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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 ($23^{\circ} 22'$
106 S, $150^{\circ} 30'$ 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 ($34^{\circ} 55'$ S; $139^{\circ} 28'$ 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 $50 - 59\text{ m}^2$ per individual, making the Large enclosure 224 m^2 , the Medium one 151 m^2 and the
126 Small one 118 m^2 . 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 m² 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

150 **Table 1. Ethogram of *L. latifrons* behaviour with categorization for analysis**
 151

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 Wombat smell	Groom	Vigorous back and forth motion of foot claws across an area of the body
				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

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

Minor behaviour [Log (count / day)]					
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	F statistic, P value
Air smell	1.24 ^a	0.50 ^b	0.37 ^b	0.12	$F_{2,6} = 27.46, P = 0.01$
Object smell	4.07 ^a	2.74 ^b	1.46 ^c	0.53	$F_{2,6} = 8.57, P = 0.008$
Scan	2.64 ^a	2.07 ^{ab}	1.23 ^b	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

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

Vigilance behaviour has been examined previously in only one wombat species – *V. ursinus* (Favreau et al., 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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354 **5.0 REFERENCES**

355

356 ARAZPA., 2007. Code of Practice of the Australasian Regional Association of Zoological Parks and Aquaria:
357 Minimum Standards for Exhibiting Wildlife in Queensland. Queensland Environmental Protection Agency.

358

359 Arenz, C.L., 2003. The group size effect on vigilance: many unanswered questions. *Behav Processes.* 63,
360 123-124.

361

362 Barboza, A., 2003. Group size effects on vigilance: we need more bricks in the wall. *Behav Processes.* 63,
363 133-134.

364

365 Beauchamp, G., 2001. Should vigilance always decrease with group size? *Behav Ecol Socio.* 51, 47-52.

366

367 Beauchamp, G. 2007. Exploring the role of vision in social foraging: What happens to group size,
368 vigilance, spacing, aggression and habitat use in birds and mammals that forage at night? *Biol Rev.* 82,
369 511-525.

370

371 Beauchamp, G., 2008. What is the magnitude of the group-size effect on vigilance? *Behav Ecol.* 19, 1361-
372 1368.

373

374 Beauchamp, G., 2009. How does food density influence vigilance in birds and mammals? *Anim Behav.* 78,
375 223-231.

376

377 Beauchamp, G., Ruxton, G.D., 2003. Changes in vigilance with group size under scramble competition.
378 *Am Nat.* 161, 672-675.

379

380 Blumstein, D.T., Daniel, J.C., Schnell, M.R., Ardon, J.G., Evans, C.S., 2002. Antipredator behaviour of
381 red-necked pademelons: a factor contributing to species survival? *Anim Conserv.* 5, 325-331.

- 382
- 383 Blumstein, D.T., Daniel, J.C., Sims, R., 2003. Group size but not distance to cover influences agile wallaby
- 384 (*Macropus agilis*) time allocation. *J Mammal.* 84 (1), 197-204.
- 385
- 386 Burger, J., 2003. The search for mechanisms for group size effects on vigilance. *Behav Processes.* 63, 125-
- 387 126.
- 388
- 389 Burger, J., Gochfeld, M., 1994. Vigilance in African mammals: Differences among mothers, other females
- 390 and males. *Behav.* 131 (304), 153-169.
- 391
- 392 Cameron, E.Z., Du Toit, J.T., 2005. Social influences on vigilance behavior in giraffes, *Giraffa*
- 393 *camelopardalis*. *Anim Behav.* 69, 1337-1344.
- 394
- 395 Caro, T.M., 2005. Antipredator Defenses in Birds and Mammals. Chicago: University of Chicago Press.
- 396
- 397 Descovich, K.A., Lisle, A.T., Johnston, S.D., Nicolson, V., Phillips, C.J.C., 2012a. Differential responses
- 398 of captive southern hairy-nosed wombats (*Lasiorhinus latifrons*) to the presence of faeces from difference
- 399 species and male and female conspecifics. *Appl Anim Behav Sci.* DOI: 10.1016/j.applanim.2012.01.017.
- 400
- 401 Descovich, K.A., Reints Bok, T.E., Lisle, A.T., Phillips, C.J.C., 2012b. Auditory laterality in a nocturnal,
- 402 fossorial marsupial (*Lasiorhinus latifrons*) in response to bilateral stimuli. *Laterality.* DOI:
- 403 10.1080/1357650X.2011.626562.
- 404
- 405 Estevez, I., Andersen, I., Nævdal, E., 2007. Group size, density and social dynamics in farm animals. *Appl*
- 406 *Anim Behav Sci.* 103, 185-204.
- 407
- 408 Evans, M., Green, B., Newgrain, K., 2003. The field energetics and water fluxes of free-living wombats
- 409 (Marsupialia: Vombatidae).

