



# Brushtail possum terrestrial activity patterns are driven by climatic conditions, breeding and moonlight intensity

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## Abstract

Ecological studies of common brushtail possums (*Trichosurus vulpecula*) in their extant range have been limited by technology and the species' nocturnal habit. However, camera traps now allow the investigation of possum ethology without observer interference. Here, we analysed terrestrial possum activity patterns using a large dataset collected over 3 years from 133 camera traps in mesic eucalypt woodland and open forest in three national parks on the New England Tablelands, New South Wales, Australia. We investigated how weather and moonlight intensity influenced possum activity patterns throughout the night, and across seasons and years, by using the timestamps assigned to each detection by the camera trap. Terrestrial possum activity increased as ambient temperatures decreased in autumn and peaked in winter when females were rearing offspring. Nightly possum detections decreased significantly with rain and increasing mean temperature. Possums were almost exclusively nocturnal, with most terrestrial activity earlier in the evening in winter and later at night in summer. During longer nights, higher temperatures also delayed activity. While nightly detection rates were not affected by lunar phase, possums preferred parts of the night with the highest moonlight intensity, and this effect was stronger on brighter nights. Overall, brushtail possums were most active on the ground when temperatures were mild and moonlight bright, presumably assisting foraging and predator avoidance, and during the breeding season; they avoided rain. These patterns suggest that reproduction, thermoregulation and risk of predation strongly shape the nocturnal activity cycle. Furthermore, our research adds to the evidence that camera traps can help greatly expand our knowledge of the ecology and behaviour of nocturnal mammals.

**Keywords** Camera trap · Lunar cycle · Predator avoidance · Activity patterns

## Introduction

The common brushtail possum, *Trichosurus vulpecula* (Kerr, 1792), is a medium-sized (1.2–4.5 kg) marsupial endemic to Australia and widely distributed, with five subspecies across the continent (Jackson and Groves 2015). It falls into the category of 'critical weight range' — between approximately 35 and 5500 g — in which the highest risk of mammal decline and extinction has been observed in Australia (Burbidge and McKenzie 1989). Following European settlement, some urban and agricultural regions have maintained robust populations, and possums have successfully adjusted to living in cities (Eymann et al. 2006). At the same time, the species has suffered a decline as well as local and regional extinction throughout much of its range, particularly in central Australia, tropical savannas and parts of inland New South Wales and Western Australia. Its decline has been attributed primarily to land clearing, hunting, predation

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by introduced predators (dingoes, *Canis familiaris*; European red fox; *Vulpes vulpes*; and feral cat, *Felis catus*) and increasing aridity (Kerle et al. 1992; How and Hillcox 2000; Goldingay and Jackson 2004; Stobo-Wilson et al. 2019). There have been attempts to reintroduce brushtail possums, with varied success, into sites within its historic range, such as Ikara-Flinders Ranges National Park in South Australia (Bannister et al. 2020) and Wadderin Sanctuary in Western Australia (Short and Hide 2014).

Successful management of wildlife species relies on knowledge of their biology, ecology and ethology. Brushtail possum ecology and ethology have long been studied (Tynedale-Biscoe 1955; Dunnet 1956; Kerle et al. 1992; Marsh et al. 2003; Mella et al. 2014). Research has been particularly focused on New Zealand where the species was introduced in the nineteenth century and subsequently became a major pest, damaging plantations and native forests, preying on native bird species and posing a risk as a vector of bovine tuberculosis (Paterson et al. 1995; Montague 2000; Nugent and Sweetapple 2000; Nugent et al. 2001, 2015; Glen et al. 2012). Nevertheless, studying activity patterns has been limited by the species' nocturnal habits and available technologies. VHF radio collars and GPS tags have provided further insight (Ball et al. 2005; Harper 2006; Whyte et al. 2014), but these methods are resource- and time-intensive and tend to provide detailed information on a subset of individuals rather than describing populations. Overall, the effects of environmental variables on fine-scale temporal activity and long-term seasonal changes are still largely unknown. Recent advances in wildlife monitoring with camera traps allow continuous recording of animal activity at a landscape scale, providing both spatially and temporally explicit information at a population level (Meek et al. 2014; Rovero and Zimmerman 2016). Camera traps combine the benefits of high temporal resolution and long-term monitoring, allowing investigation of seasonal changes in activity as well as fine-scale diel activity patterns. To our knowledge, there is no long-term dataset from continuous monitoring of common brushtail possum activity at landscape scale over multiple years in their native range in Australia.

Here we analysed camera trap data collected over 3 years to detect terrestrial activity patterns of brushtail possums in the New England Tablelands at different temporal scales — nightly, and within and between seasons and years. We also sought to identify the influence of environmental factors, such as weather conditions and moonlight illumination, on these patterns. We did not attempt to estimate population densities at our study sites but rather focused on activity indices, analysing general patterns at a landscape scale.

We recognise that our results represent patterns of possum activity on the ground, but their overall activity patterns might differ. However, no other research method allows for continuous monitoring of animal activity on a

landscape scale across multiple seasons. There have been attempts to survey Australian arboreal fauna at tree canopy level (e.g. Cotsell and Vernes 2016), but placing cameras on tree branches or directed at tree hollows restricts the effective detection area of each camera to a branch or hollow. Because possums use multiple dens within their home range and rarely share dens (Paterson et al. 1995), a substantially higher number of canopy cameras would be required to collect a comparable dataset of arboreal activity.

