats denning by themselves were more vigilant than those that were sharing a burrow. While  
310 denning congregations in wombats and other species are recognized as strategies for thermoregulation  
311 (Shimmin et al., 2002) and energetic conservation (Walker et al., 2007), our study is the first to suggest that  
312 denning in congregations may also serve an anti-threat purpose, either from intruder wombats or predators.  
313 *L. latifrons* wombats burrow-share more frequently than *V. ursinus*, which are rarely found in the same  
314 warren system (Favreau et al., 2009) at the same time, and therefore it is possible that *L. latifrons* are more  
315 susceptible to, or aware of, attack risk and recognize the protective advantage of denning in a group.  
316

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

328

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

334

335 In conclusion, this study of social influences on vigilance and general activity in *L. latifrons* wombats in  
336 different group sizes demonstrated patterns more commonly observed in social species. Vigilance  
337 decreased as group size increased, and this pattern was apparent over the entire active period, as well as in  
338 the burrows. Vigilance decreased when conspecifics were closer in proximity. Other behaviour was largely  
339 unaffected by group size, with the exception of walking, which was performed most frequently by animals  
340 in the largest group. It is concluded that *L. latifrons* modify anti-threat behaviour with social context and  
341 perceive a protective advantage from the presence of conspecifics, even within the burrow system.  
342 Furthermore, the hypothesis that semi-solitary species will reduce vigilance in larger groups if observed in  
343 conditions under which aggregation is likely to have occurred is supported by these results, however further  
344 research is needed to determine if this is supported under a variety of environmental or external conditions.

345

## 346 **ACKNOWLEDGEMENTS**

347 The authors would like to thank the Wombat Foundation for their financial support, and the Rockhampton  
348 Regional Council and staff for animal husbandry and access to the facilities and animals at the  
349 Rockhampton Botanic Gardens and Zoo. Technical advice and equipment were kindly provided by Dr Alan  
350 Horsup of the Queensland Department of Environmental and Resource Management. The authors also  
351 acknowledge the work of volunteers who generously donated their time at the Wombat Research Centre  
352 during this study, most notably Joel Irwin and Benjamin Descovich. Finally, the authors would like to  
353 thank two anonymous reviewers that provided feedback on the manuscript.

354

355

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507

#### 508 **FUNDING SOURCE**

509

510 This work was supported by the Wombat Foundation. The funding source played no role in conducting this  
511 experiment or preparing the manuscript for publication. Additionally, the Wombat Foundation was not  
512 involved in the study design, or the collection, analysis and interpretation of data, or in the decision to

513