

Notornis, 2021, Vol. 68: 1-12

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Nocturnal activity of the western weka (*Gallirallus australis australis*) in an open environment

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Abstract: Understanding how animal behaviours are affected by external factors such as time of day/year and weather conditions is fundamental to understanding the basic biology of a species and can thus help with conservation management. Weka (*Gallirallus australis*) is typically crepuscular in its habits, but there is some evidence to suggest that it can also be nocturnal. We conducted a longitudinal study of the nocturnal habits of the western weka (*G. australis australis*) located at Manaroa in New Zealand's Marlborough Sounds. We used model selection information criterion to examine how the numbers of weka in an open environment (lawn) changed with time of night and season, as well as differing weather and moonlight conditions. In addition, we undertook night-time behavioural observations during a four-month subset of the study period. Numbers of weka declined through the night and increased non-linearly around dawn. Weka were more likely to be present during moonlit nights and at warmer temperatures during the evening. There was considerable seasonal variation, with the highest number of weka during autumn and lowest during summer. Behavioural observations demonstrated that weka were active throughout the night, with foraging being the most frequently-observed behaviour.

Lamb, S.D.; Taylor, H.R.; Powlesland, R. 2021. Nocturnal activity of the western weka (*Gallirallus australis australis*) in an open environment. *Notornis* 68(1): 1-12.

Keywords: weka, *Gallirallus australis australis*, nocturnal, behaviour, activity, weather, moonlight

INTRODUCTION

Understanding how patterns of activity in animals are influenced by external factors is important for understanding the basic biology of a species, and in turn, could be important for contributing

to conservation management strategies. Weather conditions (e.g. temperature, rainfall, wind speed) can have enormous effects on how an animal behaves and the choices it makes while trying to meet its biological needs (Daly *et al.* 1992; Lengagne *et al.* 1999; Mougeot & Bretagnolle 2000; Dänhardt & Lindström 2001; Lengagne & Slater 2002; Sergio 2003). For example, little owls (*Athene noctua*) tend

Received 23 September 2019; accepted 22 September 2020

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to shift habitat use depending on temperature, altering their foraging strategy for expected prey types (Sunde *et al.* 2014). At times, weather conditions may impart physical challenges on animals (Lengagne *et al.* 1999; Lengagne & Slater 2002). At others cueing in on favourable conditions may allow animals to exploit different resources or spend less energy when there is a need to be active (Dänhardt & Lindström 2001). Nocturnal animals are additionally affected by moonlight and tend to change foraging strategies, habitat use or general activity levels in response (Daly *et al.* 1992; Brown 1999; Mougeot & Bretagnolle 2000; Kronfeld-Schor *et al.* 2013; Prugh & Golden 2014). For predators that rely on visual cues to detect their prey, increased moonlight can improve their foraging ability. Conversely, prey species typically exhibit moonlight avoidance by damping activity levels and restricting themselves to cover when moving through their environment, whereas predators tend to be more active (Daly *et al.* 1992; Brown 1999; Mougeot & Bretagnolle 2000; Kronfeld-Schor *et al.* 2013).

The weka (*Gallirallus australis*) is a flightless rail endemic to New Zealand and occupies a variety of habitat types (Beauchamp 1997; Bramley & Veltman 2000a). Over time, the population and range of weka has declined due to a combination of factors, particularly habitat loss with predation by introduced mammals (especially by ferrets (*Mustela furo*) and stoats (*M. erminea*) (Beauchamp 1997; Beauchamp *et al.* 1999, 2009; King 2017; Watts *et al.* 2017). Weka can be particularly susceptible to the presence of introduced predatory mammals, and re-introduction attempts to historic ranges often incur high mortality rates (Bramley & Veltman 1998; Watts *et al.* 2017). Despite their fragmented distribution throughout the North Island, weka populations remain relatively abundant on offshore islands and in some areas of the South Island (Robertson *et al.* 2007). The conservation status of western weka (*G. australis australis*) is 'not threatened', whereas other subspecies are classified as 'recovering', 'stable' or 'relict' (Robertson *et al.* 2017). The weka is a controversial species for conservation management owing to its tendency to depredate other endangered species (Imber *et al.* 2003; Miskelly & Beauchamp 2004; Harper 2006; Lettink *et al.* 2010). Indeed, weka have been removed from some parts of their natural range for the protection of other native species (Miskelly & Beauchamp 2004). Weka provide important ecosystem functions (Carpenter *et al.* 2018, 2019) and understanding aspects of their behavioural ecology could be useful for identifying areas of risk based on facets of their behaviour (e.g. colour preference and consumption of toxic baits for mammals by weka; Hartley *et al.* 2000).

Weka typically exhibit a crepuscular activity profile with activity peaks occurring at dawn and dusk (Bramley 1994). However, there is some evidence that weka may also be active throughout the night (Beauchamp 1987a, 1987b; Beauchamp *et al.* 2009; RP *pers. obs.*). Previous research has found that call rates of weka around dusk are unaffected by weather conditions, but are influenced by time of the year (Bramley & Veltman 2000b). Furthermore, weka exhibit habitat preferences towards patches with cover and away from open environments (Bramley & Veltman 2000a). This is thought to change, however, depending on the time of day and with the presence/absence of moonlight (Beauchamp *et al.* 2009). We conducted a longitudinal study on a western weka (*G. australis australis*) population during evening and night-time hours for 16 months, from August 2013 to November 2014. We sought to understand how time of night, season, and weather conditions may influence the number of weka nocturnally active in an open environment. In addition, we recorded night-time behaviours during a four-month subset of the study period to gain further insight into what nocturnal behaviours may be typical of weka.