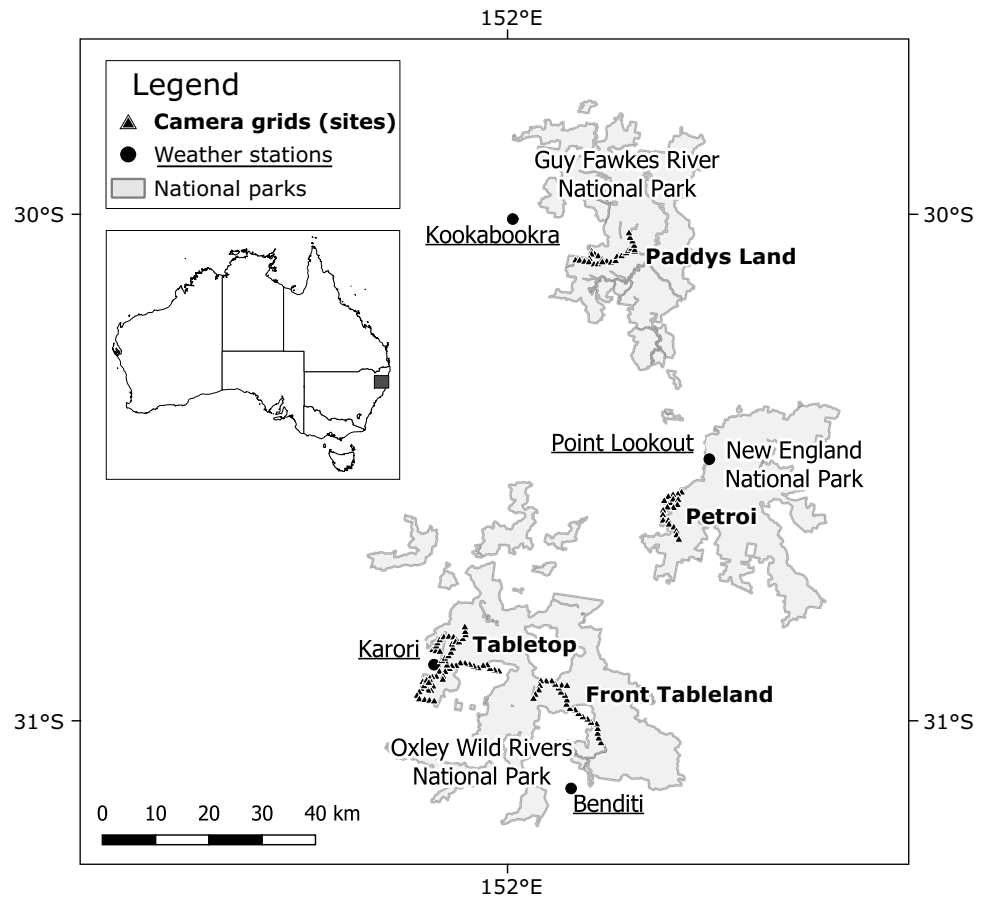
## Material and methods

### Study area

Our study was conducted in the New England Tablelands in north-eastern New South Wales, Australia (Fig. 1). This region encompasses the Great Escarpment, with steep, rugged gorges and boulder-strewn slopes in the east (1500 m a.s.l.) and undulating plateaus in the west (600 m a.s.l.). The four monitoring sites were situated towards the east of the plateau and were: Tabletop (30°53'30" S, 151°52'50" E) and Front Tableland (30°59'3" S, 152°7'8" E) in Oxley Wild Rivers National Park (NP), Paddys Land (30°4'49" S, 152°12'0" E) in Guy Fawkes River NP and Petroi (30°35'12" S, 152°19'27" E) in New England NP (Fig. 1). Vegetation is a combination of sclerophyll forests and woodlands with pockets of subtropical dry rainforest in gullies and gorges. Dominant vegetation types vary between sites, with dry sclerophyll forests at Tabletop, a combination of dry and wet sclerophyll forests at Front Tableland and Paddys Land and wet sclerophyll and rainforest at Petroi (Office of Environment and Heritage 2016). The altitudinal range of camera locations was similar for all study sites, with the lowest cameras at 854–916 m a.s.l. and the highest at 1104–1281 m a.s.l. The climate is temperate with the highest temperatures in January and the lowest in July. Rainfall is distributed throughout the year, with the highest rainfall in summer, from November to February (Bureau of Meteorology (BOM) 2020). The four study sites were located within 100 km and, due to topography, represented comparable but sufficiently different climatic and weather conditions (Table 1) to test the effects of environmental factors on activity.

The study sites were located in extensive areas of native vegetation, with distances ranging from 0 to 7.5 km to agricultural land, predominantly sheep and cattle farms, where dingo and red fox populations are controlled to varying degrees by toxic baiting, trapping, shooting and exclusion boundary fences. During the study period, two of the study sites (Tabletop and Front Tableland) were also subjected to aerial predator baiting programmes, typically undertaken in May to June by the NSW National Parks and Wildlife Service (NPWS).

**Fig. 1** Location of study sites, camera trap transects and weather stations. Inset shows map range in relation to Australia



**Camera trap monitoring**

A permanent camera trap monitoring network consisting of 20–60 Reconyx Hyperfire HC600 cameras (RECONYX LLC, Holmen, WI, USA) per site was established in the four study sites. From a random starting point, camera traps were placed on perpendicular poles located at ~1 km spacing along management trails. Camera traps were approximately 50 cm above the ground, faced along the trail and angled at ~22.5° towards the axis of the trail. As this camera placement was optimised for the detection of introduced predators (Ballard et al. 2014), we tested it for reliable detection of slightly smaller possums. For a limited time, a second

camera was fitted 25 cm above the ground for a subset of cameras (approximately one-third of all cameras at two study sites). While the lower mounted cameras were more effective in detecting possums, the cameras mounted at the standard height of 50 cm detected possums consistently albeit at a reduced rate; our data was, therefore, a representative subset of all possum movements on the ground (M.K.Š. unpublished). We did not need to know the exact numbers of detections because we assumed that the detection probability was constant among camera traps. Because our dataset is large (> 10,000 independent possum detections), collected over a long period (3 years) and the ratio of detections was consistent between paired cameras set at different heights,

**Table 1** Mean annual rainfall, mean annual temperature and mean temperature in January and July for each of the study sites (mean values extracted from maps of average climatic conditions for a 2-km buffer around each camera line (BOM 2020))

Site	Mean annual rainfall (mm)	Mean annual temperature (°C)	Mean temperature in January (°C)	Mean temperature in July (°C)
Front Tableland	1022	13.4	19.1	6.8
Petroi	1199	13.4	18.8	7.1
Paddys Land	1010	13.8	19.4	7.2
Tabletop	886	12.5	18.6	5.6

we are confident that our detections were drawn randomly from all real events.

Cameras were serviced approximately every 2 months when batteries and SD cards were replaced. All photos were then downloaded to a PC, tagged to species level and filtered for those containing *T. vulpecula*. A threshold of 5 min was applied to define individual activity events (i.e. subsequent detections within a 5-min period were ignored). These activity events (hereafter referred to as ‘events’) were used in subsequent analyses (Table 2).

## Environmental variables

### Temperature

For each site, the temperature information encoded in metadata of each picture taken by the camera trap was used to initially calculate mean temperature values for 1-h intervals from all available readings in that hour. On average, 3.6 readings ( $SD = 3.63$ ) were recorded per 1-h block, and at least one reading was recorded for 50,362 out of the 70,462 one-hour blocks. Missing values were interpolated, and data further condensed to calculate an average value for the 12-h block between 18:00 and 06:00, representing the average nightly temperature. The intermediate step of calculating 1-h blocks was used because motion triggers were often clustered (e.g. animals grazing continuously in front of a camera), and such a cluster would skew a mean towards values recorded in that cluster.

### Sunlight and moonlight

We defined night as the period between sunset and sunrise. Each event was placed in the context of astronomical events (such as sunrise, sunset, moonrise, moonset), and these were calculated using the package ‘suncalc’ (Agafonkin and Thieurmel 2018). To account for seasonal changes in the length of the night, as well as shifts in the time of sunset and sunrise, we standardised the time of each event by converting it to a relative position of that event within a night. Each nocturnal observation took a fractional value between 0 (at sunset) and 1 (at sunrise), with a value of 0.5 for astronomical midnight.

Furthermore, moonlight illumination was calculated as the ambient intensity of moonlight on the ground using a custom model, taking into account brightness of the lunar disc, distance to the moon, position of the moon in the sky and light propagation in the atmosphere (Śmielak 2023). For each night at each of the study sites, we calculated mean moonlight intensity and the time of the lunar noon (the point when the moon is at its highest over the horizon and thus the brightest). The moonlight illumination model did not consider cloud cover; therefore, an interaction variable (moonlight intensity  $\times$  mean cloud cover) was included in the global model. Time of lunar noon was standardised relative to the duration of each respective night.

### Rainfall and cloud cover

Rainfall records were obtained from historical weather data services (Bureau of Meteorology (BOM) 2020), with the distance of each camera trap to the nearest weather station

**Table 2** Monitoring periods, number of camera traps, survey effort and number of possum activity events at each of four sites in north-east NSW

Site	Code	Location	Start date	End date	Monitoring period (days)	Number of camera traps	Camera trap nights	Total <i>T. vulpecula</i> events	Detection rate (events/100 trap nights)	
Front Table-land	FT	Oxley Wild Rivers NP 30°59'3" S, 152°7'8" E	14/03/2015	18/12/2017	1010	26	26,260	2228	8.5	
Petroi	NE	New England NP 30°35'12" S, 152°19'27" E	17/03/2015	16/10/2017	944	20	18,880	1032	5.5	
Paddys Land	PL	Guy Fawkes River NP 30°4'49" S, 152°12'0" E	15/12/2014	11/12/2017	1092	27	29,484	4518	15.3	
Tabletop	TT	Oxley Wild Rivers NP 30°53'30" S, 151°52'50" E	17/12/2014	21/12/2017	1100	60	66,000	2259	3.4	
					Total	4146	134	140,624	10,037	7.1

