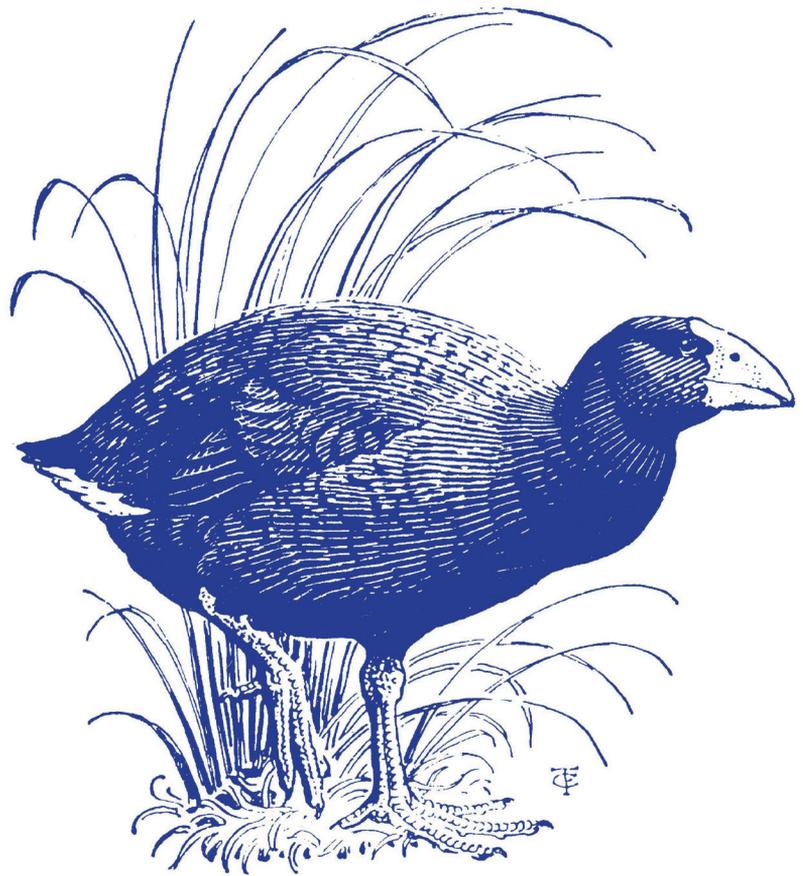


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Nocturnal activity of the western weka (*Gallirallus australis australis*) in an open environment

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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.

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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

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2003). For example, little owls (*Athene noctua*) tend 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).

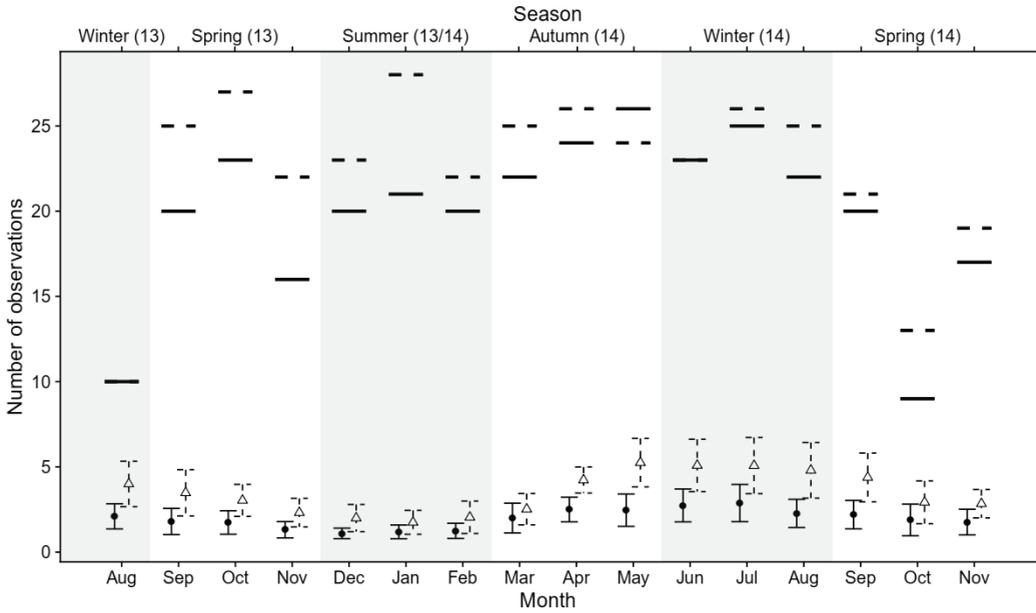


Figure 1. The sampling effort over each month for each season (year following in parentheses) throughout the study (August 2013 – November 2014). Points indicate the mean number of nightly observations for each month and errors bars indicate the standard deviation of the mean. Circles represent the dusk 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).

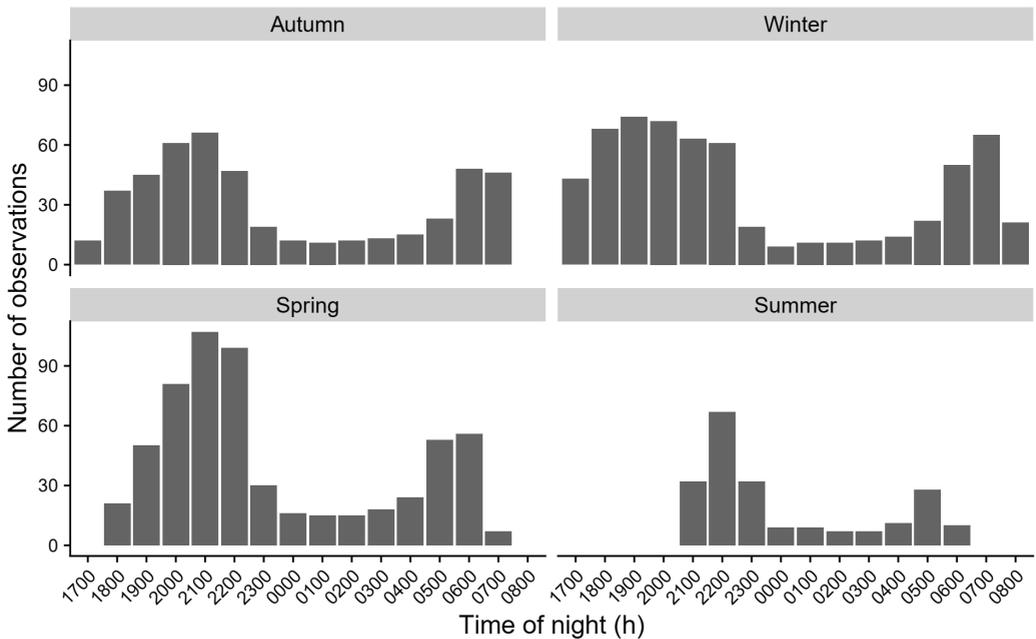


Figure 2. The sampling effort for observing weka at each time point (from 1700 h to 0800 h) for each season throughout the study (August 2013 – November 2014). Bars indicate the total number of nightly observations.

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 ΔBIC of ≤ 2 was considered as the criterion for retaining predictors. Models with ΔBIC of ≤ 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], $t\text{-ratio} = 5.912$, $P\text{-value} < .0001$; 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], $t\text{-ratio} = 0.31$, $P\text{-value} = 0.9498$).

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], $t\text{-ratio} = 2.78$, $P\text{-value} = 0.028$; winter vs summer, Est. 0.42 ± 0.13 se, [0.09, 0.76 95% CI], $t\text{-ratio} = 3.25$, $P\text{-value} = 0.007$). 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], $t\text{-ratio} = 2.00$, $P\text{-value} = 0.190$). 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], $t\text{-ratio} = 0.88$, $P\text{-value} = 0.814$), 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], $t\text{-ratio} = -3.307$, $P\text{-value} = 0.006$; summer vs spring, Est. -0.71 ± 0.24 se, [-1.34, -0.09 95%CI], $t\text{-ratio} = -2.94$, $P\text{-value} = 0.018$). 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

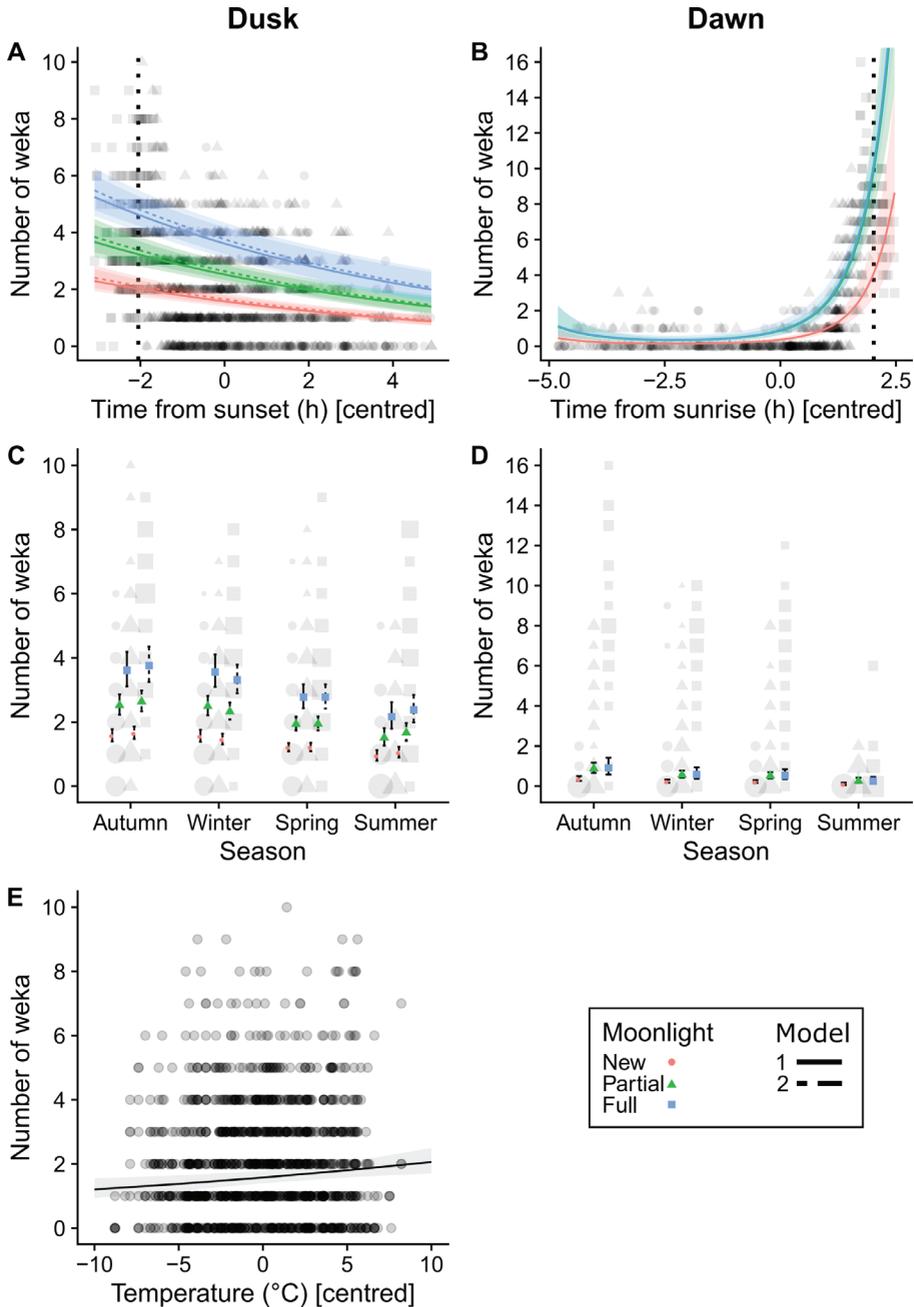


Figure 3. The relationship between the predicted number of weka \pm 95% CI present at the study site during the dusk (1700 h – 0000 h; left side) and dawn (0100 h – 0800 h; right side) under differing weather and moonlight conditions. A) and B) time from sunset/sunrise (h) [centred] for each category 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.

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LITERATURE CITED

- Akaike, H. 1998. Information theory and an extension of the maximum likelihood principle. *In: Selected papers of Hirotugu Akaike*: 199–213. Springer.
- Bang, B. 1968. Olfaction in Rallidae (Gruiformes), a morphological study of thirteen species. *Journal of Zoology* 156: 97–107.
- Bartón, K. 2019. *MuMIn: multi-model inference, R package*.
- Bates, D.; Mächler, M.; Bolker, B.; Walker, S. 2014. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48.
- Beauchamp, A.; Hanbury, J.; Hanbury, R. 2009. Changes in the population size of North Island weka (*Gallirallus australis greyi*) during establishment on Pakatoa Island, Hauraki Gulf, New Zealand. *Notornis* 56: 124–133.
- Beauchamp, A.J. 1987a. A population study of the weka *Gallirallus australis* on Kapiti Island. Unpubl. PhD Thesis, Victoria University, Wellington, New Zealand.
- Beauchamp, A.J. 1987b. The social structure of the weka (*Gallirallus australis*) at Double Cove, Marlborough Sounds. *Notornis* 34: 317–325.

- Beauchamp, A.J. 1997. The decline of the North Island weka (*Gallirallus australis greyi*) in the East Cape and Opotiki Regions, North Island, New Zealand. *Notornis* 44: 27–36.
- Beauchamp, A.J.; Butler, D.; King, D.R. 1999. Weka (*Gallirallus Australis*) Recovery Plan, 1999–2009. Threatened Species Recovery Plan 29. Biodiversity Recovery Unit, Department of Conservation.
- Beauchamp, A.J.; Van Berkum, B.; Closs, M.J. 1998. The decline of North Island Weka (*Gallirallus australis greyi*) at Parekura Bay, Bay of Islands. *Notornis* 45: 31–43.
- Bramley, G. 1994. The autecology and conservation of the North Island Weka (*Gallirallus australis greyi*). Unpubl. MSc Thesis, Massey University, Palmerston North, New Zealand.
- Bramley, G. 2001. Dispersal by juvenile North Island weka (*Gallirallus australis greyi*). *Notornis* 48: 43–46.
- Bramley, G.; Veltman, C. 2000a. Directions for future management of North Island Weka *Gallirallus australis greyi* to improve survival and productivity in situ. *Bird Conservation International* 10: 241–253.
- Bramley, G.; Veltman, C. 2000b. Call survey method for monitoring endangered North Island weka (*Gallirallus australis greyi*). *Notornis* 47: 154–159.
- Bramley, G.N.; Veltman, C.J. 1998. Failure of translocated, captive-bred North Island weka *Gallirallus australis greyi* to establish a new population. *Bird Conservation International* 8: 195–204.
- Brooks, M.E.; Kristensen, K.; van Benthem, K.J.; Magnusson, A.; Berg, C.W.; Nielsen, A.; Skaug, H.J.; Machler, M.; Bolker, B.M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9: 378–400.
- Brown, J.S. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. *Evolutionary Ecology Research* 1: 49–71.
- Carpenter, J.K.; Kelly, D.; Moltchanova, E.; O'Donnell, C.F. 2018. Introduction of mammalian seed predators and the loss of an endemic flightless bird impair seed dispersal of the New Zealand tree *Elaeocarpus dentatus*. *Ecology and Evolution* 8: 5992–6004.
- Carpenter, J.K.; O'Donnell, C.F.; Moltchanova, E.; Kelly, D. 2019. Long seed dispersal distances by an inquisitive flightless rail (*Gallirallus australis*) are reduced by interaction with humans. *Royal Society Open Science* 6: 190397.
- Carroll, A. 1963a. Breeding cycle of the North Island weka. *Notornis* 10: 300–302.
- Carroll, A. 1963b. Food habits of the North Island weka. *Notornis* 10: 289–300.
- Colbourne, R.; Baird, K.; Jolly, J. 1990. Relationship between invertebrates eaten by little spotted kiwi, *Apteryx owenii*, and their availability on Kapiti Island, New Zealand. *New Zealand Journal of Zoology* 17: 533–542.
- Coleman, J.D.; Warburton, B.; Green, W. 1983. Some population statistics and movements of the western weka. *Notornis* 30: 93–107.
- Cunningham, H.F. 2006. The comparative ecology of Stewart Island weka (*Gallirallus australis scotti*) on islands with and without seabirds. Unpubl. MSc Thesis, University of Otago, Dunedin, New Zealand.
- Daly, M.; Behrends, P.R.; Wilson, M.I.; Jacobs, L.F. 1992. Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. *Animal Behaviour* 44: 1–9.
- Dänhardt, J.; Lindström, Å. 2001. Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. *Animal Behaviour* 62: 235–243.
- Freeman, S. 2010. Western weka road-kill at Cape Foulwind, Buller, New Zealand. *New Zealand Journal of Zoology* 37: 131–146.
- Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine* 27: 2865–2873.
- Grueber, C.; Nakagawa, S.; Laws, R.; Jamieson, I. 2011. Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology* 24: 699–711.
- Harper, G. 2006. Weka (*Gallirallus australis*) depredation of sooty shearwater/titi (*Puffinus griseus*) chicks. *Notornis* 53: 318–320.
- Hartig, F. 2020. DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models, R package.
- Hartley, L.; Waas, J.; O'Connor, C.; Matthews, L. 2000. Colour preferences and coloured bait consumption by weka *Gallirallus australis*, an endemic New Zealand rail. *Biological Conservation* 93: 255–263.
- Heather, B.; Robertson, H. 2015. *The field guide to the birds of New Zealand*. Auckland, New Zealand, Penguin.
- Holdaway, R.N.; Worthy, T.H.; Tennyson, A.J. 2001. A working list of breeding bird species of the New Zealand region at first human contact. *New Zealand Journal of Zoology* 28: 119–187.
- Imber, M.; West, J.A.; Cooper, W.J. 2003. Cook's petrel (*Pterodroma cookii*): historic distribution, breeding biology and effects of predators. *Notornis* 50: 221–230.
- King, C.M. 2017. Contemporary observations of predation on the buff weka (*Gallirallus australis hectori*) by ferrets in the South Island during the nineteenth century. *Notornis* 64: 52–55.
- Kronfeld-Schor, N.; Dominoni, D.; de la Iglesia,

- H.; Levy, O.; Herzog, E.D.; Dayan, T.; Helfrich-Forster, C. 2013. Chronobiology by moonlight. *Proceedings of the Royal Society B: Biological Sciences* 280: 20123088.
- Kross, S.M.; Tylianakis, J.M.; Nelson, X.J. 2013. Diet composition and prey choice of New Zealand falcons nesting in anthropogenic and natural habitats. *New Zealand Journal of Ecology* 37: 51–59.
- Lengagne, T.; Aubin, T.; Lauga, J.; Jouventin, P. 1999. How do king penguins (*Aptenodytes patagonicus*) apply the mathematical theory of information to communicate in windy conditions? *Proceedings of the Royal Society of London. Series B: Biological Sciences* 266: 1623–1628.
- Lengagne, T.; Slater, P.J. 2002. The effects of rain on acoustic communication: tawny owls have good reason for calling less in wet weather. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 269: 2121–2125.
- Lenth, R.; Singmann, H.; Love, J.; Buerkner, P.; Herve, M. 2018. *Emmeans: Estimated marginal means, aka least-squares means, R package*.
- Lettink, M.; Hopkins, G.; Mayhew, K. 2010. Conservation status, threats and management options for the Open Bay Island skink (*Oligosoma taumakae*). *New Zealand Journal of Zoology* 37: 225–234.
- Lüdtke, D. 2018. *ggeffects: Create tidy data frames of marginal effects for 'ggplot' from model outputs, R package*.
- Marchant, S.; Higgins, P. 1993. *Handbook of Australian, New Zealand and Antarctic Birds, Volume 2 Raptors to Lapwings*. Melbourne, Oxford University Press.
- Mellanby, K. 1939. Low temperature and insect activity. *Proceedings of the Royal Society of London. Series B-Biological Sciences* 127: 473–487.
- Miskelly, T.; Beauchamp, T. 2004. Weka, a conservation dilemma. In: *Restoring Kapiti: Nature's second chance*: 81–88. Christchurch, New Zealand: University of Otago Press.
- Mougeot, F.; Bretagnolle, V. 2000. Predation risk and moonlight avoidance in nocturnal seabirds. *Journal of Avian Biology* 31: 376–386.
- Prugh, L.R.; Golden, C.D. 2014. Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *Journal of Animal Ecology* 83: 504–514.
- R Core Team, R.F. for S.C., Vienna, Austria. 2018. R: A language and environment for statistical computing.
- Ripley, S.D.; Lansdowne, J.F.; Olson, S.L. 1977. *Rails of the world: a monograph of the family Rallidae*. Boston, Massachusetts, David R. Godine Publisher.
- Robertson, C.; Hyvönen, P.; Fraser, M.; Pickard, C. 2007. *Atlas of bird distribution in New Zealand 1999–2004*. Wellington, New Zealand: Ornithological Society of New Zealand.
- Robertson, H.A.; Baird, K.; Dowding, J.E.; Elliott, G.P.; Hitchmough, R.A.; Miskelly, C.M.; McArthur, N.; O'Connell, C.F.J.; Sagar, P.M.; Scofield, P.; Taylor, G.A. 2017. *Conservation status of New Zealand birds, 2016. New Zealand threat classification series 19*. New Zealand Department of Conservation.
- Sergio, F. 2003. From individual behaviour to population pattern: weather-dependent foraging and breeding performance in black kites. *Animal Behaviour* 66: 1109–1117.
- Sunde, P.; Thorup, K.; Jacobsen, L.B.; Rahbek, C. 2014. Weather conditions drive dynamic habitat selection in a generalist predator. *PloS One* 9: e88221.
- Taylor, B.; van Perlo, B. 1998. *A guide to rails, crakes, gallinules and coots of the world*. Sussex, Pica Press.
- Tinnemans, J.S.; Elliott, G.P.; Rawlence, T.E.; McDonald, A.; Bell, M.A.N.; Bell, C.W.; Moran, K.J. 2019. Costs and benefits of aerial 1080 operations to Western weka (*Gallirallus australis australis*). *New Zealand Journal of Ecology* 43(1): 3353.
- Watts, J.O.; Moore, A.; Palmer, D.; Molteno, T.C.; Recio, M.R.; Seddon, P.J. 2017. Trial reintroduction of buff weka to an unfenced mainland site in central South Island, New Zealand. *Austral Ecology* 42: 198–209.

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Clutch sizes and hatching success of Canada geese nesting in Canterbury, New Zealand

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Dedicated to Earnest Selwyn Bucknell (Buck) 1926–2001, outdoorsman, colleague, tutor, and friend.

Abstract: Nesting outcomes of Canada geese (*Branta canadensis maxima*) in Canterbury, New Zealand were recorded from a sedentary population nesting at coastal Lake Forsyth (1967–70) and from a seasonally migratory population nesting in headwater valleys of the Waimakariri River (1966–80). Mean clutch size in 462 Lake Forsyth nests was 5.3 ($sd = 1.3$) eggs, with clutches of 4, 5, and 6 eggs comprising 17%, 30% and 30% respectively of the total. Goslings hatched from 67.4% of 1,602 eggs in 298 monitored nests, and the entire clutch hatched successfully in 42.6% of the monitored nests. Mean productivity at hatching was 3.6 ($sd = 2.3$) goslings per nest. Mean clutch size in 1,211 Waimakariri River headwaters nests was 4.5 ($sd = 1.3$), with clutches of 4, 5, and 6 eggs comprising 25%, 32%, and 20% respectively of the total. Goslings hatched from 63.3% of 3,952 eggs in 871 monitored nests, and the entire clutch hatched successfully in 30.5% of the monitored nests. Mean productivity at hatching was 2.9 ($sd = 1.9$) goslings per nest. Relative to Canada geese in their native North American range, geese nesting at Lake Forsyth laid clutches of similar size, had similar hatching success but higher nest success whereas geese nesting in the Waimakariri River headwaters laid, on average, conspicuously smaller clutches, had similar hatching success, but higher nest success.

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Keywords: Canada goose, *Branta canadensis*, nesting, clutch size, hatching success, New Zealand

INTRODUCTION

Following an importation of 50 birds in 1905, and a plethora of liberations of their captive-raised progeny, wild populations of Canada goose (*Branta canadensis maxima*) soon established in scattered headwaters of New Zealand's eastern South Island rivers, from North Canterbury to central Otago (Imber & Williams 2015). As their numbers

increased, so did the antipathy of pastoral farmers on whose lands the birds grazed, the geese being viewed as grazing competitors with their farm stock, polluters of pastures, and damagers of newly-sown grass and of autumn-saved pastures being withheld to support stock through winter. Introduced to provide sport for hunters, the goose's troublesome feeding choices saw it declared unprotected in 1931, merely 25 years after its introduction. While not an auspicious start to life in a new land, it was, nevertheless, a portent of the travails to follow, and

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which persist to this day (McDowall 1994; Spurr & Coleman 2005; Williams 2011).

The persistent challenge for historic wildlife management agencies (Acclimatisation Societies, Wildlife Service of Department of Internal Affairs) was to limit Canada goose populations to numbers pastoral farmers could reluctantly tolerate but which also ensured adequate sporting opportunity for gamebird hunters. Population “control” was attempted, mainly, by pricking or destroying eggs in nests of geese breeding in headwater valleys of some Canterbury rivers (e.g. Waimakariri, Poulter, Rakaia, Wilberforce, Harper, Avoca), by culling of moulting birds, and, between 1963–72 by late-summer hunting at Lake Ellesmere and in its environs, including at Lake Forsyth (Imber & Williams 1968).

Canterbury’s Canada goose population was, by the 1960s, perceived to be seasonally migratory. It was known that most nesting occurred in headwater tributary valleys of major Canterbury rivers, especially Waimakariri River, and once nesting and brood rearing had been completed, the geese dispersed to autumn and winter pastoral and lake-side habitats at lower elevations, or to coastal wetlands (Imber 1971a, 1985). The Canterbury-wide population at this time was estimated to be c. 20,000 (Imber 1971a) and the majority were thought to share an annual residency at Lake Ellesmere (Te Waihora) on Canterbury’s east coast. It was at this lake that many failed breeders, non-breeders and pre-breeding geese of this population moulted each year, and to which many successful breeders brought their fledglings in late February-early March annually. A small (400–500) and presumed sedentary population of Canada geese resided at adjacent Lake Forsyth.

To assess the reproductive performance of Canada geese coincidental with the attempted “control” measures, nesting studies were initiated by the former New Zealand Wildlife Service (NZWS). Records of these studies, at Lake Forsyth 1967–70 and in Waimakariri River headwaters (Esk River and Cox River catchments) 1966–80, were lodged in (now archived) files of the NZWS (IAD 25/4/10) where they remained unevaluated. Retrospectively, and to the extent that the archived records allow, we summarise these nesting records, the only nesting study of Canada geese in New Zealand to date.

STUDY AREAS

Lake Forsyth (Te Roto o Wairewa) is a small (620 ha), shallow and hypertrophic barrier-bar lake impounded by coastal gravels at the south-western flank of Banks Peninsula (43.805°S, 172.741°E) and lies 4 km east of Lake Ellesmere. From within a

catchment of 108 km², it is fed by the small Okana and Okuti Rivers (which coalesce to form the short Takiritawai River) and by drainage from its flanking hills. Its catchment is entirely of steep pastoral slopes. Resident geese nested on the lower 100 m of the steep pastoral slopes on the lakes’ eastern flank and grazed pastoral flats at the head of the lake (Fig. 1).



Figure 1. Lake Forsyth looking south towards its terminal barrier and coast. Arrows delimit Canada goose shoreline nesting area. A sliver of Lake Ellesmere, 4 km distant, is visible in upper right corner of this image. Photo: Kelvin Nicholle.

The Waimakariri River headwaters study area (hereafter referred to as “headwaters”) included three sites within the tributary catchments of Esk River and Cox River. Within the Esk River catchment, the broad dry alluvial terraces, and boggy flats, of the tributary Pūkio Stream (pre-2016 name Nigger Stream) adjacent to Little Flora Knoll (42.962°S, 172.067°E) and about Flora Stream (42.950°S, 172.054°E) were where nest searches were concentrated initially. This comprised a terrace of 2.52 km² and boggy flats 1.85 km² in extent, both at an altitude of 750 m. Surveys extended over 5–10 km of main stem Esk River’s extensive braided flats (Fig. 2) and those of tributary streams (650–700 m altitude), mostly upriver from the river’s confluence with Ant Stream (42.955°S, 172.116°E). The section of Cox River valley surveyed was at 650 m altitude, and comprised 2.27 km² of braided river flats extending upriver of Ball Creek Hut (42.893°S, 171.968°E) to Montgomery Stream (7 km) and approximately 2 km downriver of the hut in a valley that, but for an ancient landslide, was an extension of the Pūkio Stream valley.



Figure 2. Esk River valley, looking upriver from near the river's confluence with Pūkio Stream. Photo: J.S. Adams

The two nesting areas contrasted climatically and topographically. At Lake Forsyth September – November temperatures averaged 9–12°C, and rain about 11 mm monthly. Orientated SW–NE, the lake's narrow valley funnels winds averaging 16 km/h. The headwaters area comprised broad (1.5–2.0 km) sub-alpine valleys flanked by ridges rising 500–600 m above the valley floors. Mean daily September – November temperatures averaged 5.5–10°C with 10–14 mm of precipitation monthly, including snowfalls which, in most years, extend to mid-October.

METHODS

Prior banding

The study was supported by annual banding of geese moulting at Lakes Ellesmere and Forsyth. Banding at Lake Ellesmere commenced in 1957 (Imber & Williams 1968) but only after 1966 were yearlings discriminated (by bursa probing: Elder 1946) and colour banded to denote year class. Additionally, and commencing in 1969, tags were inserted in the webs of newly-hatched goslings at the headwaters nesting sites allowing those caught the following year, or later, moulting at Lake Ellesmere to have coloured leg bands applied to denote year class. Banding commenced at Lake Forsyth in 1966 where, annually, most of each year's cohort of goslings were captured (and colour-banded to denote year class) together with their moulting parents and some pre-breeders. The colour bandings at both moulting sites, and web-tagging of goslings, were to allow ages of nesting birds to be identified in the field.

Nesting study

Visits to the study areas commenced once nesting was well underway (Lake Forsyth, mid-October)

or when spring thaw of winter snow permitted vehicular access to the remote headwaters sites, which was seldom before the third week of October. Observers were continuously present in the headwaters sites until approximately 20 November each year, whereas at Lake Forsyth the nesting area was visited for 3-day periods usually four times between 12 October and 20 November.

Initial nest searches comprised methodical pattern searches of the landscape and all nests detected were indicated with markers of some kind e.g. colour-tipped bamboo stakes, marking tape on nearby conspicuous vegetation etc. Once located, the nest was revisited on subsequent days to confirm laying had ceased (and thus clutch completed), thereafter infrequently during incubation sufficient to assess egg fertility (by field candling; Weller 1956) and deduce likely hatching date, and then, near and during hatching, daily to confirm hatching success. Where goslings hatched and departed a marked nest without being observed, hatching outcome was assessed from number of egg-shell membranes and unhatched eggs present in or alongside the nest bowl.

Details of colour bands observed on nesting adults were recorded alongside their breeding records, and banded non-breeding geese observed were recorded also.