MATERIAL AND METHODS

Sampling location, observations and environmental measurements

The study took place at Manaroa, near Pelorus Sound, Marlborough Sounds, New Zealand (41°07'47.1"S, 174°02'32.4"E) from August 2013 to November 2014. The sampling location was an area of shortly-mowed lawn (measuring c. 1,150 m²), adjacent to bush. The bush consisted primarily of tall macrocarpa (*Cupressus macrocarpa*) and pine trees (*Pinus radiata*), with an understorey of mainly mahoe (*Meliccytus ramiflorus*), wineberry (*Aristotelia serrata*), karamu (*Coprosma robusta*), kanono (*C. grandifolia*), marble leaf (*Carpodetus serratus*), and kaikomako (*Pennantia corymbosa*) trees and shrubs. Beyond the study site, the landscape consisted of rank grass and farmland.

Observations involved taking counts of weka on the lawn during a 10-minute period centred on the hour, from 1700 h to 0800 h. The observer (RP) was located on a 1-metre high deck directly adjacent to the lawn. Little artificial light emanated from the building. Observations of weka were achieved using a white-light LED head torch.

Across the study period, there was an average of 4.9 observations per night (range 1–11) and an average of 117.9 observations per month (range 55–204). Overall, there was an average of 24 unique nights sampled per month (range 12–29; 385 total nights sampled; Fig. 1). The total number of observations varied across each hour of the night and varied across each season (Fig. 2).

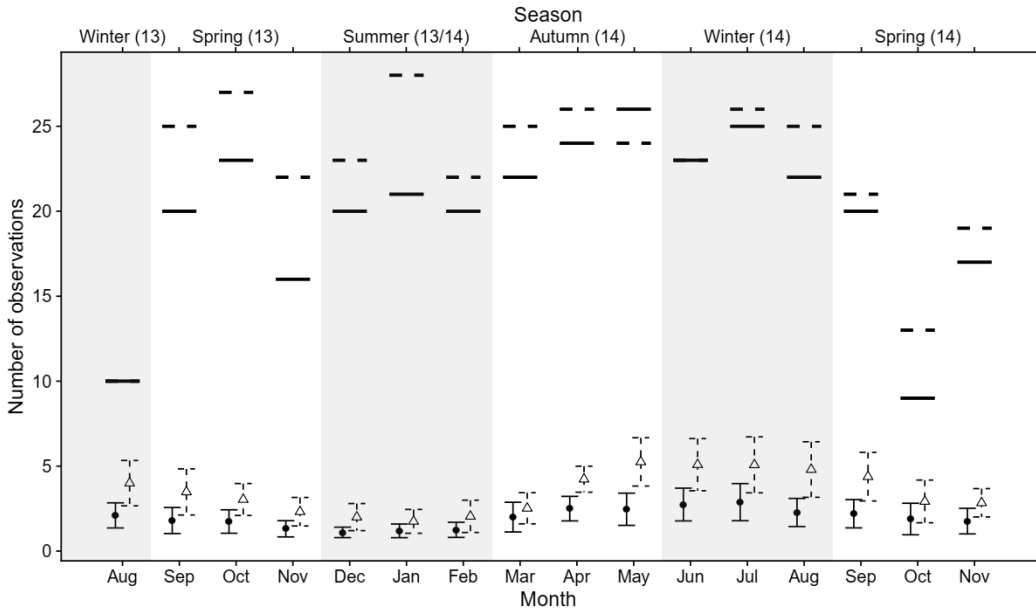


Figure 1. The sampling effort over each month for each season (year following in parentheses) throughout the study (August 2013 – November 2014). Points indicate the mean number of nightly observations for each month and errors bars indicate the standard deviation of the mean. Circles represent the dusk timeframe and triangles the dawn timeframe. Horizontal lines indicate the number of unique days sampled per month (solid lines indicate dusk and dashed indicate the dawn time-frame).