**Table 3** Result of model selection (based on the Akaike information criterion (AIC)) from among negative binomial GLMs of the daily number of common brushtail possum detections. Headings for columns are as follows: AIC, Akaike information criterion;  $\Delta AIC$ , difference in AIC related to the optimal model;  $w$ ,  $\Delta AIC$  weight;  $acc\ w$ , cumulative Akaike weight;  $ER$ , evidence ratio. Cumulative Akaike weight for selected models was 0.98. Predictors for site and day not shown

Model	(Intercept)	Mean temperature at night	Rainfall	Night length	Mean moon illumination	Mean cloud cover	Mean temperature at night $\times$ mean cloud cover	Mean temperature at night $\times$ night length	Mean temperature at night $\times$ rainfall	Mean cloud cover $\times$ mean moon illumination	AIC	$\Delta AIC$	$w$	$acc\ w$	ER
1	0.78	-0.29	-0.69	-0.03	NA	0.04	-0.10	0.24	0.17	NA	14,479.20	0.00	0.40	0.40	
2	0.78	-0.29	-0.69	-0.03	0.02	0.04	-0.10	0.24	0.17	NA	14,479.36	0.16	0.37	0.77	1.09
3	0.78	-0.29	-0.69	-0.03	0.02	0.04	-0.10	0.24	0.17	-0.01	14,480.48	1.29	0.21	0.98	1.90
Predictor weight	0.98	0.98	0.98	0.98	0.58	0.98	0.98	0.98	0.98	0.21					

**Table 4** Results of model selection (based on the AIC criteria) from among beta GLMs of the temporal distribution of detections. Headings for columns are as follows: AIC, Akaike information criterion;  $\Delta AIC$ , difference in AIC related to the optimal model;  $w$ ,  $\Delta AIC$  weight;  $acc\ w$ , cumulative Akaike weight;  $ER$ , evidence ratio. Cumulative Akaike weight for selected models is 0.73

Model	(Intercept)	Mean temp. at night	Mean temp. at night $\times$ length	Mean temp. at night $\times$ mean cloud cover	Mean moon illumination	Lunar moon illumination	Lunar moon $\times$ mean moon illumination	AIC	$\Delta AIC$	$w$	$acc\ w$	ER
1	-0.17	0.02	-0.22	0.02	-0.01	0.08	0.08	-2618.87	0.00	0.39	0.39	
2	-0.18	0.02	-0.22	NA	-0.01	0.08	0.08	-2617.34	1.53	0.18	0.57	2.15
3	-0.17	0.02	-0.23	0.03	NA	0.08	0.08	-2617.15	1.72	0.16	0.73	2.36
Predictor weight	0.73	0.73	0.73	0.55	0.57	0.73	0.73					

**Table 5** Changes in long-term patterns of activity. Model-averaged parameter estimates for the negative binomial GLM describing the effects of environmental factors, days since the commencement of the study and study site on possum daily detection rates

Predictors	Log mean	95% confidence interval	p
(Intercept)	0.78	0.71–0.85	<0.001
Mean cloud cover	0.04	0.01–0.07	0.019
Mean temp. at night	–0.29	–0.34––0.24	<0.001
Night length	–0.03	–0.07–0.01	0.123
Rainfall	–0.69	–0.78––0.60	<0.001
Mean cloud cover × mean temp. at night	–0.10	–0.13––0.07	<0.001
Mean temp. at night × night length	0.24	0.20–0.28	<0.001
Mean temp. at night × rainfall	0.17	0.07–0.28	0.002
Mean moon illumination	0.02	–0.01–0.04	0.209
Mean moon illumination × mean cloud cover	–0.01	–0.04–0.01	0.345
Day	–0.29	–0.36––0.22	<0.001
Site [NE]	–0.61	–0.72––0.51	<0.001
Site [PL]	0.66	0.58–0.74	<0.001
Site [TT]	–0.03	–0.12–0.06	0.491
Day × site [NE]	0.39	0.28–0.50	<0.001
Day × site [PL]	0.58	0.50–0.66	<0.001
Day × site [TT]	0.16	0.07–0.25	<0.001
Observations		3.928	
Conditional $R^2$		NA	
Marginal $R^2$		0.571	

ranging from 1.7 to 24.3 km. Daily measurements were taken around 09:00 h and represented total rainfall over the previous 24 h. Across the four sites, rainfall records were unavailable for 218 out of 4146 days, and those days were removed from analysis.

Cloud cover data were obtained from the NCEP/NCAR Reanalysis 1 project using the R package RNCEP (Kemp et al. 2020). For each study site, cloud cover data for the nearest grid cell was downloaded in a 6-h series, and an average cloud cover for each night was calculated as a weighted mean (weights were 0.25 for 18:00 h, 0.5 for 00:00 h and 0.25 for 06:00 h).

### Statistical analysis

All analyses were performed using R Statistical Software (version 4.2.2, R Core Team 2022). We identified candidate models by applying the ‘dredge’ function in the MuMIn package (Bartoń 2020) to a global model containing all variables and interactions. The best candidate models were chosen based on the Akaike information criterion (AIC), and models with  $\Delta AIC < 2$  (Symonds and Moussalli 2011) are presented in Tables 3 and 4. All numerical explanatory variables were standardised by subtracting the mean value and dividing by one standard deviation (Schielzeth 2010). Models were fitted using R package ‘glmmTMB’ (Magnusson et al. 2020).

**Table 6** Changes in short-term (within-night) patterns of activity. Model-averaged parameter estimates for the beta GLMM describing the impact of environmental factors on the standardised time of activity of brushtail possums (where  $y=0$  at sunset and  $y=1$  at sunrise).  $R^2$  represents range for candidate models

Predictors	Estimates	95% confidence interval	p
(Intercept)	–0.17	–0.23––0.12	<0.001
Lunar noon	0.08	0.05–0.12	<0.001
Mean moonlight intensity	–0.00	–0.02–0.02	0.999
Mean cloud cover	–0.01	–0.03–0.01	0.360
Mean temp. at night	0.02	–0.01–0.05	0.125
Night length	–0.22	–0.25––0.20	<0.001
Lunar noon × mean moonlight intensity	0.08	0.03–0.14	0.002
Mean cloud cover × mean temp. at night	–0.02	–0.04––0.00	0.028
Mean temp. at night × night length	0.02	0.00–0.04	0.046
$N_{\text{Camera}}$		122	
Observations		9588	
Conditional $R^2$		0.734–0.735	
Marginal $R^2$		0.374–0.375	

To analyse the influence of environmental conditions on daily detection rates, we fitted a generalised linear model (GLM) with a log link function and a negative binomial error distribution. The response variable was the number of events in a 24-h period (from noon to noon) across all cameras for a given site. Explanatory variables in the global model were mean temperature at night, rainfall, night length, mean moonlight illumination, mean cloud cover and the interactions between mean temperature and mean cloud cover, mean temperature and night length, mean temperature and rainfall and mean moonlight illumination and mean cloud cover. Because of the length of the study, long-term changes in detection rates, which varied between sites, were present in our data. We accounted for this temporal trend, as well as the different number of cameras per site, by including the interaction between two explanatory variables — day since the beginning of the study and site — in the model. Three candidate models with  $\Delta\text{AIC} < 2$  were identified, and they were averaged using `model.avg()` function in MuMIn to produce the final model.

