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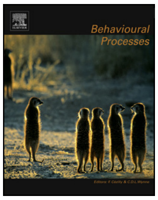

The effect of group size on vigilance in a semi-solitary, fossorial marsupial (*Lasiorhinus latifrons*)

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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.

1. 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 (Schoepf 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

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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*, *Lasiorhinus 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 cm × 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. Methods

2.1. Study animals

This study was conducted at the Rockhampton Botanic Gardens and Zoo, Rockhampton, Australia (23°22′ S, 150°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 intra-specific aggression. In their place, a new wombat was substituted on commencement of the next experimental period.

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