For 1977–80 inclusive, the approximate location of all surveyed nests within Pūkio Stream and Cox River were plotted on large-scale field maps (1:31680 = 2 inches-to-the-mile). These maps were too crude to allow inter-nest distances to be calculated but the margins of the surveyed areas were sufficiently well defined on the maps to allow a coarse estimation of nesting density. For Pūkio Stream, this was done by constructing a minimum convex polygon to encompass all nests and calculating its area using Google Earth measuring tool; for Cox River, the area of riverbed surveyed was consistently 2.27 km². No nest location maps were compiled for the Esk River study site, nor for Lake Forsyth. However, at Lake Forsyth, the 100 m contour along 2.5 km of the its eastern shore delimited almost all nest placements (see Fig. 1) and this area was also calculated using the Google Earth measuring tool.

The data set

Nest records from Lake Forsyth were accumulated over four summers 1967–70 inclusive. The annual nest summaries and field notebooks provided dates of nest visits and details of nest content at each viewing. Nest status (e.g. laying, incubating, abandoned, hatched) was reported and an assessment of egg fertility was recorded, usually when incubation had extended for at least one week. The number of nests monitored annually

(105–123) was considered to comprise most nesting attempts at Lake Forsyth.

Archived nest records from the headwaters area were from 1966 to 1980 but varied between the three valleys and in their completeness between years. For Pūkio Stream, complete nest records were for 1966–68, 1971–73, 1975, 1977–80 with summarised data reported for 1974 and 1976. For Esk River, complete nest records were from 1977–80 with summarised data for 1971–73. For Cox River, complete nest records were from 1976–80 with summarised data for 1971–74. Complete nest records provided details of dates of nest visits, details of nest content at each viewing, and nest status (laying, incubating, abandoned, hatched). An assessment of egg fertility was recorded soon after incubation had commenced (consistently only for Pūkio Stream nests). Summarised data reported numbers of nests encountered, mean clutch size, and sometimes mean number hatched per nest (there are no hatching records for Esk River and Cox River sites other than 1977–80 inclusive). Nest records from all three valleys have been amalgamated for this analysis.

Definition of terms

Key terms used in this account are: clutch size – the maximum number of eggs observed in a nest; number hatched – number of goslings that emerged completely from eggs in the nest; hatching success – percentage of eggs from which a gosling emerged (equivalent to egg success in some literature); nest success – percentage of total nests in which one or more eggs hatched.

RESULTS

Nesting environment and nest density

At Lake Forsyth most nests were constructed on sloping ground and in association with low vegetation e.g. rushes (*Juncus* spp.) or small prostrate herbs/shrubs in an otherwise pastoral environment. Narrow ledges on the slopes and bared areas of former small landslips were common nest sites. Most nest sites afforded the incubating and guarding adults a wide uninterrupted view. No nest density assessment was reported but nests were scattered along approximately 2.5 km of the lake's south-eastern hillside (see Fig. 1) and at low elevation (< 100m above lake level). In effect, all nests were established within a long, narrow hillside area of approximately 0.4–0.6 km², equivalent to a density of approximately 200 nests/km². It was a quasi-colonial distribution despite some altitudinal separation between nesting pairs and the hillside and shoreline indentations ensuring many nests were established out of direct sight of others.

Nest sites of headwaters geese were all on the valley floors and affording a wide vista. The Pūkio Stream nesting environment, especially the alluvial terrace, had a patchy covering of *Halocarpus bidwillii* shrubs amongst extensive grassland comprised of *Agrostis capillaris*, *Festuca novae-zelandiae*, *Anthoxanthum odoratum* and *Holcus lanatus*. *Chionocloa rubra* was prominent on the boggy flats (Hustedt 2002). Most nests were associated with low or prostrate herbs in dry sites (Fig. 3) and with *Carex* spp. and *Poa cita* in wet areas. Nests established on the Esk River and Cox River flats were often on bare shingle but associated with woody debris, small hummocks of river sediment, or sparse plant clumps. Although nests were widely distributed and proximity of neighbours highly variable (as interpreted from the nest distribution field maps), the overall nest density in years 1977–80, was 20–30 nests/km². Within Pūkio Stream valley, nest density on the drier alluvial terrace was more similar across these four years (range 23.1–27.5 nests/km²) than on the boggy flats (range 18.3–35.1 nests/km²). On the Cox River flats, the range of nest densities was 18.5–25.6 nests/km². It was not possible to deduce nest density on the Esk River flats from the filed records nor the precise limits of the surveyed area in any year.



Figure 3. Typical headwaters nesting environment on the dry valley floor of Pūkio Stream. Photo: J. L. Kendrick, NZ Wildlife Service.

Nesting chronology

Initial visits to both study sites post-dated the commencement of nesting in every year.

At Lake Forsyth, initial visits in each year 1967–70 were between 12–15 October. At this time 79%, 48%, 84%, and 84% of the nests in 1967, 1968, 1969, and 1970 respectively from which clutch size information was obtained were active, most of which at that time (83%, 62%, 70% and 74% respectively) were being incubated. Only in 1968 were new nests (6) established later than 25 October.

The timing of snow thaw and ability to traverse challenging vehicle tracks meant access to headwater areas was rarely possible prior to 23 October, by which date the first eggs were beginning to hatch (see hatching results below). Of 705 nests monitored in Pūkio Stream valley across all years of study, just 39 (5.5%) were established later than 27 October.

Clutch size

Lake Forsyth

Over four years 1967–70, clutch sizes in 462 nests averaged 5.3 ($sd = 1.3$) eggs and ranged from 1 to 10 eggs (Table 1). Clutches of 5 and 6 eggs were the most common, each 30% of total clutches. Clutches of 1 and 2 eggs (4 and 6 nests respectively) were all recorded as being incubated but, as with all nests, prior egg loss cannot be excluded. For larger clutches of 8–10 eggs (14 nests) there was no record to indicate any comprised eggs from multiple females.

Variability in mean annual clutch size ranged from 5.1 ($sd = 1.4$) in 1969 to 5.5 ($sd = 1.0$) in 1970. The mean clutch size in 1969 was significantly lower than in the previous or subsequent year (1968 v. 1969, $z = 2.261$, $P = 0.023$; 1969 v. 1970, $z = 2.964$, $P = 0.003$) but not 1967 ($z = 0.643$, $P = 0.520$), and was a consequence of the higher number of 4-egg clutches laid in 1969 (Table 1). Clutches of ≤ 4 eggs comprised 27.6%, 21.1%, 30.8%, and 14.9% of total known clutches across the four years, and 23.6% overall.

For female geese of known age, mean clutch sizes were 4.7 ($sd = 1.5$, $n = 3$) for 2-year-olds, 4.8 ($sd = 0.9$, $n = 27$) for 3-year-olds, and 5.3 ($sd = 1.0$, $n = 15$) for 4-year olds.

Headwaters

Between 1966–80, clutches in 1211 headwaters nests averaged 4.5 ($sd = 1.3$) eggs and ranged from 1 to 8 eggs (Table 2). Clutches of five eggs comprised almost one-third, and those of four eggs almost one-quarter, of total clutches. Clutches of 1 and 2 eggs (93 (7.7%) nests in total) were all recorded as being incubated. There were no records reporting a clutch had been contributed to by multiple females.

At Pūkio Stream, the only headwaters valley surveyed in all years, there was non-significant annual variability in mean clutch size of nests (Table 3) (e.g. 1967 v. 1971, $z = 1.816$, $P = 0.069$, NS)

Mean sizes of clutches of females of known age and found 1977–80, were 3.0 ($sd = 1.6$, $n = 5$) for 3-year-olds, 4.1 ($sd = 0.8$, $n = 8$) for 4-year-olds, and 5.0 ($sd = 0.9$, $n = 19$) for >4-year olds. Three 2-year-old females were recorded alongside sparse nest bowls which never contained eggs.

Table 1. Annual and overall percentage frequency distribution of clutch sizes, and annual and overall mean (\bar{x} , sd) clutch sizes of Canada geese nesting at Lake Forsyth 1967–70.

Clutch size	Year				All years
	1967	1968	1969	1970	
1	2.9	0	0.8	0	0.9
2	2.9	0.8	1.7	0	1.3
3	4.8	7.3	5.8	0.1	4.8
4	17.1	13.0	22.5	14.0	16.7
5	24.8	28.5	32.5	34.2	30.1
6	31.4	31.7	24.2	35.1	30.5
7	14.3	13.0	10.0	14.0	12.8
8	0.9	4.1	2.5	1.8	2.4
9	0	0.8	0	0	0.2
10	0.9	0.8	0	0	0.4
\bar{x}	5.2	5.5	5.1	5.5	5.3
sd	1.5	1.4	1.3	1.0	1.3
n	105	123	120	114	462

Table 2. Percentage size frequency distribution of 1,211 clutches of Canada geese nesting at three Waimakariri River headwaters valleys 1966–80 (combined data from Pūkio Stream 1966–68, 71–73, 75, 77–80; Esk River 1977–80; Cox River 1976–80).

Clutch size	1	2	3	4	5	6	7	8
Frequency (%)	0.6	7.1	12.5	24.8	32.1	20.2	2.5	0.2

Table 3. Mean (\bar{x} , sd) annual clutch sizes of Canada geese nesting at Pūkio Stream 1966–80. (nr = not recorded).

year	1966	1967	1968	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
\bar{x}	4.5	4.2	4.6	4.7	4.3	4.5	4.3	4.4	4.7	4.4	4.4	4.5	4.4
sd	1.0	1.3	1.0	1.2	1.3	1.3	nr	1.2	nr	1.0	1.1	1.3	1.1
n	42	45	32	50	47	59	47	61	57	58	66	54	90

Comparison between areas

Mean clutch size at Lake Forsyth was significantly larger than at any one of the three headwaters sites, and all headwaters sites combined ($z = 11.51$, $P < 0.001$). When this comparison is restricted to the two years when data were collected from both areas coincidentally (1967, 1968), mean clutch size at Lake Forsyth was 5.4 eggs ($sd = 1.4$, $n = 228$) and at Pükio Stream 4.3 eggs ($sd = 1.2$, $n = 77$), a highly significant difference ($z = 5.91$, $P < 0.001$).

A principal difference between the two study areas was in the proportions of small clutches, i.e. those containing ≤ 4 eggs (Lake Forsyth 23.7%, headwaters 45.0%) and ≤ 3 eggs (Lake Forsyth 7.0%, headwaters 20.2%; Tables 1,2).

Hatching*Lake Forsyth*

Visitation frequency and duration did not allow a hatching chronology to be compiled. However, no hatchings were recorded prior to 25 October in any year but by 10 November annually, eggs had hatched in 47–74% of monitored nests.

Over the four years combined, hatching outcomes were recorded for 298 nests (Table 4); these nests contained 1,602 eggs, of which 1,079 (67.4%) hatched, an overall mean hatch per nesting attempt of 3.6 ($sd = 2.3$) eggs.

In 127 (42.6%) nests all eggs hatched and in 59 (19.8%) nests none hatched. Of the latter, 32 were recorded as being “abandoned”, including consequent to cattle trampling the nest (3), and “predation” (27). References to some nests being “abandoned/predated” indicates these were not necessarily exclusive categories.

In 112 (37.6%) nests, which in total contained 629 eggs, less than the full clutch hatched. In 48 nests just 1 egg failed to hatch of which 17 contained a near full term embryo, 16 a gosling that was unable to emerge completely from its shell, and 15 recorded

as “addled” or “infertile”. In 64 nests multiple eggs failed to hatch successfully (191 (52.5%) of 364 eggs); of 106 egg fates recorded, 18 goslings failed to emerge, 24 eggs contained a near full-term embryo, 25 were early embryo deaths, and 39 recorded as “infertile” or “addled”. Reported scavenging and predation by black-backed gulls (*Larus dominicanus*) of eggs remaining in recently hatched nests suggests the status of some unhatched eggs may not have been identified.

There was no consistent evaluation of egg fertility; many nest records were devoid of a fertility assessment, some reported evaluations of unhatched eggs only, while in others, assessments were at variable times during the laying-incubation periods. However, there were 138 nests whose total of 741 eggs were candled to determine evidence of embryo development during days 10–24 of the incubation period; 586 (79.1%) eggs were recorded as “fertile”.

Hatching rates (percentage of eggs hatching) were significantly lower in nests containing small clutches (2–3 eggs) than in all others (e.g. in 5-egg clutches, $\chi^2 = 14.18$, $P < 0.001$), and was a consequence of their higher nest failure (Table 4). In 13 (68%) of 19 2–3 egg clutches no eggs hatched compared to 14 (10%) of 140 6–7 egg clutches, a significant difference ($\chi^2 = 7.08$, $P = 0.008$). Hatching success in 5-egg clutches was significantly lower than in 6-egg ($\chi^2 = 25.33$, $P < 0.001$) and 7-egg ($\chi^2 = 21.09$, $P = 0.0001$) clutches, a statistical outcome arising from the higher whole clutch failure within this cohort (Table 4).

Hatching outcomes from nests of known age females were: 2-year-olds, $n = 3$, 1 partial hatch (3 of 5 eggs), 2 failed; 3-year-olds, $n = 13$, 2 complete hatch, 9 partial hatch (33 of 43 eggs), 2 failed; 4-year-olds, $n = 6$, 2 complete hatch, 4 partial hatch (16 of 20 eggs); older females, $n = 12$, 6 complete hatch, 4 partial hatch (17 of 23 eggs), 2 failed.

Table 4. Hatching outcomes relative to clutch size, and overall, in 298 Canada goose nests at Lake Forsyth, 1967–70.

Clutch size	All nests			All hatch		None hatch	
	No. nests	No. eggs	% eggs hatching	No. nests	% all nests	No. nests	% all nests
2	3	6	33.3	1	33.3	2	66.7
3	16	48	31.3	5	31.3	11	68.8
4	50	200	64.5	21	42.0	10	20.0
5	83	415	58.6	32	38.6	21	25.3
6	97	582	73.7	45	46.4	9	9.3
7	43	301	75.1	21	48.8	5	11.6
8–10	6	50	70.0	2	40.0	1	20.0
Totals	298	1,602	67.4	127	42.6	59	19.8

After hatching, almost all broods of young goslings and their attendant adults congregated on pastoral flats at the head of the lake feeding as a flock or as large creches.

Headwaters

The continuous presence of observers during the nesting period allowed a hatching distribution to be compiled (Fig. 4); in 68% of 725 successful (and assumed successful) nests eggs hatched in the first 12 days of November while, by 18 November, only in 16% of nests were eggs yet to hatch, thus indicating a high level of nesting synchrony. [An approximate nesting chronology can be deduced from this hatching distribution by taking into account an egg-laying frequency of 1 egg each 1.5 days and an average 28 days of incubation (Brakhage 1965); initial egg-laying in late September and peak egg-laying during 1–10 October is implied.]

Hatching outcomes were recorded for 871 nests (Table 5); these nests contained 3,952 eggs, of which 2,502 (63.3%) hatched, an overall mean hatch per nesting attempt of 2.9 (*sd* 1.9) eggs.

In 266 (30.5%) of nests all eggs hatched and in 141 (16.2%) nests none hatched. In the other 464 (53.3%) nests, which in total contained 2,199 eggs, less than the full clutch hatched. In 218 just 1 egg failed to hatch successfully and records of 154 of these report the unhatched egg contained a fully-formed gosling that had either failed to break the eggshell or could not escape from it (74), the egg was infertile or early embryo death had occurred (68), or the egg was broken or predated (12). In 246 nests multiple eggs failed to hatch successfully (668 (54.8%) of 1,220 eggs); of 301 egg fates recorded, 105 were “dead in shell” (gosling either failing to emerge successfully from egg or a full-term embryo not having pipped the egg), 28 were “early embryo deaths”, and 168 recorded as “infertile” or “addled”.

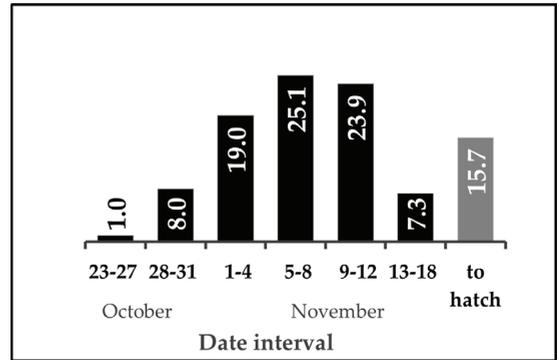


Figure 4. Percentage frequency distribution of hatching dates of 725 headwaters Canada goose nests, 1966–80.

Of the 141 (16.2%) nests that failed to hatch any eggs, 61 were abandoned (mostly during incubation) and 80 suffered apparent predation of some or all eggs both during egg laying and incubation (black-backed gulls were identified as an egg predator).

A fertility assessment of incubated eggs at Pūkio Stream 1971–73 recorded 511 of 571 (89.5%) eggs in 127 nests as “fertile”.

Hatching rate (the percentage of eggs hatching) was similar across all clutch sizes (Table 5), except for 6-egg clutches being significantly higher than for 2-egg ($\chi^2 = 10.04$, $P = 0.0015$), 3-egg ($\chi^2 = 12.29$, $P = 0.0004$) and 4-egg ($\chi^2 = 11.99$, $P = 0.0005$) clutches, and 5-egg clutches exceeding that of 2-egg clutches ($\chi^2 = 5.34$, $P = 0.027$).

Across nine of the years between 1968–80, annual hatching rate in Pūkio Stream nests averaged 69.7% (*sd* = 7.5%), varying between 62.2% and 78.5%.

Hatching outcomes from nests of known age females 1976–80 were: 3-year-olds, $n = 4$, 1 complete

Table 5. Hatching outcomes relative to clutch size, and overall, in 871 Canada goose nests at three Waimakariri River headwaters valleys combined, data from 1966–80.

Clutch size	All nests			All hatch		None hatch	
	No. nests	No. eggs	% eggs hatching	No. nests	% nests	No. nests	% nests
2	69	138	54.3	26	37.7	21	30.4
3	106	318	57.2	37	34.9	25	23.6
4	210	840	60.2	67	31.9	40	19.0
5	285	1,425	64.3	76	26.6	34	11.9
6	176	1,056	67.9	54	38.4	18	10.9
7–8	25	175	62.3	6	24.0	3	12.0
Totals	871	3,952	63.3	266	30.5	141	16.2

Table 6. Comparative hatching outcomes for Canada geese at Lake Forsyth and headwaters study areas. (Statistical comparisons: ¹ $z = 4.73$, $P < 0.001$; ² $\chi^2 = 14.51$, $P < 0.001$; ³ NS; ⁴ $\chi^2 = 8.14$, $P = 0.004$; ⁵ NS; ⁶ $\chi^2 = 5.08$, $P = 0.024$.)

Study area	No. of nests	$\bar{x} \pm sd$ hatchlings per nest ¹	% nests all eggs hatch ²	% nests no eggs hatch ³	Hatching rate (%)		
					in all nests ⁴	in clutches ≤ 4 eggs ⁵	in clutches 5–7 eggs ⁶
Lake Forsyth	298	3.6 \pm 2.3	42.6	19.8	67.4	57.5	69.2
Headwaters	871	2.9 \pm 1.9	30.5	16.2	63.3	58.9	65.6

hatch, 2 partial hatch (3 of 6 eggs), 1 failed; 4-year-olds, $n = 7$, 2 complete hatch, 4 partial hatch (11 of 18 eggs), 1 failed; older females, $n = 14$, 2 complete hatch, 6 partial hatch (19 of 31 eggs), 6 failed.

In the early aftermath of hatching, goslings and their parents remained in discrete family units, mostly alongside each valley's watercourses.

Comparison between areas

Hatching outcomes differed between the two study areas (Table 6). Only hatching rate of clutches ≤ 4 eggs and percentage of nests in which no eggs hatched were similar whereas the differences for all other comparisons were statistically significant (Table 6). Additionally, amongst successful nests (those in which at least 1 egg hatched), the proportion in which all eggs hatched at Lake Forsyth (53.1%) was significantly higher than in headwaters nests (36.4%; $\chi^2 = 20.82$, $P < 0.001$). The relative proportions of single to multi-egg failures in successful nests did not differ between the study areas ($\chi^2 = 0.62$, $P = 0.43$, NS).

DISCUSSION

Study context and intent

The field study reported here sought to record nesting outcomes of geese at a time when extensive "control measures" were being applied; egg pricking or whole nest destruction within some Canterbury headwater valleys (but not in Esk and Cox River valleys), widespread culls of moulting geese, hunting without kill limits during the annual gamebird hunting seasons (May–July), and, between 1963 and 1972, immediate post-moult hunting of the largest moult aggregation at Lake Ellesmere (also including Lake Forsyth). The study was intended to be complemented by an estimation of age-specific annual survival rates of geese from analyses of bands returned by hunters and from recaptures of already banded geese at moulting sites, thereby extending the analyses of Imber & Williams (1968).

The choice of two study areas, Lake Forsyth and Waimakariri River headwaters, was strictly pragmatic. Lake Forsyth was a readily accessible nesting and capture location whereas the

headwaters valleys, where most nesting occurred, were remote and challenging to access. There was no prior expectation that nesting outcomes might differ between study areas other than, perhaps, as a consequence of their differing age structures (Imber 1971a). The single perceived difference between geese nesting at the two locations was their annual dispersion: Lake Forsyth geese were year-round residents whereas, after nesting, the headwaters geese dispersed across inland and coastal Canterbury, but mainly to Lake Ellesmere.

The anticipated importance of the age composition of nesting females was responded to by banding goslings at hatching or before fledging. At Lake Forsyth, following four years of banding all goslings before fledging, females 4-years old or younger comprised 21% of those nesting in 1970 but age-related breeding performances of only 45 females had, by then, accrued. A more prolonged period of annual banding of goslings was, at that point, considered necessary so the nesting study was stopped with the intent of recommencing four years later. Annual banding of goslings continuing to 1982 but, for reasons unrecorded, the nesting study was never recommenced.

The headwaters nesting study proved even more daunting in this respect. Between 1969 and 1977, 2,196 goslings were tagged at hatching but, by 1980, just 270 (12.3%) had been recaptured at Lake Ellesmere. Between 1967 and 1973, 1,569 yearling females were captured and banded with an age-denoting colour band at Lake Ellesmere. Despite this effort, known-aged females comprised a mere 5.9–7.4% of those nesting in the study area annually in years 1977–80.

While NZWS staff persisted with the headwaters nesting study throughout the 1970s, farmer agitation for a reduction in goose numbers ensured the focus on Canada goose management gradually shifted to annual aerial surveys across areas of inland Canterbury, increased culls of geese moulting at inland lakes, and to an assessment of grazing impact on farming economics (references in Spurr & Coleman 2005). In effect, the extensive nesting study reported here ceased to be directly relevant to contemporary goose management and the intended survivorship analyses were never pursued.

Interpreting between-area differences

A conspicuous outcome of the study was the differing clutch sizes and hatching outcomes at the two areas. Geese nesting at Lake Forsyth laid larger clutches, hatched more of their eggs in more of their nests, and thus were significantly more productive. Was this a consequence of different age structures of nesting females, or might other factors have contributed?

Age composition of nesting females

North American nesting studies (e.g. Brakhage 1965; Cooper 1978), confirm that young Canada geese lay smaller clutches than those of older age. Age-related clutch size data from this study, while minimal, are in accordance. Thus, small clutches (of ≤ 4 eggs), which were twice as frequent in headwaters nests than at Lake Forsyth, could indicate the presence of, proportionately, many more young nesters there.

One pathway by which a difference in age structure of nesters could have arisen was by restriction of breeding opportunity. At Lake Forsyth, high nesting density could have excluded young breeders from nesting amongst older, more dominant, and experienced nesters. By this means the relative contribution of young geese, with their smaller clutches, to the annual mean clutch size would be restricted. Conversely, the expansive headwaters nesting grounds may have imposed little or no restriction on nesting opportunity for young geese and, thus, their smaller clutches would contribute proportionately more to the overall annual mean clutch size. The significantly different proportions of clutches of ≤ 4 eggs in the two populations (Forsyth 23.6% (1967–70) *c.f.* headwaters 45.0% (1966–80), and Pukio Stream alone 1966–68, 50.4%) are, nevertheless, stark, but for age composition to be a primary explanation for their difference implies other vital statistics (e.g. age-related survival, mean adult longevity) must have been profoundly different also. Regrettably, those survival characteristics were not appraised beyond 1967 (Imber & Williams 1968).

Body condition

Clutch size in waterfowl reflects nutrient reserves of the female at time of laying (Lack 1967), although other demands of the breeding process, especially incubation and brood rearing, influence energy allocated to clutch formation (Winkler & Walters 1983; Erikstad *et al.* 1993). Ryder's (1970) elaboration of Lack's original idea as an "energy reserve hypothesis" found favour as an explanation for clutch size variation and evolution in many arctic-nesting waterfowl that fly long distances from winter feeding to spring breeding grounds, nesting immediately upon arrival (see Alisauskas &

Ankney (1992) for review). By not relying on food on the nesting grounds to fuel egg production, their body reserves are mobilised instead. Could female Canada geese travelling to nest in the remote Waimakariri River headwaters valleys arrive there with, on average, lower energy reserves than those of resident geese preparing to nest at Lake Forsyth?

Lake Forsyth was a benign pastoral feeding, nesting, and brood-rearing environment. The pastoral flats at the head of the lake would have offered fresh and nutritious pre-breeding fodder. Not so the headwaters nesting areas wherein snow cover could linger into October and where first nests, established in the last third of September when snow remained lying in many areas, probably post-dated those at Lake Forsyth by two weeks. The immediate headwater nesting environs were most unlikely to have been significant pre-breeding assembly or feeding areas, and the geese would have needed to accrue or maintain body reserves on snow-free pastures either further down the Waimakariri River valley, or at their winter habitat of Lake Ellesmere, 80 km distant and at 700 m lower altitude.

There are no data from which to assess possible differences in body condition. However, one hatching outcome could imply the lesser condition of headwater nesting females – the significantly differing proportions of total nests in which all eggs hatched (Lake Forsyth 42.6% *c.f.* headwaters 30.5%) and, in successful nests, the significantly differing proportions hatching all eggs (Lake Forsyth 53.1% *c.f.* headwaters 36.4%). Among the many determinants of hatching success (which include female age and weather) is consistency of incubation. Body condition of incubating females demonstrably influences the frequency and duration of incubation recesses in Canada geese (Aldrich & Raveling 1983; Ankney *et al.* 1991). Cooper 1978 reported incubation constancy in Canada geese extending to 96% of each day, and incubating females spending as little as nine hours off the nest during the entire 26–28-day incubation period with less than one-third of that time devoted to feeding. In New Zealand conditions, however, incubation behaviour remains unreported.

Evolving population-specific response

The differences in clutch sizes and hatching outcomes between the two study areas might also reflect an evolving response arising from 40–50 years of breeding separation. Although a small introduction of geese directly to Lake Forsyth occurred in 1921, it is likely that the lake was colonised directly from nearby Lake Ellesmere at which initial headwaters releaseses aggregated during autumn and winter from the early 1910s (Imber & Williams 2015).

Migratory Canada geese in North America demonstrate nesting ground philopatry, especially by females, and this is thought to have contributed to extensive genetic and morphological structuring within the *Branta canadensis* complex (van Wagner & Baker 1986, 1990). In a sedentary British population, there was especially strong natal philopatry by young female geese (Lessells 1985). The extensive marking of goslings at both Lake Forsyth and headwaters nesting areas provided evidence of nesting ground philopatry. For example, just five (1 male, 4 females) of 2,196 goslings tagged at headwater sites 1969–77 were amongst moulting adults caught annually along with goslings at Lake Forsyth 1971–80, while between 1974–80 just three females of 2,861 goslings colour-banded at Lake Forsyth 1968–78 were sighted at headwater sites.

Any evolving response to nesting alongside a consistent and year-round food supply may lead to an increase in average clutch size mediated via higher food quality and less energy expended to obtain it.

Comparisons with Canada goose nesting elsewhere

North America

Nesting studies of various Canada goose subspecies in North America were a popular professional and student pursuit in the 1940–1960 period with results summarised in relevant North American journals e.g. *Journal of Wildlife Management*, and in U. S. State and Federal agency publications e.g. California Department of Fish and Wildlife, U.S. Fish & Wildlife Service (see references in Hanson & Eberhardt (1971) and comparisons of early studies in Klopman (1958) and Brakhage (1965)).

How the nesting characteristics of the two Canterbury populations compared with those from some historic North American studies is summarised in Table 7. Lake Forsyth nesting outcomes matched many North American examples, e.g. Hanson & Browning (1959) and Geis (1956) reported mean clutch sizes and clutch size distributions almost identical to those from Lake Forsyth and whereas other North American comparisons differ slightly, they appear to reflect different field methodologies at sites also with differing predator impacts. However, headwaters clutches were significantly lower ($t = -7.888$, $df = 3282$, $P < 0.001$) than the lowest of the compared North American clutch sizes (Guerena *et al.* 2016).

Both Canterbury populations distinguish themselves by their generally higher nest success, a consequence of proportionately fewer nests losing their entire contents relative to those in North American studies and, most likely, reflecting a lesser mammalian predator impact in New Zealand.

Great Britain and Fennoscandia

Canada geese have established feral populations in Great Britain and Fennoscandia and are presently expanding in lowland western Europe (Andersson *et al.* 1999). Nesting studies akin to those from North America are not extensively reported.

In Great Britain where the species is essentially sedentary, Wright & Giles (1988) reported a mean clutch of 6.1 ($sd = 1.4$, $n = 88$), a nest success of 69% ($n = 146$ nests), a hatch of 433 goslings in 79 successful nests (5.5 goslings/nest), and a productivity of 2.9 fledglings per successful nest, outcomes broadly akin to those reported from Lake Forsyth and some North American studies (Tables 6, 7). Conversely,

Table 7. Comparative nesting statistics of New Zealand and North American populations of Canada goose. North America studies are, 1 – Hanson & Browning 1959 (¹calculated from Fig. 4); 2 – Geis 1956; 3 – Steel *et al.* 1957; 4 – Cooper 1978 (²calculated from Fig. 3); 5 – Guerena *et al.* 2016 (³calculated from Table 1). \bar{x} = mean, sd = standard deviation, nr = not recorded.

Location	New Zealand			North America				
	Population/Source	Forsyth	Headwaters	1	2	3	4	5
Clutch size	n	462	1,211	1,032	358	361	466	2,073
	\bar{x}	5.3	4.5	5.4 ¹	5.3	5.2	5.6	4.9
	sd	1.3	1.3	1.2 ¹	1.3	nr	1.2 ²	1.8
Hatching rate	n	1,602	3,952	nr	2,501	1,810	2,912	10,075
	%	67.4	63.3	nr	55.6	69.3	68	61
Nest success	n	298	871	1,033	423	361	542	1,967
	%	80.2	83.8	70.9	61.5	79.5	75.0	59.0
Hatching rate in successful nests	n	1,321	3,376	3,947	1,364	1,458	1,871	nr
	%	81.7	85.4	92.0	89.5	86.0	96.6	nr
Hatch/ nest (all)	\bar{x}	3.6	2.9	3.5	2.8	3.5	3.8	3.0 ³

Johnson & Sibley (1993) reported a mean clutch of 5.1 ($sd = 1.9$, $n = 71$; calculated from their Fig. 4) and high nest failure with just 148 goslings hatched within 69 study nests (2.1 goslings/nest). Nevertheless, a 7–9% annual growth reported for the Great Britain population (Ogilvie 1977; Allan *et al.* 1995; Austin *et al.* 2007) indicates both high annual productivity and survival.