To analyse the influence of environmental conditions on the temporal distribution of possum activity, we removed seven anomalous diurnal data points from the dataset and fitted a generalised linear mixed model (GLMM). The response variable, standardised diel time of activity, took values from 0 to 1 (see above). Therefore, a beta distribution with a logit link function was used in the model. Explanatory variables in the global model were mean temperature

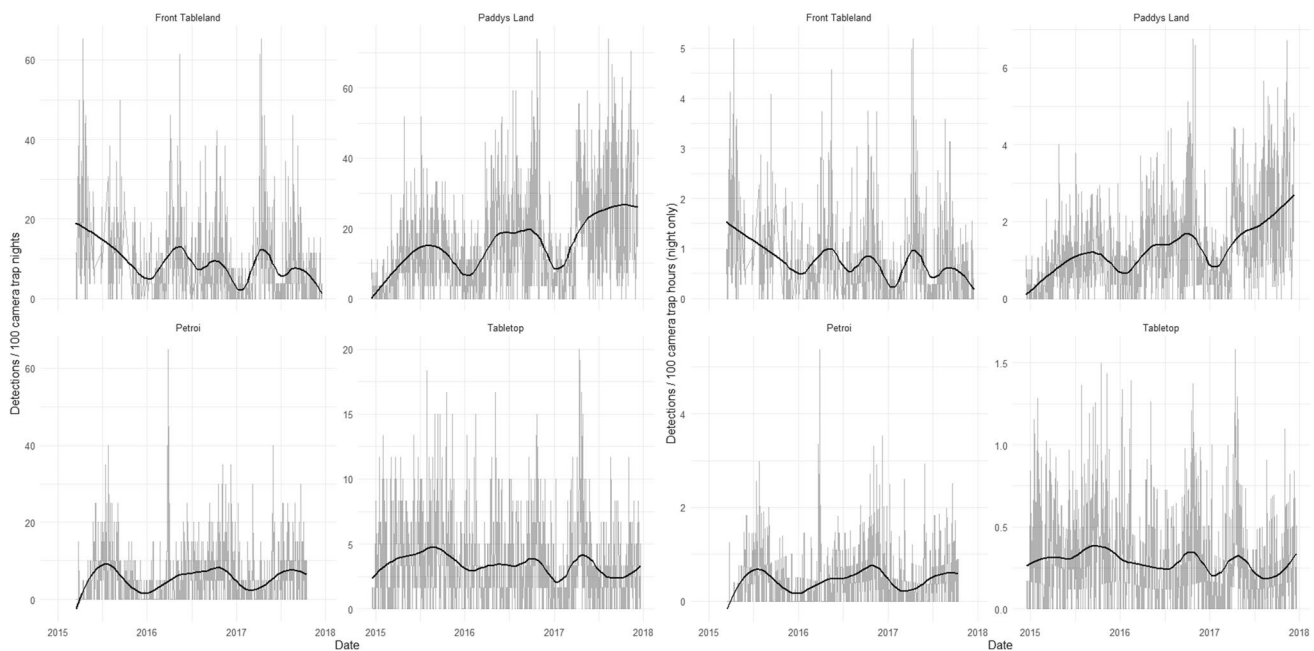
at night, night length, time of lunar noon, mean moonlight intensity, mean cloud cover and interactions between mean temperature at night and night length, mean temperature at night and mean cloud cover and the time of lunar noon and mean moonlight intensity. Camera trap identity was included as a random variable, and three candidate models with  $\Delta\text{AIC} < 2$  were identified and averaged using `model.avg()` function in MuMIn to produce the final model.

## Results

### Detection rates

Over the 3 years, 10,037 common brushtail possum activity events were recorded with an average of 7.1 events per 100 camera trap nights (Table 2). The lowest mean detection rate was recorded at Tabletop (3.4 events per 100 camera trap nights) and the highest at Paddys Land (15.3 events per 100 camera trap nights). We observed seasonal patterns with higher nightly detection rates in winter than in summer. This was also true for nocturnal hourly detection rates, indicating that higher daily detection rates were not due to a wider window of detection on longer winter nights (Fig. 2).

The mean nightly temperature was 10.9 °C (range –2.0–27.2 °C), and the mean cloud cover was 39% (range 0–99%). The mean daily rainfall recorded was



**Fig. 2** Daily (per 100 camera trap nights; left) and hourly (per 100 camera trap hours, night only; right) detection rates (grey) and moving average (solid line) for each study site. For all sites, there was an

increase in activity mid-year (winter) and a decrease around the new year (summer), to varying degrees. Moving average calculated using ‘loess’ function and moving window of 0.3

2.4 mm (range 0–158 mm), and no rainfall was recorded on 66% of the nights with data.

Possum daily detection rates were significantly affected by three two-way interactions, all involving mean nightly temperature: mean cloud cover, night length and rainfall (Table 5). Possum terrestrial activity declined with increasing mean nightly temperature but to a much greater degree on cloudy nights than on cloudless nights (Fig. 3c). The impact of increasing nightly temperature on declining possum activity was only evident on rain-free nights (Fig. 3a) and was much greater on short summer nights than in mid-winter, when the effect was almost but not significantly reversed (Fig. 3b). Modest rainfall nullified the effect of nightly temperature on possum activity, and heavy rain reversed the pattern, with significantly more possum activity on the warmest nights with heavy rain and virtually none on the coldest, very wet nights.

### Temporal distribution of terrestrial activity

Common brushtail possum activity was almost exclusively nocturnal, with 10,030 of the 10,037 events recorded at night. There was a seasonal pattern observed across all study sites, with activity being recorded, on average, earlier during the night in winter than in summer (Fig. 4).

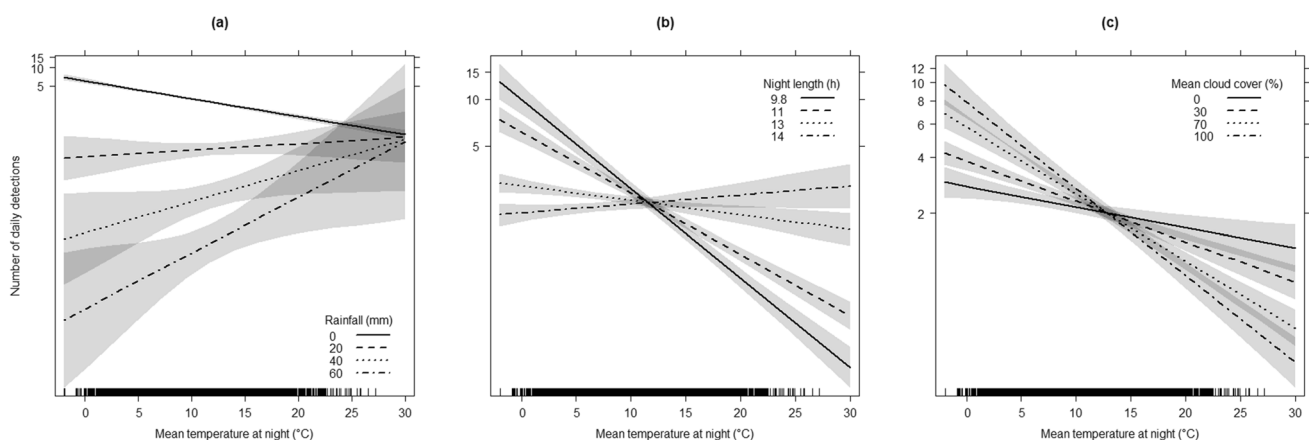
The time of nocturnal possum activity was significantly influenced by three two-way interactions: between mean temperature at night and night length; between mean temperature at night and cloud cover; and between time of lunar noon and mean moonlight intensity (Table 6). The effect of night length was inversely related to the timing of possum activity, with possums more active earlier in the evening in midwinter than in midsummer (Fig. 5a). However, this effect was modulated by the mean temperature at night, with possums active earlier in the evening on cold than on warmer

winter evenings. In midsummer, the mean temperature had no effect on possums becoming active later in the night. The effect of mean temperature was also modulated by mean cloud cover: on colder nights, possums were active later when there were clouds, and the opposite was true for the warmest nights (Fig. 5b). The timing of possum activity was also positively influenced by the time of lunar noon when moonlight is most intense, with possums most active early in the evening when the lunar noon was early but delaying their activity until later in the night when the lunar noon was late (Fig. 5c). This relationship was strongest on bright nights, while on nights with no moonlight, the time of lunar noon had no impact on the timing of possum activity.

