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Moon phase and nocturnal activity of native Australian mammals

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Abstract. Moon phase and variation in ambient light conditions can influence predator and prey behaviour. Nocturnal predators locate prey visually, and prey may adjust their activity to minimise their predation risk. Understanding how native mammals in Australia respond to varying phases of the moon and cloud cover (light) enhances knowledge of factors affecting species' survival and inference regarding ecological and population survey data. Over a two-year period within a fenced conservation reserve, in south-eastern Australia, with reintroduced native marsupial predator and prey species (eastern barred bandicoot, southern brown bandicoot, long-nosed potoroo, rufous bettong, Tasmanian pademelon, brush-tailed rock-wallaby, red-necked wallaby, eastern quoll, spotted-tailed quoll, and naturally occurring swamp wallaby, common brushtail possum, common ringtail possum), we conducted monthly spotlight surveys during different moon phases (full, half and new moon). We found an interaction between cloud cover and moon phase, and an interaction of the two depending on the mammal size and class. Increased activity of prey species corresponded with periods of increasing cloud cover. Predators and medium-sized herbivores were more active during times of low illumination. Our findings suggest that moon phase affects the nocturnal activity of mammal species and that, for prey species, there might be trade-offs between predation risk and foraging. Our findings have implications for: ecological survey design and interpretation of results for mammal populations across moon phases, understanding predator and prey behaviour and interactions in natural and modified (artificial lighting) ecosystems, and potential nocturnal niche partitioning of species.

Additional keywords: animal movement, foraging, marsupial, predation risk, predator–prey interactions, temporal activity.

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Introduction

The movement and activity of animals are determined by a range of behavioural, ecological and physiological factors. Individuals will attempt to optimise their energetic and reproductive gains against the risk of predation (Halle and Stenseth 2012). Abiotic factors influence animal behaviour, and moon phase, for example, can influence biological processes such as the timing of breeding, foraging and navigation (Pyle *et al.* 1993; Lang *et al.* 2006; Grant *et al.* 2009). Higher nocturnal illumination is associated with increased antipredator vigilance behaviour in sugar gliders (*Petaurus breviceps*) and artificial street lighting has been associated with reduced activity and richness of insectivorous bats (Barber-Meyer 2007; Nersesian *et al.* 2012; Linley 2017).

While moon phase is known to affect the activity of some nocturnal species, effects may vary depending on a species' trophic position, ecology, and sensory systems for detecting

predators or prey (Prugh and Golden 2014). Nocturnal illumination has the potential to reduce prey activity as it aids in their detection and capture (Clarke 1983; Griffin *et al.* 2005). As such, the activity and hunting success of nocturnal predators may be increased when there is more nocturnal illumination. Short-eared owls (*Asio flammeus*) are more successful at hunting deermice (*Peromyscus maniculatus*) when illumination is high (Clarke 1983). In turn, antipredator avoidance behaviours are heightened by some prey species during periods of high nocturnal illumination (Clarke 1983; Sabato *et al.* 2006; Harmsen *et al.* 2011). Snowshoe hares' (*Lepus americanus*) nocturnal movements decreased and they favoured foraging in dense vegetation when illumination was high (Griffin *et al.* 2005; Gigliotti and Diefenbach 2018). The activity of prey species can increase during decreased nocturnal illumination, allowing for increased fitness (Clarke 1983; Harmsen *et al.* 2011). Although illumination plays a significant regulatory role in activity, abiotic factors,

such as rainfall, cloud cover, temperature, and biotic factors, such as food availability and canopy cover, can also have an effect on the activity of both predators and prey (Laurance 1990; Read and Moseby 2001; Fernandez-Duque 2003; Saldaña-Vázquez and Munguía-Rosas 2013). Responses to nocturnal illumination can vary: tamar wallabies (*Notamacropus eugenii*) have been shown to not respond to increased illumination; whereas black ‘swamp’ wallabies (*Wallabia bicolor*) may increase their activity during periods of low light and these findings are likely to be influenced by local predation pressures (Biebow and Blumstein 2003; Bennett and Coulson 2014).