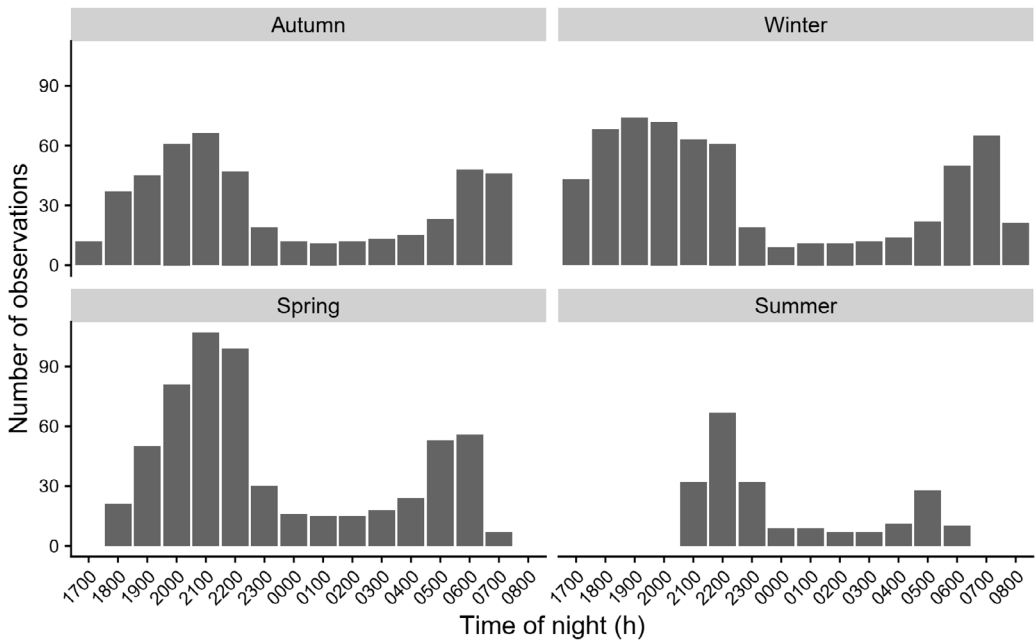


Figure 2. The sampling effort for observing weka at each time point (from 1700 h to 0800 h) for each season throughout the study (August 2013 – November 2014). Bars indicate the total number of nightly observations.

Phase of the moon (moonlight) was recorded *in situ* at three levels: none (no moonlight), partial moonlight ($\frac{1}{4}$ – $\frac{3}{4}$ moon) and full moonlight ($\frac{7}{8}$ moon to full moon). Wind speed was recorded *in situ* at three levels based on the Beaufort Wind Force Scale: calm (no wind to leaves rustling), moderate (leaves and small twigs in constant motion and small branches moving), and strong (small trees sway and large branches in motion). Cloud cover was recorded *in situ* at three levels: clear (<10% cloud cover), partly cloudy (11–89% cloud cover) and overcast ($\geq 90\%$ cloud cover). Temperature (minimum, daily mean, and maximum; °C) and rainfall (mm) data were obtained from the Pelorus Sound weather station (weather station agent number 4232, network number G13195 located at Crail Bay, 41°06′04.0″S, 173°57′51.0″E, approximately 7.3 km away from the study site). Measures of temperature and rainfall were recorded daily by the weather station at 0900 h. The historical weather data used in this study are publicly available from The National Climate Database (<https://cliflo.niwa.co.nz/>).

Behavioural observations

In addition to the counts of weka, from August 2014 to November 2014, RP recorded the nocturnal behaviour of weka using a Yukon Newton 4 x 50 night-vision monocular on the hour from 1900 h to 0600 h (taking approximately 10 min to record the activity of all weka present on the lawn during each observation). Activity was identified and recorded at first sighting. Six classifications of mutually exclusive behaviours were recorded; walking, scanning, probing the ground, prey capture, preening, and resting (see Table 1 for definitions and descriptions of each classified behaviour). Some observations were unclear and have been recorded as “other”. There was an average of 2.4 observations per night (range 1–5) and an average of 33 (range 4–54) observations per month.

Statistical analysis

We conducted all analyses in R (R Core Team 2018). To determine what environmental factors may have influenced weka numbers on the open lawn, we conducted a generalised linear mixed effect model (GLMM) with a Poisson error-function using the ‘lme4’ package (Bates *et al.* 2014). To facilitate the analysis of time of night, we split the data into two time-frames: a ‘dusk’ time-frame (1700 h to 0000 h) and a ‘dawn’ time-frame (0100 h to 0800 h) and analysed them separately. We then calculated the time from sunset (for the dusk time-frame) and sunrise (for the dawn time-frame) for each observation using sunset and sunrise times specified for the Blenheim region (data publicly available from <https://www.timeanddate.com/>). The response variable was the number of weka observed, and the categorical predictor variables considered were: moonlight, cloud cover, wind speed, and season. The continuous predictor variables considered were: time from sunset (dusk time-frame)/ sunrise (dawn time-frame), average daily temperature (°C), minimum (min) daily temperature (°C), maximum (max) daily temperature (°C), and daily rainfall (mm). Because weka are crepuscular, we additionally included time from sunrise as a non-linear term (sunrise²) for the analysis of the dawn time-frame to test for non-linear increases in counts occurring during sunrise (Bramley 1994). Because the temperature variables were significantly correlated with one another (average vs min correlation = 0.84, *P-value* <0.001; average vs max correlation = 0.76, *P-value* <0.001; min vs max correlation = 0.56, *P-value* <0.001), we decided to retain the min temperature (and exclude the mean and max daily temperatures from the model), as this is more likely to reflect night time temperatures. Because moonlight is known to strongly influence nocturnal activity across many taxa (Daly *et al.* 1992; Brown 1999; Mougeot & Bretagnolle 2000; Kronfeld-Schor *et al.* 2013; Prugh & Golden 2014), we additionally tested for

Table 1. Description of mutually exclusive behaviours observed by weka.