## Discussion

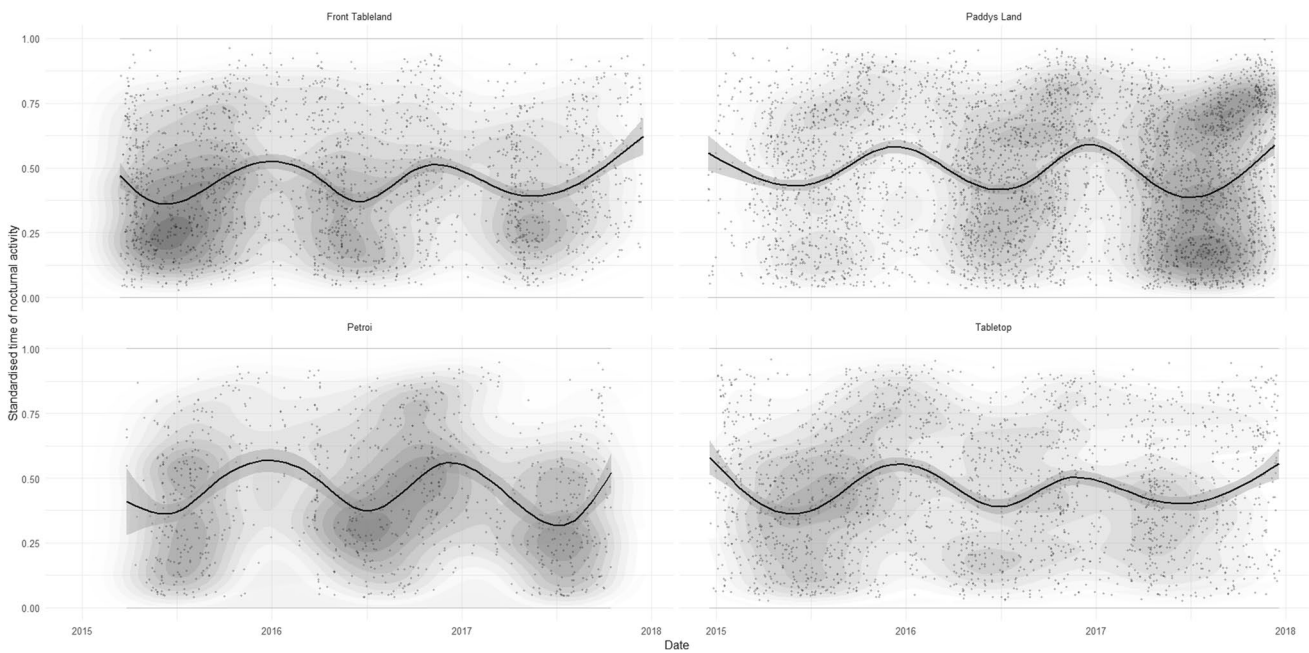
### Seasonal changes

During the study, possums were more active on the ground between autumn and spring when ambient temperature was the lowest. Higher detection rates can be explained by a likely increase in the number of individuals, greater possum activity due to increased energy requirements during cold winter weather and/or increased mobility when searching for mates. Reproduction in possums in temperate regions appears to be moderately seasonal with a birth pulse in autumn (April to May) followed in some years by a second, spring birth pulse (Cowan 2014). Similar patterns have been observed previously at one of our study sites (Clinchy et al. 2004). Furthermore, pregnancy and rearing offspring combined with lower temperature in winter increase energetic requirements, likely explaining the correlation between seasonal temperatures and detection rates. During the



**Fig. 3** Interaction plots for pairs of environmental variables: mean temperature at night and **a** rainfall, **b** night length and **c** mean cloud cover in the negative binomial GLM of daily detection rates





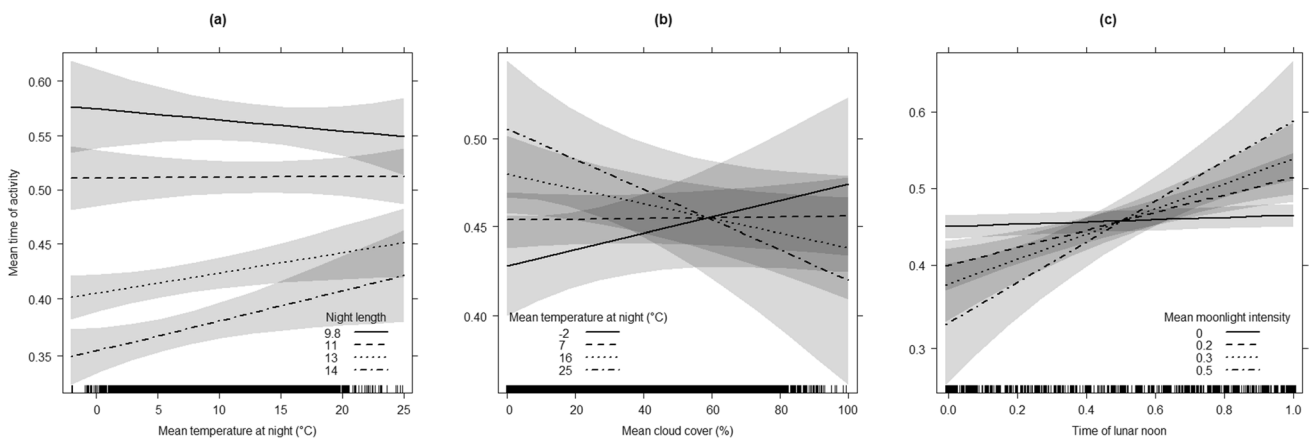
**Fig. 4** The standardised time of possum activity at four study sites. Horizontal lines represent sunset ( $y=0$ ) and sunrise ( $y=1$ ). Black line represents the moving mean of the time of activity calculated

using ‘loess’ function and moving window of 0.3, with the mean time of detection closer to sunset in winter, and closer to sunrise in summer. Shading represents density of observations

autumn breeding season, activity is extended (Paterson et al. 1995), and males have been found to lose body condition (Gilmore 1969), likely due to longer movements as they increase their home range (Green 1984). The cyclic change in detection rate is most likely primarily due to seasonal changes in population size through recruitment, mortality and migrations, which is behaviourally modulated by greater mobility associated with reproduction, greater energetic requirements of rearing offspring and colder ambient temperatures.

**Weather**

Without rain, possums were more active on the ground on colder nights, which was expected given that increased movement increases thermogenesis for behavioural thermoregulation (Terrien et al. 2011). The lower critical temperature (the temperature below which the basal rate of heat production does not compensate for heat loss to the environment, therefore incurring thermoregulatory costs) for brushtail possums in still air is between 7 and 10 °C (van



**Fig. 5** Interaction plots for pairs of environmental variables: **a** night length and mean temperature at night, **b** cloud cover and mean temperature at night and **c** mean moonlight intensity and time of lunar noon in the beta GLMM of standardised time of activity

den Oord et al. 1995). Hence, moderately cool nights incur little energetic penalty. The situation changes significantly with rain and wind. Simulated rain by itself increased the lower critical temperature by 6 °C and in conjunction with wind by 8 °C (van den Oord et al. 1995). We observed a strong negative impact of rainfall on activity on cool nights, which is consistent with previous research (Herbert and Lewis 1999). Effect of rainfall was, however, minimal on the warmest nights, showing that temperature can minimise the energetic penalty of rain on thermoregulation. The sugar glider (*Petaurus breviceps*), a related smaller possum species, is significantly less active and often enters torpor on cold and rainy nights (Körtner and Geiser 2000). Therefore, although possums were more active on colder nights, which presumably increased thermogenesis, rain likely increased the costs of thermoregulation to a point where it was difficult to offset it by increased food intake. As a result, reducing activity, and presumably denning, likely became the preferred strategy on cold rainy nights.