In Australia, little work has been done investigating the nocturnal behaviour of predators and prey in fenced, conservation reserves, ecosystems that may have mammal assemblages that more closely resemble those before European colonisation and the extinction of many native mammal species. It remains poorly understood how lunar cycles affect native mammal behaviour in response to different amounts of illumination. For conservation and reintroduction programmes, it is essential for us to understand the effect of nocturnal illumination on native mammal behaviour, especially given the increase of artificial light and light pollution closer to urban areas. To address this knowledge gap we aimed to determine whether the activity of native Australian mammals was affected by nocturnal illumination (i.e. moon phase and/or cloud cover). We predicted that: (1) prey species would reduce their activity during high illumination (i.e. full moon and low cloud cover); (2) predators would increase their activity during low illumination (i.e. new moon and high cloud cover); and (3) the activity of large herbivores will not be heavily regulated by illumination (Laurance 1990; Fernandez-Duque 2003; Prugh and Golden 2014).

Methods

We conducted our study at Mount Rothwell Conservation and Research Centre (Mt Rothwell), a 453-ha fenced reserve located 65 km south-west of Melbourne, Victoria. Mt Rothwell comprises three habitat types: remnant box woodlands (177 ha), basalt grasslands (147 ha) and granite outcrops (129 ha). Two of the habitats had no canopy while box woodlands had an open canopy. Several locally extinct mammal species have been reintroduced, including: the eastern barred bandicoot (*Perameles gunnii*), southern brown bandicoot (*Isodon obesulus*), long-nosed potoroo (*Potorous tridactylus*), rufous bettong (*Aepyprymnus rufescens*), Tasmanian pademelon (*Thylogale billardierii*), brush-tailed rock-wallaby (*Petrogale penicillata*), red-necked wallaby (*Macropus rufogriseus*), eastern quoll (*Dasyurus viverrinus*), and spotted-tailed quoll (*D. maculatus*). The swamp wallaby (*Wallabia bicolor*), common brushtail possum (*Trichosurus vulpecular*), and common ringtail possum (*Pseudocheirus peregrinus*) occur naturally in Mt Rothwell reserve. The reserve is free from invasive vertebrate predators, although the European rabbit (*Oryctolagus cuniculus*) persists and fluctuates in abundance.

We quantified the activity of native mammals over a two-year period (January 2015 – December 2016) by conducting trimonthly surveys using two transects (2 km) that covered all three habitats. In total, 141 surveys were conducted. Within each month, transect surveys of mammal activity were undertaken at

the full ($n = 48$ transects over 24 nights), half ($n = 53$ transects over 27 nights) and new moon phase ($n = 40$ transects over 20 nights). Transect surveys commenced within 30 min of sunset and were conducted using a 4WD vehicle driving consistently at 10 km h^{-1} . We used the vehicle’s headlights to count native mammals 20 m in front of the vehicle and 3 m either side of the vehicle. In addition, we visually estimated cloud cover at the beginning of surveys (on a scale of 0–4, 0 being no cloud cover and 4 being full cover). We estimated native mammal species’ activity using counts similar to Read and Eldridge (2010).

We grouped identified species into three categories defined by their body mass (Johnson and Isaac 2009) and trophic position: critical weight range (CWR) prey (eastern barred bandicoot, brush-tailed rock-wallaby, common brushtail possum, rufous bettong, Tasmanian pademelon, southern brown bandicoot, long-nosed potoroo, common ringtail possum), predators (eastern quoll, spotted-tailed quoll), and large herbivores (swamp wallaby, red-necked wallaby; i.e. herbivore species that are not preyed upon in the study area due to lack of large predators). To investigate the illumination factors affecting the activity of native mammal species, we created three candidate generalised linear mixed-effects models (GLMM) with a Poisson distribution. We set the total number of CWR prey species as the response variable, and lunar phase and cloud cover, plus their interaction, as explanatory variables, with month and transect ID as random factors. We then repeated this with the total number of CWR predator species and non-predated herbivores as the response variable. We assessed collinearity between independent explanatory variables before analysis using variance inflation factors (VIF) and Spearman rank correlation tests, ensuring that all variables had VIF values < 2 in the final statistical models. To identify the best model(s), we used model selection based on the Akaike Information Criterion (AIC_c) and also measured the goodness of fit (R^2) of the highest-ranked models. We performed all statistical analyses and created all figures in RStudio 1.0.136 (R Core Team 2008), using the packages lme4 (Bates *et al.* 2015) and MuMIn (Barton 2013).