- 410
- 411 Favreau, F., Jarman, P.J., Goldizen, A., Dubot, A., 2009. Vigilance in a solitary marsupial, the common
412 wombat (*Vombatus ursinus*). Aust J Zool. 57, 363-371.
- 413
- 414 Furrer, R.D., Kyabulima, S., Willems, E.P., Cant, M.A., Manser, M.B., 2011. Location and group size
415 influence decisions in simulated intergroup encounters in banded mongooses. Behav Ecol. 22, 493-500.
- 416
- 417 Grand, T.C., Dill, L.M., 1999. The effect of group size on the foraging behaviour of juvenile coho salmon:
418 reduction of predation risk or increased competition? Anim Behav. 58, 443-451.
- 419
- 420 Hebblewhite, M., Pletscher, D.H., 2002. Effects of elf group size on predation by wolves. Can J Zool. 80
421 (5), 809.
- 422
- 423 Hogan, L., Phillips, C.J.C., Lisle, A., Horsup, A.B., Janssen, T., Johnston, S.D., 2009. Remote monitoring
424 of the behavior and activity of captive southern hairy-nosed wombats (*Lasiorhinus latifrons*). Aust
425 Mammal. 31, 123-135.
- 426
- 427 Hogan, L.A., Johnston, S.D., Lisle, A., Keeley, T., Wong, P., Nicolson, V., Horsup, A., Janssen, T.,
428 Phillips, C.J.C., 2011a. Behavioral and physiological responses of captive wombats (*Lasiorhinus latifrons*)
429 to regular handling by humans. Appl Anim Behav Sci. 134, 217-228.
- 430
- 431 Hogan, L.A., Phillips, C.J.C., Horsup, A.B., Janssen, T., Johnston, S.D., 2011b. Technique for faecal
432 marking in group-housed southern hairy-nosed wombats (*Lasiorhinus latifrons*) (Marsupialia:
433 Vombatidae). Aust Zool. 35 (3), 649-654.
- 434
- 435 Johnson, C.N., 1998. The Evolutionary Ecology of Wombats, in: Wells, R.T., Pridmore, P.A., (Eds.), Wombats.
436 Surrey Beatty and Sons Pty Ltd. Chipping Norton, pp. 34-39.
- 437