Ambient temperatures are rarely constant throughout the night. Generally, night temperatures are the highest at sunset and decrease until sunrise as heat is radiated from the ground. On cloudy nights, some of the radiated heat is reflected towards the ground, which means temperatures drop more slowly. While this could be advantageous on cold nights, on warm nights, it could mean that temperature can potentially stay uncomfortably high for longer — an effect that was especially pronounced during shorter summer nights. Possums can tolerate ambient temperatures up to 40 °C (Halse and Rose 1988), but evaporative cooling, respiratory rate and metabolic rate begin to increase rapidly above 25 °C in resting possums (upper critical temperature). Activity would further lower this threshold as an activity-related increase in metabolic rate requires enhanced heat dissipation, which in turn requires more energy and water use. Moreover, high temperatures can suppress food intake as they reduce hepatic detoxification capacity (Beale et al. 2022). Hence, warmer ambient temperatures can be as problematic as cold and rainy conditions. As a result, on cold nights with clouds, the optimal window of activity widened, whereas on warm clear nights it shrank, and detection rate decreased. This effect was further reinforced on shorter nights or mitigated when the night was sufficiently long.

Changes in ambient climatic conditions over the course of the evening meant that activity varied throughout the night. Previous studies have shown that possums exposed to outdoor conditions in pens commenced activity after sunset, but the timing was modulated by environmental factors, such as rain and wind (Herbert and Lewis 1999). Paterson et al. (1995), using direct observations from a hide, found that possum activity started after sunset, reached its peak between 23:00 and 02:30 h and then gradually decreased towards sunrise. Our long-term study revealed modulations

as possums commenced activity later after sunset on shorter (and warmer) nights than on longer (and colder) ones. On long winter nights, higher temperatures delayed activity significantly, whereas, on short summer nights, temperature had little or no impact. Nights in summer were either too short to allow for much flexibility or, during summer, temperatures at sunset were generally above the optimum, and therefore, possums delayed activity as much as possible. As expected, higher cloud cover allowed possums to be active later in the night on colder nights as temperature dropped more slowly. At the same time on warm nights, possums were active earlier when the sky was overcast. A possible explanation is that warm nights already have a narrow window of activity and with the slower temperature decline; delaying activity might not have been worth the lost feeding opportunity.

### Moonlight

Unlike the environmental factors discussed above, moonlight does not impinge on energy expenditure directly, and its cyclic changes are unrelated to season or the 24-h day–night cycle. One of the interesting findings of our study was that the terrestrial detection rate for possums did not change with moonlight intensity. This contrasts with several previous studies that showed that feeding activity increases during a new moon (Lennon James 1998) and that possums in open woodland are stationary for more time on brighter nights, which might indicate predator avoidance behaviour (MacLennan 1984). Eyre (2004) found that moonlight negatively affected detections of common brushtail possums, mountain brushtail possums (*Trichosurus cunninghami*) and some gliders (Petauroidea). Other studies found no effect of moon phase on brushtail possum activity in New South Wales (Pickett 1999) and koomal (*Trichosurus vulpecula hypoleucus*) detections in south-western Australia (Wayne et al. 2005), which is consistent with our results. Interestingly, Parisi (2011) found that in New Zealand, possum activity was the highest during full moon and decreased significantly around new moon, particularly under canopy cover.

Moon phase is not linearly related to moonlight intensity (e.g. when 50% of lunar disc is illuminated, its brightness is only around 8% of that of a full moon). Around full moon, small daily changes in lunar phase (1–2%) can translate into major changes in moon brightness (up to 40%), while around new moon, there is minimal change in actual brightness despite large changes in moon phase (Śmielak 2023). Also, moon phase does not account for position of the moon in the sky, and its visibility above the horizon and overall is a poor proxy for lunar illumination (Kyba et al. 2020). Brushtail possums are relatively small folivores with an energy-poor diet high in tannins, require a steady food intake and are unable to enter torpor. In temperate eucalypt forests, foliage comprises on average half of their diet and presents significant challenges in meeting energy needs due to the

high concentration of digestion-inhibiting compounds found in leaves (Hume 1999). These challenges lead to digestive and metabolic adaptations; for instance, the mean retention time of food by arboreal marsupials is similar to that of large ruminant and fermenting herbivores, ranging between 37 and 100 h (Cork and Foley 1991). The main factor limiting energetic intake in possums feeding on leaves is not the availability of food, but rather the quality of it and the time needed to digest, absorb and detoxify it (Nugent et al. 2000; Edwards et al. 2010). To maximise intake and mitigate the impact of plant chemical defences, possums have to either feed longer or travel further so they can frequently switch diets (Wiggins et al. 2003, 2006; Marsh et al. 2006). In the absence of better food sources such as fruit or invertebrates (particularly at times of increased energetic need, detailed earlier), possums are unlikely to be able to significantly decrease activity for the multiple days required for a large change in moon phase. Therefore, a preference towards a particular moon phase may not be noticeable. However, temporal modifications of activity are evident not between but within nights.

We found that possum terrestrial activity was correlated with the time of the lunar noon. This effect was stronger on brighter nights, which indicates that common brushtail possums preferred higher moon illumination. Since possums spent approximately 16% of their time feeding and 30% travelling (MacLennan 1984), we hypothesise that they exhibited within-night resource selection and focused their locomotor activity in the part of the night with optimal moonlight levels.

We hypothesise that this preference for moonlit parts of the night indicates that higher illumination levels provide an advantage to possums (improved foraging efficiency and/or predator detection) that outweigh the increased risk of predation that would result from spending more time on the ground. Few studies have assessed the effects of on-the-ground moonlight intensity, rather than moon phase, on animal activity. Gilmore (2016) rightly pointed out that previous studies of possum ecology struggled to use biologically meaningful measures of moonlight exposure, which might explain the inconclusive results that have been reported, ranging from lunar phobia (Lennon James 1998; Linley et al. 2020) to lunar philia (Cowan and Clout 2000; Parisi 2011). In studies where artificial light was used to simulate moonlight, possums in captive trials perceived illuminated patches as less risky (Nersesian et al. 2012), but no such effect was found when tested on possums in the wild (Mella et al. 2014). However, all these studies, using either moon phase or artificial light, assumed constant light levels through the night. The only study undertaken where light levels were measured hourly through the night revealed that illumination, but not moon phase, affected activity of five nocturnal pest species in New Zealand (Gilmore 2016). Due to the short duration of the study (12 nights) and resultant

small sample sizes, the effect of illumination on possums specifically could not be analysed and was therefore modelled for all five pest species combined and was negative, which could be a type II error. Pooling the species could have contributed to the negative result because of the different ecological niches occupied by the five pest species, which ranged in size from mice to feral cats. We argue that understanding the effect of moonlight on animal activity requires higher temporal resolution of data, and, therefore, lunar illumination should either be measured or estimated using appropriate models (Śmielak 2023).

## Conclusions

Our study provides a valuable contribution towards understanding common brushtail possum biology at different temporal scales. Furthermore, our work greatly expands knowledge of the temporal niche of possums in Australia, an aspect that has not been studied in detail before either in possums or in nocturnal mammals in general, predominantly due to technical limitations. Our study presents a novel approach to analysing changes in activity, with a higher temporal resolution than has commonly been used. Time-stamped records of activity, combined with a custom model of moonlight intensity, allowed us to detect subtle modulations in terrestrial activity from night to night.

We analysed drivers of terrestrial possum activity at various temporal scales using an extensive camera trap dataset collected over multiple years, which permitted temporal replication. Both temperature and rainfall were identified as important drivers, with results suggesting hot rather than cold weather limited possum terrestrial activity. This is particularly important in the context of climate change and can contribute to better predictions of how the species will respond to rising temperature, extreme weather and other climatic events and the likelihood of reestablishment in hotter environments where possums are locally extinct.