Behaviour	Description
Probing	Foraging; frequent quick touches to the soil surface with beak between steps
Prey capture	Foraging
Scanning	Staggered gait; slow stepping, with intermittent freezing of the body, sometimes in mid-step so that the bird was standing on one leg
Walking	Continuous gait
Preening	Preening feathers
Resting	Resting or asleep
Other	Observation was unclear

interactive effects of moonlight with the continuous predictors (i.e. min temperature °C, rainfall mm and time elapsed since sunset/sunrise h). The time after sunset/sunrise, min temperature and rainfall were mean centred (Gelman 2008; Grueber *et al.* 2011). We used date as a random effect to account for multiple observations per night and potentially multiple observations of the same individual (as we were unable to distinguish between individuals between sampling points). We assessed model validation using the ‘DHARMA’ package (Hartig 2020). The model for the dawn time-frame was found to be over-dispersed and was re-analysed using a negative binomial error distribution using the ‘glmmTMB’ package (Brooks *et al.* 2017).

Given the number of variables in the model, we applied a model selection approach using Bayesian Information Criterion (BIC) using the ‘MuMin’ package using the ‘dredge’ function

(Bartón 2019). Bayesian Information Criterion was used rather than the Akaike’s Information Criterion (Akaike 1998) as BIC enacts a greater penalty for the number of predictor variables included in the model (see Grueber *et al.* 2011). Again, considering the high number of predictor variables during model selection, a conservative $\Delta\text{BIC} \leq 2$ was considered as the criterion for retaining predictors. Models with $\Delta\text{BIC} \leq 2$ were averaged together. Significant differences between factor levels (i.e. levels of moonlight) were compared using the ‘pairs’ function from the package ‘emmeans’ with a ‘Tukey’ adjustment (Lenth *et al.* 2018). Model predictions were calculated using the ‘ggpredict’ function in the ‘ggeffects’ package (Lüdtke 2018). No statistical analyses were carried out on weka behavioural observations as these were purely descriptive.

Table 2. Bayesian Information Criterion (BIC) results of generalised linear mixed models investigating the effects of weather conditions, categories of moonlight, and season on the number of weka on the lawn. Results show the 10 highest ranked models. Models shown in bold are the most parsimonious models based on $\Delta\text{BIC} \leq 2$. k is the number of parameters, ΔBIC is the change in BIC relative to the top model, weight is the model probability (the likelihood of a particular model against all other models). Note, time in the dusk time-frame indicates time from sunset and time in the dawn time frame indicates time from sunrise.

Time-frame: Dusk						
Rank	Model	k	BIC	ΔBIC	weight	
1	Time + Moonlight + Season + Temp	10	4,330.9	0.00	0.398	
2	Time + Moonlight + Season	9	4,331.4	0.46	0.316	
3	Time + Moonlight + Season + Temp + Wind	12	4,334.0	3.06	0.086	
4	Time + Moonlight + Season + Wind	13	4,335.2	4.31	0.046	
5	Time + Moonlight + Season + Cloud	10	4,335.9	4.93	0.034	
6	Time + Moonlight + Season + Wind	10	4,336.5	5.59	0.024	
7	Time + Moonlight + Season + Temp + Wind + Cloud	13	4,337.4	6.44	0.016	
8	Time + Moonlight + Season + Rain	9	4,337.6	6.65	0.014	
9	Time + Moonlight + Season + Temp + Rain	10	4,337.9	6.99	0.012	
10	Time + Moonlight + Season + Time*Moonlight	10	4,338.3	7.43	0.010	
Time-frame: Dawn						
1	Time + Time ² + Moonlight + Season	11	1,626.1	0.00	0.818	
2	Time + Time ² + Moonlight + Season + Time*Moonlight	13	1,629.5	3.39	0.135	
3	Time + Time ² + Moonlight + Season + Rain	12	1,630.7	4.64	0.072	
4	Time + Time ² + Moonlight + Season + Temp	12	1,632.5	6.40	0.030	
5	Time + Time ² + Moonlight + Season + Rain + Time*Moonlight	14	1,634.4	8.35	0.011	
6	Time + Time ² + Moonlight + Season + Temp + Time*Moonlight	14	1,635.9	9.82	0.005	
7	Time + Time ² + Moonlight + Season + Rain + Temp	13	1,637.0	10.92	0.003	
8	Time + Time ² + Moonlight + Season + Wind	13	1,638.3	12.25	0.002	
9	Time + Time ² + Moonlight + Season + Cloud	13	1,638.7	12.60	0.001	
10	Time + Time ² + Moonlight + Season + Rain + Temp + Time*Moonlight	15	1,640.8	12.68	0.000	

Table 3. Results of model averaged generalised linear mixed models investigating the effects of weather condition, categories of moonlight and season on the number of weka on the lawn. Reported are the estimates, standard errors (SE) / adjusted SE for the averaged model/ variance (var) for random effects, lower and upper 95% confidence intervals (CI), Z-values and P-values. Continuous variables, minimum daily temperature °C (Temp) and time after sunset h (dusk time-frame) / sunrise h (dawn time-frame) was mean centred. Moonlight(none) was the reference group for Moonlight(partial) and Moonlight(full), Season(autumn) was the reference group for Season(winter), Season(spring), and Season(summer).