Sjöberg & Sjöberg (1992) reported mean clutch sizes over five years in four Swedish populations were between 4.8 ($sd = 1.4$, $n = 102$) and 5.3 ($sd = 1.6$, $n = 133$) with their annual variability ranging between means of 4.6 and 5.6. In two further Swedish nesting studies, hatching rates of 51% and 72% were reported (Fabricius 1983, quoted in Andersson *et al.* 1999).

These data on nesting of Canada geese beyond their native range indicate the two New Zealand populations had broadly similar nesting outcomes to those elsewhere. Despite the New Zealand and Fennoscandian introductions arising from small numbers released (Imber & Williams 2015; Heggberget 1991; Jansson *et al.* 2008) their nesting outcomes are akin to those recorded within North America, albeit influenced by their differing nesting densities and predator suites. Even so, the mean size of Waimakariri River headwaters clutches is the lowest reported.

Contemporary relevance of study

Since this study was undertaken, Canada goose numbers in New Zealand have increased significantly (Spurr & Coleman 2005; Robertson *et al.* 2007) both within long-established South Island regional distributions and in many North Island locations following deliberate 1980s introductions (Imber & Williams 2015). At one North Island site (Lake Wairarapa) their annual rate of increase over 20 years (1985–2005) was >12% (Spurr & Coleman 2005: Fig. 3). During the decade 2000–2010, and in the absence of deliberate culls, annual increases of some regional populations (e.g. Otago, West Coast, Marlborough, Waikato, Bay of Plenty) have ranged between 5–15% (relevant Fish & Game Councils, *unpubl. data*).

In the absence of modern assessments, outcomes of this 40–50-year-old nesting study can be used to infer productivity of Canada geese now nesting throughout New Zealand. The modern expansion of Canada goose distribution, especially in lowland North Island, has been typified by many initially small but rapidly expanding flocks derived from family groupings wherein pairs nest in near proximity and have limited feeding ranges. In these circumstances, which are akin to those reported for Lake Forsyth, each nesting female will lay 5–6 eggs and goslings will hatch from approximately two-

thirds of all eggs laid. Gosling survival to fledging is unquantified in New Zealand but if it lies in the upper range reported in lowland pastoral English conditions (45–77%, Allan *et al.* 1995) then, on average, each nesting pair will fledge goslings from half of their eggs annually.

The Canada goose has been a remarkably successful, if somewhat controversial, exotic addition to New Zealand's avifauna. Evaluation of its contemporary breeding performance and survival, especially in lowland pastoral North Island and at peri-urban sites, would serve to prepare responses to its inevitable further expansion and concomitant decline in public endearment.

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LITERATURE CITED

- Aldrich, T.W.; Raveling, D.G. 1983. Effects of experience and body weight on incubation behaviour of Canada geese. *The Auk* 100: 670–679.
- Alisauskas, R.T.; Ankney, C.D. 1992. The cost of egg-laying and its relationship to nutrient reserves in waterfowl. pp 30–61 *In*: Batt, B.J.D. *et al.* (eds.) *The ecology and management of breeding waterfowl*. Minneapolis, Minnesota University Press.
- Allan, J.R.; Kirby, J.S.; Feare, C.J. 1995. The biology of Canada geese (*Branta canadensis*) in relation to the management of feral populations. *Wildlife Biology* 1: 129–143.
- Andersson, Å; Madsen, J.; Mooij, J.; Reitan, O. 1999. Canada goose *Branta canadensis*: Fennoscandia/continental Europe. pp. 236–245 *In*: Madsen, J.; Cracknell, G.; Fox, A.D. (eds). *Goose populations of the Western Palearctic*. Wetlands International Publications No. 48, Wetlands International, Wageningen, The Netherlands. National Environmental Research Institute, Rönde, Denmark. 344pp.
- Ankney, C.D.; Afton, A.D.; Alisauskas, R.T. 1991. The role of nutrient reserves in limiting waterfowl reproduction. *Condor* 93: 1029–1032.
- Austin, G.E.; Rehfish, M.M.; Allan, J.R.; Holloway, S.J. 2007. Population size and differential population growth of introduced Greater Canada geese *Branta canadensis* and re-established Greylag Geese *Anser anser* across habitats in Great Britain in the year 2000. *Bird Study* 54: 343–352.
- Brakhage, G.K. 1965. Biology and behavior of tub-nesting Canada geese. *Journal of Wildlife Management* 29: 751–771.
- Cooper, J.A. 1978. The history and breeding biology of the Canada geese of Marshy Point, Manitoba. *Wildlife Monographs* 61: 3–87.
- Elder, W.H. 1946. Age and sex criteria and weights of Canada geese. *Journal of Wildlife Management* 10: 93–111.
- Erikstad, K.E.; Bustnes, J.O.; Moum, T. 1993. Clutch size determination in precocial birds: a study of the common eider. *The Auk* 110(3): 623–628.
- Fabricius, E. 1983. Kanadagasen i Sverge (Canada goose in Sweden). *Naturvardsverket Rapport* 1678. (not viewed, quoted in Alisauskas & Ankney 1992).
- Geis, M.B. 1956. Productivity of Canada geese in the Flathead Valley, Montana. *Journal of Wildlife Management* 20: 409–419.
- Guerena, K.B.; Castelli, P.M.; Nichols, T.C.; Williams, C.K. 2016. Factors affecting nest survival in resident Canada geese. *Journal of Wildlife Management* 80: 1022–1030.
- Hanson, W.C.; Browning, R.L. 1959. Nesting studies of Canada geese on the Hanford reservation 1953–56. *Journal of Wildlife Management* 23: 129–137.
- Hanson, W.C.; Eberhardt, L.L. 1971. A Columbia River Canada goose population, 1950–1970. *Wildlife Monographs* 28: 3–61.
- Heggberget, T.M. 1991. Establishment of breeding populations and population development in the Canada goose *Branta canadensis* in Norway. *Ardea* 79: 365–370.
- Hustedt, S. 2002. The ecology and conservation of a threatened shrub: *Hebe armstrongii* (Scrophulariaceae), Canterbury, New Zealand. Unpubl. M. Forestry Science thesis, University of Canterbury.
- IAD 25/4/10. Wildlife Research: Canada goose (Item R5080471). Archived file of the Department of Internal Affairs, Archives New Zealand, Wellington. (see also file 46/52/19).
- Imber, M.J. 1971a. Canada geese studies in Canterbury. *Ammohouse Bulletin* 1(30): 6–8.
- Imber, M.J. 1971b. The identity of New Zealand's Canada geese. *Notornis* 18: 253–261.
- Imber, M.J. 1985. Giant Canada goose. pp. 140 *In*: *Reader's Digest complete book of New Zealand birds*. Sydney, Reed Methuen and Reader's Digest.
- Imber, M.J.; Williams, G.R. 1968. Mortality rates of a Canada goose population in New Zealand. *Journal of Wildlife Management* 32: 256–267.
- Imber, M.J.; Williams, M. 2015. Disseminations which established Canada goose (*Branta canadensis*) throughout New Zealand. *Notornis* 62: 219–230.
- Jansson, K.; Josefsson, M.; Weidema, I. 2008: NOBANIS – Invasive Alien Species Fact Sheet – *Branta canadensis*. From: Online Database of the North European and Baltic Network on Invasive Alien Species – NOBANIS www.nobanis.org. Date of access 01/08/2019.
- Johnson, I.P.; Sibley, R.M. 1993. Pre-breeding behaviour affects condition, assessed by

- abdominal profile, and hence breeding success of Canada geese *Branta canadensis*. *Wildfowl* 44: 60–68.
- Klopman, R.B. 1958. The nesting of the Canada goose at Dog Lake, Manitoba. *The Wilson Bulletin* 70: 168–183.
- Lack, D. 1967. The significance of clutch-size in waterfowl. *Wildfowl* 18: 125–128.
- Lessells, C.M. 1985. Natal and breeding dispersal of Canada geese *Branta canadensis*. *Ibis* 127: 31–41.
- McDowall, R.M. 1994. *Gamekeepers for the nation: the story of New Zealand's acclimatisation societies 1861–1990*. Christchurch: Canterbury University Press.
- Ogilvie, M. 1977. The numbers of Canada geese in Britain, 1976. *Wildfowl* 28: 8–12.
- Robertson, C.J.R.; Hyvönen, P.; Fraser, M.J.; Pickard, C.R. 2007. *Atlas of bird distribution in New Zealand 1999–2004*. Wellington, Ornithological Society of New Zealand.
- Ryder, J.P. 1970. A possible factor in the evolution of clutch size in the Ross' goose. *Wilson Bulletin* 82: 5–13.
- Sjöberg, G.; Sjöberg, K. 1992. Geographic variation in reproductive investment in Canada geese (*Branta canadensis*) in Sweden. *Journal für Ornithologie* 133: 403–412.
- Spurr, E.B.; Coleman, J.D. 2005. *Review of Canada goose population trends, damage, and control in New Zealand*. Landcare Research Science Series No. 30. Lincoln, Manaaki Whenua Press
- Steel, P.E.; Dalke, P.D.; Bizeau, E.G. 1957. Canada goose production at Gray's Lake, Idaho, 1949–1951. *Journal of Wildlife Management* 21: 38–41.
- van Wagner, C.E.; Baker, A.J. 1986. Genetic differentiation in populations of Canada geese *Branta canadensis*. *Canadian Journal of Zoology* 64: 940–947.
- van Wagner, C.E.; Baker, A.J. 1990. Association of mitochondrial DNA and morphological evolution in Canada geese. *Journal of Molecular Evolution* 31: 373–382.
- Weller, M.W. 1956. A simple field candler for waterfowl eggs. *Journal of Wildlife Management* 20: 111–113.
- Williams, M. 2011. Boo hoo for the goose. *Fish & Game New Zealand* 74: 66–69.
- Winkler, D. W.; Walters, J.R. 1983. The determination of clutch size in precocial birds. *Current Ornithology* 1: 33–68.
- Wright, R.; Giles, N. 1988. Breeding success of Canada and Greylag geese *Branta canadensis* and *Anser anser* on gravel pits. *Bird Study* 35: 31–36.

Appendix: A record of egg size in Canada geese.

A sample of eggs was measured at each study area. These data were originally intended to contribute to an assessment of the race of Canada goose established in New Zealand (Imber 1971b) but were never published.

- From Lake Forsyth, 179 eggs had a mean length of 87.9 mm (sd = 4.1, range 75.6–103.2 mm) and a mean width of 58.3 mm (sd = 1.6, range 53.6 – 62.5 mm).
- From Pūkio Stream, 48 eggs had a mean length of 88.0 mm (sd = 4.9, range 76.5–98.5 mm) and a mean width of 58.0 mm (sd = 2.1, range 53.3–62.8 mm). The eggs sizes did not differ between the two study areas (length: $z = 1.64$, $P = 0.55$; width: $z = 1.96$, $P = 0.36$).
- Eggs laid at Lake Forsyth by females of known age included 76 eggs from 16 3-year olds which had mean dimensions of 88.9 (sd = 3.0) x 58.0 (sd = 1.7) mm, and 15 eggs from three 4-year-olds with mean dimensions of 88.1 (sd = 3.9) x 58.2 (sd = 1.1) mm.

The food and foraging of *Collocalia* and *Aerodramus* swiftlets: a review

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Abstract: Swiftlets (*Collocalia*, *Aerodramus*) make up a guild of birds which prey on a wide range of aerial insects and spiders. The studies reviewed here show their prey to include 19 orders and 55 families of insects plus spiders. Most swiftlets seem to take whatever is available at the time and place, with site to site and year to year differences noted. One species (black-nest swiftlet) appears to be a swarm-feeding specialist. Prey size ranged from <1 to 13 mm in body length and is related to swiftlet body size. Habitat and elevational differences may represent resource partitioning in foraging strategies.

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INTRODUCTION

Birds and insects have “intricate and fundamental ecological interrelationships” (Morse 1971). This is particularly true in cases where flying insects are exploited by guilds of avian predators. Guilds, as formulated by Root (1967), are made up of groups of birds which utilize similar environmental resources in a similar way regardless of their taxonomic relatedness. One particularly recognizable guild would consist of aerial insectivores, all of which

capture their arthropod food on the wing. In Malaysia and other parts of south-eastern Asia this guild could consist of as many as 15 species of swallows, swifts, swiftlets, and treeswifts. However, not all of these may be resident species or ones that occur sympatrically. A more focused subset might be a guild made up of only swiftlets in the genera *Collocalia* and *Aerodramus*. This is a group of small to medium sized Apodiform birds which occur widely from the Seychelles in the western Indian Ocean eastward to India, Malaysia, north-eastern Australia, and islands of the Pacific Ocean as far east as Tahiti, and the Marquesas Islands (Holyoak

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& Thaibault 1978; Lim & Cranbrook 2002). Swiftlets are also noted for their utilization of caves as nesting and roosting sites. Individual caves can house up to 3–4 million swiftlets (Medway 1962a; Francis 1987; Lim & Cranbrook 2002). Swiftlets in the genus *Aerodramus* are known for their ability to utilize echolocation to navigate within nesting and roosting caves (Medway & Pye 1977; Collins & Murphy 1994; Price *et al.* 2004).

Aspects of the breeding biology have been documented in earlier studies of several swiftlet species (Medway 1962b; Harrison 1974; Langham 1980; Hails & Amirrudin 1981; Waugh & Hails 1983; Tarburton 1986, 1993; Lourie & Tompkins 2000; Tarburton 2017). In addition to documenting the great diversity of prey items taken by some swiftlets, these studies have also directed attention to possible differences in foraging areas utilized by particular species (Medway 1962a; Diamond 1972; Harrison 1974; Waugh & Hails 1983; Lourie & Tompkins 2000; Collins 2000a). Elsewhere, studies including a variety of other larger species of swifts have shown their diets to include a wide diversity of both taxa and sizes of prey, with substantial variation from place to place (Lack & Owen 1955; Gory 2008), season to season (Harrison 1974; Cucco *et al.* 1993) as well as year to year at the same site (Tarburton 1993; Collins 2010). Local weather conditions may also influence short-term prey type availability and consumption (Lack & Owen 1955). In this review we summarize previous studies, and personal observations, of swiftlets from various regions of their extensive range. We give particular attention to their food and their foraging behaviour.

METHODS

In this review, we have summarized data presented in 20 earlier studies of 11 species of *Collocalia* and *Aerodramus* swiftlets and our personal observations. We also present new data on the diets of three swiftlets from Malaysia (Appendix 1). Body weight data were mostly derived from swiftlets which were weighed in the field at the point of capture. Some additional data were obtained from museum specimens. Data on prey type and size are largely from boluses of food, mostly insects, carried in the mouth by adults feeding nestlings. Boluses were usually ejected when the adults were captured in nets or if their mouth was gently opened. Adults were then released unharmed at the site of capture. To prevent possible detrimental effects on nestling growth, boluses in our studies were not collected on consecutive days from the same colony. The body size of prey items was measured from the tip of the head to the tip of the abdomen, excluding antennae or caudal appendages (Tarburton 1986, 1993, 2017).

As noted previously (Collins *et al.* 2009; Collins

2010, 2015) such food boluses are only available during the chick-rearing portion of the annual cycle. However, such samples may be more informative than the examination of stomach contents and faeces obtained at other times of the year which could underestimate smaller soft-bodied prey items which are subject to rapid fragmentation and digestion (Hartley 1948; Kopij 2000).

The waterfall swift (*Hydrochous gigas*), formerly known as the giant swiftlet, has been excluded from this analysis. It is much larger (37.8 g; Becking 2006b), does not use echolocation (Medway & Wells 1969; Medway & Pye 1977), and its behind-waterfall nest sites (Becking 2006a), nestling development (Becking 2006b) as well as its flight behaviour (King 1987) contribute to a rather problematic relationship to the more typical *Collocalia* and *Aerodramus* swiftlets (Collins 2000b). However, recent DNA analyses have again supported a relationship with *Aerodramus* (Price *et al.* 2005; Thomassen *et al.* 2005). No information is currently available on its diet or foraging behaviour.

The discussion of species limits among the swiftlets has a long history. As stated in a recent review (Cranbrook *et al.* 2013) this has “proved challenging because of their limited variation in size and plumage colouration”. Even today, there is a lack of universal agreement on the taxonomy of all swiftlets in the genera *Collocalia* and *Aerodramus*. For the purposes of this review we have adopted the species limits and common names presented in the IOC World Bird List which covers the full geographic range of this group. Similarly, we follow CSIRO (1970) for the ordinal and family classification of insect prey items of swiftlets.

RESULTS AND DISCUSSION

Foraging behaviour

As noted in several studies, swiftlets arise at or before first light of dawn and pour out of their nesting and roosting caves “by the thousands per minute” (Lim & Cranbrook 2002) to spend twelve hours or more aloft in search of aerial arthropod prey, before returning in the “gathering dusk” (Medway 1962a; Ali & Ripley 1970; Harrison 1974; Lim & Cranbrook 2002). Return entry flights may take several hours at some of the largest colonies and be extended on moonlit nights (Mane & Manchi 2017). Australian swiftlets (*A. terraereginae*) usually depart an hour later and return an hour earlier than the similar white-rumped swiftlet (*A. spodiopygius*) in Fiji which has been noted returning to their caves as late as 2230 h (Tarburton 1988). Three-toed swiftlets (*A. papuensis*) have also been observed leaving their cave before first light and returning as late as 0300h (Tarburton 2018). The Indian swiftlet (*A. unicolor*) in Sri Lanka and the Australian swiftlet in

Queensland have been observed opportunistically hawking insects in areas illuminated by floodlights hours after normal roosting times (Ali & Ripley 1970; Tarburton 1987). Similar behaviour has been observed in chimney swifts (*Chaetura pelagica*) in North America (Cottam 1932).

The foraging range of swiftlets was shown to extend for up to at least 24 km, (15 miles) from the nesting cave at Niah in Borneo, (Malaysia) (Medway 1962a) and possibly as far as 81–113 km (50–70 miles) (Harrisson 1974). In Vietnam, Germain's swiftlets (*A. germani*) make daily flights to mainland foraging areas up to 250–300 km from their island nesting caves (Nguyen Quang *et al.* 2002). Such distant and dispersed foraging ranges may be a necessity for individuals from very large colonies to find sufficient prey (Harrisson 1974).

In Malaysia, the majority of the swiftlets appear to forage between 9 and 266 m (20–800 feet) above ground level with only about 2% seen at 333 m (1,000 feet) or more above the forest canopy (Harrisson 1974). In Malaysia, a group of three species of swiftlets foraged at heights of 50–60 m (164–197 feet) above ground level which was lower than the foraging height of 114–184 m (374–604 feet) recorded for two larger swifts (Waugh & Hails 1983). Notable exceptions were the glossy swiftlet (*C. esculenta*) and black-nest swiftlet (*A. maximus*). In Malaysia, the black-nest swiftlet was stated by Medway (1962: 243) to forage higher than the sympatric mossy-nest swiftlet (*A. salangana*); this trend was not confirmed by later observations (Harrisson 1974: 380). However, black-nest swiftlets did tend to go farther from the nesting cave and stay out longer and possibly take advantage of patchily distributed swarming insects especially at dusk.

Glossy swiftlets were found to be the lowest elevation feeders among several swifts and swallows in Malaysia and closely associated with the forest canopy (Waugh & Hails 1983). They were similarly recorded foraging low over open landscapes in both rural and urban areas (Rabor 1954; Francis 1987; Lourie & Tompkins 2000). Also, in 2013, glossy swiftlets were observed foraging on *Schedorhinotermes* and *Odontotermes* sp. alates below three metres in Andaman Islands during a monsoon, when termite swarms leave the nest to seek out mates in order to form new colonies (A.M. Mane *unpubl. data*). They were observed foraging less than 3 m above the ground level and below the canopy level when sympatric with the similar sized pygmy swiftlet (*C. troglodytes*) on Palawan (Collins 2000a) and the uniform swiftlet (*A. vanikorensis*) on Vanuatu (Kratter *et al.* 2006). Glossy swiftlets were similarly observed foraging, “below the canopy level flying between trees” while the sympatric Halmahera swiftlet (*A. infuscatus*) was only observed foraging above the canopy (Riley

1997). On Karkar, Solomon Islands, two species of swiftlets had segregated foraging zones with the mountain swiftlet (*A. hirundinacea*) foraging in the open, high above the treetops while glossy swiftlets “flew over rivers, in clearings and even within the forest itself” (Diamond & LeCroy 1979). Similarly, in New Guinea, glossy swiftlets generally foraged below the level of the treetops, occasionally inside the forest in more open areas where they circled and skimmed close to the foliage, at times “even hovering at foliage like a hover-gleaning flycatcher” (Diamond 1972; Diamond & LeCroy 1979; Coates 1985). In New Guinea, there is also elevational segregation with glossy swiftlets and uniform swiftlets occurring in the lowlands and hills while the mountain swiftlet is widely distributed in mountainous areas up to 4,000 m elevation (Coates 1985).

Recently, detailed analyses have been made of the foraging behaviour of glossy swiftlets and white-nest swiftlets (*A. fuciphagus*) in the Andaman Islands, India, (Manchi & Sankaran 2010) and Germain's swiftlet in Thailand (Petkiliang *et al.* 2017). These studies indicated that swiftlet foraging habits changed in response to changes in the food supply in different habitat types as well as the time of day and season.

The white-rumped swiftlet in Fiji typically foraged above the canopy in rainforest areas but also down to 0.5 m in well vegetated residential and agricultural areas (Tarburton 1986). In Queensland, Australia the similar Australian swiftlet largely inhabits drier savannah areas, and rarely foraged below 8 m (Tarburton 1993). Individual Palau swiftlets (*A. pelewensis*) and glossy swiftlets have been observed coursing back and forth in open areas <3 m high under the canopy of isolated trees (Hails & Amirrudin 1981; CTC *pers. obs.*). Such foraging bouts may allow them to forage on such unique prey as Lepidoptera larvae lowering themselves on silk threads to pupate in the ground litter (Appendix 1 & 2).

Diet

Swiftlets, like other Apodidae, gather all their arthropod prey on the wing. Individual boluses were found to contain 49–1,104 prey items and over 50 morphotypes (Lourie & Tompkins 2000). Included in their prey are representatives from 19 orders and over 55 families of insects and spiders (Appendix 2). Insects in the orders Hymenoptera, Diptera, Coleoptera, and Homoptera were the most abundant items in food boluses usually making up 82–99% of all individuals identified. Other orders such as Strepsiptera (Nguyen Quang *et al.* 2002), Neuroptera (Tarburton 1986), and Dermaptera (Appendix 1), were only represented in one

previous study. Spiders were present in 12 of the studies summarized here (Table 1) and averaged 3.7% (0–12%) of all identified prey items.

The great diversity of prey taxa taken by swiftlets reinforces the view that they are opportunistic foragers taking whatever suitable sized prey (see below) is available at any given time and place. They are quick to exploit localized, and sometimes ephemeral, abundances of suitable prey. Mayflies (Ephemeroptera) were only present in the food boluses of three swiftlets (Table 1) but made up 26.4% of 6,924 prey items taken by white-nest swiftlets in Malaya (Langham 1980). Mayflies accounted for <1.5% of the prey taken by glossy swiftlets and white-rumped swiftlets (Table 1). Beetles (Coleoptera) were present in the boluses of all of the swiftlets in this study. They were particularly numerous (57.8–64.0%) in the prey taken by glossy swiftlets and uniform swiftlets in the Philippines (Table 1). Termites (Isoptera, Macrotermitinae), some up to 13 mm long, were prominent in the stomach contents of swiftlets collected at the Niah Great Cave in Malaysia (Harrison 1974). However, they only occurred in nine of the 20 samples examined in this study and never made up more than 6% of the prey in any one sample (Table 1). Like mayflies, termite abundance varies seasonally and thus may be an irregularly available prey type for swiftlets. Lepidoptera larvae were an unusual prey type taken by glossy swiftlets (Hails & Amirrudin 1981: Appendix 1 & 2) presumably while coursing below a tree canopy, as noted earlier.

A large portion of the prey items taken by most swiftlets were Hymenoptera, particularly winged ants (Formicidae). This was particularly true for black-nest swiftlets where 83.0–97.9% of their prey

in both Malaysia and Vietnam were ants (Table 1). Some Neotropical swifts (Cypseloidinae) take similarly large numbers of flying ants (Collins & Landy 1968; Marin 1999; Rudalevige *et al.* 2003; Potter *et al.* 2015). These swifts are thought to forage widely in search of swarms of this lipid-rich prey. The data presented here support the previous suggestions of Medway (1962b) and Harrison (1974) that black-nest swiftlets utilize a similar swarm-feeding strategy otherwise unique among the swiftlets.

Prey size

The size of the prey items swiftlets take varies substantially, ranging from 0.7 mm to 13.0 mm. The mean prey size is more consistent ranging from 1.71 mm in white-nest swiftlets to 3.64 mm in Australian swiftlets (Table 2). The exceptions are two samples consisting almost entirely of large ants taken by black-nest swiftlet, which averaged 3.74 mm and 7.39 mm (Table 2); 82.7% of their prey items were larger than 6 mm. Black-nest swiftlet also had significantly fewer prey items and morphotypes per bolus than sympatric species (Lourie & Tompkins 2000), again an indication of their specialization on large-bodied swarming ants (Lim & Cranbrook 2002). The distribution of the sizes of all prey items is available for four swiftlets (Tarburton 2017; Appendix 1). In three of the four cases the prey sizes are sharply positively skewed (Table 3); there being an abundance of smaller prey items <6 mm long (Figure 1). This presumably reflects the greater abundance of smaller prey items in the air column (Glick 1939). Larger prey items, when available, may be preferred as they would have greater energy value and proportionally less indigestible exoskeleton chitin.

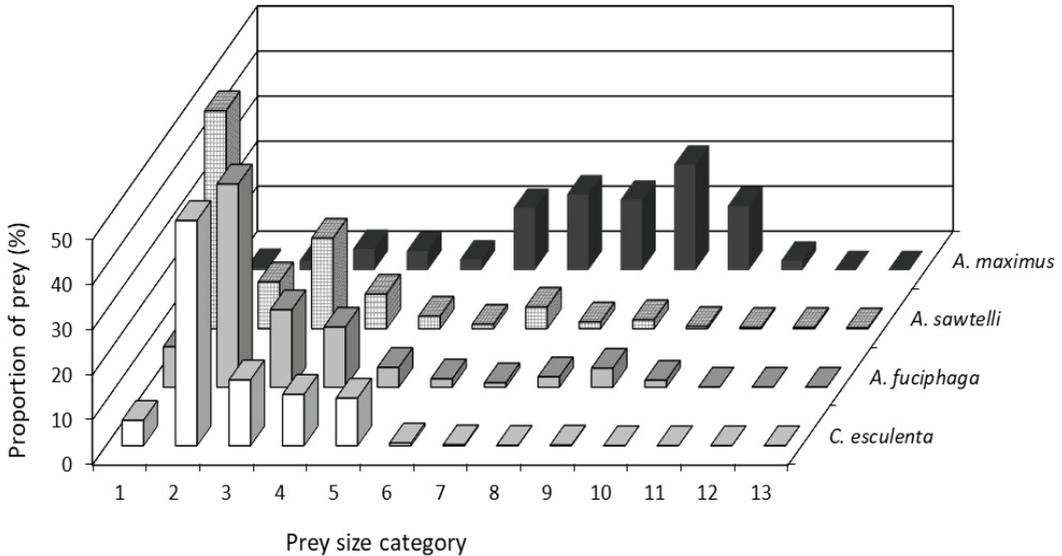
Table 2. Body weight (grams) and prey size (mm) of swiftlets (*Collocalia* and *Aerodramus*).

Species name	Body size (g)	SE	n	Source	Prey size (mm)	SE	n	Source
<i>A. fuciphagus</i> (Malaysia)	10.67	0.43	365	1	1.71	0.03	5,114	8
<i>A. fuciphagus</i> (Malaysia)	10.67	0.43	365	1	3.09	0.05	1,611	9
<i>A. spodiopygius</i> (Fiji)	8.19	0.06	102	2	2.48	0.11	7,309	2
<i>A. elaphrus</i> (Seychelles)	8.95	0.18	19	3	2.51	0.08	114	3
<i>A. sawtelli</i> (Cook Islands)	8.56	0.06	144	4	2.6	0.05	1,893	4
<i>C. esculenta</i> (Malaysia)	7.13	0.03	133	5	2.61	0.03	1,456	9
<i>C. esculenta</i> (Malaysia)	8.28	0.28	114	6	2.72	0.14	2,135	8
<i>A. salangana</i> (Malaysia)	12.7	1	304	1	2.73	0.06	4,643	8
<i>A. terraereginae</i> (Australia)	9.3	0.03	567	7	3.64	0.24	6,583	7
<i>A. maximus</i> (Malaysia)	17.98	0.30	40	1	3.74	0.04	1,989	8
<i>A. maximus</i> (Malaysia)	17.98	0.30	40	1	7.39	0.08	760	9

Sources: 1 - C. M. Francis, *unpubl. data*; 2 - Tarburton (1986); 3 - Collins & Cheke *unpubl. data*; 4 - Tarburton (2017); 5 - Francis (1987); 6 - Hails & Amirrudin (1981); 7 - Tarburton (1993); 8 - Lourie & Tompkins (2000); 9 - Appendix 1.

Table 3. Distribution of prey sizes in the diets of four swiftlet species.

Species	Mean prey size (mm)	Range	n	skewness	% prey > 6mm
Glossy swiftlet (<i>C. esculenta</i>)	2.61	0.9–8.7	1,456	1.18	<1.0
White-nest swiftlet (<i>Aerodramus fuciphagus</i>)	3.09	0.7–10.3	1,611	1.82	10.3
Atiu swiftlet (<i>Aerodramus sawtelli</i>)	2.6	1.0–13.0	1,893	1.76	10.1
Black-nest swiftlet (<i>A. maximus</i>)	7.4	0.9–11.0	760	-0.84	82.2

**Figure 1.** Proportion of prey sizes, showing abundance of smaller prey in three of the four swiftlet species (*Aerodramus*, *Collocalia*). Prey size categories indicated as follows; 1 = 0.5–1.4 mm, 2 = 1.4–2.4 mm, 3 = 2.4–3.0 mm, etc.

In the larger swifts in the genera *Apus* and *Tachymarptis* there is a positive relationship between prey size and predator body weight (Collins *et al.* 2009). For the swiftlets, there is a similar positive relationship (Table 2) although the body weights are more clumped ranging only from 7.1 g to 17.9 g (Table 2). A Spearman's Rank correlation of the data in Table 2 gives a probability of 90–95%, showing a loose correlation between body size and prey size.

SUMMARY

The food of both swifts and swiftlets consists entirely of aerial arthropods, mostly insects, captured on the wing. Swiftlets are often characterized as being opportunistic foragers taking whatever prey is available in the air column at a given time and place (Lack & Owen 1955). They can also be considered as generalists, as outlined by Morse (1971). However,

the exact prey taken by swifts and swiftlets shows a lot of variability from place to place, season to season, and even year to year, at the same location. Prey size taken has long been assumed to be related to swift body size (Brooke 1973; Salmonson 1983) and recently documented for swifts in the genera *Apus* and *Tachymarptis* (Collins *et al.* 2009) and five Neotropical species (Collins 2015). This review of prey size in the smaller swiftlets confirms this expectation and extends it to the wide array of sizes found in both the swifts and swiftlets which make up the family Apodidae. A further finding is the swarm-feeding behaviour of the black-nest swiftlet which is convergent to the similar foraging behaviour shown by Neotropical Cypseloidine swifts. There are several examples reported here of habitat partitioning among swiftlets, presumably to avoid inter-specific competition. Such niche partitioning has been examined more closely

among a guild of Neotropical swifts (Collins 2015). The widespread distribution of the 32 currently recognized species of swiftlets includes many more examples of sympatry, and opportunities for habitat partitioning, the study of which would contribute further to our understanding of the foraging behaviour of swiftlets.