Results

We identified 12 native mammal species and made 2456 individual counts during surveys across the three moon phases (Appendix 1). Most individuals observed were eastern barred bandicoots (27.7%), brush-tailed rock-wallabies (25.9%), common brushtail possums (18.5%) and rufous bettongs (15.1%).

For CWR prey species, cloud cover affected activity (Table 1). Activity increased with increasing cloud cover (Fig. 1). We found that for CWR predator species, both moon and cloud, but not their interaction, affected their activity (Table 1). Predator species were most active when the moon was either half or new (Fig. 2a), and cloud cover was marginal (Fig. 2b); however, we acknowledge the relatively low R^2 values and hence this should be interpreted conservatively. For herbivore species, cloud and moon, but not their interaction, also affected their activity (Table 1). They were slightly more active when cloud cover was mid-range (Fig. 3a) and the moon was half or new (Fig. 3b). However, the large variation around the means makes it unlikely that either have an effect.

Table 1. GLMM models, including a measure of fit (R^2), used to investigate factors affecting native mammal activity
Models with a $\Delta AIC_c \leq 2$ are highlighted in bold

Model	d.f.	Log(likelihood)	AIC_c	ΔAIC_c	Weight	R^2
Prey species						
Cloud	4	-507.01	1022.32	0.00	0.82	0.84
Cloud + Moon + Cloud \times Moon	8	-504.58	1026.25	3.93	0.11	0.84
Moon	5	-508.41	1027.26	4.94	0.07	0.84
Predator species						
Moon	5	-68.79	148.02	0.00	0.63	0.26
Cloud	4	-70.52	149.33	1.30	0.33	0.27
Cloud + Moon + Cloud \times Moon	8	-68.20	153.49	5.46	0.04	0.28
Herbivore species						
Cloud	4	-160.15	328.60	0.00	0.72	0.41
Moon	5	-160.07	330.58	1.99	0.27	0.41
Cloud + Moon + Cloud \times Moon	8	-159.82	336.74	8.14	0.01	0.40

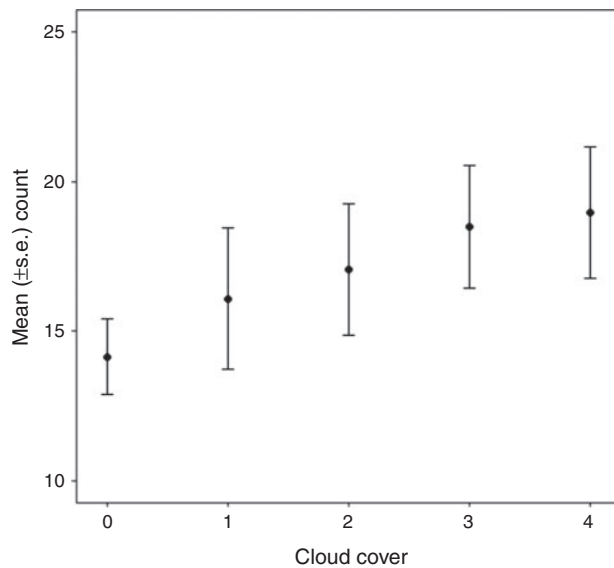


Fig. 1. Activity of prey species during increasing cloud cover.