- 438 Johnson, D.D.P., Kays, R., Blackwell, P.G., Macdonald, D.W., 2002. Does the resource dispersion hypothesis
439 explain group living? *Trends Ecol Evol.* 17 (12), 563-570.
- 440
- 441 Knott, C., 1998. Social system dynamics, ranging patterns and male and female strategies in wild Bornean
442 orangutans (*Pongo pygmaeus*). *Am J Phys Anthropol. Suppl.* 26, 140.
- 443
- 444 Krause, J. and Ruxton, G.D., 2002. *Living in Groups*. Oxford University Press, Oxford.
- 445
- 446 Le Roux, A.L., Cherry, M.I., Gygaz, L., Manser, M.B., 2009. Vigilance behavior and fitness consequences:
447 comparing a solitary foraging and obligate group-foraging mammal. *Behav Ecol Socio.* 63, 1097-1107.
- 448
- 449 Li, Z., Jiang, Z., 2008. Group size effect on vigilance: Evidence from Tibetan gazelle in Upper Bha River,
450 Qinghai-Tibet Plateau. *Behav Processes.* 78, 25-28.
- 451
- 452 Lian, X., Zhang, T., Cao, Y., Su, J., Thirgood, S., 2007. Group size effects on foraging and vigilance in
453 migratory Tibetan antelope. *Behav Processes.* 76, 192-197.
- 454
- 455 Makenbach, S.A., Waterman, J.M., Roth, J.D., 2013. Predator detection and dilution as benefits of
456 associations between yellow mongooses and Cap ground squirrels. *Behav Ecol Sociobiol.* 67, 1187-1194.
- 457
- 458 McDonough, C.M., Loughry, W.J., 1995. Influences on vigilance in nine-banded armadillos. *Ethology.*
459 100, 50-60.
- 460
- 461 McGowan, A., Sharp, S.T., Simeon, M., Hatchwell, B.J., 2006. Competing for position in the communal
462 roosts of long-tailed tits. *Anim Behav.* 72, 1035-1043.
- 463
- 464 Pays, O., Dubot, A., Jarman, P.J., Loisel, P., Goldizen, A.W., 2009. Vigilance and its complex synchrony
465 in the red-necked pademelon, *Thylogale thetis*. *Behav Ecol.* 20, 22-29.

- 466
- 467 Predavec, M., Krebs, C.J., 2000. Microhabitat utilisation, home ranges and movement patterns of the
468 collared lemming (*Dicrostonyx groenlandicus*) in the central Canadian Arctic. Can J Zool. 78, 1885-1890.
- 469
- 470 Pulliam, H.R., 1973. On the advantages of flocking. J Theor Biol. 38, 419-422.
- 471
- 472 Schoepf, I., Schradin, C.. 2012. Better off alone! Reproductive competition and ecological constraints
473 determine sociality in the African striped mouse (*Rhabdomys pumilio*). J Anim Ecol. DOI: 10.1111/j.1365-
474 2656.2011.01939.x
- 475
- 476 Schradin, C., Schubert, M., Pillary, N., 2006. Winter huddling groups in the striped mouse. Can J Zool. 84,
477 5.
- 478
- 479 Shimmin, G.A., Skinner, J., Baudinette, R.V., 2002. The warren architecture and environment of the
480 southern hairy-nosed wombat (*Lasiorhinus latifrons*). J Zool. 258, 469-477.
- 481
- 482 Sugardjito, J., te Boekhorst, I.J., van Hooff, J.A.R.A.M., 1987. Ecological constraints on the grouping of
483 wild Orang-utans (*Pongo pygmaeus*) in the Gunung Leuser National Park, Sumatra, Indonesia. Int J
484 Primatol. 8, 17-41.
- 485
- 486 Taggart, D.A., Finlayson, G.R., Richings, N., Shimmin, G.A., Dibben, R., Adcock, J., Temple-Smith, P.D.,
487 2003. Environmental factors affecting the capture of southern hairy-nosed wombats (*Lasiorhinus latifrons*)
488 by stunning. Wildl Res. 30, 539-546.
- 489
- 490 Taylor, R.J., 1993. Observations on the behavior and ecology of the common wombat *Vombatus ursinus* in
491 northeast Tasmania. Aust Mammal. 16, 1-7.
- 492
- 493 Treves, A., 2000. Theory and method in studies of vigilance and aggregation. Anim Behav. 60, 711-722.

494

495 Triggs, B., 2009. Wombats, second ed. CSIRO Publishing, Melbourne.

496

497 Walker, F.M., Sunnucks, P., Taylor, A.C., 2006. Genotyping of "captured" hairs reveals burrow-use and
498 ranging behavior of southern hairy-nosed wombats. J Mammal. 87, 690-699.

499

500 Walker, F.M., Taylor, A.C., Sunnucks, P., 2007. Does soil type drive social organization in southern hairy-
501 nosed wombats? Mol Ecol. 16 (1), 199-208.

502

503 Whitfield, D.P., 2003. Redshank *Tringa totanus* flocking behavior, distance from cover and vulnerability of
504 sparrowhawk *Accipiter nisus* predation. J Avian Biol. 34, 163-169.

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