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LITERATURE CITED

- Ali, S.; Ripley, S.D. 1970. *Handbook of the birds of India and Pakistan. Volume 4.* Bombay, Oxford University Press.
- Becking, J.H. 2006a. Notes on Waterfall Swift *Hydrochous gigas*: I. Occurrence and nesting. *Bulletin of the British Ornithologists' Club* 126: 117–122.
- Becking, J.J. 2006b. Notes on Waterfall Swift *Hydrochous gigas* II. nestling plumage, and phylogenetic relationships. *Bulletin of the British Ornithologists' Club* 126: 123–136.
- Brooke, R.K. 1973. Distributional and biological notes on the Mottled Swift in Rhodesia. *Ostrich* 44: 106–110.
- Coates, B.J. 1985. *The birds of Papua New Guinea, Volume 1.* Alderley, Queensland, Australia, Dove Publications.
- Collins, C.T. 2000a. Foraging of Glossy and Pygmy Swiftlets in Palawan, Philippines. *Forktail* 16: 53–55.
- Collins, C.T. 2000b. Subfamilies of the swifts (Apodiformes, Apodidae): *Schoutedenapus* revisited. *Durban Museum Novitates* 25: 36–39.
- Collins, C.T. 2010. Notes on the breeding biology of the White-throated Swift in southern California. *Bulletin of the Southern California Academy of Sciences* 109: 23–36.
- Collins, C.T. 2015. Food habits and resource partitioning in a guild of Neotropical swifts. *Wilson Journal of Ornithology* 127: 239–248.
- Collins, C.T.; Landy M.J. 1968. Breeding of the Black Swift in Veracruz, Mexico. *Bulletin of the Southern California Academy of Sciences* 67: 266–268.
- Collins, C.T.; Murphy, R. 1994. Echolocation acuity of the Palawan Swiftlet (*Aerodramus palawanensis*). *Avocetta* 17: 157–162.
- Collins, C.T.; Tella, J.L.; Colahan, B.D. 2009. Food habits of the Alpine Swift on two continents: Intra- and interspecific comparisons. *Ardeola* 56: 259–269.
- Cottam, C. 1932. Nocturnal habits of the Chimney Swift. *Auk*, 49: 479–481.
- CSIRO, 1970. *The Insects of Australia: A Textbook for Students and Research Workers.* Melbourne University Press. 1029 pp.
- Cucco, M.; Bryant, D.M.; Malacarne, G. 1993. Difference in the diet of the Common (*Apus apus*) and Pallid (*A. pallidus*) Swifts. *Avocetta* 17: 131–138.
- Cranbrook, Earl of; Goh, W.L.; Lim, C.K.; Rahman, M.A. 2013. The species of White-nest Swiftlets (Apodidae, Collocaliini) of Malaysia and the origins of house-farm birds: morphometric and genetic evidence. *Forktail* 29: 107–119.
- Diamond, J.M. 1972. Avifauna of the eastern highlands of New Guinea. *Publications of the Nuttall Ornithological Club* 12: 1–438.
- Diamond, J.; LeCroy, M. 1979. Birds of Karkar and Bagbag Islands, New Guinea. *Bulletin of the American Museum of Natural History* 164: 467–531.
- Francis, C.M. 1987. The management of edible bird's nest caves in Sabah. Wildlife Section, Sabah Forest Department.
- Glick, P.A. 1939. The distribution of insects, spiders, and mites in the air. *Technical Bulletin U.S. Department of Agriculture* 673: 1–150.
- Gory, G. 2008. Le regime alimentaire du Martinet Noir *Apus apusen* region Mediterranean. *Revue Ecologie (Terre et Vie)* 63: 251–260.
- Harrison, T. 1974. The food of the *Collocalia* swiftlets (Aves, Apodidae) at Niah Great Cave in Borneo. *Journal of the Bombay Natural History Society* 71: 376–393.
- Hartley, B.H.T. 1948. The assessment of the food of birds. *Ibis* 90: 361–381.
- Hails, C.J.; Amirrudin, A. 1981. Food samples and selectivity of the White-bellied Swiftlet *Collocalia esculenta*. *Ibis* 123: 328–333.
- Holyoak, D.T.; Thibault, J.C. 1978. Notes on the biology and systematic of Polynesian swiftlets, *Aerodramus*. *Bulletin of the British Ornithologists' Club* 98: 59–65.
- King, B. 1987. The Waterfall Swift. *Bulletin of the British Ornithologists' Club* 107: 36–37.
- Kopij, G. 2000. Diet of swifts (Apodidae) and swallows (Hirundinidae) during breeding season in South African grassland. *Acta Ornithologica* 35: 203–206.
- Kratter, A.W.; Kirchman, J.J.; Steadman, D.W. 2006. Upland bird communities on Santo, Vanuatu, Southwest Pacific. *Wilson Journal of Ornithology* 118: 295–308.
- Lack, D.; Owen, D.F. 1955. Food of the swift. *Journal of Animal Ecology* 24: 120–136.
- Langham, N. 1980. Breeding biology of the edible nest swiftlet *Aerodramus fuciphagus*. *Ibis* 122: 447–461.

- Lim, C.K.; Cranbrook, Earl of. 2002. Swiftlets of Borneo. Builders of edible nests. *Natural History Publications (Borneo)*, Kota Kinabalu. 171 pp.
- Lourie, S.A.; Tompkins, D.M. 2000. The diets of Malaysian swiftlets. *Ibis* 142: 596–602.
- Manchi, S.S.; Sankaran, R. 2010. Foraging habits and habitat of Edible-nest and Glossy Swiftlets in the Andaman Islands, India. *The Wilson Journal of Ornithology* 122: 259–272.
- Mane, A.M.; Manchi, S.S. 2017. Roosting patterns of the Edible-nest Swiftlet (*Aerodramus fuciphagus*) of the Andaman Islands: effects of lunar phase and breeding chronology. *Emu* 117(4): 325–332.
- Marin, M. 1999. Food, foraging and time of breeding of the Black Swift in California. *Wilson Bulletin* 111: 30–37.
- Medway, Lord. 1962a. The swiftlets (*Collocalia*) of Niah Cave, Sarawak. Part 1. Breeding biology. *Ibis* 104: 45–66.
- Medway, Lord. 1962b. The swiftlets (*Collocalia*) of Niah Cave, Sarawak. Part 2. Ecology and the Regulation of breeding. *Ibis* 104: 228–245.
- Medway, Lord; Pye, J.D. 1977. Echolocation and the systematics of swiftlets. pp 225–238 In: Stonehouse, B.; Perrins, C. (eds) *Evolutionary Ecology*. London, Macmillan.
- Medway, Lord; Wells, D.R. 1969. Dark orientation by the Giant Swiftlet, *Collocalia gigas*. *Ibis* 111: 609–611.
- Morse, D.H. 1971. The insectivorous bird as an adaptive strategy. *Annual Review of Ecology and Systematics* 2: 177–200.
- Nguyen Quang, P.; Quang, Y. Vo.; Voisin, J.-F. 2002. The White-nest Swiftlet and the Black-nest Swiftlet. Paris, Société Nouvelle des Éditions Boubée.
- Nituda, C.J.P.; Nuneza, O.M. 2016. Diet composition of two species of swiftlets from caves of northern Mindanao, Philippines. *Bulletin of Environment, Pharmacology and Life Sciences* 5: 48–52.
- Petklian, N.; Gale, G.A.; Brunton, D.H.; Bumrungari, S. 2017. Wetland forest, and open paddy land are the key foraging habitats for Germain's Swiftlet (*Aerodramus germaini*) in southern Thailand. *Tropical Conservation Science* 10: 1–12.
- Potter, K.M.; Gunn, C.; Beason, J.P. 2015. Prey items of the Black Swift (*Cypseloides niger*) in Colorado and a review of historical data. *Wilson Journal of Ornithology* 127: 411–420.
- Price, J.J.; Johnson, K.P.; Bush, S.E.; Clayton, D.H. 2005. Phylogenetic relationships of the Papuan Swiftlet *Aerodramus papuensis* and implications for the evolution of avian echolocation. *Ibis* 147: 790–796.
- Price, J.J.; Johnson, K.P.; Clayton, D.H. 2004. The evolution of echolocation in swiftlets. *Journal of Avian Biology* 35: 135–143.
- Rabor, D.S. 1954. Notes on the nesting of some Philippine swifts on Negros and Mindanao. *The Suliman Journal* 1: 45–53.
- Rahman, S.R.S.; Nor, H.M.; Burhanuddin, M. 2016. Diversity of the insects in the diet of Edible-nest Swiftlets in old palm plantations. *Journal of Biodiversity and Environmental Sciences* 8: 39–48.
- Riley, J. 1997. The birds of Sangihe and Talaud, North Sulawesi. *Kukila* 9: 3–36.
- Root, R.B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. *Ecological Monographs* 37: 317–315.
- Rudalevige, A.D.; Underwood, D.L.A.; Collins C.T. 2003. Diet of breeding White-throated and Black Swifts in southern California. *Western Birds* 34: 209–215.
- Salmonson, F. 1983. Revision of the Melanesian swiftlets (Apodes, Aves) and their conspecific forms in the Indo-Australian and Polynesian regions. *Kongelige Danske Videnskabernes Selskab Biologiske Skifter* 23(5): 1–112.
- Tarburton, M.K. 1986. The food of the White-rumped Swiftlet (*Aerodramus spodiopygius*) in Fiji. *Notornis* 33: 1–16.
- Tarburton, M.K. 1987. The population status, longevity and mortality of the White-rumped Swiftlet in Fiji. *Corella* 11: 97–110.
- Tarburton, M.K. 1988. Calls of the White-rumped Swiftlet. *Notornis* 35: 77–83.
- Tarburton, M.K. 1993. The diet of the White-rumped Swiftlet (*Aerodramus spodiopygius*) in Queensland's savannah. *Avocetta* 17: 125–129.
- Tarburton, M.K. 2017. Diet of the Atiu Swiftlet (*Aerodramus sawtelli*): an aerial insectivore on a small island in the South Pacific. *Notornis* 64: 106–108.
- Tarburton, M.K. 2018. Difficulties identifying Three-toed Swiftlets *Aerodramus papuensis* in New Guinea. *Australian Field Ornithology* 35: 126–128.
- Thomassen H.A.; den Tex, R.-J.; de Bakker, M.A.G.; Povel, G.D.E. 2005. Phylogenetic relationships amongst swifts and swiftlets: a multi locus approach. *Molecular Phylogenetics and Evolution* 37: 264–277.
- Valdez, E.W.; Wiles, G.F.; O'Shea, T.F. 2011. Diets of the sympatric Sheath-tailed Bat (*Emballonura semicaudatus totensis*) and Mariana Swiftlet (*Aerodramus bartschi*) on Aguiguan, Mariana Islands. *Pacific Science* 65: 301–309.
- Waugh, D.R.; Hails, C.J. 1983. Foraging ecology of a tropical aerial feeding bird guild. *Ibis* 125: 200–217.

Appendix 1. Arthropods in the diets of three swiftlets in Sabah, Malaysia: the black-nest swiftlet (*Aerodramus maximus*), the white-nest swiftlet (*Aerodramus fuciphagus*), and glossy swiftlet (*Collocalia esculenta*). Prey items were identified in food boluses obtained from black-nest and white-nest swiftlets living in the Gomantong Caves (Sabah, Malaysia) and the glossy swiftlets near Sandakan (Sabah, Malaysia). See Tarburton (2017) for details about collection and identification procedures.

Order	Family/Super family	Glossy Swiftlet	White-nest Swiftlet	Black-nest Swiftlet
Hymenoptera		639	685	744
	Formicidae	511	576	741
	Apoidea	22	1	
	Apocrita	101	108	2
	Brachonidae	-	-	1
	Colletidae	1	-	-
	Ichneumonidae	2	-	-
	Sphecidae	2	-	-
Coleoptera		136	554	5
	Bostrichidae	1	-	-
	Bruchidae	2	-	-
	Buprestidae	2	-	-
	Chrysomelidae	12	82	-
	Carabidae	-	-	1
	Curculionidae	51	6	-
	Coccinellidae	5	1	-
	Dermestidae	13	3	-
	Elateridae	4	-	-
	Histeridae	4	1	-
	Nitidulidae	2	2	-
	Ostomidae	-	7	-
	Phalocoidea	-	2	-
	Scaphididae	1	-	-
	Platypodidae	10	25	1
	Scarabeidae	-	2	-
	Scolytidae	15	303	3
	Staphylinidae	12	119	-
	Unidentified	2	1	-
Diptera		456	247	4
	Asilidae	3	-	-
	Bibionidae	2	1	-
	Chironomidae	2	-	-
	Dolichopodidae	1	-	-
	Otitidae	-	3	-
	Muscidae	-	-	1
	Mycetophilidae	7	-	-
	Nematocera	19	-	-
	Playpezidae	1	1	2
	Sepsidae	31	1	-
	Stratiomyidae	6	3	-
	Syrphidae	-	5	-

Appendix 1. continued

Order	Family/Super family	Glossy Swiftlet	White-nest Swiftlet	Black-nest Swiftlet
	Tachinidae	2	1	-
	Tephritidae	-	1	-
	Tipulidae	1	-	-
	Unidentified	381	231	1
Homoptera		27	54	4
	Aphididae	16	45	2
	Cicadellidae	2	2	-
	Fulgoroidea	7	5	2
	Membracidae	1	1	-
	Psyllidae	1	1	-
Hemiptera		2	4	1
	Aratidae	2	-	-
	Thomastocoridae	-	3	-
	Tingidae	-	1	-
	Unidentified	-	-	1
Lepidoptera		180		
	Gracillaridae	180	-	-
Thysanoptera			53	
	Phallothripidae	-	53	-
Isoptera				1
	Termitidae	-	-	1
Psocoptera			1	
	Unidentified	-	1	-
Dermaptera			1	
	Unidentified	-	1	
Araneae		16	12	1
	Unidentified	16	12	1
Total		1,456	1,611	760

Appendix 2. Orders and families of insects recorded as prey of one or more species of swiftlets (*Aerodramus*, *Collocalia*).

Hymenoptera: Formicidae, Apidae, Apocrita, Brachonidae, Colletidae, Ichneumonidae, Sphecidae, Pteromalidae, Torymidae.

Coleoptera: Bostrichidae, Bruchidae, Bupestidae, Chrosomelidae, Carabidae, Curculionidae, Coccinellidae, Dermestidae, Elateridae, Histeridae, Nitidulidae, Ostomidae, Phalocidae, Scaphididae, Scolytidae, Staphylinidae, Cryptophagidae, Mordellidae.

Diptera: Asilidae, Bibionidae, Chironomidae, Dolichopodidae, Otitidae, Muscidae, Mycetophilidae, Playpezidae, Sepsidae, Stratiomyidae, Syrphidae, Tachinidae, Tephritidae, Tipulidae, Tamypedidae, Sciaridae, Chloropida.

Homoptera: Aphididae, Cicadellidae, Fulgoridae, Membracidae, Psyllidae.

Hemiptera: Aratidae, Thomastocoridae, Tingidae.

Ephemeroptera: Ephemeridae.

Blattodea: Blattidae.

Lepidoptera: Gracillaridae.

Thysanoptera: Phallothripidae.

Isoptera: Termitidae.

Psocoptera: Pseudocaecillidae.

No families were identified for prey in the following orders: Dermaptera, Neuroptera, Strepsiptera, Phasmatodea, Orthoptera, Thysanura, Odonata, Trichoptera.

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Erect-crested penguins on the Bounty Islands: population size and trends determined from ground counts and drone surveys

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Abstract: In October 2019, an expedition to the subantarctic Bounty Islands provided the opportunity to conduct comprehensive ground counts of erect-crested penguins to assess population size and compare numbers to previous surveys. The entirety of Proclamation Island, an erect-crested penguins' stronghold, was surveyed and number of active penguin nests was determined via ground counts. Drone surveys aiming at assessing seal numbers, provided high-resolution aerial photography allowing spatial analysis of penguin nest densities on four islands, i.e. Proclamation, Tunnel, Spider, and Ranfurly Islands. A total of 2,867 penguin nests were counted on Proclamation Island between 24 and 29 October. Adjusting for the earlier timing of the survey compared to counts conducted since 1997, nest numbers were only marginally lower (~2.4%) than in 1997 and 2004 suggesting that the penguin population has remained stable for the past 20 years; a ~10% reduction in penguin numbers in 2011 seems to be related to warmer than average ocean temperatures that year. Density analysis from drone imagery showed highly heterogenous distribution of penguin nests, with birds preferring areas sheltered from prevailing south-westerly winds. This also means that a previous estimate from 1978 which relied on uniform extrapolation of nest densities to what was assumed to be suitable breeding areas substantially overestimated the true population size, thereby contributing to the species current 'endangered' threat ranking.

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INTRODUCTION

Crested penguins (*Eudyptes* spp.) are the most diverse genus of extant penguins (García-Borboroglu & Boersma 2013). The International Union for the Conservation of Nature (IUCN) currently recognizes seven different species all of which are listed as threatened or near threatened on the IUCN Red List of Threatened Species (IUCN 2019). Four species breed in the New Zealand region (Mattern & Wilson 2019a): Snares crested penguin (*E. robustus*) confined to the Snares Islands archipelago 200 km south of New Zealand's South Island; Fiordland crested penguin (tawaki; *E. pachyrhynchus*) inhabiting the southwestern coastline of New Zealand's South Island; eastern rockhopper penguin (*E. filholi*) whose populations are found on Antipodes, Campbell, and Auckland Islands; and erect-crested penguin (*E. sclateri*), which breeds on the Bounty and Antipodes Islands.

Some crested penguin populations have experienced significant population declines in the past decades (García-Borboroglu & Boersma 2013). Rising ocean temperatures and associated reduction of productivity in the subantarctic region have been identified as an important factor contributing to these declines (e.g. Weimerskirch *et al.* 2003; Hilton *et al.* 2006; Morrison *et al.* 2015).

In New Zealand, some crested penguin species seem to be faring better with Snares penguins (Hiscock & Chilvers 2016) and tawaki considered stable (Long 2017; Mattern & Long 2017) and potentially even having experienced a population increase (Mattern & Wilson 2019b). Only eastern rockhopper penguins are known to have declined substantially on the New Zealand subantarctic islands over the second half of the 20th century (Hiscock & Chilvers 2014; Morrison *et al.* 2015). Similarly, the population of erect-crested penguin on the Antipodes Islands experienced reduction in numbers with estimates of their decline ranging between 23% and 74% since the late 1970s (Taylor 2006; Davis 2013; Hiscock & Chilvers 2014).

However, the situation for erect-crested penguin on the Bounty Islands is less well known; to date there are few reliable population estimates for the species from this location (Wilson & Mattern 2019).

While early visitors to the Bounty Island provide figures of '1 million' (Anonymous 1890a) to '3 million penguins' (Anonymous 1890b), the first scientific attempt at estimating erect-crested penguin population size was made in 1978. Robertson and van Tets (1982) estimated the total penguin population to be 115,000 breeding pairs. Almost two decades later, in 1997, a survey that included comprehensive ground counts on Proclamation and Depot Islands (*Totorore* Expedition; Clarke *et al.* 1998) put the Bounty Island erect-crested penguin population at 27,956 pairs (Taylor 2000).

Both estimates used different approaches limiting the usefulness of a direct comparison (Taylor 2000; Wilson & Mattern 2019). However, a re-count on Proclamation Island in 2004 (*Mahalia* Expedition; De Roy & Amey, 2004) found no change in breeding pair numbers there suggesting that the population had remained stable between 1997 and 2004.

Erect-crested penguin population estimates for the entire Bounty Islands archipelago available to date (Robertson & van Tets 1982; Taylor 2000) were derived by extrapolation of nest density to the planar area of what was presumed suitable habitat. However, there are substantial topographical differences between and even within islands (Taylor 2006) that likely have a significant effect on nest densities, so simple extrapolation may substantially over- or underestimate true population size. Repeat counts of discrete locations such as surveys conducted on Proclamation Island (e.g. Clarke *et al.* 1998; De Roy & Amey 2004) should provide more meaningful information about the species' population trajectory.

In late October 2019, we conducted ground counts of breeding erect-crested penguins on Proclamation Island using the methods employed since the 1997 counts. Furthermore, trials of an unmanned aerial vehicle (UAV or 'camera drone') to survey New Zealand fur seals (*Arctocephalus forsteri*) (Rexer-Huber & Parker 2020) enabled aerial photographic counts of erect-crested penguins on four islands (including Proclamation Island) as well as an examination of the distribution and densities of penguins on the islands. Additional count data from 2011 have also become available. Here, we provide new information on the status of erect-crested penguins on the Bounty Islands, examine the validity of previous estimates, and discuss population developments and factors influencing penguin numbers.

METHODS

Study site

The Bounty Islands are a small archipelago comprising 18 named, unvegetated granite islets as well as several unnamed rock stacks located about 870 km due east of Stewart Island (Fig. 1). With a combined area of around 135 hectares and an average elevation of approximately 40 m, the Bounty Islands provide breeding habitat for three other species of seabirds; Salvin's albatross (*Thalassarche saluini*), fulmar prion (*Pachyptila crassirostris*), and the endemic Bounty Island shag (*Leucocarbo ranfurlyi*) (Taylor 2006). When discovered and named in 1788 by William Bligh after his ship the *HMS Bounty*, the Bounty Islands also harboured a large population of >50,000 New Zealand fur seals. However, these were reduced by sealers to just a

Bounty Islands

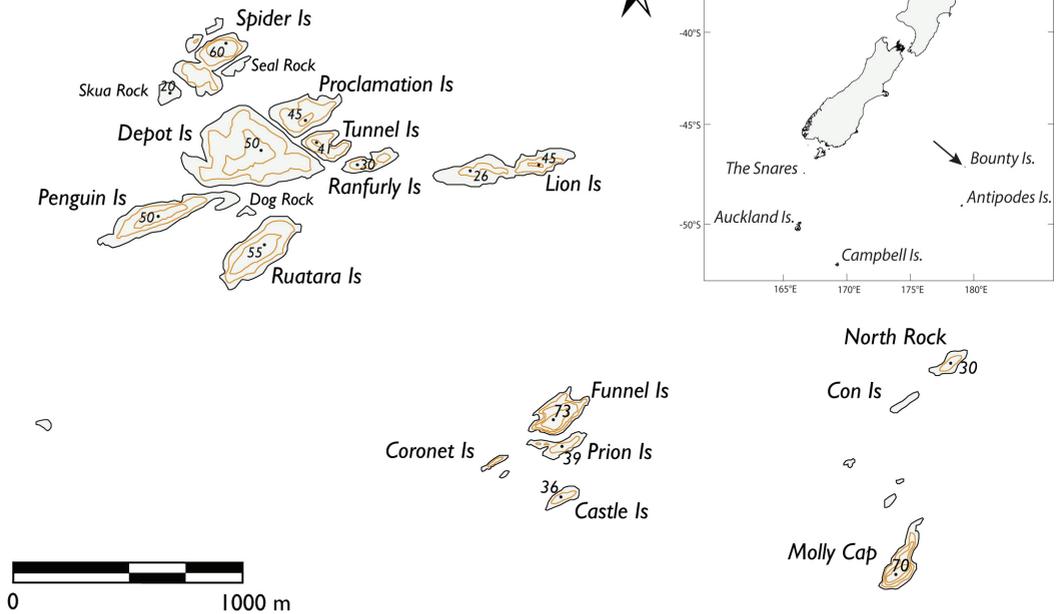


Figure 1. Map of the Bounty Island archipelago (based on LINZ Topo Map 25, 2011). Inset provides overview of New Zealand's subantarctic islands; arrow indicates location of the Bounty Islands.

few individuals in the early 1800s and the local fur seal population has been slowly recovering since the early 20th Century to about 16,000 individuals in the 1980s (Taylor 1982). The exposed, rugged nature of the archipelago makes access difficult so that only few scientific expeditions have visited the island in the past decades (Taylor 2006).

2019 Bounty Island Expedition

An expedition to the Bounty Island was conducted between 22 October and 1 November 2019 to conduct various studies ranging from deployment of satellite transmitters on Salvin's albatross and investigations of fulmar prion morphology, to ground counts of albatross and penguins (Parker *et al.* 2019) and trials of camera drone surveys of fur seals that provided the opportunity to assess penguin and albatross numbers (Rexer-Huber & Parker 2020). A team of six researchers arrived at the Bounty Islands on board the research yacht *Evohe* in the morning of 24 October. Between 24 and 29 October, the team spent three full and two half days working on Proclamation Island¹. Access to the island was difficult and only possible under reasonably calm conditions.

Ground counts of penguin nests

Following the methodology described in Clarke *et al.* (1998) and de Roy & Amey (2004), ground counts were conducted between 25 and 29 October 2019 by sectioning Proclamation Island into eight counting blocks (Fig. 2). The outlines of the blocks were established during the 1997 expedition and refined using a professional grade Global Positioning System solution (Garmin Pro XR GPS, Garmin Ltd., Schaffhausen, Switzerland) in 2004 (De Roy & Amey 2004). For this study, the GPS boundaries of the 2004 counting blocks were loaded to a handheld GPS device (Garmin GPSMAP 64s) and used in conjunction with the GPS device's track function to accurately limit counts to each counting block. GPS Exchange Format (GPX) files of the counting blocks are accessible online (<https://doi.org/10.6084/m9.figshare.12159948>).

Counts were conducted by carefully walking through each block, checking potential penguin nests for their contents either passively, or by slipping one hand under the bird to lift it up slightly from a prone position until nest contents were visible. Only nests that contained an egg were counted using a tally counter; each nest counted was then marked with a dab of blue stock marker paint to prevent double counts. Approximately 98% of the island was accessible for direct counts. Some

¹ see: Bounty Islands 2019 - <https://vimeo.com/417809116>

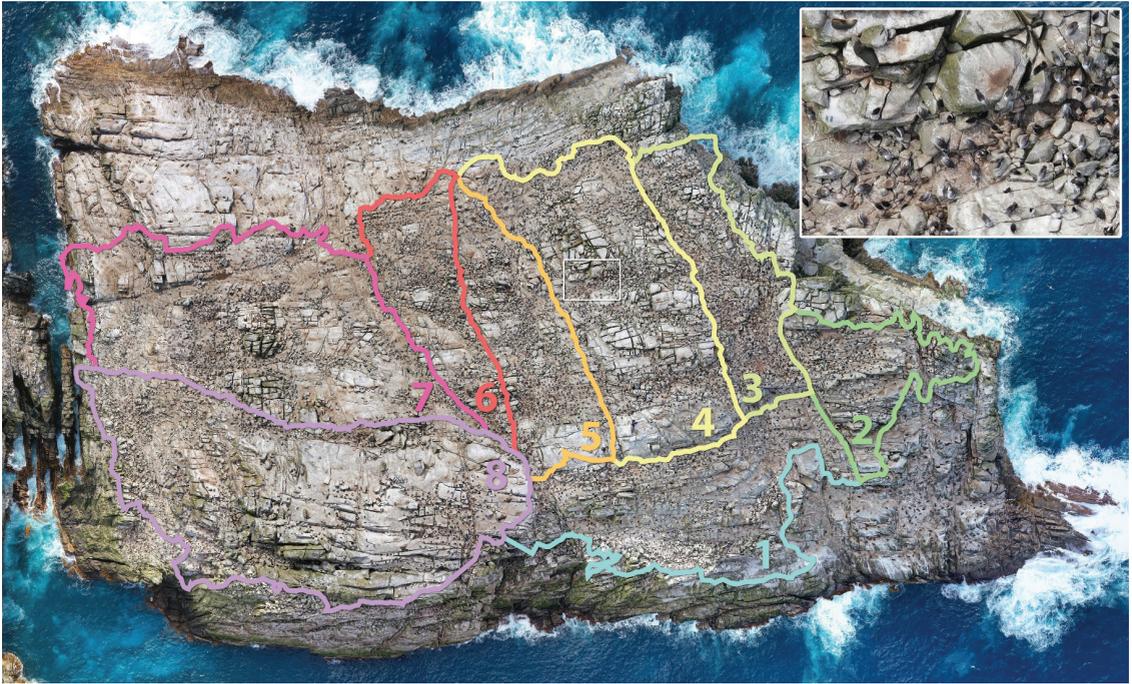


Figure 2. Composite image of Proclamation Island stitched from 799 individual images. Inset shows level of detail of the composite image; white rectangle indicates location of inset. Coloured polygons indicate the eight main counting blocks. Blocks were established during the 1997 *Totorore* Expedition (Clarke *et al.* 1998) and refined and accurately georeferenced in 2004 during the *Mahalia* Expedition (De Roy & Amey 2004).

rock ledges over steep drops in blocks 2 and 8 could not be reached on foot and had to be counted from a vantage point using binoculars. In this case, nest contents could not be determined; however, body postures (e.g. sitting semi-prone with extended brood pouch) provided an indication of whether one bird in a pair was incubating allowing an estimation of active nest numbers. Due to time constraints, as well as concerns about undue disturbance of breeding birds early in the incubation phase, we omitted the final transect counts as conducted during previous surveys that were used to assess observer errors and adjust final count results in each counting block (Clarke *et al.* 1998). All ground counts of penguin nests were conducted by a single person (TM).

Blocks 3 and 4 were counted on 25 October 2019, followed by Blocks 5, 6, and 7 on 26 October. Landing was not possible on 27 October due to unfavourable winds and high seas. Swells also prevented landing on the morning of the 28 October; after the seas eased in the afternoon, Block 8 could be counted. The ground counts were completed on 29 October with the counting of Blocks 1 and 2.

In this study, ground counts were conducted an average of 21 days earlier when compared to the

previous surveys which were conducted between 15 and 23 November. Therefore, a correction factor was applied to our counts to derive figures that are directly comparable. During the 1997 study, nest fates of 66 penguin nests were followed over the course of 50 days (14 November 1997 – 03 January 1998, JA *unpubl. data*). A total of 16.1% nests were lost during this period which translates to nest loss of 6.72% over 21 days. Our counts were adjusted by subtracting this percentage from our total counts in each block.

Camera drone imagery

We used a Mavic Pro 2 (SZ DJI Technology Ltd., Shenzhen, Guangdong China) drone which features a 20-megapixel Hasselblad L1D-20c camera mounted with a 3-axis gimbal. The camera lens' field of view was 77°, which equates to approximately 24 mm focal length of a traditional camera.

Since the effect of drone overflight on animals at this island group was unknown, trials were first conducted to assess the risk of negative effects on animals and determine actions to mitigate any such effects (Rexer-Huber & Parker 2020). All drone trials and photographic flights were conducted by one of two qualified drone pilots (KR-H and GP).