Discussion

Moon phase, specifically the level of nocturnal illumination, plays an integral role in regulating nocturnal mammal activity (Clarke 1983; Prugh and Golden 2014). We found that mammal activity was affected by moon phase and cloud cover or a combination of the two factors differently depending on mammal body size and class. During periods of increasing cloud cover, activity of CWR prey species increased. During periods of low illumination (half and new moon) CWR predator species showed increased activity whereas medium-sized herbivore species showed less variation in activity in response to nocturnal illumination and cloud cover. Nocturnal illumination can negatively affect the activity of some mammals (Barber-Meyer 2007; Linley 2017), with the general consensus suggesting that prey are typically less active during periods of high lunar illumination, but conjecture exists (Lockard and Owings 1974; Clarke 1983; Prugh and Golden 2014).

Human modification of the environment (i.e. light pollution) is causing temporal shifts in mammal populations, which is expected to dramatically alter ecosystems (Benítez-López 2018). Nocturnal illumination affects the behaviour and foraging efficiency of prey by increasing their risk of detection and predation, and hence can increase the foraging success of predators (Prugh and Golden 2014). Optimal foraging theory points to the trade-off between marginal fitness gains obtained through foraging versus the risk of predation (Charnov 1976). Our results, especially those during half and new moon phases, suggest a possible trade-off between increased activity and elevated predation risk during periods of lowest light and cloud cover. Further work is needed to examine whether such a trade-off exists, and could be done by tracking individuals, their foraging behaviour and survival (predation frequency) under different illumination treatments (moon phases).

In ecosystems where predation pressure is reduced or absent, mammals may adjust their behaviour to maximise foraging time and reward (Terborgh 2015; Linley *et al.* 2017). While larger native predators (spotted-tailed quolls) do exist within Mt Rothwell, their relatively low abundance may mean that predation pressure on CWR prey species within the reserve is lower than is typical for wild populations elsewhere (Körtner *et al.* 2004; Claridge *et al.* 2005). An additional explanation is that the presence of European rabbits could also alter predation pressure/risk, as rabbits make up a significant proportion of the diet of quolls (Glen and Dickman 2006), including at Mt Rothwell (Linley *et al.* 2020). This may mean that native prey accept a relatively low risk of nocturnal exposure to predators in order to forage during the full moon and compete for resources with conspecifics and/or other species.

Our findings highlight the importance of moon phase, and cloud cover, in affecting patterns of mammalian activity and, potentially, species interactions. Further, our results have implications for: (1) ecological survey design and interpretation (as different species may be observed in varying numbers through time due to behavioural differences in responses to ambient light, inference about populations, communities and species interactions must account for this), and (2) understanding the potential effects of artificial illumination on the