Time-frame: Dusk							
Variable	Model	Estimate	SE/ SE adjusted/ Var	95% CI	Z-value	P-value	
Intercept	M1	0.45	0.06	0.33, 0.57	7.35	<0.001	
	M2	0.50	0.06	0.38, 0.62	8.37	<0.001	
	Average	0.48	0.07	0.35, 0.60	7.26	<0.001	
Time from sunset	M1	-0.12	0.02	-0.15, -0.09	-7.05	<0.001	
	M2	-0.12	0.02	-0.16, -0.09	-7.09	<0.001	
	Average	-0.12	0.02	-0.16, -0.09	-7.06	<0.001	
Moonlight (partial)	M1	0.47	0.05	0.37, 0.57	8.90	<0.001	
	M2	0.47	0.05	0.36, 0.57	8.80	<0.001	
	Average	0.47	0.05	0.37, 0.57	8.84	<0.001	
Moonlight (full)	M1	0.83	0.07	0.70, 0.96	12.17	<0.001	
	M2	0.82	0.07	0.69, 0.96	12.04	<0.001	
	Average	0.83	0.07	0.69, 0.96	12.09	<0.001	
Season (winter)	M1	-0.01	0.08	-0.17, 0.15	-0.15	0.884	
	M2	-0.13	0.07	-0.27, 0.02	-1.72	0.086	
	Average	-0.06	0.10	-0.25, 0.13	-0.64	0.520	
Season (spring)	M1	-0.26	0.07	-0.40, -0.12	-3.67	<0.001	
	M2	-0.30	0.07	-0.44, -0.16	-4.28	<0.001	
	Average	-0.28	0.07	-0.43, -0.14	-3.78	<0.001	
Season (summer)	M1	-0.51	0.09	-0.70, -0.33	-5.43	<0.001	
	M2	-0.46	0.09	-0.64, -0.27	-4.91	<0.001	
	Average	-0.49	0.10	-0.68, -0.30	-4.99	<0.001	
Temp	M1	0.03	0.01	0.008, 0.05	2.78	0.005	
	Average	0.03	0.01	0.008, 0.05	2.78	0.005	
Random effect variance	M1	-	0.09	-	-	-	
	M2	-	0.09	-	-	-	
	Average	-	0.09	-	-	-	
Time-frame: Dawn							
Intercept		-1.01	0.16	-1.33, -0.69	-6.17	<0.001	
Time from sunrise		0.83	0.07	0.70, 0.96	12.56	<0.001	
Time from sunrise ²		0.18	0.02	0.13, 0.23	7.32	<0.001	
Moonlight (partial)		0.88	0.15	0.58, 1.18	5.76	<0.001	
Moonlight (full)		0.92	0.20	0.52, 1.32	4.54	<0.001	
Season (winter)		-0.44	0.09	-0.62, -0.25	-4.63	<0.001	
Season (spring)		-0.52	0.10	-0.72, -0.32	-5.14	<0.001	
Season (summer)		-1.23	0.24	-1.70, -0.77	-5.19	<0.001	
Random effect variance		-	0.011	-	-	-	

RESULTS

Weka presence at the study site during the dusk time-frame (between 1700 h and 0000 h) was predominantly influenced by a combination of moonlight, temperature, time after sunset, and season. Among all models tested, two models had a $\Delta\text{BIC} \leq 2$ and included the predictor variables moonlight, time from sunset, season (in both models) and minimum daily temperature (in one model; Table 2). During the dawn time-frame (between 0100 h and 0800 h), only one model had a $\Delta\text{BIC} \leq 2$ and included the predictor variables: moonlight, time from sunrise, time from sunrise² (i.e. a non-linear term) and season (Table 2). We found no statistical support during either time-frame for the variables cloud cover, wind speed and rainfall influencing weka presence, as all these variables were present in models with $\Delta\text{BIC} \geq 2$ (Table 2). Likewise, there was a lack of support for interactive effects between moonlight and the other variables tested.

We found that weka numbers significantly decreased after sunset (Fig 3A; Table 3); however, based on counts and on behavioural observations, it appears that a small proportion of weka continue to be active throughout the night up until approximately one hour preceding sunrise when weka numbers begin to increase non-linearly (Fig. 3B; Table 3). During the dusk time-frame we found that weka were more likely to be present during partial moonlight (Fig. 3A Table 3), and even more likely under a full moon, with the difference in weka numbers being statistically significant when compared to partial moonlight (Est. 0.36 ± 0.06 se, [0.22, 0.50 95%CI], t -ratio = 5.912, P -value <.0001; Fig. 3A). Likewise, during the dawn time-frame, weka were more likely to be present during moonlight (Fig. 3B; Table 3); however, there was no statistical difference between partial and full moonlight (Est. 0.04 ± 0.12 se, [-0.25, 0.32 95%CI], t -ratio = 0.31, P -value = 0.9498).