The main concerns when using drones to survey seabird populations are, (a) the potential disturbance of breeding birds by the noise created by the drone, (b) the risk of stampede of irritated seals through nesting regions, and (c) the potential for collisions of the drone with flying birds (Brisson-Curadeau *et al.* 2017; Egan *et al.* 2020; Rexter-Huber & Parker 2020). During the drone flights on the Bounty Islands penguins and albatross on the ground showed no visible reaction to the drone's presence; there was no indication of mass movement among seals; and except for black-backed gulls (*Larus dominicanus*) occasionally circling the airborne drone, no flying bird interacted with the unit (Rexter-Huber & Parker 2020).

Once parameters for safe operation were determined, flights for aerial photography were conducted. Using the software Pix4Dcapture (Pix4D Inc., Denver, Colorado, USA) the drone was programmed to fly along parallel paths within a predefined polygon outlining the island to be surveyed. The drone autonomously took photos at a 90° angle (i.e. facing straight down) and maintained an overlap of 80% between consecutive images.

Four islands were surveyed by drone: Proclamation, Spider, Tunnel, and Ranfurly (Fig. 1) on 28 and 29 October 2019. Islands were photographed at 40, 60, or 80 m above launch height (Table 1), with the launch site on Proclamation Island at ~40 m above sea level. Varying flight altitudes were due to different elevations of the islands and to fulfil trial requirements (Rexter-Huber & Parker 2020). The ground sampling distance (GSD, calculated in Pix4DCapture) depended on flight altitude so photo GSD varied from 0.94 to 1.87 cm per pixel (Table 1).

For each island, an image composite was created from respective photos using the software Image Composite Editor (Microsoft Corporation, Redwood, Washington, USA). The software automatically aligned photos, performed lens correction, and stitched the images using a

transverse Mercator projection. Stitched images are accessible online (<https://bit.ly/bounty-island-2019-data>, see Table 1 for corresponding DOIs).

Composite image analysis

Composite image analysis served two purposes. Firstly, counts of penguins were used to compare to results of the ground survey. Secondly, the image count data allowed spatial and density analysis of penguin distribution on the islands. As fur seal presence likely influences penguin distribution due to the risk of nest loss in areas with high seal densities, seal numbers and distribution were also determined.

Penguins and seals were counted in each composite image. For the Proclamation Island composite, an overlay was created outlining the eight different counting blocks, that were individually analysed. All other islands were counted in their entirety. Counts were conducted in the open-source image annotation software "DotDotGoose" (American Museum of Natural History, Centre for Biodiversity and Conservation, New York City, New York, USA; <https://github.com/persts/DotDotGoose/>).

Using the object classes "penguin single", "penguin pair", "penguin commuting", and "fur seal" each image was systematically annotated by clicking the identified object, marking it with a colour-coded dot. The software overlays a counting grid which facilitates systematic annotation and provides a dot count for each of the object classes. It also allows the export of a table containing object coordinates relative to the image dimensions. These data were used to perform a density analysis.

Spatial distribution and density analysis

Point data generated from the composite image analysis contain the pixel coordinates of each marked individual animal along the images' x

Table 1. Flight number & composite image details of drone camera surveys of erect-crested penguins and New Zealand fur seals on the Bounty Islands, October 2019.

	Proclamation Is.	Tunnel Is.	Ranfurly Is.	Spider Is.
Date	28 October 2019	29 October 2019	29 October 2019	29 October 2019
Mission No	1	3	4	5
Flight altitude (m)	40	60	60	80
Total flight time (mins)	35	12	10	30
GSD (cm/px)	0.94	1.41	1.41	1.87
Composite dimensions (px)	32,763x28,592	21,466x15,392	19,153x9,036	24,975x19,000
DOI	10.6084/ m9.figshare.10725248	10.6084/ m9.figshare.10723544	10.6084/ m9.figshare.10724828	10.6084/ m9.figshare.10724483

and y axes. For each composite image ground sampling distance was known, so that pixel values could be converted to metres by multiplying point coordinates with the corresponding GSD. As GSD was calculated automatically by the Pix4DCapture software (see above), GSD for the respective image composites was validated by measuring distances between notable landmarks discernible on both composite images and georeferenced satellite images (ESRI World Imagery & Google Maps Imagery) in ArcGIS 10.4 (ESRI Inc., Redlands, California, USA). A correction factor was calculated by averaging the differences of measurements between composite and georeferenced images for each island and applying this factor to the composite coordinates.

Converted point data were imported into ArcGIS using an equiarectangular geographic map projection (NZGD_2000_Antipodes_Island_TM_2000). Points were then grouped according to animal class and different spatial analyses were performed. We used the ArcGIS “Point Density” analysis function to determine densities for penguins and seals on all four islands. This function overlays a raster on the point data and, for each raster cell, the number of points within a defined radius (‘neighbourhood’) are totalled and divided by area of the neighbourhood. This way, the average number of points (i.e. individuals) per square metre is calculated for each grid cell. We used a raster cell size of 1 m with a neighbourhood radius of 10 m. The resulting point density raster was then transformed to isopleth polygons by using the ArcGIS ‘Contour’ function on the raster with contour intervals of 0.1 individuals/m² for penguins.

Average densities for each surveyed island were determined by calculating raster statistics. For that,

raster cells with values of individual densities of zero were omitted from the calculation to focus the statistics on breeding areas. Resulting density maps for all islands are accessible online (<https://bit.ly/bounty-island-2019-data>).

To determine the relative overlap of seal distributions with penguin breeding areas, a kernel density analysis was conducted using the Geospatial Modelling Environment (Beyer 2012) and the Kernel Smoothing ‘ks’ package run in R (R Core Team & R Development Core Team 2014). The resulting kde rasters were used to calculate isopleths delineating the 0.5 kernel density quantiles which outline core occupancy areas (i.e. regions where 50% of all counted animals were located).

Penguin presence on other islands

To supplement ground and drone surveys, penguin presence on the other islands of the Bounty Islands archipelago was determined via ship-based observations. On 29 October 2019, the *Evohe* circumnavigated the remaining islands to allow scan checks of occupancy, using binoculars. Reliable counts were impossible due to the varying topography of the islands, so that penguins were classified as either ‘abundant’ (breeding or presumed breeding), ‘rare’, or ‘absent’. The boat survey was conducted by AJDT.

RESULTS

Ground counts

A total of 2,867 active penguin nests were counted for all blocks (Table 2) on Proclamation Island during a cumulative search time of 22 hours. Many nests were still occupied by pairs; unfortunately,

Table 2. Numbers of erect-crested penguin nests on the Bounty Island from ground counts on Proclamation Island 1997, 2004, 2011, and 2019. For 2019, adjusted counts are given to account for the difference in timing compared to the previous surveys (see Methods for details); unadjusted counts are given in parentheses.

	12–16 November 1997 (Clarke <i>et al.</i> 1998)	15–23 November 2004 (De Roy & Amey 2004)	15–23 November 2011 (JA <i>unpubl. data</i>)	25–29 October 2019 (this study)
Proclamation Is.				
Block 1	313	325	305	229 (243)
Block 2	112	108	95	124 (132)
Block 3	231	313	284	356 (382)
Block 4	337	316	356	331 (359)
Block 5	258	305	315	352 (381)
Block 6	257	195	151	150 (161)
Block 7	581	370	339	438 (469)
Block 8	547	785	669	696 (740)
Total	2,743	2,717	2,514	2,676 (2,867)

no exact records of single vs pair nests were kept. Several pairs were not or no longer associated with a nest; to which extent these pairs represented failed breeders or non-breeders is unknown. There was evidence of failed penguin nests with abandoned or broken eggs present in the colony that often could not be reliably associated with nests and were, thus, not counted. Therefore, the total number of nests determined during the counts is lower than the actual number of nests that were established by penguins at the beginning of the season (i.e. early October; Wilson & Mattern 2019).

Compared to previous counts, adjusted nest numbers were only marginally lower during this study (Table 2). A noticeable drop of around 200 nests is apparent in 2011 compared to the previous two surveys, while numbers have picked up again in 2019 (+353 nests compared to 2011).

Drone image counts

On 28 October 2019, conditions for the drone survey were ideal with moderate to low winds and a slightly overcast sky creating flat light with little to no shadows. On the drone composite image of Proclamation Island (28 October 2019, Fig. 2), a total of 5,468 penguins were counted (Table 3). About

two thirds of these (3,588 birds, 65%) were present in pairs, the remaining 1,880 birds were single birds. 30 penguins were counted at or close to the main landing platforms and, thus, defined as commuting. Counts from drone images taken of the other islands were complicated by the higher flight altitude reducing the level of detail in the composite images. Moreover, clear weather and sunshine on the 29 October 2019 resulted in higher contrast and an increased amount of shadow. Thus, it was sometimes difficult to distinguish between single penguins and pairs; penguins located in shadowy areas were difficult to discern. Penguin counts for Spider, Tunnel and Ranfurly Islands were lower than on Proclamation Island (Table 3); pairs were in a minority and made up 43–50% of all penguins on the three islands.

Penguin and seal densities

On Proclamation Island, relatively high penguin densities (>0.5 penguins/m²) were found on the western slopes (counting Blocks 7 and 8) that drop into the gut between Proclamation and Depot Islands.

Penguin densities varied greatly between the four islands surveyed (Figs 3a–d). Raster calculation

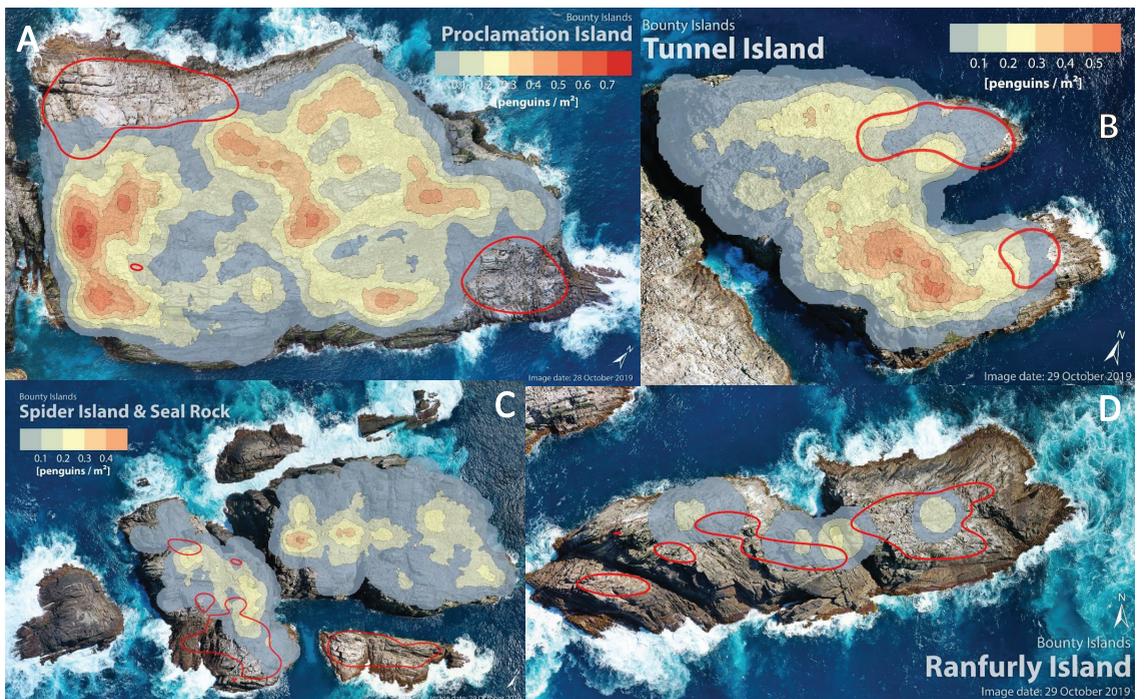


Figure 3. Point density (shaded polygons) of erect-crested penguins on four islands of the Bounty Island archipelago surveyed with camera drone on 28 & 29 October 2019. Red line features indicate 50% kernel density distribution of New Zealand fur seals.

of the point densities show that Proclamation Island had the greatest average density of penguins (0.19 individuals/m²), followed by Tunnel Island (0.15 individuals/m²), while penguin densities on Spider (0.08 individuals/m²) and Ranfurly Islands (0.03 individuals/m²) were considerably lower.

On Proclamation and Tunnel Islands, most seals were hauled out at and around the main landing platforms in the east and north of the islands (Figs 3a&b). Similarly, there was little overlap between seals and penguins on Spider Island, primarily due to there being very few seals on the larger eastern plateau and high densities of seals on seal rock where no penguins were present (Fig. 3c). Greatest overlap of penguins and seals was apparent on Ranfurly Island (Fig. 3d).

Penguin presence on other islands of the group

Besides the four surveyed islands, erect-crested penguins were recorded on six other islands in the archipelago; on four of these they were recorded as 'abundant' (Depot, Penguin, Prion Islands, and North Rock). Few penguins were recorded on Ruatara and Funnel Islands. The ship-based survey recorded penguin presence on Seal Rock; however, no penguins were visible on the drone imagery of

this rock. Erect-crested penguins were therefore present on 10 of 18 named islands of the Bounty archipelago.

DISCUSSION

Our results suggest erect-crested penguin numbers on Proclamation Island have remained relatively stable between 1997 and 2019. Our study highlights the potential of drone surveys to determine population sizes of surface nesting seabirds, illustrates the varying densities of penguins on the four islands surveyed by a drone, and allows the assessment of factors determining the heterogeneous distribution of penguin nests. The results suggest that numbers of erect-crested penguins reported in 1978 and which are a cornerstone for the species' current threat rating, likely represent a substantial overestimation.

Recent population trends in erect-crested penguins on the Bounty Islands

Surveying erect-crested penguins is a challenging undertaking as the species is confined to remote and difficult to access subantarctic islands. In the case of the Bounty Islands, the penguins are distributed

Table 3. Drone counts of erect-crested penguins and New Zealand fur seals for four of the 18 named islands in the Bounty Island archipelago, 28 & 29 October 2019.

	Erect-crested penguin			New Zealand fur seal
	<i>singles</i>	<i>pairs</i>	TOTAL	
Proclamation Island				
<i>Block 1</i>	284	184	652	23
<i>Block 2</i>	76	89	254	38
<i>Block 3</i>	289	146	581	11
<i>Block 4</i>	318	192	702	71
<i>Block 5</i>	118	197	512	30
<i>Block 6</i>	192	100	392	41
<i>Block 7</i>	191	263	717	147
<i>Block 8</i>	382	623	1,628	90
Outside*	30	-	30	651
Total	1,880	1,794	5,468	1,102
Spider Island	1,314	655	2,658	801
Tunnel Island	1,227	469	2,230	376
Ranfurly Island	53	22	97	391

* Penguins counted outside Blocks were commuting from the ocean to their nests so that no penguins were counted as pairs.

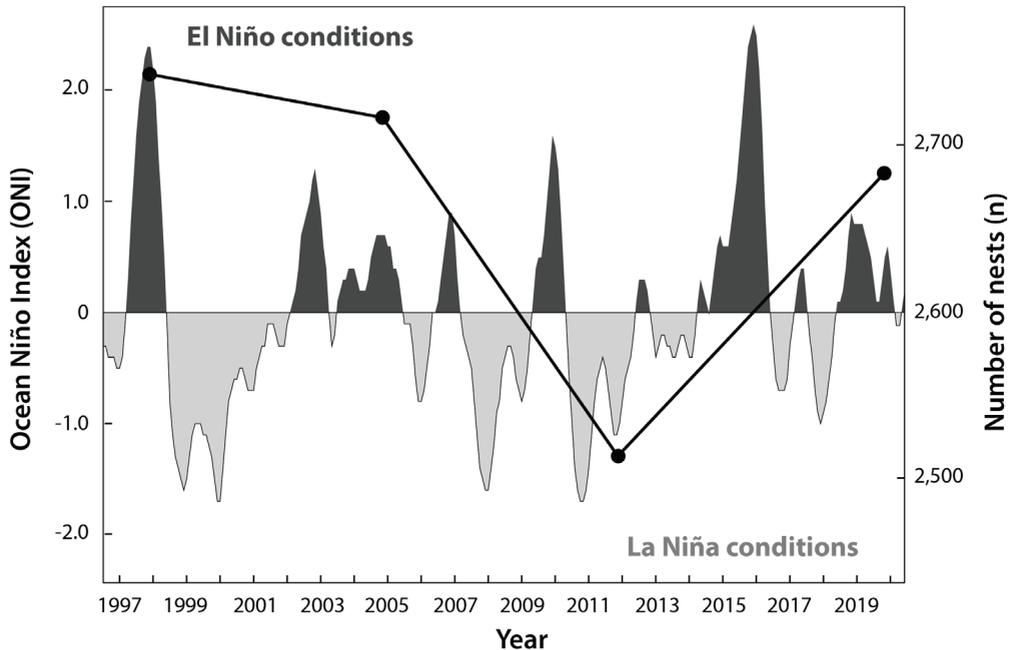


Figure 4. Ocean Niño Index (ONI*) over the time-period of the four comprehensive ground counts of erect-crested penguins on Proclamation Island (1997–2019). The ONI is a measure of the departure from normal sea surface temperatures in the east-central Pacific; positive values indicate El Niño conditions (i.e. higher than the average sea temperatures) while negative values are associated with La Niña conditions (lower sea temperatures). In the subantarctic region south-east of New Zealand this relationship is reversed so that ocean temperatures are lower during El Niño episodes and higher if La Niña conditions persist. Trajectory of erect-crested penguin nest numbers is given as black line plot.

* Data source: https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php

across 10 different islands none of which are easy to land on. Under these circumstances, it is practically impossible to conduct accurate ground-based counts of the entire erect-crested penguin population at the Bounty Islands. As a result, current estimates of the penguin breeding population on the Bounty Islands were derived from extrapolations of ground counts conducted primarily on Proclamation Island (e.g. Robertson & van Tets 1982; Taylor 2000), although some counts also have been conducted on Depot and Funnel Islands (De Roy & Amey 2004). However, extrapolation risks substantially under- or overestimating numbers, especially if penguin densities determined on one island do not apply on the others.

Comprehensive ground surveys conducted since 1997 allow robust assessment of penguin numbers on Proclamation Island. Besides Depot Island, Proclamation Island is considered to hold the greatest numbers of breeding penguins (Robertson & van Tets 1982; Clarke *et al.* 1998; De Roy & Amey 2004), so that population changes observed on that island likely reflect trends for the entire Bounty archipelago.

Comparing count results of the four surveys

shows fairly stable numbers for 1997, 2004, and 2019 (Fig. 4). In 2004, nest numbers were <1% lower than in 1997 (Table 2); and 2019 counts were 2.4% lower when compared to 1997. This latter difference could be explained by variations in the onset breeding season between the years. For example, if breeding started 8 days earlier in 2019 than in 1997, the estimated loss of 0.32% of nests per day could account for the different numbers between both years. Hence, survey results of these three years do not indicate significant changes in erect-crested penguin population size.

In 2011, numbers were between 162–229 nests (6–8%) lower when compared to the other three surveys (Table 2). While this decrease in numbers probably falls within of what can be considered normal annual variation, it nevertheless is interesting to note that it occurred in a year where the Pacific region experienced a moderate La Niña event, while all other surveys coincided with years of weak to strong El Niño conditions (Fig. 4).

La Niña result in higher-than-average ocean temperatures in the subantarctic region south-east of New Zealand, while the opposite effect occurs in years with El Niño conditions (Hopkins *et al.* 2010).

Higher than normal ocean temperatures have been found to negatively impact on yellow-eyed penguin (*Megadyptes antipodes*) survival rates (Mattern *et al.* 2017) and increasing ocean temperatures have long been thought to be a major driver for the decline of rockhopper penguins in New Zealand (Cunningham & Moors 1994; Morrison *et al.* 2015). Therefore, it appears as if warmer ocean conditions also influence erect-crested penguin numbers. Considering that numbers in 2019 were again comparable to the earlier surveys, La Niña impacts do not seem to have lasting effects on the population. However, if the trend of globally rising ocean temperatures continues (Stocker 2014), this may affect future erect-crested penguin numbers on the Bounty Islands.

At this stage, however, it can be concluded that penguin numbers on Proclamation Island have remained stable for at least the past 22 years.

Shifting of nests between counting blocks?

Considering changes in nest numbers in the eight counting blocks on Proclamation Island, it appears as if a spatial shift in penguin distribution may be occurring. There were fewer nests in Blocks 1 and 6 with a comparable increase in nest numbers in adjacent blocks (Table 3). Both blocks are located along the two main access ramps for fur seals in the East (Block 1) and Northwest (Block 6) (compare Figs 2 & 3a). Fur seal numbers appear to be slowly recovering after being hunted to local extinction on the Bounty Islands in the early 19th century (Taylor 1982). Increasing seal abundance may have a negative effect on penguin nest survival in the vicinity of the main areas used by seals, potentially causing penguins to move nesting attempts to blocks further from seals. The apparent effect of seals on penguins is further underpinned by point density distributions derived from drone imagery, which show that penguin density is lowest where fur seal concentrations are highest (Figs 3a & b).

Distribution and density of penguins and fur seals

Until recently, aerial photography has been the only feasible method of conducting animal surveys of the entire Bounty archipelago. Overflights are expensive and challenging due to often rapidly changing weather and deteriorating flight conditions (Baker *et al.* 2014). Moreover, nest numbers and breeding status cannot be determined from a plane and require ground truthing. Today, high quality camera drones provide the best of both worlds; they allow the combination of ground counts with aerial photography of unprecedented detail (e.g. Weimerskirch *et al.* 2018; Hodgson *et al.* 2018).

Spatial analysis of animal densities on the islands highlight their irregular distribution. On Proclamation Island, two main factors seem to determine where penguins concentrate – seal presence and topography.

There are no detailed data about the topography of islands in the Bounty archipelago. The topographic maps of the Bounty Islands published by Land Information New Zealand (<https://data.linz.govt.nz/layer/50860-nz-bounty-islands-topo25-maps/>) are of insufficient accuracy to allow meaningful spatial analysis. However, based on the observations of terrain on Proclamation Island, densities of penguins appear to correlate strongly with areas sheltered from wind and sea spray, such as rock gullies, channels and crevices. Highest densities of penguins were found on the western slopes of Proclamation Island located in the wind shadow of Depot Island, rendering the area the least exposed to the dominant subantarctic westerly and south-westerly winds. Similarly, the eastern slopes of Depot Island facing away from prevailing winds also appear densely populated by penguins (Fig. 5).

Topography is also affecting access to breeding areas. This could explain the lower densities of erect-crested penguins on Spider Island, where access to the main breeding plateau requires a steep and treacherous climb up an almost vertical cliff face. However, albatross densities on the island are equally low (Parker *et al. unpubl. data*) and it appears that exposure to the elements plays a far greater role in governing distribution of both species on the Bounty Islands.

The heterogenic distribution of penguins resulting from local topography will inevitably introduce a substantial error when extrapolating nest densities to what is considered suitable breeding habitat. This error can be aggravated if extrapolation factors derive from density estimates in sheltered, densely populated area. For example, while nest densities on the western slopes of Proclamation Island range mainly between 0.4 and 0.8 individuals/m², the average density across the entire island averages 0.19 individuals/m². Hence, a population size estimate extrapolated from western slope densities to the full area occupied by penguins on the island would overestimate the true number of penguins on Proclamation Island two to four-fold. Even greater would be the error if this extrapolation would be applied to low density islands like Spider and Ranfurly. Such substantial extrapolation errors are evident in the first published estimate of erect-crested penguin numbers on the Bounty Islands (Robertson & van Tets 1978) discussed below.

Validity of the 1978 population estimates

Erect-crested penguins are ranked 'endangered'



Figure 5. Photo looking west across Proclamation Island (from counting block 4) onto the eastern slopes of Depot Island, showing penguin and albatross occupation on the side of the island sheltered from southerly storms and the prevailing westerlies. Yellow line indicates the delineation of Proclamation Island (below line) and Depot Island (above).

by the IUCN red list due to a ‘suspected rapid population size reduction of $\geq 50\%$ over three generations’ (A2b) (IUCN 2019). This assessment is to a large degree based on population size estimations made by Robertson & van Tets (1982) in 1978 and subsequent survey data compiled in Taylor (2000).

Robertson & van Tets (1982) provided an estimate of 115,000 breeding pairs of erect-crested penguins on the Bounty Islands based on a rough extrapolation of an average nest density of 0.9 nests/m². The authors only provided a generalized graphic to explain how nest densities were determined (see Fig. 6 in Robertson & van Tets 1982). This density value was then uniformly applied to land area presumed to be suitable for breeding after ‘plotting the breeding areas of birds from visual mapping and air photographs’ (see Fig. 2 in Robertson & van Tets 1982). For Proclamation Island, this resulted in an estimate of 15,580 breeding pairs of erect-crested penguins (Taylor 2000), which is over five times the counts of about 2,700 breeding pairs between 1997 and 2019 (Table 2).

While comparing these figures directly is

problematic due to the lack of reproducible methods in Robertson & van Tets (1982), the discrepancy raises the question about whether the erect-crested penguin has indeed undergone a significant population decline prior to 1997, or if the earlier figures represent an overestimation of penguin numbers.

Aerial photographs from 7 November 1978 and 15 January 1998 were analysed in the early 2000s (JA *unpubl. data*). In these photographs counting Blocks 2–7 were visible, and penguins and albatross could adequately be distinguished and counted. The 1978 counts gave 1,400 penguins; the 1998 counts resulted in 1,118 penguins. However, the photos were taken during different stages in the breeding cycle (i.e. incubation in 1978, post guard in 1998), so at least a part of the lower numbers in the 1998 photographs can be attributed to ongoing nest loss over the breeding period. Applying the nest loss correction factor (0.32 nests/day, see above) to adjust the 7 November 1978 counts to account for the 69-day-difference to 15 January would result in 1,126 penguins, i.e. differing only by eight nests from the 1998 counts. Even if the birds present in

the 1998 photograph are mostly pre-fledging chicks, it can be assumed that most breeding adults were at sea to acquire food for their offspring at the time of the photograph so that counts still provide an adequate representation of nest numbers.

Therefore, the population size estimate published by Robertson & van Tets (1982) must be considered a substantial overestimation of the actual population size of erect-crested penguins on the Bounty Islands at that time. Hence, only data recorded since the 1997 ground survey provide robust information about population trends and suggest a stable population within the Bounty archipelago.

In contrast, erect-crested penguin numbers have declined in the past decades on the Antipodes Island, the species' other breeding stronghold 200 km south of the Bounty Islands. Between 1995 and 2011 a 23% difference in breeding pairs was recorded on the Antipodes Island (Hiscock & Chilvers 2014). A subsequent survey in 2014 found a further drop in nest numbers at those colonies censused by an average 23%, with landslides burying whole colonies during severe storms being a major factor of this decline (Chilvers & Hiscock 2019). The lack of topsoil on the Bounty Islands means that landslides pose no risk to the local penguin population, although the projected higher frequency and increased severity of storms (Hoegh-Guldberg *et al.* 2018) may become problematic for penguins in the more exposed areas of the archipelago in the future.

Historic population size of erect-crested penguins on the Bounty Islands

While the reports of 'millions of penguins' (e.g. Anonymous 1890a) likely exaggerate the true numbers of penguins in the late 1800s, some historic photography (e.g. Ref: 1/2-056479-F. Alexander Turnbull Library, Wellington, New Zealand, <https://natlib.govt.nz/records/23196041>) seem to suggest a higher density of penguins on the Bounty Islands than what we observed during this survey. However, bear in mind that many of the historic photos were taken in February, i.e. during the moult when most of the erect-crested penguins would be confined to land (Wilson & Mattern 2019). At this stage, all breeding birds plus non-breeders are present on the island which more than doubles the numbers ashore compared to our survey which occurred when many breeders were at sea. Nevertheless, analysis of historic photos may allow it to determine if erect-crested penguins used to be more numerous on the Bounty Islands in the past. Photos taken by William Dougall in February 1888 (held by Te Papa, <https://collections.tepapa.govt.nz/agent/6043>) and Rollo Beck in February 1926 (held by the American Museum of Natural History) provide clearly identifiable vantage points on Depot

and Proclamation Islands that allow reproduction of their photos and subsequent comparative bird counts. Both visited the islands during the late breeding/early moulting season so that penguin numbers visible are not comparable to census data presented here. Therefore, to adequately investigate historic trends using this method it would be necessary to reproduce historic photos in February/March.

CONCLUSIONS

The erect-crested penguin remains the least known and least studied penguin species in the world (Mattern & Wilson 2019a). This study demonstrates how a lack of data contributes to threat classifications that paint a seemingly grim picture of New Zealand's state of conservation (IUCN 2019). Yet, despite its 'endangered' classification, at least the Bounty Island population of erect-crested penguins appears to remain stable in contrast to the species' ongoing decline on the Antipodes Islands located 200 km to the south. It is important that erect-crested penguins receive closer scientific attention. Further research is vital to avoid future decisions for the species' conservation remaining based on sketchy or invalid assumptions. Conservation is most effective when it is based on prior knowledge of species ecology (Ropert-Coudert *et al.* 2019) and the current lack of data could prove fatal if the erect-crested penguin experiences more severe population declines, as has already been documented in other New Zealand penguin species (e.g. Morrison *et al.* 2015; Mattern *et al.* 2017).