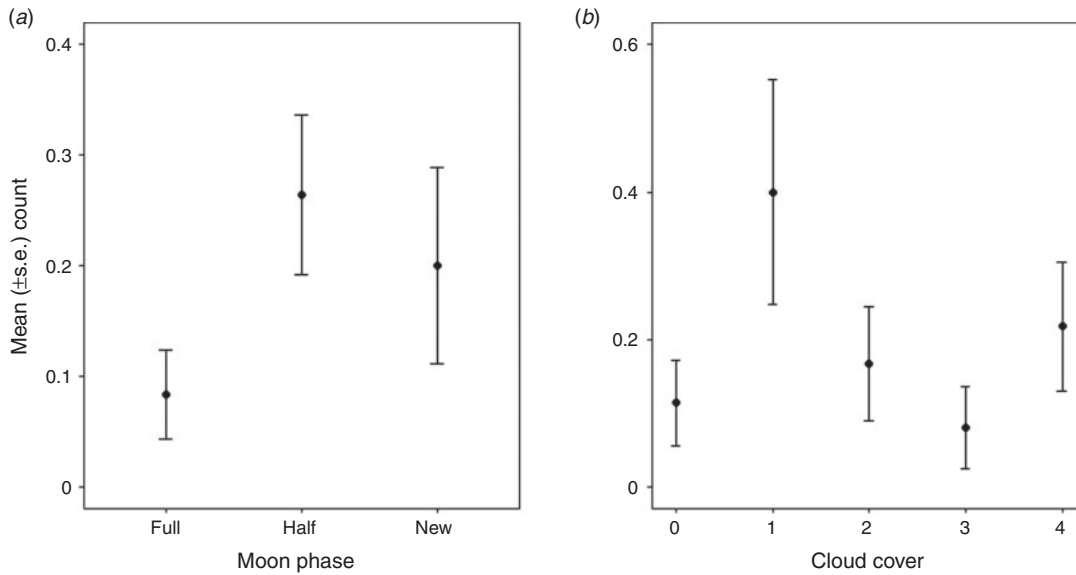


Fig. 2. Activity of predator species during (a) each moon phase, and (b) increasing cloud cover.

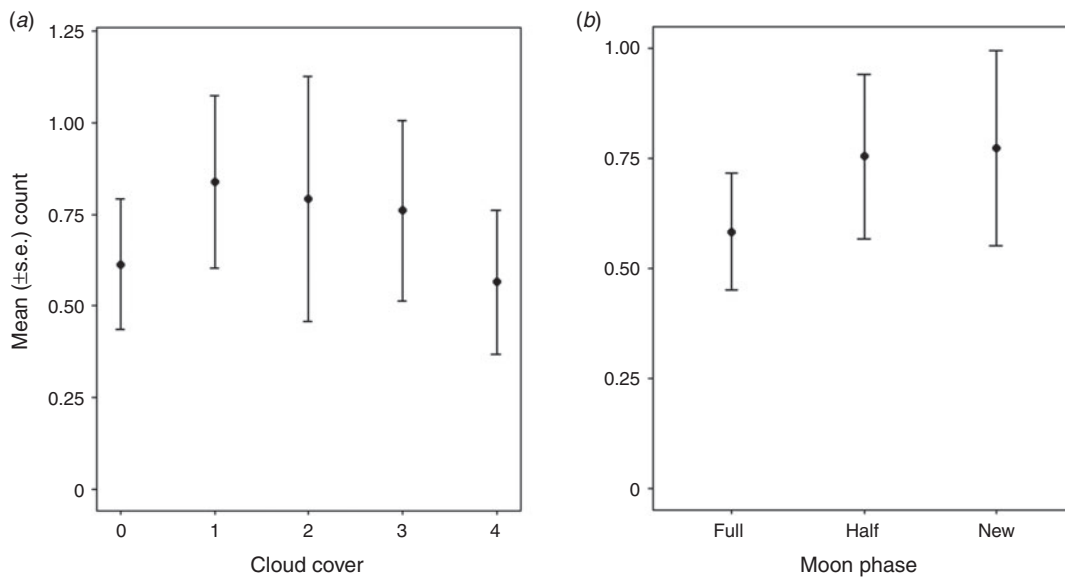


Fig. 3. Activity of non-predated herbivores during (a) increasing cloud cover, and (b) each moon phase.

behaviour of species, an increasing issue globally and particularly in urban/periurban areas (Longcore and Rich 2004, 2006).

Future studies should further investigate how different lunar phases affect mammal and other species' behaviours, including measuring vigilance, in order to better understand how species react to abiotic factors and their variation.

Conflicts of interest

The authors declare no conflicts of interest.

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Appendix 1. Counts of native mammal species recorded at each moon phase during the study period

		New	Full	Half
Prey	<i>Peremeles gunnii</i>	168	242	270
	<i>Petrogale penicillata</i>	179	228	229
	<i>Trichosurus vulpecula</i>	95	171	189
	<i>Aepyprymnus rufescens</i>	102	130	140
	<i>Thylogale billardieri</i>	19	48	41
	<i>Isodon obesulus</i>	10	12	14
	<i>Potorous tridactylus</i>	7	17	10
	<i>Pseudocheirus peregrinus</i>	2	5	3
Predator	<i>Dasyurus viverrinus</i>	7	4	12
	<i>Dasyurus maculatus</i>	1	0	2
Herbivore	<i>Wallabia bicolor</i>	18	23	33
	<i>Macropus rufogriseus</i>	13	5	7