In our study, possums exhibited a very strong diel pattern of terrestrial activity, with all but seven of the recorded detections being nocturnal. Possums adjusted timing of their activity based on the season (night length) while modulating it in response to temperature and changes in moonlight intensity. Besides seasonal changes, weather and lunar illumination levels clearly regulated patterns of on-ground locomotion and therefore detection. An adverse effect of one environmental factor was often mitigated by another one; for instance, rain reduced activity on cold but not on warm nights. This shows that the temporal niche of possums is more complex than previously thought.

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**Data availability** The raw data analysed during this study (camera trap detections) are included as a supplementary material.

**Code availability** R code to replicate the analysis is provided in a dedicated public data repository ([https://github.com/msmielak/Brushtail\\_possum\\_activity](https://github.com/msmielak/Brushtail_possum_activity)).

## Declarations

**Ethics approval** This study was carried out under the University of New England Animal Ethics Committee permit AEC14-079.

**Consent to participate** Not applicable.

**Consent for publication** Not applicable.

**Conflict of interest** The authors declare no competing interests.

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## References

- Agafonkin V, Thieurmel B (2018) *suncalc*: compute sun position, sun-light phases, moon position and lunar phase. <https://CRAN.R-project.org/package=suncalc>. Accessed 5 Dec 2018
- Ball SJ, Ramsey D, Nugent G et al (2005) A method for estimating wildlife detection probabilities in relation to home-range use: insights from a field study on the common brushtail possum (*Trichosurus vulpecula*). *Wildl Res* 32:217–227. <https://doi.org/10.1071/WR03125>
- Ballard G, Meek P, Doak S et al (2014) Camera traps, sand plots and known events: what do camera traps miss? In: Meek P, Fleming P, Ballard G et al (eds) *Camera trapping for wildlife management and research*. CSIRO Publishing, Australasian Wildlife Management Society, Royal Zoological Society of NSW, Collingwood, pp 189–202
- Bannister HL, Brandle R, Delean S et al (2020) Supportive release techniques provide no reintroduction benefit when efficacy and uptake is low. *Oryx* 54:206–214. <https://doi.org/10.1017/S0030605317001843>
- Bartoń K (2020) MuMIn: multi-model inference. <https://CRAN.R-project.org/package=MuMIn>. Accessed 13 Oct 2020
- Beale PK, Connors PK, Dearing MD et al (2022) Warmer ambient temperatures depress detoxification and food intake by marsupial folivores. *Front Ecol Evol* 10:888550. <https://doi.org/10.3389/fevo.2022.888550>
- Burbidge AA, McKenzie NL (1989) Patterns in the modern decline of western Australia's vertebrate fauna: causes and conservation implications. *Biol Conserv* 50:143–198. [https://doi.org/10.1016/0006-3207\(89\)90009-8](https://doi.org/10.1016/0006-3207(89)90009-8)
- Bureau of Meteorology (BOM) (2020) Historical weather observations and statistics. <http://www.bom.gov.au/climate/data-services/station-data.shtml>. Accessed 3 Feb 2020
- Clinchy M, Taylor AC, Zanette LY et al (2004) Body size, age and paternity in common brushtail possums (*Trichosurus vulpecula*). *Mol Ecol* 13:195–202. <https://doi.org/10.1046/j.1365-294X.2003.02029.x>
- Cork SJ, Foley WJ (1991) Digestive and metabolic strategies of arboreal mammalian folivores in relation to chemical defenses in temperate and tropical forests. In: Palo RT, Robbins CT (eds) *Plant Defenses Against Mammalian Herbivory*. CRC Press, Boca Raton, Florida, pp 133–166
- Cotsell N, Vernes K (2016) Camera traps in the canopy: surveying wildlife at tree hollow entrances. *Pac Conserv Biol* 22:48–60. <https://doi.org/10.1071/PC15030>
- Cowan P (2014) Variability in the seasonality of breeding by the common brushtail possum, *Trichosurus vulpecula*: its possible causes and management implications. *Aust Mammal* 36:131–136
- Cowan PE, Clout MN (2000) Possums on the move: activity patterns, home ranges, and dispersal. In: Montague TL (ed) *The brushtail possum; biology, impact and management of an introduced marsupial*. Manaaki Whenua Press, Lincoln, pp 24–34
- Dunnet GM (1956) A live-trapping study of the brush-tailed possum *Trichosurus vulpecula* Kerr (Marsupialia). *CSIRO Wildl Res* 1:1–18. <https://doi.org/10.1071/cwr9560001>
- Edwards MJ, Wallis IR, Foley WJ (2010) Acid loads induced by the detoxification of plant secondary metabolites do not limit feeding by common brushtail possums (*Trichosurus vulpecula*). *J Comp Physiol B* 180:247–257. <https://doi.org/10.1007/s00360-009-0404-y>
- Eymann J, Herbert CA, Cooper DW (2006) Management issues of urban common brushtail possums *Trichosurus vulpecula*: a loved or hated neighbour. *Aust Mammal* 28:153–171. <https://doi.org/10.1071/am06025>
- Eyre TJ (2004) Distribution and conservation status of possums and gliders in South Australia. In: Goldingay RL, Jackson SM (eds) *The Biology of Australian Possums and Gliders*. Surrey Beatty & Sons, Sydney, pp 1–25
- Gilmore DP (1969) Seasonal reproductive periodicity in the male Australian Brush-tailed possum (*Trichosurus vulpecula*). *J Zool* 157:75–98. <https://doi.org/10.1111/j.1469-7998.1969.tb01690.x>
- Gilmore SE-R (2016) The influence of illumination and moon phase on activity levels of nocturnal mammalian pests in New Zealand. Lincoln University, Thesis
- Glen AS, Byrom AE, Pech RP et al (2012) Ecology of brushtail possums in a New Zealand dryland ecosystem. *N Z J Ecol* 36:29–37
- Goldingay R, Jackson S (eds) (2004). *Surrey Beatty & Sons, Sydney*