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LITERATURE CITED

- Anonymous. 1890a. The Islands of the Far South. The Hinemoa's Cruise - VII. The Bounty Islands. *Otago Witness*: 35. <https://paperspast.natlib.govt.nz/newspapers/OW18900313.2.96>
- Anonymous. 1890b. Destruction of sea birds:

- penguin threatened with extermination. *The Press*: 6. <https://paperspast.natlib.govt.nz/newspapers/CHP18900815.2.61>
- Baker, B.G.; Jenz, K.; Sagar, P. 2014. 2013 Aerial survey of Salvin's albatross at the Bounty Islands. Wellington, New Zealand, <https://deepwatergroup.org/wp-content/uploads/2015/11/SEA2015P2D6-Bounties-pop2012-06-salvins-albatross-aerial-population-estimate.pdf>
- Beyer, H.L. 2012. Geospatial Modelling Environment (Version 0.7.3.0). <http://www.spatial ecology.com/gme>
- Brisson-Curadeau, É.; Bird, D.; Burke, C.; Fifield, D.A.; Pace, P.; Sherley, R.B.; Elliott, K.H. 2017. Seabird species vary in behavioural response to drone census. *Scientific Reports* 7(1): 17884. doi: 10.1038/s41598-017-18202-3
- Chilvers, B.L.; Hiscock, J.A. 2019. Significant decline of endangered Antipodes Island penguins: Is extreme weather an additional impact? *Aquatic Conservation: Marine and Freshwater Ecosystems* 29(4): 546–553. doi: 10.1002/aqc.3034
- Clarke, G.; Booth, A.; Amey, J.M. 1998. The "Totorore" Expedition to the Bounty Islands, New Zealand. Report to Department of Conservation, Wellington. doi: 10.6084/m9.figshare.12408011
- Cunningham, D.M.; Moors, P.J. 1994. The decline of Rockhopper Penguins *Eudyptes chrysochome* at Campbell Island, Southern Ocean and the influence of rising sea temperatures. *Emu* 94: 27–36. doi: 10.1071/MU9940027
- Davis, L.S. 2013. Erect-crested penguin (*Eudyptes sclateri*). pp. 144–151. In: García-Borboroglu, P.; Boersma P.D. (eds.) *Penguins: Natural History and Conservation*. Seattle & London, University of Washington Press.
- Egan, C.C.; Blackwell, B.F.; Fernández-Juricic, E.; Klug, P.E. 2020. Testing a key assumption of using drones as frightening devices: Do birds perceive drones as risky? *The Condor* 122: 1–15. doi: 10.1093/condor/duaa014
- García-Borboroglu, P.; Boersma, P.D. 2013. *Penguins: Natural History and Conservation*. Seattle & London, University of Washington Press.
- Hilton, G.M.; Thompson, D.R.; Sagar, P.M.; Cuthbert, R.J.; Cherel, Y.; Bury, S.J. 2006. A stable isotopic investigation into the causes of decline in a sub-Antarctic predator, the rockhopper penguin *Eudyptes chrysochome*. *Global Change Biology* 12: 611–625. doi: 10.1111/j.1365-2486.2006.01130.x
- Hiscock, J.; Chilvers, L. 2016. Snares crested penguins *Eudyptes robustus* population estimates 2000–2013. *New Zealand Journal of Ecology* 40(1): 108–113. doi: 10.20417/nzjecol.40.12
- Hiscock, J.A.; Chilvers, B.L. 2014. Declining eastern rockhopper (*Eudyptes filholi*) and erect-crested (*E. sclateri*) penguins on the Antipodes Islands, New Zealand. *New Zealand Journal of Ecology* 38(1): 124–131.
- Hodgson, J.C.; Mott, R.; Baylis, S.M.; Pham, T.T.; Wotherspoon, S.; Kilpatrick, A.D.; Raja Segaran, R.; Reid, I.; Terauds, A.; Koh, L.P. 2018. Drones count wildlife more accurately and precisely than humans. *Methods in Ecology and Evolution* 9(5): 1160–1167. doi: 10.1111/2041-210X.12974
- Hopkins, J.; Shaw, A.G.P.; Challenor, P. 2010. The Southland Front, New Zealand: Variability and ENSO correlations. *Continental Shelf Research* 30(14): 1535–1548. doi: 10.1016/j.csr.2010.05.016
- Hoegh-Guldberg, O.; Jacob, D.; Bindi, M.; Brown, S.; Camilloni, I.; Diedhiou, A.; Djalante, R.; Ebi, K.; Engelbrecht, F.; Guiot, J.; Hijioka, Y. 2018. Impacts of 1.5°C of Global Warming on Natural and Human Systems. *Global Warming of 1.5°C. An IPCC Special Report*. IPCC Secretariat, pp. 175–311.
- IUCN. 2019. The IUCN Red List of Threatened Species. Version 2019-2. <https://www.iucnredlist.org>
- Long, R. 2017. A survey of Fiordland crested penguins / tawaki (*Eudyptes pachyrhynchus*) from Cascade River to Martins Bay, South Westland, New Zealand, 2014. *Notornis*. 64: 206–210.
- Mattern, T.; Long, R. 2017. Survey and population size estimate of Fiordland penguin / tawaki (*Eudyptes pachyrhynchus*) in Milford Sound / Piopiotahi, New Zealand. *Notornis*. 64(2): 97–101.
- Mattern, T.; Meyer, S.; Ellenberg, U.; Houston, D.M.; Darby, J.T.; Young, M.J.; van Heezik, Y.; Seddon, P.J. 2017. Quantifying climate change impacts emphasises the importance of managing regional threats in the endangered Yellow-eyed penguin. *PeerJ* 5(5): e3272. doi: 10.7717/peerj.3272
- Mattern, T.; Wilson, K.-J. 2019a. State of Penguins. Dunedin, New Zealand, New Zealand Penguin Initiative, Dunedin, New Zealand. doi: 10.36617/SoP
- Mattern, T.; Wilson, K.-J. 2019b. Fiordland penguin / tawaki. In: *State of Penguins*. Dunedin, New Zealand, New Zealand Penguin Initiative, Dunedin, New Zealand. doi: 10.36617/SoP.tawaki.2019-04
- Morrison, K.W.; Battley, P.F.; Sagar, P.M.; Thompson, D.R. 2015. Population dynamics of Eastern Rockhopper Penguins on Campbell Island in relation to sea surface temperature 1942–2012: current warming hiatus pauses a long-term decline. *Polar Biology* 38(2): 163–177. doi: 10.1007/s00300-014-1575-x
- Parker, G.C.; Mattern, T.; Tennyson, A.J.D.; Rexer-Huber, K.; Sagar, P.M. 2019. Trip report to DOC

- Murihiku: Bounty Islands seabird and fur seal research, Proclamation Island, 22 October 2019 – 1 November 2019. Wellington, Department of Conservation, New Zealand. doi: 10.6084/m9.figshare.12408029.v1
- R Core Team; R Development Core Team. 2014. R: A Language and Environment for Statistical Computing. <http://www.r-project.org>
- Rexer-Huber, K.; Parker, G.C. 2020. Bounty Islands drone trials: feasibility for population assessment of NZ fur seal. Wellington, Department of Conservation, New Zealand. <https://www.doc.govt.nz/globalassets/documents/conservation/marine-and-coastal/marine-conservation-services/reports/final-reports/pop-2019-05-fur-seal-bounty-islands-final-report.pdf>
- Robertson, C.; van Tets, G. 1982. The status of the birds at the Bounty Islands. *Notornis* 29: 331–336.
- Ropert-Coudert, Y.; Chiaradia, A.; Ainley, D.; Barbosa, A.; Boersma, P.D.; Brasso, R.; Dewar, M.; Ellenberg, U.; García-Borboroglu, P.; Emmerson, L.; Hickcox, R.; Jenouvrier, S.; Kato, A.; McIntosh, R.R.; Lewis, P.; Ramírez, F.; Ruoppolo, V.; Ryan, P.G.; Seddon, P.J.; Sherley, R.B.; Vanstreels, R.E.T.; Waller, L.J.; Woehler, E.J.; Trathan, P.N. 2019. Happy feet in a hostile world? The future of penguins depends on proactive management of current and expected threats. *Frontiers in Marine Science* 6. doi: 10.3389/fmars.2019.00248
- De Roy, T.; Amey, J.M. 2004. Mahalia Bounties/Antipodes Expedition. Report to Department of Conservation, Wellington, New Zealand. doi: 10.6084/m9.figshare.12408044
- Taylor, G.A. 2000. Action plan for seabird conservation in New Zealand. Part A: threatened seabirds. Wellington, Department of Conservation, New Zealand.
- Taylor, R.H. 1982. New Zealand fur seals at the Bounty Islands. *New Zealand Journal of Marine and Freshwater Research* 16(1): 1–9. doi: 10.1080/00288330.1982.9515942
- Taylor, R.H. 2006. Straight through from London: the Antipodes and Bounty Islands, New Zealand. Christchurch, New Zealand, Heritage Expeditions New Zealand.
- Weimerskirch, H.; Inchausti, P.; Guinet, C.; Barbraud, C. 2003. Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. *Antarctic Science* 15(2): 249–256. doi: 10.1017/S0954102003001202
- Weimerskirch, H.; Prudor, A.; Schull, Q. 2018. Flights of drones over sub-Antarctic seabirds show species- and status-specific behavioural and physiological responses. *Polar Biology* 41(2): 259–266. doi: 10.1007/s00300-017-2187-z
- Wilson, K.-J.; Mattern, T. 2019. Erect-crested penguin. *In: State of Penguins*. Dunedin, New Zealand Penguin Initiative, Dunedin, New Zealand. doi: 10.36617/SoP.erec.2019-04

Dominance interactions among New Zealand albatrosses and petrels at ecotourist boats

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Abstract: Aggressive interactions among species competing for resources are common and usually asymmetric, leading to consistent dominance hierarchies. Here, we document aggressive interactions among six albatross and three petrel species off southern New Zealand, in response to supplemental food provided by ecotourism boats. For species with sufficient sampling, we found a consistent dominance hierarchy, with *Diomedea antipodensis gibsoni* > *D. epomophora* > *Macronectes halli* > *Thalassarche cauta* > *T. salvini* > *T. bulleri* > *Daption capense*. The heavier species was dominant in most species pairs. Dominant species monopolised the food provided by displacing subordinates. However, subordinate species appeared to gain access to some food through fast responses, greater manoeuvrability, and feeding on small pieces of food ignored by dominants. Similar congregations and interactions at natural food sources suggest that dominance hierarchies may play an important role in structuring the diverse seabird communities in the southern oceans.

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Keywords: dominance interactions, albatross, petrel, interference competition, behavioural dominance, aggressive interactions, seabird communities

INTRODUCTION

Interference competition plays a central role in the structuring of ecological communities (Morse 1974; Persson 1985; Martin 2015; Grether *et al.* 2017), particularly among closely related species that share ecological traits, preferences, and resources (Martin & Ghalambor 2014). Aggressive, competitive interactions among species are usually asymmetric, leading to consistent selective pressures acting on species as a function of their position within a dominance hierarchy (Morse 1974; Freshwater *et al.* 2014; Martin *et al.* 2017). The extent to which

these dominance interactions influence the traits and distributions of species is poorly known, in part, because dominance relationships among most species are undescribed (Martin *et al.* 2020).

Here, we document dominance relationships among albatrosses and petrels in a diverse marine community in New Zealand. We first summarise the outcomes of aggressive contests among nine focal species, and use these data to test for consistent dominance relationships among pairs of species. We then qualitatively describe the behaviour and ecology of focal species in the context of their dominance and relative body mass. All data and observations came from albatrosses and petrels foraging on fish discards provided by ecotourism operators in southern New Zealand.

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METHODS

Study area

We recorded the outcomes of aggressive interactions among albatrosses and petrels that congregated behind ecotourism boats off Stewart Island/Rakiura, Southland (three trips, 24.5 hours total, 14–28 February 2020), and off Kaikoura, Canterbury (three trips, 6.5 hours total, 5–13 March 2020), New Zealand (Fig. 1). Stewart Island/Rakiura observations came from waters east of the island, from Halfmoon Bay (Oban) south to Wreck Reef and surrounding areas. Kaikoura observations came from areas offshore from South Bay to Goose Bay (The Sea Mount, The Royal, South Point, The Lump, The Outer Hole, and Trench off Barney's Rock). We obtained additional data from videos recorded by other observers and posted to YouTube (<https://www.youtube.com/>) or archived with the Macaulay Library (<https://www.macaulaylibrary.org/>), mostly recorded at Kaikoura, but with additional video recorded at Stewart Island/Rakiura and at an unspecified location in New Zealand.

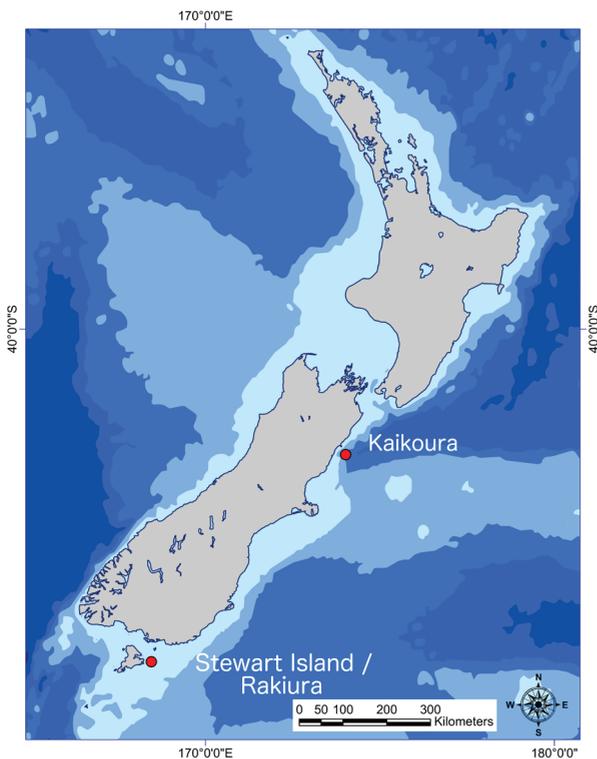


Figure 1. Map of New Zealand, showing the general locations of the two study sites (red dots). Boats moved around these sites, and thus dots show only the general locations. Shaded oceans show water depths of 0–200m, 200–1,000m, 1,000–2,000m, 2,000–3,000m, and 3,000–4,000m as progressively darker shades of blue. Map courtesy of Natural Earth (naturalearthdata.com).

Focal species

We recorded the outcomes of aggressive interactions involving six species of albatross (Procellariiformes: Diomedidae): the Gibson's subspecies of Antipodean Albatross (*Diomedea antipodensis gibsoni*), Southern Royal Albatross (*Diomedea epomophora*), Black-browed Mollymawk (*Thalassarche melanophris*), Buller's Mollymawk (*Thalassarche bulleri*), White-capped Mollymawk (*Thalassarche cauta*), and Salvin's Mollymawk (*Thalassarche salvini*). We did not try to identify subspecies of *T. bulleri* or *T. cauta*; most or all *T. cauta* were likely *T. c. steadi* based on bill colouration and geographic location, while both *T. b. bulleri* and *T. b. platei* appeared to be present based on bill and head colouration and bill shape (Howell & Zufelt 2019), studied in photographs taken on the trips. We also recorded the outcomes of aggressive interactions involving three species of petrels (Procellariiformes: Procellariidae): Northern Giant Petrel (*Macronectes halli*), Cape Petrel (*Daption capense*), and White-chinned Petrel (*Procellaria aequinoctialis*). Focal species at Stewart Island/Rakiura were: *D. epomophora*, *T. bulleri*, *T. cauta*, *T. salvini*, and *D. capense*; focal species at Kaikoura were: *D. a. gibsoni*, *D. epomophora*, *T. cauta*, *T. salvini*, *M. halli*, *D. capense*, and *P. aequinoctialis*. Observations of aggressive contests involving *T. melanophris* came from online video exclusively. Birds were initially identified by expert tour leaders on the ecotourism trips (see Acknowledgements); birds and interactions recorded on video were identified using Howell & Zufelt (2019). It was not possible to estimate exact numbers of each focal species on each trip, but off Stewart Island/Rakiura, the minimum numbers of individuals recorded on each trip (range of minimum estimates across trips): *D. epomophora*: 10–30, *T. bulleri*: 5–10, *T. cauta*: 60–120, *T. salvini*: 6–20, *Daption capense*: 1–40. Other species of seabirds were observed during Stewart Island/Rakiura trips (e.g. Wandering/Antipodean Albatross [*Diomedea exulans/antipodensis*], Northern Royal Albatross [*Diomedea sanfordi*], *M. halli*, *P. aequinoctialis*); however, we did not observe these species engaging in aggressive contests for food around the boat. Off Kaikoura, the numbers of focal species per trip (range of estimates across trips) were: *D. antipodensis gibsoni*: 5–7, *D. epomophora*: 1–5, *T. cauta*: 2–4, *T. salvini*: 2–3, *M. halli*: 7–14, *Daption capense*: 20–40, *P. aequinoctialis*: 2–8. Again, other species were observed during Kaikoura trips (e.g. *T. melanophris*, *T. bulleri*, Westland Petrel [*Procellaria westlandica*]), but we did not observe these species engaging in aggressive contests. Numbers are minimum estimates because birds were not marked, and some birds followed the boat while others left and new birds arrived. Two other procellariids also fed on fish discards from our boats at Stewart

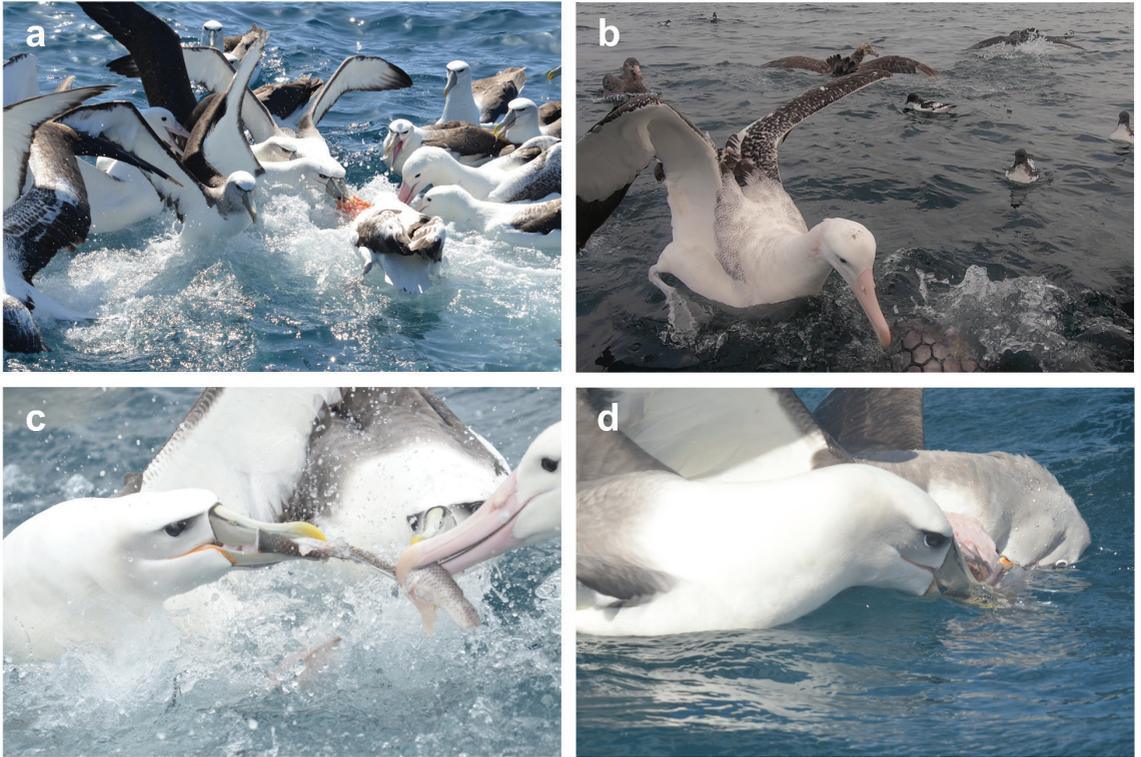


Figure 2. Albatrosses and petrels compete for fish discards behind ecotourism boats in southern New Zealand. (a) *Diomedea epomophora*, *Thalassarche cauta*, and *T. salvini* (front, centre-left) compete for fish scraps off Stewart Island/Rakiura, February 2020. (b) *Diomedea antipodensis gibsoni* controls fish within a mesh container, with *Macroneustes halli* and *Daption capense* in the background, off Kaikoura, March 2020. Photo from video. (c) *Thalassarche cauta* and *Diomedea epomophora* pull at scraps of fish off Stewart Island/Rakiura, February 2020. (d) *Thalassarche cauta* forces *T. salvini* under water as it attempts to take away its fish off Stewart Island/Rakiura, February 2020.

Island/Rakiura: Short-tailed Shearwater (*Puffinus tenuirostris*), and Sooty Shearwater (*Puffinus griseus*) (the latter on 21 February only). These species did not engage in aggressive interactions with other species; we discuss the behaviours that allowed them to feed without interacting directly with the other species.

Food provisioning

All trips were commercial ecotourism excursions that used fish discards to attract seabirds to the boats. None of the trips were research driven; we simply joined pre-planned ecotourism excursions and recorded observations and video during the course of these trips. Off Stewart Island/Rakiura, tour leaders provided discards from commercial fishing, thrown individually from the back of the boat (Fig. 2a). Off Kaikoura, tour leaders provided fish discards within a mesh container attached by rope to the back of the boat (Fig. 2b).

Dominance interactions

We recorded the outcomes of aggressive interactions between two individuals of different focal species, where there was a clear winner (dominant) and loser (subordinate). These interactions are referred to as 'dominance interactions'. Aggressive interactions incorporated, (1) chases, where one species actively pursued another in the air or on the water, (2) supplants/displacements, where one species flew, lunged, pushed, pecked, or bit at another species, causing the other species to leave its location, (3) fights, where two species pecked, bit, grabbed, grappled, or hit (e.g. with wings) each other, resulting in the losing species retreating from the interaction, and (4) kleptoparasitism, where one species aggressively engaged another species that was in possession of food, successfully taking the food away from the other species (Freshwater *et al.* 2014). We excluded observations that involved more than one individual of each species (following Freshwater *et al.* 2014) because larger groups

may have an advantage in aggressive contests, although we observed no evidence of individuals coordinating their aggression towards others. We also excluded cases where two (or more) birds had a hold on the same fish, pulling in different directions (Fig. 2c), because the fish often ripped apart, providing both individuals with some food. In these cases, dominance interactions typically did not occur – no one individual was in control of the fish, and any individual trying to displace, supplant, or fight directly with another individual would lose the fish to one or more of the many other competing individuals. To the categories of Freshwater *et al.* (2014), we added cases of active avoidance, where one individual quickly moved out of the way of another individual, even if the second individual did not use aggressive behaviours like lunging, biting, or bill clacking; all avoidance interactions were taken from video so that we could verify that the behaviour of the first (subordinate) individual occurred in response to the second. We included these avoidance behaviours in our study because they were common in some smaller species (*T. bulleri*, *Daption capense*) that actively avoided close proximity to larger species, and thus avoided pecking, biting, and other more overt interactions.

We obtained data on the outcomes of aggressive interactions among birds from both direct observations on the boats and from videos later transcribed. We recorded videos using a GoPro HERO7 Black video recorder (GoPro Inc., San Mateo, California, USA). For Stewart Island/Rakiura, we recorded the outcomes of 117 interactions from direct observations and 123 interactions from 123.5 minutes of recorded video. For Kaikoura, we recorded the outcomes of 73 interactions from direct observations and 182 interactions from 40.6 minutes of recorded video. We supplemented these data with data on the outcomes of 27 interactions from videos available online¹.

Mass

Larger mass provides an advantage in aggressive contests among birds (Morse 1974; Peters 1983; Robinson & Terborgh 1995), particularly among closely related species (Martin & Ghalambor 2014), and thus we compiled mass data for our focal species from Marchant & Higgins (1990) (Tables 1 & 2). We exclusively used masses of live and unemaciated adult birds. Average mass was used to test the hypothesis that larger species are typically dominant to smaller species in interactions.

Statistical analyses

We tested for asymmetric dominance relationships among our focal species pairs using binomial tests (*binom.test*; R Core Team 2018). Binomial tests detect significant deviations from equality; we tested if the number of aggressive interactions between a species pair was greater than expected by chance (i.e. $P < 0.05$), thus reflecting an asymmetry in dominance. We only conducted tests on species pairs with at least six recorded interactions, as this is the minimum sample required for a significant binomial test.

As the majority of our focal birds were not banded, we could not keep track of individuals involved in interspecific interactions. Thus, some of our interactions involved the same individuals, creating pseudoreplication in our data. We addressed this limitation by including three trips at each location, where different birds were likely to be involved in interactions on each trip. The tour boats visited a number of different sites on each trip, and although some birds followed the boat, each site clearly included new individuals. We also compiled information on as many interactions as possible, reducing the bias caused by one or a few oddly dominant or subordinate individuals.

RESULTS

Aggressive interactions

We recorded the outcomes of 522 aggressive interactions: 240 interactions from Stewart Island/Rakiura, 255 from Kaikoura, and 27 from published video from New Zealand (mostly from Kaikoura) (Tables 1 & 2). Aggressive interactions were common among species, but varied in frequency. Dominance interactions among species averaged 0.70/minute off Stewart Island/Rakiura (range 0–5.2/minute) and 4.0/minute off Kaikoura (range 0–10.0/minute) across all birds visible in the video frame (video clips ranged from 2–386 seconds, average = 71 seconds, $n = 137$ video clips).

Aggressive interactions in Kaikoura were usually associated with control of food (either fish in the mesh container, or pieces of fish dislodged from the container). At Stewart Island/Rakiura, dominance interactions were common around the boat in the absence of food, as birds jockeyed for position in anticipation of fish being thrown. In response to fish thrown, most individuals focused on quickly obtaining and swallowing fish, with large scums of albatross pulling on pieces of fish in different directions; in these cases, dominance interactions were most evident in cases of kletoparasitism, where one individual pursued and took possession of fish initially controlled by another individual, usually by pursuing the individual in possession of the fish from the side and behind (e.g. Fig. 2d).

¹ <https://youtu.be/Ni0JsDzHvI0> (Kaikoura); <https://www.youtube.com/watch?v=wt89NjgEe0s> (Kaikoura); <https://www.youtube.com/watch?v=QVsF-XaGfIU> (Kaikoura); <https://www.youtube.com/watch?v=pMZGCK4zyOM> (Kaikoura); https://www.youtube.com/watch?v=8Wvf_FAiCz0 (unknown location, New Zealand); <https://www.youtube.com/watch?v=Z08HcAe4ck4> (unknown location, New Zealand); and Macaulay Library ML201457441 (Stewart Island/Rakiura)

Aggressive interactions among species usually involved displacements or supplants, often enabled by open or snapping bills or biting. For example, in video, displacements/supplants made up 101 of 123 interactions (82.1%; Stewart Island/Rakiura) and 146 of 182 interactions (80.2%; Kaikoura), while avoidance occurred 17 times (13.8%, Stewart Island/Rakiura) and 36 times (24.7%, Kaikoura), respectively. Prolonged chases were uncommon other than the pursuit of birds with fish (one time, 0.8%, Stewart Island/Rakiura; zero times, Kaikoura). Kleptoparasitism occurred only two times (1.6%, Stewart Island/Rakiura; zero times, Kaikoura) on video, but was more common when fish were thrown off the back of the moving boat (Stewart Island/Rakiura) because this situation was more likely to allow one individual to gain possession of a fish before others arrived (these were too distant to video using our camera). Prolonged fights (>2 seconds) only occurred in cases where *D. epomophora* attacked *T. cauta* (recorded on two occasions on our video [1.6%], four times overall, at Stewart Island/Rakiura).

Dominance hierarchies

We observed significant asymmetries in the outcomes of all pairwise interactions among species analysed with binomial tests. *Diomedea* spp. were dominant to all other seabirds, followed by

Macronectes halli, then *Thalassarche* spp., and finally *Daption capense* (Tables 1 & 2). Within *Diomedea*, *D. antipodensis gibsoni* was dominant to *D. epomophora*; within *Thalassarche*, *T. cauta* was dominant to both *T. bulleri* and *T. salvini*, while *T. salvini* was dominant to *T. bulleri* (Table 1). The outcomes of interactions between dominant and subordinate species were typically lopsided, with subordinates rarely winning aggressive interactions (Tables 1 & 2). An exception involved interactions between *T. cauta* and *T. salvini*, where the subordinate *salvini* won 15% of the aggressive contests with *cauta* (Table 1; Stewart Island). Overall, the outcomes of aggressive interactions suggest a consistent dominance hierarchy among our focal albatross and petrel species.

Body mass and dominance

The heavier species was dominant in aggressive contests in 12/13 species pairs (92.3%; Tables 1 & 2). The only case where the lighter species was dominant involved *Diomedea*, where *D. antipodensis gibsoni* was dominant to *D. epomophora* despite *epomophora* averaging 51.0% heavier than *antipodensis gibsoni* (Table 1; Fig. 3a,b).

Behaviour and ecology of focal species

Diomedea antipodensis gibsoni – *D. antipodensis gibsoni* was the behaviourally dominant species

Table 1. Outcomes of aggressive interactions among albatross species observed off Stewart Island/Rakiura and Kaikoura, New Zealand (N=259), supplemented with observations from published video from New Zealand (N=10). ‘Species A wins’ and ‘Species B wins’ are the number of aggressive interactions won by Species A and Species B, respectively. *P* values are from binomial tests of asymmetries in the outcomes of aggressive interactions among each species pair. ‘Species A mass’ and ‘Species B mass’ provide the average mass in grams for Species A and Species B, respectively, with sample sizes in brackets, from Marchant & Higgins (1990).

Species A	Species B	Species A wins	Species B wins	<i>P</i>	Species A mass	Species B mass	Location
<i>Diomedea a. gibsoni</i>	<i>Diomedea epomophora</i>	7	0	0.0156	5,960 (10)	9,000 (18)	Kaikoura
<i>Diomedea a. gibsoni</i>	<i>Thalassarche melanophris</i>	1	0	n/a	5,960 (10)	3,613 (98)	Kaikoura
<i>Diomedea a. gibsoni</i>	<i>Thalassarche cauta</i>	8	0	0.0078	5,960 (10)	3,983 (49)	Kaikoura
<i>Diomedea a. gibsoni</i>	<i>Thalassarche salvini</i>	7	0	0.0156	5,960 (10)	3,795 (29)	Kaikoura
<i>Diomedea epomophora</i>	<i>Thalassarche melanophris</i>	2	0	n/a	9,000 (18)	3,613 (98)	unspecified
<i>Diomedea epomophora</i>	<i>Thalassarche bulleri</i>	9	0	0.0039	9,000 (18)	2,793 (78)	Stewart I.
<i>Diomedea epomophora</i>	<i>Thalassarche cauta</i>	160	0	0.0000	9,000 (18)	3,983 (49)	Stewart I.; unspecified
<i>Diomedea epomophora</i>	<i>Thalassarche salvini</i>	10	0	0.0020	9,000 (18)	3,795 (29)	Stewart I.; Kaikoura; unspecified
<i>Thalassarche cauta</i>	<i>Thalassarche bulleri</i>	32	1	0.0000	3,983 (49)	2,793 (78)	Stewart I.
<i>Thalassarche cauta</i>	<i>Thalassarche salvini</i>	22	4	0.0005	3,983 (49)	3,795 (29)	Stewart I.
<i>Thalassarche salvini</i>	<i>Thalassarche bulleri</i>	6	0	0.0313	3,795 (29)	2,793 (78)	Stewart I.

Table 2. Outcomes of aggressive interactions involving petrel species observed off Stewart Island/Rakiura and Kaikoura, New Zealand ($N=236$), supplemented with observations from published video from New Zealand ($N=17$). ‘Species A wins’ and ‘Species B wins’ are the number of aggressive interactions won by Species A and Species B, respectively. P values are from binomial tests of asymmetries in the outcomes of aggressive interactions among each species pair. ‘Species A mass’ and ‘Species B mass’ provide the average mass in grams for Species A and Species B, respectively, with sample sizes in brackets, from Marchant & Higgins (1990).

