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

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

While conspecific effects on vigilance have been extensively tested in gregarious animals, species that operate within other social systems (e.g. solitary, semi-solitary, facultatively social) are underrepresented in the literature. Existing results indicate that solitary species should increase vigilance in the presence of conspecifics (e.g. *Sarcophilus harrisii:* Jones, 1998; *Dasypus novemcinctus:* McDonough and Loughry, 1995), while semi-solitary species display a more mixed response (e.g. *Thylogale thetis:* Blumstein et al., 2002; Pays et al., 2009). The propensity of a semi-solitary species to modulate group size vigilance patterns in a given direction is influenced by the conditions and situations that would normally encourage this species to aggregate or disperse. For example, the solitary forager, the yellow mongoose (*Cynictis penicillata*) increases vigilance when conspecifics are present if engaged in feeding behaviour (le Roux et al., 2009) but decreases vigilance when aggregating near sleeping burrows (Makenbach et al. 2013). Studies of vigilance performed while grazing are important because they depict a trade-off of energy input with threat avoidance, however, it is clear that this alone cannot provide a full picture of how conspecifics influence vigilance behaviour, particularly for semi-social / semi-solitary animals, or those that are reliant on non-feeding behaviour (e.g. long resting periods or denning) to maintain energetic balance, such as the three wombat species (*Lasiorhinus latifrons, L. krefftii* and *Vombatus ursinus*: Evans et al., 2003). Recently, the solitary common wombat (*V. ursinus*) was examined for social-vigilance patterns (Favreau et

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

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

2.0 METHODS

2.1 Study Animals

This study was conducted at the Rockhampton Botanic Gardens and Zoo, Rockhampton, Australia (23º 22'

S, 150º 30' E) using nine adult *L. latifrons* (3♂, 6♀) per experimental period. All but one wombat from

this study were wild-caught as adults from Swan Reach, South Australia (34˚55'S; 139˚28'E) prior to 2005,

with the remaining one born at the facility in 2003. Wombats were organized into three groups using a

randomized blocked design: Large (1♂, 3♀), Medium (1♂, 2♀) and Small (1♂, 1♀). Groups were blocked

to ensure that none contained multiple males as these could become aggressive towards each other and

cause severe injury (ARAZPA, 2007), and wherever possible to avoid animals experiencing the same

treatment or group members in consecutive experimental periods. All groups were given comparable

facilities comprised of an interior section with two air-conditioned sleeping dens and an external pen

containing a digging chamber, large log covered with dirt, feed-house and grassed areas. Carrots, chaff and

macropod pellets (Riverina Australia Pty Ltd., West End, Australia) were provided each afternoon. Each

wombat wore a collar with a distinctive reflective pattern (Titley Electronics, Ballina, Australia) for

identification on video. Approval for this experiment was granted by the University of Queensland Animal

Ethics Committee (SAS/288/09).

2.2 Study Design

Four consecutive experimental periods occurred in total, with each period comprised of one of each group

size. New wombat groups were formed on day one of each experimental period and behavioural

observations were then taken on day 7, 14 and 21 to account for possible changes over time. The size of the

interior of the enclosures could not be altered, however, the external enclosures were adjusted for group

size at $50 - 59$ m^2 per individual, making the Large enclosure 224 m^2, the Medium one 151 m^2 and the

Small one 118 m^2. The research facility was off-display to avoid interference by zoo patrons and the

wombats were able to freely move between both sections of their enclosure. Not all animals experienced

each treatment during the study, as more animals were needed for the Large group than for the Medium or

Small. Also, three original participants (one from each group size) were removed during or after an

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.

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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^2 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.

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

Behaviour	Category	Description
		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

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2.3 Statistical analysis

2.3.1 General treatment of data

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

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

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

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

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

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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.

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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.

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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.

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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

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

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

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

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

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

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

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

Vigilance behaviour while grazing was affected by group size in a pattern similar to that recorded over the entire observation period (Table 4). Air smelling occurred more frequently in the Small group compared to 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 ($t_6 = 2.58$, $P = 0.04$).

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.

Behaviour (count / 5 min grazing interval)	Small	Medium	Large	Pooled SED	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	$F_{2,6} = 20.70$, $P = 0.002$

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 ($r_{64} = -0.22$, $P = 0.083$).

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.

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

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

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

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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.

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