We found several seasonal differences in weka numbers during both time-frames (Fig 3C, 3D). During the dusk time-frame, we found that weka were equally likely to be present during autumn and winter (Fig. 3C; Table 3); however, the number of weka was significantly higher in autumn and winter compared to spring and summer (Table 3; winter vs spring, Est. 0.22 ± 0.08 se, [0.02, 0.42 95%CI], t -ratio = 2.78, P -value = 0.028; winter vs summer, Est. 0.42 ± 0.13 se, [0.09, 0.76 95% CI], t -ratio = 3.25, P -value = 0.007). The number of weka present on the lawn during the dusk time-frame in spring and summer were similar (Est. 0.21 ± 0.10 se, [-0.06, 0.47 95%CI], t -ratio = 2.00, P -value = 0.190). During the dawn time-frame, weka were more likely to be present in autumn compared to all other seasons (Fig. 3D; Table 3). There was no significant

difference in the number of weka during winter and spring (Est. 0.08 ± 0.10 se, [-0.16, 0.33 95%CI], t -ratio = 0.88, P -value = 0.814), and the number of weka during summer was significantly less than all other seasons (Table 3; summer vs winter, Est. -0.80 ± 0.24 se, [-1.42, -0.18 95%CI], t -ratio = -3.307, P -value = 0.006; summer vs spring, Est. -0.71 ± 0.24 se, [-1.34, -0.09 95%CI], t -ratio = -2.94, P -value = 0.018). During the dusk time-frame, we found that weka numbers increased with higher minimum daily temperatures (Fig. 3E; Table 3).

Finally, behavioural observations made between August and November 2014 indicated that, during the night, weka engaged predominantly in scanning and foraging (Table 4).

DISCUSSION

We found that during the dusk time-frame (1700 h to 0000 h), a model encompassing moonlight, temperature, time after sunset, and season were important predictors of the number of weka recorded at the study site. During the dawn time-frame (0100 h to 0800 h), we found that moonlight, time after sunrise, time after sunrise², and season were the important predictors. Conversely, cloud cover, wind speed, and rainfall appeared to have little effect on weka numbers. Additionally, there was little support for any interactive effects of moonlight with the other variables.

Given that the predominant activity we observed weka engaging in during the nightly observations was foraging (Table 4), our data suggest that weka are using the increased illumination provided by moonlight to extend foraging times. By day, weka tend to show avoidance of open habitats (Beauchamp *et al.* 2009), and exhibit a strong preference for environments with adequate bush cover (Bramley & Veltman 2000a). This is likely in response to an evolutionary history of predation by diurnal avian raptors, i.e. the New Zealand falcon (*Falco novaeseelandiae*) and the extinct Eyles's hawk (*Circus eylesi*) (Holdaway *et al.* 2001; Kross *et al.* 2013). The swamp harrier (*C. approximans*), though a recent arrival (<1,000 years in New Zealand; Holdaway *et al.* 2001), is also known to prey on weka (Beauchamp *et al.* 1999). This raptor is smaller than the extinct hawk, but arguably fills the niche left by *C. eylesi*. Indeed, at this study site (but outside the study period), two separate instances of harriers and one instance of a New Zealand falcon swooping down to attack a weka occurred during the day (RP *pers. obs.*). Moonlight may therefore improve visibility sufficiently to enable weka to use open habitats for nocturnal foraging, when at other times (i.e. during the day) they would be discouraged from doing so due to the threat of predation. It was not unusual to see weka at the study site foraging at night