- Green WQ (1984) A review of ecological studies relevant to the management of the common brushtail possum. In: Smith AP, Hume ID (eds) Possums and gliders. Surrey Beatty & Sons, Sydney, pp 483–499
- Halse SA, Rose RW (1988) Variation in the basal body temperature of the common brushtail possum (*Trichosurus vulpecula*) in Tasmania. *Mammalia* 52:225–232. <https://doi.org/10.1515/mamm.1988.52.2.225>
- Harper MJ (2006) Home range and den use of common brushtail possums (*Trichosurus vulpecula*) in urban forest remnants. *Wildl Res* 32:681–687. <https://doi.org/10.1071/WR04072>
- Herbert PA, Lewis RD (1999) The chronobiology of the brushtail possum, *Trichosurus vulpecula* (Marsupialia:Phalangeridae): tests of internal and external control of timing. *Aust J Zool* 47:579–591. <https://doi.org/10.1071/zo99035>
- How RA, Hillcox SJ (2000) Brushtail possum, *Trichosurus vulpecula*, populations in south-western Australia: demography, diet and conservation status. *Wildl Res* 27:81–89. <https://doi.org/10.1071/wr98064>
- Hume ID (1999) Marsupial nutrition. Cambridge University Press, Cambridge
- Jackson S, Groves C (2015) Taxonomy of Australian mammals. CSIRO Publishing, Clayton South. <https://www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi?id=9337>
- Kemp MU, van Loon EE, Shamoun-Baranes J, Bouten W (2020) RNCEP: obtain, organize, and visualize NCEP weather data. <https://CRAN.R-project.org/package=RNCEP>. Accessed 26 May 2020
- Kerle JA, Foulkes JN, Kimber RG, Papenfus D (1992) The decline of the brushtail possum, *Trichosurus vulpecula* (Kerr 1798), in arid Australia. *Rangel J* 14:107–127. <https://doi.org/10.1071/rj9920107>
- Körtner G, Geiser F (2000) Torpor and activity patterns in free-ranging sugar gliders *Petaurus breviceps* (Marsupialia). *Oecologia* 123:350–357. <https://doi.org/10.1007/s004420051021>
- Kyba CCM, Conrad J, Shatwell T (2020) Lunar illuminated fraction is a poor proxy for moonlight exposure. *Nat Ecol Evol* 4:318–319. <https://doi.org/10.1038/s41559-020-1096-7>
- Lennon James S (1998) The effect of moonlight intensity and moon phase on feeding patterns of common brushtail possums. Lincoln University, Thesis
- Linley GD, Pauligk Y, Marneweck C, Ritchie EG (2020) Moon phase and nocturnal activity of native Australian mammals. *Aust Mammal* 43:190–195. <https://doi.org/10.1071/AM19070>
- MacLennan DG (1984) The feeding behaviour and activity patterns of the brushtail possum, *Trichosurus vulpecula*, in an open eucalypt woodland in southeast Queensland. In: Smith A, Hume I (eds) Possums and gliders. Surrey Beatty & Sons in association with the Australian Mammal Society, Chipping Norton, N.S.W., pp 155–161
- Magnusson A, Skaug H, Nielsen A et al (2020) glmmTMB: generalized linear mixed models using template model builder. <https://CRAN.R-project.org/package=glmmTMB>. Accessed 6 Jun 2020
- Marsh KJ, Foley WJ, Cowling A, Wallis IR (2003) Differential susceptibility to Eucalyptus secondary compounds explains feeding by the common ringtail (*Pseudocheirus peregrinus*) and common brushtail possum (*Trichosurus vulpecula*). *J Comp Physiol B* 173:69–78. <https://doi.org/10.1007/s00360-002-0318-4>
- Marsh KJ, Wallis IR, McLean S et al (2006) Conflicting demands on detoxification pathways influence how common brushtail possums choose their diets. *Ecology* 87:2103–2112. [https://doi.org/10.1890/0012-9658\(2006\)87\[2103:cdodpi\]2.0.co;2](https://doi.org/10.1890/0012-9658(2006)87[2103:cdodpi]2.0.co;2)
- Meek P, Fleming P, Ballard G et al (eds) (2014). CSIRO Publishing, Australasian Wildlife Management Society, Royal Zoological Society of NSW, Collingwood
- Mella VSA, Banks PB, McArthur C (2014) Negotiating multiple cues of predation risk in a landscape of fear: what scares free-ranging brushtail possums? *J Zool* 294:22–30. <https://doi.org/10.1111/jzo.12146>
- Montague TL (2000) The brushtail possum : biology, impact and management of an introduced marsupial. Manaaki Whenua Press, Lincoln
- Nersesian CL, Banks PB, McArthur C (2012) Behavioural responses to indirect and direct predator cues by a mammalian herbivore, the common brushtail possum. *Behav Ecol Sociobiol* 66:47–55. <https://doi.org/10.1007/s00265-011-1250-y>
- Nugent G, Fraser W, Sweetapple P (2001) Top down or bottom up? Comparing the impacts of introduced arboreal possums and ‘terrestrial’ ruminants on native forests in New Zealand. *Biol Conserv* 99:65–79. [https://doi.org/10.1016/S0006-3207\(00\)00188-9](https://doi.org/10.1016/S0006-3207(00)00188-9)
- Nugent G, Buddle B, Knowles G (2015) Epidemiology and control of *Mycobacterium bovis* infection in brushtail possums (*Trichosurus vulpecula*), the primary wildlife host of bovine tuberculosis in New Zealand. *N Z Vet J* 63:28–41. <https://doi.org/10.1080/00480169.2014.963791>
- Nugent G, Sweetapple P, Colman J, Suisted P (2000) Possum feeding patterns: dietary tactics of a reluctant folivore. In: Montague TL (ed) The Brushtail Possum; Biology, impact and management of an introduced marsupial. Manaaki Whenua Press, Lincoln, pp 10–23
- Office of Environment and Heritage (2016) New England Tableland Bioregion. <https://www.environment.nsw.gov.au/bioregions/NewEnglandTablelandBioregion.htm>. Accessed 11 Nov 2019
- Parisi J (2011) The influence of lunar phase on indirect indices of activity for the common brushtail possum (*Trichosurus vulpecula*) on Banks Peninsula. Georg-August-Universität Göttingen, Germany and Lincoln University, New Zealand, New Zealand
- Paterson BM, Morris RS, Weston J, Cowan PE (1995) Foraging and denning patterns of brushtail possums, and their possible relationship to contact with cattle and the transmission of bovine tuberculosis. *N Z Vet J* 43:281–288. <https://doi.org/10.1080/00480169.1995.35907>
- Pickett K (1999) Sublethal impacts of risk of predation by the introduced red fox on the common brushtail possum (*Trichosurus vulpecula*) in New South Wales. Master of Science, University of Toronto, Australia
- Rovero F, Zimmerman F (eds) (2016). Pelagic Publishing Ltd, Exeter
- R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. *Methods Ecol Evol* 1:103–113. <https://doi.org/10.1111/j.2041-210X.2010.00012.x>
- Short J, Hide A (2014) Successful reintroduction of the brushtail possum to Waddarin Sanctuary in the eastern wheatbelt of Western Australia. *Aust Mammal* 36:229–241
- Śmielak MK (2023) Biologically meaningful moonlight measures and their application in ecological research. *Behav Ecol Sociobiol* 77:21. <https://doi.org/10.1007/s00265-022-03287-2>
- Stobo-Wilson AM, Murphy BP, Cremona T, Carthew SM (2019) Contrasting patterns of decline in two arboreal marsupials from Northern Australia. *Biodivers Conserv* 28:2951–2965. <https://doi.org/10.1007/s10531-019-01807-7>
- Symonds MRE, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike’s information criterion. *Behav Ecol Sociobiol* 65:13–21. <https://doi.org/10.1007/s00265-010-1037-6>
- Terrien J, Perret M, Aujard F (2011) Behavioral thermoregulation in mammals: a review. *Front Biosci Landmark Ed* 16:1428–1444. <https://doi.org/10.2741/3797>
- Tyndale-Biscoe CH (1955) Observations on the reproduction and ecology of the Brush-tailed possum. *Trichosurus vulpecula* Kerr (Marsupialia), in New Zealand. *Aust J Zool* 3:162–184. <https://doi.org/10.1071/zo9550162>
- van den Oord QGW, van Wijk EJA, Lugton IW et al (1995) Effects of air temperature, air movement and artificial rain on the heat production of brushtail possums (*Trichosurus vulpecula*): an exploratory study. *N Z Vet J* 43:328–332. <https://doi.org/10.1080/00480169.1995.35914>

- Wayne A, Cowling A, Rooney J et al (2005) Factors affecting the detection of possums by spotlighting in Western Australia. *Wildl Res* 32:689–700
- Whyte BI, Ross JG, Blackie HM (2014) Differences in brushtail possum home-range characteristics among sites of varying habitat and population density. *Wildl Res* 40:537–544. <https://doi.org/10.1071/WR13063>
- Wiggins NL, McArthur C, McLean S, Boyle R (2003) Effects of two plant secondary metabolites, cineole and gallic acid, on nightly feeding patterns of the common brushtail possum. *J Chem Ecol* 29:1447–1464. <https://doi.org/10.1023/A:1024221705354>
- Wiggins NL, McArthur C, Davies NW (2006) Diet switching in a generalist mammalian folivore: fundamental to maximising intake. *Oecologia* 147:650–657. <https://doi.org/10.1007/s00442-005-0305-z>

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