Species A	Species B	Species A wins	Species B wins	P	Species A mass	Species B mass	Location
<i>Diomedea a. gibsoni</i>	<i>Macronectes halli</i>	203	0	0.0000	5,960 (10)	4,180 (235)	Kaikoura
<i>Diomedea a. gibsoni</i>	<i>Daption capense</i>	8	0	0.0078	5,960 (10)	438 (179)	Kaikoura
<i>Diomedea epomophora</i>	<i>Macronectes halli</i>	3	0	n/a	9,000 (18)	4,180 (235)	Kaikoura; unspecified
<i>Thalassarche cauta</i>	<i>Daption capense</i>	1	0	n/a	3,983 (49)	438 (179)	Stewart I.
<i>Thalassarche salvini</i>	<i>Daption capense</i>	2	0	n/a	3,795 (29)	438 (179)	Kaikoura
<i>Thalassarche salvini</i>	<i>Procellaria aequinoctialis</i>	1	0	n/a	3,795 (29)	1,233 (80)	Kaikoura
<i>Macronectes halli</i>	<i>Thalassarche cauta</i>	1	0	n/a	4,180 (235)	3,983 (49)	Kaikoura
<i>Macronectes halli</i>	<i>Thalassarche salvini</i>	6	0	0.0313	4,180 (235)	3,795 (29)	Kaikoura
<i>Macronectes halli</i>	<i>Daption capense</i>	28	0	0.0000	4,180 (235)	438 (179)	Kaikoura

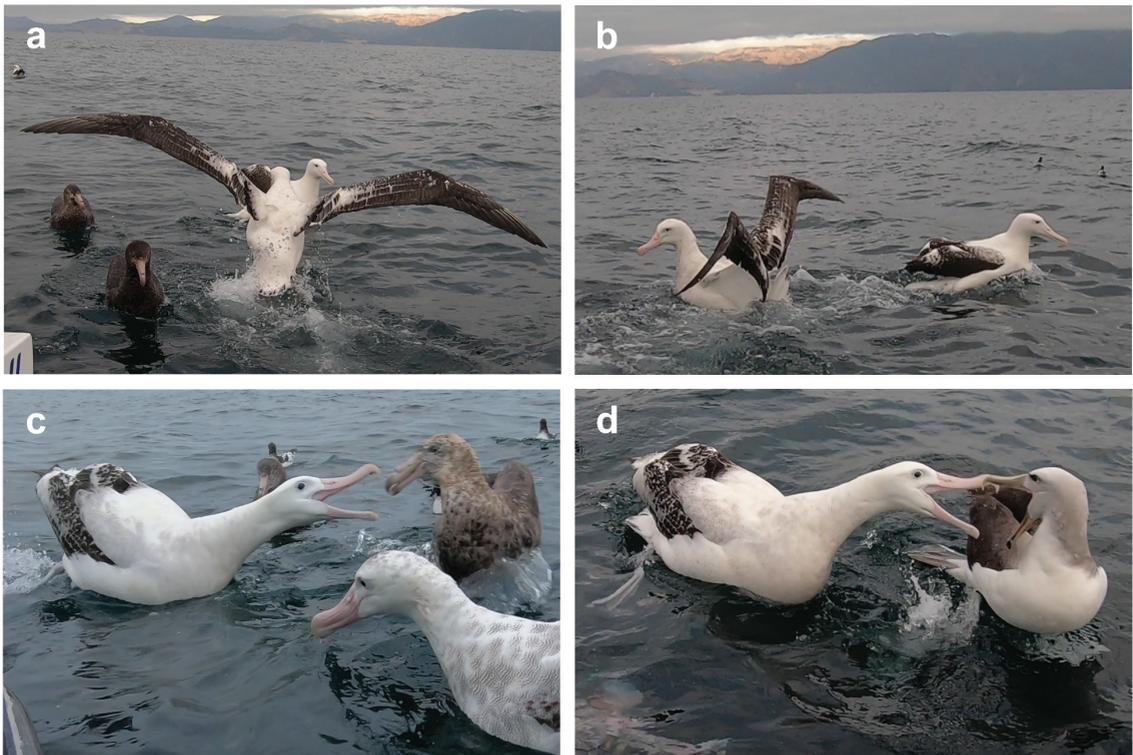


Figure 3. (a, b) *Diomedea antipodensis gibsoni* charges at the larger *D. epomophora*, forcing the latter to turn and retreat, off Kaikoura, March 2020. (a) The initial charge, followed by (b), the same birds immediately after the interaction, with *D. antipodensis gibsoni* (left) turning to return to the food, and *D. epomophora* (right) retreating. *Diomedea antipodensis gibsoni* snaps at (c) *Macronectes halli* and (d) *Thalassarche salvini* off Kaikoura, March 2020. All photos from video.

off Kaikoura. Typically, one or two individuals controlled and fed from the mesh container, snapping and sometimes chasing *M. halli* individuals that attempted to feed (Fig. 3c). The majority of interspecific aggressive interactions observed at Kaikoura involved *D. antipodensis gibsoni* snapping at *M. halli* near the fish (Table 2). *Thalassarche cauta* and *T. salvini* that attempted to feed on the fish were also chased off by *D. antipodensis gibsoni*, typically with bill snapping and a brief pursuit (Fig. 3d). *Daption capense* was occasionally displaced by *D. antipodensis gibsoni*, but more commonly ignored; *D. capense* avoided *D. antipodensis gibsoni* by scurrying out of their way. The most prolonged aggressive interactions involved conspecifics, where a dominant individual would displace the individual previously controlling the fish. Many of the behaviours used in conspecific interactions were also used in interactions with other species, including approaches with outstretched wings and upturned tail, lunges, bill clapping and chases with outstretched wings and open or snapping bills.

In contrast, *D. antipodensis gibsoni* was not observed to feed on fish off Stewart Island/Rakiura

(only two *D. exulans/antipodensis* were observed off Stewart Island/Rakiura, not identified to species; neither fed on fish near the boat).

Diomedea epomophora – *D. epomophora* was the behaviourally dominant albatross off Stewart Island/Rakiura. *Diomedea epomophora* typically responded more slowly to fish being thrown than the smaller albatrosses (*Thalassarche* spp.); even fish thrown in front of *epomophora* were typically first seized by *T. cauta*. Most *D. epomophora* waited until a piece of fish had been seized by multiple, tugging *Thalassarche*, and then muscled through to grab the fish (Fig. 4a). *Diomedea epomophora* that were able to grab onto fish were usually successful in obtaining some food, with fish often breaking apart so that multiple birds obtained parts.

Diomedea epomophora, however, often arrived too late to obtain fish, particularly when *Thalassarche* could swallow the fish quickly. Large pieces of fish that were occasionally thrown could not be quickly swallowed by *Thalassarche*, and eventually became controlled by *D. epomophora* (Fig. 4b), with

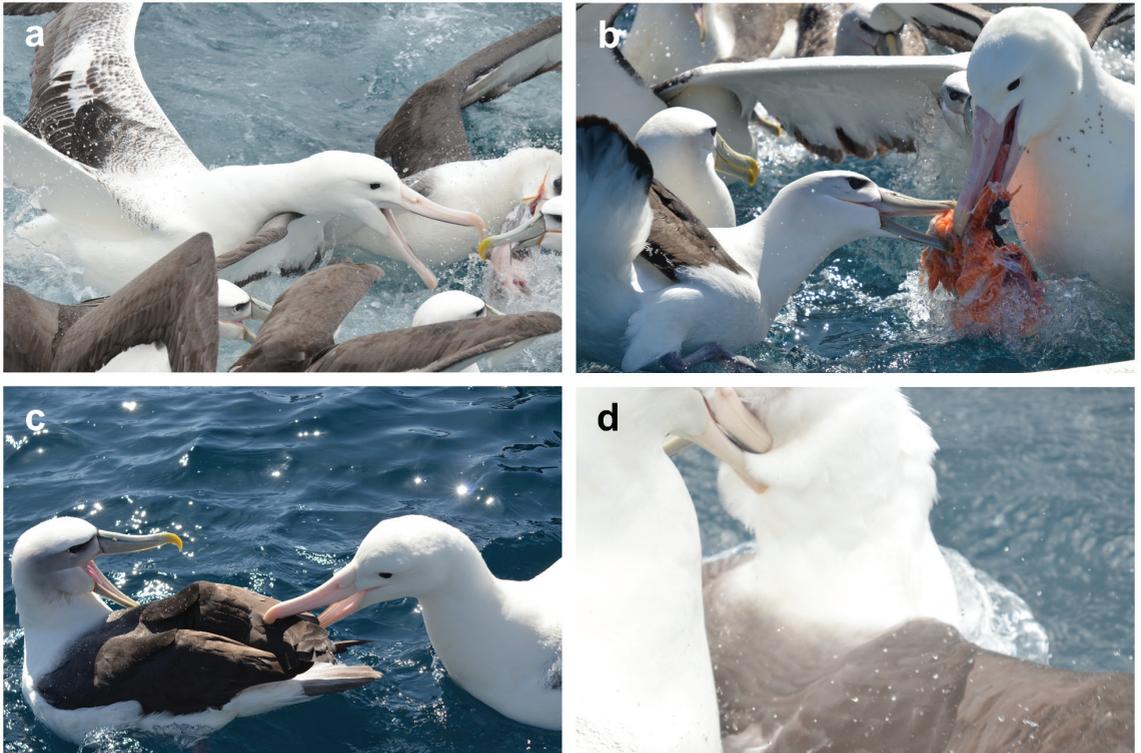


Figure 4. *Diomedea epomophora* (a) forces its way through other albatrosses to grab fish being contested by *Thalassarche cauta*, and (b) monopolises a larger piece of fish, off Stewart Island/Rakiura, February 2020. *Diomedea epomophora* bites *Thalassarche cauta* off Stewart Island/Rakiura, February 2020, (c) in the absence of fish, and (d) during contests for thrown fish.

up to six individuals pulling in different directions. We did not observe *D. epomophora* dive for fish, despite *Thalassarche* spp. regularly diving.

Most dominance interactions at Stewart Island/Rakiura involving *D. epomophora* occurred in the absence of food, as birds jockeyed for position and displaced *Thalassarche* nearby. *Diomedea epomophora* commonly bit, bill clapped, snapped at, or pulled feathers of *T. cauta* (Fig. 4c) and *T. salvini*; most *T. bulleri* avoided *D. epomophora* and quickly moved out of the way of any *epomophora*. *Diomedea epomophora* also bit *T. cauta* during scrambles for fish, including deep bites on the neck (Fig. 4d). *Diomedea epomophora* directed aggressive displays towards other species, including approaching with outstretched wings and bill (Fig. 4a), lunges, and bill clapping; these displays were similar to those used in conspecific interactions (and similar to *D. antipodensis gibsoni* aggressive displays).

The most striking examples of dominance involved repeated cases of *D. epomophora* grabbing

a *T. cauta* by the neck or head, pulling them away, and repeatedly shaking them, holding on for >20 seconds and sometimes pushing their heads under water (Fig. 5a). This behaviour was observed on four occasions off Stewart Island/Rakiura and appeared violent enough to cause injury to *T. cauta*.

At Kaikoura, *D. epomophora* was subordinate to *D. antipodensis gibsoni* and was never observed to successfully feed on the fish discards. Individuals that approached *D. antipodensis gibsoni* in control of the fish retreated when *D. antipodensis* turned to face them, lunged at them, or chased them off (Fig. 3a,b). Even when *D. epomophora* occurred in numbers (three *epomophora*, with two *D. antipodensis gibsoni* near the food), they sat at the periphery, with individuals moving towards the fish, but then retreating each time. One bird appeared to challenge *D. antipodensis gibsoni* at the food, approaching, extending its bill forward, and giving a low guttural call; this bird was immediately chased off by the *D. antipodensis gibsoni* in control of the food (Fig. 3a,b). Kaikoura *D. epomophora* included some younger birds (including first cycles), but also adults (c.f.

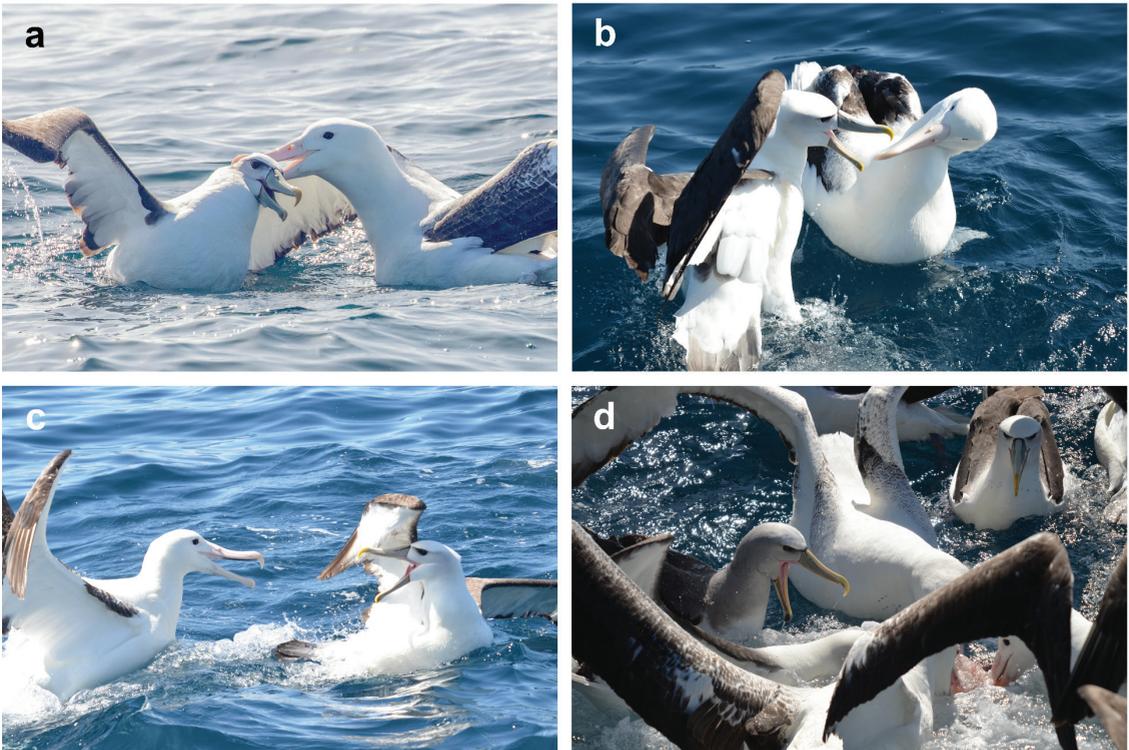


Figure 5. (a) *Diomedea epomophora* holds *Thalassarche cauta* by the neck, intermittently shaking it, off Stewart Island/Rakiura, February 2020. Photo by Dan Barton. (b, c) *Thalassarche cauta* responds to being bitten by *Diomedea epomophora* off Stewart Island/Rakiura, February 2020. (d) *Thalassarche salvini* (centre left) calls after being pushed aside by *Diomedea epomophora* and *T. cauta* off Stewart Island/Rakiura, February 2020.

Howell & Zufelt 2019), and thus the dominance of *D. antipodensis gibsoni* (which included mostly adults) seems unlikely to simply reflect age class differences between the species; all *D. epomophora* were visibly larger than the *D. antipodensis gibsoni*. *Thalassarche bulleri* – *T. bulleri* was the most subordinate albatross studied, losing almost all dominance interactions with other *Thalassarche* and *D. epomophora*, and often avoiding larger albatrosses (especially *D. epomophora*) and intense scums of albatrosses competing for fish. *Thalassarche bulleri* was observed on all trips to Stewart Island/Rakiura and regularly came in to fish scraps; only one *T. bulleri* was observed off Kaikoura, and this individual did not land or engage with other birds at fish behind the boat.

Thalassarche bulleri were generally quicker than other albatrosses, and thus sometimes obtained fish or smaller fish pieces and swallowed them before other species. This approach was particularly successful on occasions where fish were tossed from a moving boat, and thus few albatrosses were able to respond. If *T. bulleri* was the first to reach the food and swallowed it before other species of albatross had settled, then they were successful; if other *Thalassarche* (usually *T. cauta*) reached them before they could swallow the fish, then they usually lost the fish to the dominant species (e.g. Macaulay Library video, ML201457441).

When fish was thrown behind a stationary boat (as was typical), *T. bulleri* stood out as one of the few species actively scurrying away from the fish in the opposite direction of most albatrosses, avoiding the large scums. Food thrown immediately in front of *T. bulleri* was sometimes passed up by *bulleri* if larger numbers of *T. cauta* were nearby. Even when food was not present, *T. bulleri* often remained at the periphery of waiting albatrosses, especially when large numbers of *T. cauta* and *D. epomophora* had congregated. *Thalassarche bulleri* also left the area during some periods when large numbers of *T. cauta* and *D. epomophora* were present.

Nonetheless, some *T. bulleri* engaged within the albatross scums, and even participated in pulling matches with *T. cauta*, with individuals of each species pulling a piece of fish in different directions. If this led to the fish breaking, *T. bulleri* obtained part or even most of the fish. *Thalassarche bulleri* also commonly moved actively about the edges of scums, eating smaller pieces of fish that had torn off, and diving under water to secure sinking pieces of fish. *Thalassarche bulleri* was most often displaced by *T. cauta* (Table 1), with *T. cauta* individuals lunging, charging, or bill snapping; *T. bulleri* regularly scurried out of the way of both *T. cauta* and especially *D. epomophora*, avoiding more direct interactions. *Thalassarche salvini* displaced *T. bulleri* through bill snaps and lunges.

Thalassarche bulleri was rarely an initiator of aggressive interactions (Tables 1 & 2). When attacked by other species, or retreating from scums of albatrosses, *T. bulleri* sometimes elevated its head, opened its bill wide, and called, moving its head side to side, highlighting the bill, gape, and mouth colouration, and the bright ridges of skin running posterior to the gape along the cheek. Similar displays were used in interactions with conspecifics.

Thalassarche cauta – *T. cauta* was the most abundant focal species off Stewart Island/Rakiura, with large numbers gathering at the boat in response to fish discards. *Thalassarche cauta* were quick, and thus usually the first species to grab fish, with each individual trying to swallow the fish before other albatrosses. Multiple individuals would grab a fish, leading to tugging and chaotic scums of albatrosses, all battling for pieces of fish (Fig. 2a,c). *Thalassarche cauta* sometimes dove underwater for sinking pieces of fish.

Dominance interactions involving *T. cauta* occurred as they waited for fish to be thrown, and involved *T. cauta* pulling at feathers on the back half of the recipient, often from the side or behind, biting, bill snapping or clacking, and lunging. *Thalassarche cauta* also placed their bills overtop the backs of *T. salvini* and lowered their bills to the water, with their lower mandible coming in contact with the primaries or rump of the other bird; this behaviour would result in the recipient scurrying away. Bill fighting, where two birds faced each other and knocked their partly open bills repeatedly, occurred regularly between *T. cauta* and *T. salvini*, and between *T. cauta* and *D. epomophora*; however, these interactions often did not produce a clear winner (and thus were not considered dominance interactions), but instead lead to both birds backing off. All aggressive interactions of *T. cauta* that were directed toward other species were also used towards conspecifics.

Thalassarche cauta kleptoparasitised *T. bulleri* and *T. salvini*, typically by approaching a bird with a fish from the side and behind, grabbing the fish, and then wrestling the fish away by pulling back and away. One individual appeared to force the head of *T. salvini* under water as they wrestled for the fish (Fig. 2d). *Thalassarche cauta* that engaged in tugging on opposite ends of a piece of fish (e.g. Fig. 2c) often failed to obtain all of the fish from the other species.

Diomedea epomophora was particularly aggressive towards *T. cauta* (Table 1), notably on the 28 February 2020 trip when multiple individuals continuously bit at any *Thalassarche* within biting distance (usually *T. cauta*; Fig. 4c,d), creating a ring of space around each *epomophora*. *Diomedea*

epomophora were also observed grabbing *T. cauta* by their head or neck after they swallowed fish, shaking them and sometimes holding their heads under water (Fig. 5a), presumably to force *T. cauta* to regurgitate food.

Thalassarche cauta that were attacked by other species, or involved in battles for fish, often responded by opening their bills to varying degrees and calling, highlighting their bill, gape, and mouth colouration, and the bright ridges of skin running posterior to the gape along the cheek (c.f. Marchant & Higgins 1990). These birds often pointed their bills at the other albatross(es), sometimes with wings partially open (Fig. 5b,c), but usually did not bite. In large groups of albatrosses, they often held their heads up, moving their bills side to side. Similar displays were used in interactions with conspecifics.

Thalassarche cauta was also present on all Kaikoura trips, albeit in small numbers. These individuals usually stayed peripheral to the fish controlled by *D. antipodensis gibsoni*, but occasionally approached in an attempt to feed. *Diomedea antipodensis gibsoni* responded to *T. cauta* by chasing them away while bill snapping.

Thalassarche salvini – Off Stewart Island/Rakiura, *T. salvini* was consistently present around the boat, but in smaller numbers than *T. cauta*. *Thalassarche salvini* behaved similarly to *T. cauta*, intermingling with *T. cauta* near the boat in anticipation of fish being thrown, and entering into scrums in pursuit of fish. Some *T. salvini* resisted moving into scrums, while others quickly moved away when large numbers of *T. cauta* wrestled for fish. *Thalassarche salvini* kleptoparasitised a fish from *T. cauta* on one occasion when fish was being thrown behind a moving boat, approaching *T. cauta* from behind and the side to secure the fish, and then wrestling it away. On at least three other occasions, however, *T. cauta* kleptoparasitised fish from *T. salvini*. Overall, *T. cauta* was dominant to *T. salvini*, although *T. salvini* occasionally displaced *T. cauta* by feather pulling/biting, bill snapping, and lunging. In contrast, *T. salvini* dominated *T. bulleri* in all observed interactions, displacing *T. bulleri* with bill snapping or lunging, sometimes with open wings. *Thalassarche salvini* usually avoided *D. epomophora*; when it approached *D. epomophora*, it was sometimes displaced by bill clacking, biting, and lunging. *Thalassarche salvini* also dove underwater for sinking pieces of fish.

Thalassarche salvini responded to attacks by other species, and battles for fish, in similar ways to other *Thalassarche* spp.: opening their bills wide and calling, highlighting bill, gape, mouth colouration, and the bright ridges of skin running posterior to

the gape along the cheek (Fig. 5d; c.f. Marchant & Higgins 1990). *Thalassarche salvini* also often pointed their bills at the other albatross(es), sometimes with wings partially open, and with heads held up, moving their bills side to side. As with the other *Thalassarche*, *T. salvini* used similar displays in interactions with conspecifics.

At Kaikoura, *T. salvini* was present in small numbers and behaved similarly to *T. cauta*. *Thalassarche salvini* usually stayed peripheral to the fish and *D. antipodensis gibsoni*; when they occasionally moved in to attempt to feed, *D. antipodensis gibsoni* responded by chasing them away while bill snapping (Fig. 3d). *Thalassarche salvini* was also displaced by *M. halli* off Kaikoura, and sometimes avoided them. On one occasion, *T. salvini* pursued *M. halli* in possession of fish, but was unable to take it from *halli*.

Macronectes halli – Off Kaikoura, *M. halli* was prominent at fish discards and commonly aggressive towards conspecifics, vocalising, displaying with bowed heads, spread wings, and upturned tails, and fighting. Aggressive displays were also directed towards *D. antipodensis gibsoni*, however, *M. halli* was consistently subordinate in aggressive interactions with *Diomedea*. Nonetheless, *M. halli* were persistent and the only other species consistently able to feed at the mesh containers of fish controlled by *D. antipodensis gibsoni*. Most *M. halli*, however, fed away from the mesh container, gathering pieces of fish that had dislodged and drifted away. While *M. halli* were subordinate to *Diomedea* in all interactions, they bit the tails of *D. antipodensis gibsoni* twice and *D. epomophora* once, always from behind. In response, *Diomedea* adjusted their positions slightly and wagged their tails side-to-side, but were not displaced and did not turn to retaliate. *Macronectes halli* displaced *Thalassarche* spp. (mainly *T. salvini*) by lunging and biting at their heads or tails. *Macronectes halli* occasionally displaced *D. capense*, but more often, *D. capense* scurried to get out of the way of (often fighting) *M. halli* that appeared to ignore *capense*.

Daption capense – *D. capense* was present around the boats at both sites, and came in to fish discards. At both sites, *D. capense* was subordinate, often energetically and erratically moving about the other seabirds, capturing small pieces of fish scattered about the water by pecking or dipping their heads and occasionally diving. When larger pieces of fish were available (e.g. when larger birds were engaged in a fight), *D. capense* would feed at the fish; however, they actively avoided larger species and showed aggression only towards conspecifics.

Daption capense were occasionally displaced or chased by larger birds; however, most larger species appeared to ignore them, with *capense* moving to keep out of the way.

Puffinus tenuirostris and *P. griseus* – At Stewart Island/Rakiura, *P. tenuirostris* (all trips), and *P. griseus* (on 21 February only), fed on fish discards at the back of the boat, but never engaged in aggressive interactions with other species. Instead, 1–4 individuals at a time sat at the periphery of the raft of albatrosses and petrels, diving and swimming underwater to collect sinking fish from underneath the other birds, and then returning underwater again to the periphery of the group. These species dove deeper than any of the albatrosses and petrels attracted to the fish discards, and appeared to actively avoid the other species, consistent with subordinate behaviour (c.f. similar avoidance behaviours of *P. tenuirostris* from the North Atlantic; Flood & Fisher 2020).

DISCUSSION

The New Zealand albatross and petrel species studied here commonly interacted with each other and showed a consistent dominance hierarchy among species. These interactions, coupled with differences in behaviours and ecological strategies among the species, suggest that dominance hierarchies and interference competition play important roles within these seabird communities, at least when food sources are clustered and shared.

The larger albatrosses (*Diomedea*) were socially dominant and monopolised defensible food sources (Kaikoura; Fig. 2b), or obtained food in battles with other species for thrown fish (Stewart Island/Rakiura; Fig. 4a,b). Mid-sized albatrosses (*T. cauta*, *T. salvini*) were subordinate to *Diomedea*, but dominant to smaller albatross and petrel species. *Thalassarche cauta* and *salvini* were quicker to obtain thrown fish than *Diomedea*, and could out-compete larger species by obtaining and swallowing food quickly. The ability to obtain and swallow food quickly did not benefit these species when food was held within one mesh container (Kaikoura); in this case, the food source was monopolised and defended by larger *Diomedea* (and to a lesser extent, *M. halli*), suggesting that the outcome of competitive interactions depends on the distribution of the food source. The smallest and most subordinate albatross, *T. bulleri*, often fed on smaller pieces of fish, and was able to find, obtain, and swallow food quickly when fewer individuals of larger species were nearby. The smallest and most subordinate species was *Daption capense*. Individual *D. capense* moved about other seabirds, picking up small pieces of fish overlooked or passed over by larger species. The intermediate-

sized *M. halli* was aggressive and persistent at Kaikoura; some individuals were able to feed, even when the food was defended by dominant *Diomedea* (Kaikoura). In such cases, the costs of excluding persistent *M. halli* from the fish may have exceeded the benefits, as *Diomedea* in control of the fish often fed for extended periods of time, regardless of *M. halli*.

Overall, the behaviours and ecological strategies of albatrosses and petrels foraging on fish discards behind ecotourism boats matched their positions within the dominance hierarchy of species. Smaller species appeared to take advantage of peripheral resources in time (quicker to a resource), space (at the edges of large groups), and size (smaller pieces of fish), and often avoided direct competition with dominant species. Dominant species instead monopolised resources when present continuously (Kaikoura), or displaced other species from anticipated locations for acquiring fish (Stewart Island/Rakiura). The difference in food presentation at the two sites may mirror different food sources in nature, with Kaikoura (defensible food in mesh bag) more similar to a large, defensible carcass dominated by fewer, large species, and Stewart Island/Rakiura (individual fish thrown from boat) more similar to ephemeral schools of fish or squid approaching the surface that are more accessible to species with different ecological strategies (dominant and subordinate species).

The dominance hierarchies observed in this study are consistent with dominance hierarchies described in other seabird communities. For example, albatrosses and petrels off the Crozet Islands, southern Australia, and southeastern South America, and in Cook Strait, New Zealand, commonly fought over food, and showed evidence for consistent dominance hierarchies among species (Bartle 1974; Milledge 1977; Barton 1979; Weimerskirch *et al.* 1986; Harper 1987; Brothers 1991; Vaske 1991; Wood 1992; Olmos 1997; Jiménez *et al.* 2011). Similarly, Southern Giant Petrels (*Macronectes giganteus*), dominated *M. halli* in aggressive contests for seal carcasses, giving *giganteus* priority access to this food source on their shared breeding sites (Johnstone 1979; de Bruyn & Cooper 2005). *Macronectes* spp. generally dominate smaller petrels and albatrosses congregating at food (e.g. Harper 1987; Jiménez *et al.* 2011), sometimes even killing and eating smaller albatrosses and petrels (e.g. *Thalassarche carteri*, *D. capense*; Harper 1987; Marchant & Higgins 1990), but were excluded at food sources by larger albatrosses (Harper 1987; Jiménez *et al.* 2011). *Daption capense* feeding on larger prey had their prey usurped by larger *Macronectes* and albatrosses if they did not consume it quickly (Harper 1987). Interactions among other procellariid species that do not feed on carrion or

approach boats remain poorly known. However, Kermadec Petrels, (*Pterodroma neglecta*), regularly kleptoparasitise other procellariids in the eastern tropical Pacific, including Juan Fernandez Petrels (*Pterodroma externa*), and Wedge-tailed Shearwaters (*Puffinus pacificus*), appearing to mimic other kleptoparasitic species (jaegers [*Stercorarius* spp.], skuas [*Catharacta* spp.]) to improve success (Spear & Ainley 1993; Carboneras *et al.* 2016). Dominance interactions may be less common when food resources are not clustered, defensible, or easily stolen. In such cases, interference competition and dominance hierarchies may be more important for structuring communities through their influence on other resources, such as nesting burrows (e.g. Ramos *et al.* 1997; Spear & Ainley 2007).

Body mass and dominance

Larger size usually confers an advantage in aggressive contests because heavier objects can displace lighter objects more easily (Peters 1983), and heavier species often have greater muscle mass and strength, thicker defensive coverings (like skin, feathers), and larger bills, wings, and feet used in fighting (Martin & Ghalambor 2014). In our study, the larger species were dominant to smaller species in 12 of 13 species pairs (92%). Previous studies of albatrosses consistently found larger species to dominate smaller species (Bartle 1974; Milledge 1977; Barton 1979; Weimerskirch *et al.* 1986; Harper 1987; Brothers 1991; Vaske 1991; Wood 1992; Olmos 1997; Jiménez *et al.* 2011), with similar results for procellariids (Johnstone 1979; Harper 1987; Spear & Ainley 1993; Ramos *et al.* 1997; de Bruyn & Cooper 2005; Jiménez *et al.* 2011). In other birds, larger species are usually dominant to smaller species (Robinson & Terborgh 1995; Freshwater *et al.* 2014), but the importance of large size for dominance declines with evolutionary distance: larger species were dominant in 93% of species pairs within the same genus, but only 71% of species pairs in different taxonomic families (Martin & Ghalambor 2014). The consistent importance of body size in interactions involving albatrosses and petrels – even among species in different taxonomic families – may reflect behavioural and ecological similarities among seabirds and the importance of size in their aggressive interactions, or the large differences in mass between the species (Tables 1 & 2), particularly compared with other groups of birds (e.g. small passerines).

The larger size-dominance exception in our study involved *Diomedea*, where the smaller *D. antipodensis gibsoni* were consistently dominant to *D. epomophora* (Kaikoura; Fig. 3a,b). We are not sure why the smaller *Diomedea* species was dominant; however, the smaller *D. antipodensis gibsoni* may

have exhibited greater aggression, speed and manoeuvrability, or risk-taking in aggressive contests, forcing the larger *epomophora* to retreat.

While the smaller, subordinate species were usually displaced or excluded from resources, small size may have provided other advantages. Smaller organisms require less food and energy to survive and reproduce, have faster response times, and are more manoeuvrable (Peters 1983). All of these benefits appeared to play an important role in New Zealand albatrosses and petrels, with smaller species taking advantage of their speed and agility to acquire food quickly (see also Milledge 1977; Harper 1987; Wood 1992), and some species focusing on gathering smaller pieces of fish that were likely profitable only to small-sized species. Some smaller species are also more likely to come closer to boats (Vaske 1991), perhaps reflecting a greater ability to take risks and evade threats, with faster response time, and greater manoeuvrability. The different benefits of larger size (behavioural dominance) versus smaller size (speed of response, manoeuvrability, etc.) illustrate an important trade-off in albatrosses and petrels that may help species of differing sizes to coexist, particularly when resources vary in space and time (e.g. Martin 2015).