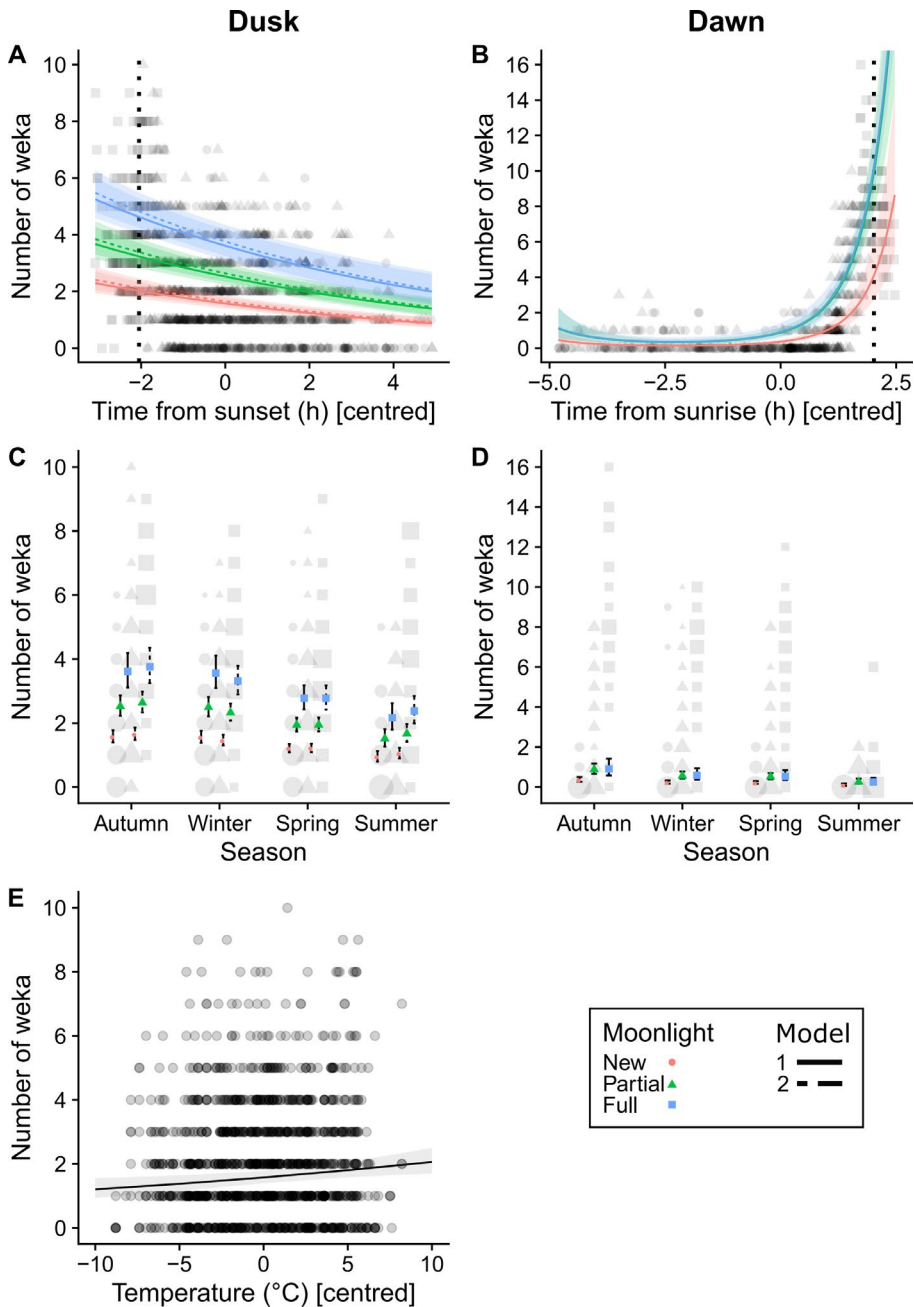


Figure 3. The relationship between the predicted number of weka \pm 95% CI present at the study site during the dusk (1700 h – 0000 h; left side) and dawn (0100 h – 0800 h; right side) under differing weather and moonlight conditions. A) and B) time from sunset/sunrise (h) [centred] for each category of moonlight. Vertical dotted line indicates sunset/sunrise (on the original scale). C) and D) across each season under different categories of moonlight. E) the minimum daily temperature ($^{\circ}\text{C}$) [centred]. Data points are partially transparent to indicate concentration of data. The size of partially transparent points indicates the relative proportion of weka observed for each season under each category of moonlight (Fig. 3C, D). Predicted values for the two top models (from the dusk time-frame only) are indicated by the different line types/ error bars (solid = model 1, dashed = model 2). Only model 1 included the minimum daily temperature (data are not subsetted by moonlight categories).

Table 4. The proportion of behaviour observed by weka between 1900 h – 0600 h. A ‘-’ indicates a behaviour not observed at that time. The proportion was calculated from the number of times a particular behaviour was observed, relative to other observed behaviours, for each time point.

Time (h)	1900	2000	2100	2200	2300	0000	0100	0200	0300	0400	0500	0600
Behaviour												
Probing	0.192	0.591	0.438	0.526	0.533	0.375	0.667	0.75	1.00	1.00	0.778	-
Prey capture	-	0.068	-	0.039	-	-	-	-	-	-	-	-
Scanning	0.577	0.25	0.419	0.368	0.333	0.625	0.333	-	-	-	0.222	0.889
Walking	0.038	0.023	-	-	-	-	-	-	-	-	-	-
Preening	-	-	0.010	-	-	-	-	-	-	-	-	-
Resting	-	-	0.010	0.013	-	-	-	-	-	-	-	-
Other	0.192	0.068	0.124	0.053	0.133	-	-	0.25	-	-	-	0.111
Total number of observations of weka at that time point	26	44	105	76	15	8	6	4	3	3	9	18
Total number of nights at that time point	12	18	35	33	8	8	4	2	2	3	8	2

over grazed pasture far from cover, a habitat they would rarely forage over during daylight (RP *pers. obs.*). It is possible that our findings of moonlight being an important predictor of weka numbers is an artifact of increased moonlight improving visibility for human observers. However, we consider this unlikely as our findings are consistent with a previous study of weka on Kapiti Island (Beauchamp 1987a), and from observations taken on the golf courses on moonlit nights at Pakatoa Island, Hauraki Gulf (Beauchamp *et al.* 2009).

Seasonal variation in weka numbers foraging over the lawn at night could reflect either a seasonal shift in habitat use or because seasonal characteristics in life-history factors influenced the number of weka. Although weka are able to breed year round, the majority of breeding occurs during winter-spring and is at a minimum during autumn (Carroll 1963a; Coleman *et al.* 1983; Beauchamp 1987a, 1987b). During incubation, one member of the pair is on the nest at all times (females typically by day, males at night; Cunninghame 2006; Tinnemans *et al.* 2019), and so fewer weka would be expected to be seen foraging when incubation is underway and while young chicks are present that need frequent brooding. It may be that incubating weka needed to extend foraging times throughout the night to meet their nutritional requirements. This might be particularly relevant for incubating females, given that they spend much of the day on the nest (Marchant & Higgins 1993; Beauchamp *et al.* 1998; Taylor & van Perlo 1998; Cunninghame 2006). Additionally, parents with dependent young are more likely to be seen foraging under cover during the day (Beauchamp *et al.* 1998, 2009),

although we did observe some families foraging on the lawn at night and over grazed pasture (RP *pers. obs.*). Another possible explanation could be due to changes in soil invertebrate availability (e.g. earthworms) during summer-autumn when the soil of the lawn is fairly dry from lack or minor rainfall.

Further declines in weka numbers on the lawn at night in summer may also be attributable to dispersal of juveniles. Recently independent young (after approximately two months of dependency) tend to disperse out of their natal territories during late spring and summer (Beauchamp 1987a; Bramley 2001). Similarly, a survey of vehicle strikes of weka at Cape Foulwind on the West Coast also found a peak in the mortality of the younger age groups (<1 year and 1–3 to years old; Freeman 2010), when young weka are likely to be dispersing and the movement of sub-adults in and out of a population are high (Beauchamp 1987a, 1987b; Bramley 2001). As we were unable to distinguish between adults and juveniles during night time observations on the lawn, we can only speculate as to what biological reasons underpinned seasonal variation in this study, but generally suggest seasonal life history and environmental factors were responsible.

The finding that the number of weka evident on the lawn at night is related to temperature during the dusk time period could be connected to invertebrate availability. Invertebrates can comprise a large portion of weka diet (Carroll 1963b; Beauchamp 1987a; Colbourne *et al.* 1990), thus weka may be using warmer temperatures as a cue for when to forage over the lawn, when invertebrates are more likely to be active (Mellanby 1939). It is also possible that weka prefer to be active

at night during warmer temperatures. However, the lack of a significant temperature effect during the dawn time-frame might suggest that the effect of temperature is weaker compared to other factors, such as moonlight. Additionally, because the temperature data were not recorded at the study site, we may not be capturing the trend completely.

When foraging, weka were frequently observed touching the soil/turf surface (i.e. probing; several times per step; Table 4), which is typical of weka when foraging through the humus level or leaf litter (Colbourne *et al.* 1990). It is unknown whether weka, like kiwi (*Apteryx* spp.), have sensory pits in the bone at the tip of their beaks for detecting prey movement underground (Heather & Robertson 2015). While it is evident that weka use sight and sound to locate prey, they may also use smell, especially during dark nights when their vision may be limited. While the sense of smell is said to be somewhat developed in rails (Bang 1968; Ripley *et al.* 1977), we are not aware that the weka's sense of smell has been investigated.

Weka at Manaroa exhibited a typical crepuscular activity profile, with peaks around one hour before and after sunrise (0600 h – 0800 h) and sunset (1700 h – 2100 h). Outside these hours (i.e. 2200 h – 0500 h), we observed only a small number of birds present on the open lawn (Fig. 3), indicating that, although not common, weka can also be nocturnal in their habits. In combination with our behavioural observations, we found that when weka are active at night, they are predominantly foraging and moving about the lawn environment. Reasons for the substantial decline of weka numbers on the lawn during the early morning hours might be a result of the restricted sampling that occurred during summer (Fig. 2) or might suggest an active shift in habitat usage that occurs over the night.

We did not record observations between 0900 h – 1600 h, but weka are also known to forage during daylight, usually being close to cover if sudden retreat is required, as well as under vegetation (Beauchamp *et al.* 2009; RP *pers. obs.*). During night-time behavioural observations, we noticed that interactions between weka were minimal and birds tended to be well spaced over the lawn (approximately ≥ 15 m away from one another). Weka are highly territorial, especially when population density is high (Beauchamp 1987a, 1987b). It may be that weka during the night restrict themselves to foraging and choose not to engage in territorial disputes, or possibly attempt to avoid them. The predominance of scanning behaviour (as opposed to continuous walking) that we observed may additionally help to minimise interaction between weka, though a more thorough sampling regime, where estimates of population size and territorial overlap can be incorporated together,

would be needed to give weight to this idea.

In this localised study, we found evidence that weka can be nocturnal in their habits and that use of open environments can be influenced by moonlight, temperature, season and time of night. Having greater insight into facets of their behaviour and how behaviour may be influenced by external factors could be helpful to manage this species effectively. There is a need for more research into the basic ecology of weka because it remains relatively understudied and some subspecies are threatened (Beauchamp *et al.* 1999; Robertson *et al.* 2017). Foraging in an open environment may increase the conspicuousness of weka to nocturnal predators, but the risk may be potentially offset if increased illumination during moonlit nights enables greater awareness of predators. Further research on the nocturnal activity of weka could examine how habitat use changes with moonlight intensity, and how moonlight may affect the probability of predation by introduced predators.

ACKNOWLEDGEMENTS

We thank Corey Mosen for the use of the night-vision monocular. We would also like to thank Stefanie Neupert for statistical assistance. Our additional thanks go to Tony Beauchamp and James Mortimer for their constructive feedback and helpful suggestions that have considerably improved the presentation of the paper.

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