Dominance interactions and seabird community structure

While the results presented here suggest that dominance hierarchies and interference interactions among species are important selective pressures for New Zealand albatrosses and petrels, the question remains: Do interactions among species in response to fish discards behind boats tell us anything about natural communities? The interactions that we observed depended on resources being shared among species, clumped in their distribution, and limiting for our focal species. Many natural food sources used by our focal albatross and petrel species mirror these characteristics. For example, at natural food sources throughout the southern oceans, *Diomedea*, *Thalassarche*, *Macronektes*, and *Daption* feed at or near the ocean surface and regularly overlap in diet (particularly squid, fish, crustaceans, and carrion) (Barton 1979; Weimerskirch *et al.* 1986; Harper 1987; Cherel & Klages 1997). These species also congregate at food sources and interact aggressively for food under natural conditions (Weimerskirch *et al.* 1986; Harper 1987; Marchant & Higgins 1990; Harrison *et al.* 1991), similar to congregations that we observed behind ecotourism boats. While *D. capense* often forage on smaller prey ignored by our larger species (e.g. through filter feeding), they also feed on larger squid when opportunities occur (e.g. 109 g *Gonatus antarcticus*) (Harper 1987). Clustering of prey

(e.g. squid) feeding on schools of krill and other zooplankton (Harper 1987), carrion regurgitated by cetaceans (Clarke *et al.* 1981), or surface prey concentrated by predatory fish, mammals, and diving birds (e.g. penguins, Spheniscidae) (Barton 1979; Marchant & Higgins 1990; Harrison *et al.* 1991), could all lead to mixed-species congregations of feeding seabirds and competitive interactions similar to those described here (e.g. Barton 1979; Harrison *et al.* 1991).

Long-term studies of seabirds also suggest that dominance hierarchies and competitive interactions help to structure communities, even at broad spatial and temporal scales. Tropical Pacific seabird communities vary with ocean productivity: most productive regions are occupied by the largest, competitively dominant species (boobies [*Sula* spp.]), regions of mid-productivity are occupied by petrels of intermediate size and dominance (*Pterodroma externa*, *Puffinus pacificus*), and regions of low productivity are left to flocks of smaller, more energy-efficient, and subordinate species (dominated by Sooty Tern [*Onychoprion fuscatus*]) (Ballance *et al.* 1997; see also studies of seabirds in other regions, Anguita & Simeone 2016; Bellier 2019). Similarly, a long-term study of the dynamics of a recovering Mediterranean seabird community suggested that asymmetric, dominance interactions among species, mediated by differences in body size, played a central role in community assembly over time (mainly Laridae; Almaraz & Oro 2011). These previous studies suggest that the consequences of interference competition and dominance hierarchies for resource acquisition may extend to influence broad patterns of seabird distributions and community structure. How such interactions influence broader patterns of albatross and petrel distributions and community structure in the southern oceans (e.g. Phillips *et al.* 2005) remains to be discovered.

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LITERATURE CITED

- Almaraz, P.; Oro, D. 2011. Size-mediated non-trophic interactions and stochastic predation drive assembly and dynamics in a seabird community. *Ecology* 92: 1948–1958.
- Anguita, C.; Simeone, A. 2016. The shifting roles of intrinsic traits in determining seasonal feeding flock composition in seabirds. *Behavioral Ecology* 27: 501–511.
- Ballance, L.T.; Pitman, R.L.; Reilly, S.B. 1997. Seabird community structure along a productivity gradient: importance of competition and energetic constraint. *Ecology* 78: 1502–1518.
- Bartle, J.A. 1974. Seabirds of eastern Cook Strait, New Zealand, in autumn. *Notornis* 21: 135–166.
- Barton, D. 1979. Albatrosses in the western Tasman Sea. *Emu* 79: 31–35.
- Bellier, E. 2019. Variation of interspecific interactions at different ecological levels within an assemblage of Arctic marine predators. *Polar Biology* 42: 99–113.
- Brothers, N. 1991. Albatross mortality and associated bait loss in the Japanese longline fishery in the Southern Ocean. *Biological Conservation* 55: 255–268.
- Carboneras, C.; Jutglar, F.; Kirwan, G.M. 2016. Kermadec Petrel (*Pterodroma neglecta*). In: del Hoyo, J.; Elliott, A.; Sargatal, J.; Christie, D.A.; de Juana, E. (eds.) *Handbook of the birds of the world alive*. Barcelona, Lynx Edicions. <http://www.hbw.com/node/52531> Accessed: May 2020.
- Cherel, Y.; Klages, N. 1997. A review of the food of albatrosses. pp. 113–136 In: Robertson, G.; Gales, R. (eds.) *Albatross biology and conservation*. Chipping Norton, Surrey Beatty & Sons.
- Clarke, M.R.; Croxall, J.P.; Prince, P.A. 1981. Cephalopod remains in regurgitations of the Wandering Albatross *Diomedea exulans* L. at South Georgia. *British Antarctic Survey Bulletin* 54: 9–21.
- de Bruyn, P.J.N.; Cooper, J. 2005. Who's the boss? Giant petrel arrival times and interspecific interactions at a seal carcass at sub-Antarctic Marion Island. *Polar Biology* 28: 571–573.
- Flood, R.L.; Fisher, E. 2020. North Atlantic seabirds: shearwaters, Jouanin's & White-chinned Petrels. Scilly, Pelagic Birds & Birding Multimedia ID Guides.
- Freshwater, C.; Ghalambor, C.K.; Martin, P.R. 2014. Repeated patterns of trait divergence between closely related dominant and subordinate bird species. *Ecology* 95: 2334–2345.
- Grether, G.F.; Peiman, K.S.; Tobias, J.A.; Robinson, B.W. 2017. Causes and consequences of behavioral interference between species. *Trends in Ecology and Evolution* 32: 760–772.
- Harper, P.C. 1987. Feeding behaviour and other

- notes on 20 species of Procellariiformes at sea. *Notornis* 34: 169–192.
- Harrison, N.M.; Whitehouse, M.J.; Heinemann, D.; Prince, P.A.; Hunt, G.L. Jr.; Veit, R.R. 1991. Observations of multispecies seabird flocks around South Georgia. *Auk* 108: 801–810.
- Howell, S.N.G.; Zufelt, K. 2019. *Oceanic birds of the world. A photo guide*. Princeton, Princeton University Press.
- Jiménez, S.; Domingo, A.; Abreu, M.; Brazeiro, A. 2011. Structure of the seabird assemblage associated with pelagic longline vessels in the southwestern Atlantic: implications for bycatch. *Endangered Species Research* 15: 241–254.
- Johnstone, G.W. 1979. Agonistic behaviour of the Giant-Petrels *Macronectes giganteus* and *M. halli* feeding at seal carcasses. *Emu* 79: 129–132.
- Marchant, S.; Higgins, P.J. (eds.) 1990. *Handbook of Australian, New Zealand and Antarctic birds. Volume 1, Part A, Ratites to petrels*. Melbourne, Oxford University Press.
- Martin, P.R. 2015. Trade-offs and biological diversity: integrative answers to ecological questions. pp. 291–308 In: Martin, L.B.; Ghalambor, C.K.; Woods, H.A. (Eds.) *Integrative organismal biology*. New York, John Wiley & Sons, Inc.
- Martin, P.R.; Freshwater, C.; Ghalambor, C.K. 2017. The outcomes of most aggressive interactions among closely related bird species are asymmetric. *PeerJ* 5: e2847.
- Martin, P.R.; Ghalambor, C.K. 2014. When David beats Goliath: The advantage of large size in interspecific aggressive contests declines over evolutionary time. *PLOS ONE* 9: e108741.
- Martin, P.R.; Kenyon, H.L.; Hayes, L. 2020. Size-dependent costs of migration: migrant bird species are subordinate to residents, but only at small body sizes. *Journal of Evolutionary Biology* 33: 495–504.
- Milledge, D. 1977. One year's observations of seabirds in continental shelf waters off Sydney, N.S.W. *Corella* 1: 1–12.
- Morse, D.H. 1974. Niche breadth and social dominance. *American Naturalist* 108: 818–830.
- Olmos, F. 1997. Seabirds attending bottom long-line fishing off southeastern Brazil. *Ibis* 139: 685–691.
- Persson, L. 1985. Asymmetric competition: are larger animals competitively superior? *American Naturalist* 126: 261–266.
- Peters, R.H. 1983. *The ecological implications of body size*. Cambridge, Cambridge University Press.
- Phillips, R.A.; Silk, J.R.D.; Croxall, J.P. 2005. Foraging and provisioning strategies of the light-mantled sooty albatross at South Georgia: competition and co-existence with sympatric pelagic predators. *Marine Ecology Progress Series* 285: 259–270.
- R Core Team. 2018. R: a language and environment for statistical computing. Version 3.5.2. Vienna, R Foundation for Statistical Computing. <https://www.R-project.org/>
- Ramos, J.A.; Monteiro, L.R.; Sola, E.; Moniz, Z. 1997. Characteristics and competition for nest cavities in burrowing Procellariiformes. *Condor* 99: 634–641.
- Robinson, S.K.; Terborgh, J. 1995. Interspecific aggression and habitat selection by Amazonian birds. *Journal of Animal Ecology* 64: 1–11.
- Spear, L.B.; Ainley, D.G. 1993. Kleptoparasitism by Kermadec Petrels, jaegers, and skuas in the eastern tropical Pacific: evidence of mimicry by two species of *Pterodroma*. *Auk* 110: 223–233.
- Spear, L.B.; Ainley, D.G. 2007. Storm-petrels of the eastern Pacific Ocean: species assembly and diversity along marine habitat gradients. *Ornithological Monographs* 62: 1–77.
- Vaske, T. Jr. 1991. Seabirds mortality on longline fishing for tuna in southern Brazil. *Ciência e Cultura* 43: 388–390.
- Weimerskirch, H.; Jouventin, P.; Stahl, J.C. 1986. Comparative ecology of the six albatross species breeding on Crozet Islands. *Ibis* 128: 195–213.
- Wood, K.A. 1992. Seasonal abundance and spatial distribution of albatrosses off central New South Wales. *Australian Bird Watcher* 14: 207–225.

SHORT NOTE

Individual long-distance migrant *Chrysococcyx* cuckoos repeat carbon and nitrogen stable isotope ratios after moulting in non-breeding range on successive migrations

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The New Zealand shining cuckoo (*Chrysococcyx lucidus lucidus* Gmelin, 1788) (Fig. 1) breeds only in the New Zealand archipelago (other subspecies breed in Australia and New Caledonia; Higgins 1999). Post-breeding, New Zealand cuckoos migrate 5,000 km, across the Tasman and Coral Seas, to the Bismarck Archipelago (New Britain, New Ireland) and the Solomon Islands, near the Equator (Fig. 1) (Higgins 1999). At least some New Zealand birds migrate via south-eastern Queensland, Australia (Gill 1983b). Mayr (1932) described the 10,000+ km trans-oceanic migration by this small (<30 g) bird as “amazing”, a sentiment echoed, in essence, by banding pioneer A. Landsborough Thomson, who described the migration as “perhaps the most remarkable trans-oceanic migration by a land bird” (Thomson 1964).

In their breeding range, shining cuckoos inhabit a wide range of habitats, including temperate rain forest, forest remnants, riparian woodlands, exotic plantations, and farmland with trees, as long as there are populations of its host species, the grey warbler (*Gerygone igata* Quoy & Gaimard, 1830) (Acanthizidae) (Higgins 1999). Shining cuckoos still breed in most areas of New Zealand (Robertson *et al.* 2007; Robertson *et al.* 2017) despite dramatic losses of natural vegetation since human settlement began (McWethy *et al.* 2010, 2014) and the species is currently not considered at risk (Robertson *et al.* 2007). However, their habitats are threatened by deforestation in their non-breeding range (Bayliss-Smith *et al.* 2003; Buchanan *et al.* 2008) potentially threatening their survival. The vegetation of the stopover area in southern Queensland is also now heavily modified, with ‘brigalow’ woodland especially fragmented (Dwyer *et al.* 2009).

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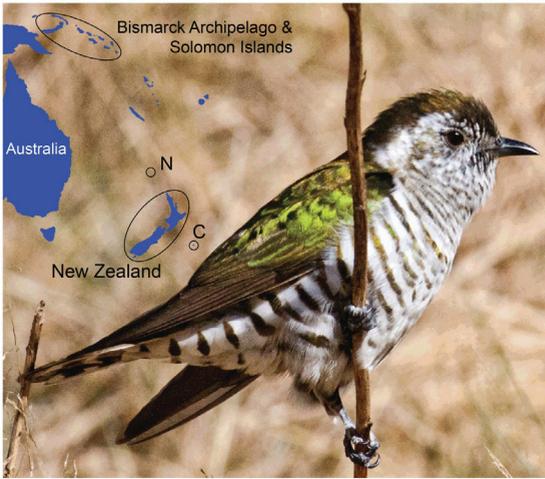


Figure 1. Shining cuckoos (*Chrysococcyx lucidus lucidus*), weighing <30 grams, breed in New Zealand, Chatham Island (C), and Norfolk Island (N) and migrate to the Bismarck Archipelago and Solomon Islands, where they moult. At least some birds migrate via eastern Australia, in a migration involving four ocean crossings totalling c. 10,000 km. Image: courtesy of Nathan Hill. © Nathan Hill, accessed via New Zealand Birds Online.

Increasing environmental change raises questions about the future conservation of the shining cuckoo, as it does for most migratory species. However, the Australasian *Chrysococcyx* cuckoos are notoriously cryptic when not calling, which they do only during the breeding season, and their distributions, ecology, and habitat requirements are poorly known away from their breeding areas (Higgins 1999; Noske 2019). Information on the habitat requirements of the species outside the breeding range is essential to understanding its threat status and for any management (Bowen *et al.* 2009).

Determining the diet and habitat of a species when it is not directly observable (Higgins 1999) can be achieved indirectly by measuring its isotopic niche (Bearhop *et al.* 2004; Newsome *et al.* 2007). For migratory species that moult in the non-breeding range, isotopic values can be measured in a relatively non-invasive fashion by sampling feathers. Stable isotopic measurements of the feathers of migratory birds have been used to determine the broad location of non-breeding areas for species inhabiting difficult and remote environments (Hobson *et al.* 2010). Where the bird's location has been established by other means, measurements of carbon and nitrogen stable isotopic ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, respectively) can provide information on habitat use and diet and hence provide a remotely-sensed window into a

bird's biology in the area where the feathers are moulted and replaced.

New Zealand shining cuckoos moult in their non-breeding ranges in the Bismarck Archipelago, Bougainville, and the Solomon Islands in the tropical southwest Pacific, but their juvenile plumage is based on the diet provided by the host species in the breeding range in New Zealand (Gill 1983a, 1998). The carbon and nitrogen stable isotopic ratios of feathers of adults caught in New Zealand should reflect the diet and isotopic niche occupied by the adults in their non-breeding range, while isotopic ratios of feathers of juveniles caught before their first migration should reflect the diet and local habitat of the host species.

Animals have $\delta^{15}\text{N}$ values higher than their food, the difference between consumer and prey being typically c. 3–4‰, where the prey are not water-stressed (Ambrose & DeNiro 1986): differences in $\delta^{13}\text{C}$ values are about one-third of those of $\delta^{15}\text{N}$ (Ambrose & DeNiro 1986). Baseline values for both ratios depend on the structure of the environment and of the food web (Ambrose & DeNiro 1986; Cerling *et al.* 2004; Hawke & Holdaway 2005; Hawke & Holdaway 2009; Holdaway *et al.* 2013; Holdaway & Rowe 2020), with each species' values reflecting its isotopic niche. Taxa with very constrained isotopic niches are likely to be vulnerable to environmental change, including availability of preferred foods and habitat structure; those with wider isotopic niches should be more resilient against change (Holdaway *et al.* 2013). Thus, an examination of the isotopic values of shining cuckoos should reveal both their isotopic niche on the wintering grounds and its variability.

Twenty-two adults and three juveniles were individually metal-banded and their feathers sampled at two sites in New Zealand between December 2014 and mid-November 2017. Birds were captured by mist-netting individuals attracted to song playback. Nets were erected with their top panels as close as possible to the canopy top, as birds rarely came lower in response to playback. Nineteen adults (9 Dec 2014 [2], 9 Nov 2016 [2], 1 Dec 2016 [1], 2 Dec 2016 [1], 3 Dec 2016 [1], 7 Dec 2016 [1], 12 Oct 2017 [3], 13 Oct 2017 [1], 24 Oct 2017 [1], 29 Oct 2017 [1], 31 Oct 2017 [1], 2 Nov 2017 [1], 5 Nov 2017 [1], 7 Nov [2]) were sampled at Kowhai Bush, Kaikoura, north-eastern South Island (42°22'37"S, 173°36'58"E), and five (16 Dec 2016 [1], 17 Dec 2016 [1], 14 Dec 2017 [1], 17 Dec 2017 [2]) at Milnthorpe Park Scenic Reserve, in the far northern South Island (40°42'47"S, 172°40'55"E) (Fig. 2).

Two of the adults at Kowhai Bush were sampled twice, in successive years (Band B122248, 7 December 2016, 5 November 2017; Band BP11568, 14 December 2016, 31 October 2, 1017). All three juveniles were sampled at Kowhai Bush on 30

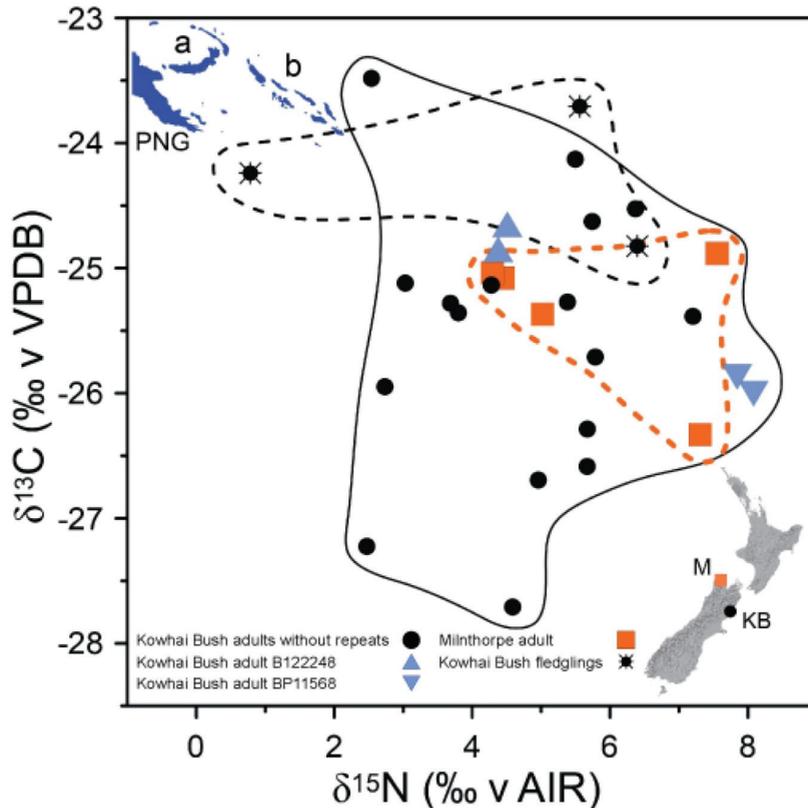


Figure 2. New Zealand shining cuckoos (*Chrysococcyx lucidus lucidus*) return to particular moulting sites within a much broader range of habitats occupied by the species during the non-breeding season. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotopic ratios for feathers replaced during moult in the non-breeding range in the Southwest Pacific by 21 adult shining cuckoos sampled once, two sampled twice (in consecutive years and listed by band number in figure), and of three juveniles raised by grey warbler (*Gerygone igata*) foster parents in New Zealand. Solid circles, solid line: adult cuckoos sampled once at Kowhai Bush. Black stars, black broken line: juvenile cuckoos sampled in breeding area at Kowhai Bush. Orange squares, broken orange line: birds sampled once at Milnthorpe Reserve. Erect and inverted triangles, bi-isotopic values for two adults sampled in successive years at Kowhai Bush. Top left: Bismarck Archipelago (a) and Solomon Islands (b); Papua New Guinea (PNG). Bottom right: New Zealand; M, Milnthorpe Reserve; KB, Kowhai Bush (Kaikoura). Outline maps not to common scale.

January 2018. Two or three breast feathers were removed from each bird under University of Canterbury Animal Ethics permit (2014/26R) and New Zealand Department of Conservation permit (39907-FAU), and stored in separate labelled glass vials until analysed.

Carbon and nitrogen stable isotopic ratios were measured at the National Institute of Water & Atmospheric Research Ltd laboratory, Greta Point, Wellington, New Zealand. Each feather was washed in 70% ethanol, and rinsed 3x in ultra-pure water, before oven drying at 60°C. Material from one side of the shaft was cut off using sterile scissors, cut further into small pieces, and mixed, before

subsampling for stable isotopic analysis. Isotopic ratios were measured in a Delta Plus automated continuous-flow isotope ratio mass spectrometer, linked to a NA1500 elemental analyser (both Thermo-Fisher Scientific, Bremen, Germany), with 2-point normalisation, using an AS 200 autosampler, against international standards. Reference materials (National Institute of Standards and Technology, NIST; United States Geological Survey, USGS) were used to determine isotopic values, following Paul *et al.* (2007).

Sample $\delta^{15}\text{N}$ values were 2-point normalised using isotopic data from the daily analysis of NIST 8573 USGS40 L-glutamic acid and NIST 8548

Table 1. Carbon and nitrogen stable isotopic ratios of feathers of adult and juvenile shining cuckoos (*Chrysococcyx lucidus lucidus*) sampled at Kaikoura and in Golden Bay. $\delta^{15}\text{N}$ reported relative to air; $\delta^{13}\text{C}$ reported relative to the Vienna PeeDee Belemnite. Mass, feather mass analysed; -a, -b, repeat recoveries; rpt, repeated measurement (B122255 repeat measurement of same sample).

Band no.	Mass (mg)	%N	$\delta^{15}\text{N}$ (‰)	%C	$\delta^{13}\text{C}$ (‰)	C:N
B104572	1.122	12.61	2.47	47.34	-27.22	3.8
B104575	0.711	13.35	4.45	47.26	-25.08	3.5
B104576	0.872	13.47	5.67	46.74	-26.29	3.5
B104577	0.673	13.26	4.96	46.12	-26.69	3.5
B104578	0.834	13.97	7.20	46.16	-25.39	3.3
B104579	1.017	13.65	5.38	46.71	-25.27	3.4
B104581	0.774	14.00	4.29	45.71	-25.04	3.3
B109463	0.753	13.59	3.03	46.87	-25.12	3.4
B109464	0.854	14.16	5.74	46.09	-24.63	3.3
B120851	0.702	13.74	5.50	46.20	-24.13	3.4
B120853	0.754	14.07	3.80	45.84	-25.36	3.3
B122245	0.683	13.79	5.79	45.87	-25.71	3.3
B122247	0.938	12.35	4.59	48.23	-27.71	3.9
B122248-a	0.675	14.14	4.51	46.55	-24.65	3.3
B122248-b_rpt	0.69	13.47	4.38	45.67	-24.85	3.4
B122249	0.726	14.55	2.54	46.00	-23.48	3.2
B122250	0.718	13.80	4.28	45.99	-25.14	3.3
B122251	0.739	13.18	5.67	45.81	-26.59	3.5
B122252	0.709	14.18	2.73	47.14	-25.95	3.3
B122253	0.887	13.76	3.68	45.83	-25.28	3.3
B122254	0.788	13.41	6.37	45.96	-24.53	3.4
B122255_rpt	0.743	13.18	5.02	45.89	-25.37	3.5
B122256	0.914	13.69	7.31	46.71	-26.33	3.4
B122257	0.789	14.26	7.55	46.59	-24.88	3.3
B122258	0.764	14.15	0.78	45.46	-24.24	3.2
B122259	0.731	13.80	6.39	45.37	-24.82	3.3
B122260	0.707	14.36	5.56	45.31	-23.71	3.2
BP11568-a	1.082	13.67	8.08	47.33	-26.00	3.5
BP11568-b	0.721	13.89	7.84	43.97	-25.87	3.2

Table 2. Measurements of nitrogen isotope ratio $\delta^{15}\text{N}$ standards against reported values. NIST, (US) National Institute of Standards and Technology; USGS, US Geological Survey; NC, not certified; ND, not determined. *, material used for data normalisation.

Standard	Reported	%N	Normalised measured		IRMS	
	$\delta^{15}\text{N} \pm \text{SD}$ (‰ v Air)		$\delta^{15}\text{N}$ Mean \pm SD	<i>n</i>	%N Mean \pm SD	<i>n</i>
NIST RM8573 USGS40 L-glutamic acid *	-4.52 ± 0.12	9.52	-4.52 ± 0.03	5	9.44 ± 0.09	5
NIST RM8548 IAEA-N-2 Ammonium sulphate*	20.40 ± 0.2	21.2	20.41 ± 0.11	6	20.97 ± 0.41	6
USGS65 Glycine	20.68 ± 0.06	18.67	20.85 ± 0.18	5	18.46 ± 0.30	5
DL Leucine	NC	10.57	13.62 ± 0.24	12	10.64 ± 0.09	11
Squid laboratory std	NC	ND	13.31 ± 0.20	6	12.53 ± 0.29	6

Table 3. Measurements of carbon isotope ratio $\delta^{13}\text{C}$ standards against reported values. NIST, (US) National Institute of Standards and Technology; USGS, US Geological Survey; IAEA, International Atomic Energy Agency; NC, not certified; ND, not determined. *, material used for data normalisation.

Standard	Reported		Normalised measured		IRMS	
	$\delta^{13}\text{C} \pm \text{SD} (\text{‰ v Air})$	%C	$\delta^{13}\text{C} \text{ Mean} \pm \text{SD}$	<i>n</i>	%C Mean \pm SD	<i>n</i>
NIST RM8573 USGS40 L-glutamic acid *	-26.39 \pm 0.09	40.82	-26.37 \pm 0.14	5	40.27 \pm 0.34	5
NIST RM8542 IAEA-CH-6 Sucrose*	-10.45 \pm 0.07	42.11	-10.45 \pm 0.12	6	41.68 \pm 0.30	6
USGS65 Glycine	-20.29 \pm 0.04	32	-20.20 \pm 0.14	5	31.46 \pm 0.17	5
DL Leucine	NC	54.38	-28.53 \pm 0.14	12	54.61 \pm 0.48	11
Squid laboratory std	NC	ND	-18.22 \pm 0.10	6	42.23 \pm 0.42	6

IAEA-N2 ammonium sulphate. Sample $\delta^{13}\text{C}$ values were 2-point normalised using isotopic data from the daily analysis of NIST 8573 USGS40 L-glutamic acid and NIST 8542 IAEA-CH-6 Sucrose. Precision was determined by the repeat analysis of the working laboratory standard DL-Leucine (DL-2-Amino-4-methylpentanoic acid, $\text{C}_6\text{H}_{13}\text{NO}_2$, Lot 127H1084, Sigma, Australia). Data from the daily analysis of USGS65 Glycine was used to check accuracy and precision. Repeat analysis of Squid lab standard provided a further check on precision.

Carbon and nitrogen stable isotopic ratios of the feather samples are shown in Table 1, and the results for the nitrogen and carbon standards in Table 2 and Table 3, respectively.

Our results display two contrasting features of cuckoo isotopic niche use (Fig. 2). Firstly, the species as a whole has a broad isotopic niche. Single factor ANOVA showed no differences between the isotopic values for any combination of site and age. The $\delta^{15}\text{N}$ values were consistent with the birds' consuming the same diet, primarily herbivorous caterpillars, recorded in New Zealand (Higgins 1999), and in the subcanopy or canopy of a tropical rain forest (Cerling *et al.* 2004). The $\delta^{13}\text{C}$ values suggested a range of habitats, from the undergrowth of closed forest (c. -27.8‰) to open forest and shrubland (c. -23.5‰ to -24‰) (Ambrose & DeNiro 1986; Cerling *et al.* 2004; Hawke & Holdaway 2009; Holdaway *et al.* 2013; Johnston 2014; Hawke *et al.* 2017; Holdaway & Rowe 2020). The $\delta^{13}\text{C}$ value for the three juveniles sampled at Kowhai Bush reflected the known natal habitat of low-canopied kanuka (*Kunzea robusta* de Lange et Toelken, 2014) open woodland. The isotopic spectrum of our samples, from two populations, suggests that the species as a whole has the capacity to cope with significant environmental change, so long as sufficient woody vegetation remains to support its preferred foods.

Despite the broad range of habitats occupied by the species in general, individuals appear to occupy only specific and narrow isotopic habitats. Both adults sampled at Kowhai Bush in successive years moulted in the same isotopic space they had occupied the previous year, but at remarkably different positions in the species' isotopic range (Fig. 2). This implies that the individuals either returned to exactly the same geographic (and habitat) location, or to different locations with the same isotopic values. Either way, both birds reached, and stayed in, the same isotopic niche for the duration of their moult period. These results imply that, while the species may be resilient, local populations in the non-breeding areas are vulnerable to environmental change. Both birds were from the same breeding area which suggests that the local population can be subject to losses occurring in different areas in the non-breeding areas in Australasia and the South-west Pacific. The similarity between the isotopic values of three cuckoos sampled at Milnthorpe to that of a repeat-sampled individual from Kowhai Bush, suggests that populations at both sites in New Zealand could be adversely affected by events elsewhere. A similar reduction in the breadth of its isotopic niche was associated with the near-extinction of the New Zealand brown teal (*Anas chlorotis* G.R. Gray, 1845) (Holdaway *et al.* 2013).

Our results show that small migrant birds may have broad habitat requirements as a species but that individuals may be tied to particular habitats, and possibly locations, at each end of their migration path, and at any stopover point. Other taxa may occupy non-breeding habitats structurally similar to their breeding habitats but whose isotopic values are different as a result of different climate (e.g. cloudiness [Helama *et al.* 2018]) or vegetation (e.g. C3 versus C4). Hence, they may shift their

isotopic niche (Hahn *et al.* 2013) without changing their physical niche. The relationship between isotopic and conventional niche is still unclear (Flaherty & Ben-David 2010).

Removal of particular favoured habitats, such as that represented by the group of individuals occupying the moulting habitat represented by the isotopic space near $\delta^{13}\text{C} \sim -25\text{‰}$ and $\delta^{15}\text{N} \sim +4\text{‰}$ (Fig. 2), would jeopardize the survival of birds breeding in two different areas in New Zealand. Site specificity away from the breeding grounds is difficult to detect. However, it may be general, showing that more research is needed into what may be a significant factor in the declines of small terrestrial migrant birds.

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LITERATURE CITED

- Ambrose, S.H.; DeNiro, M.J. 1986. The isotopic ecology of East African mammals. *Oecologia* 69: 395–406.
- Bayliss-Smith, T.; Hviding, E.; Whitmore, T. 2003. Rainforest composition and histories of human disturbance in Solomon Islands. *Ambio* 32(5): 346–352.
- Bearhop, S.; Adams, C.E.; Waldron, S.; Fuller, R.A.; MacLeod, H. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology* 73: 1007–1012.
- Bowen, M.E.; McAlpine, C.A.; Seabrook, L.M.; House, A.P.; Smith, G.C. 2009. The age and amount of regrowth forest in fragmented brigalow landscapes are both important for woodland dependent birds. *Biological Conservation* 142: 3051–3059.
- Buchanan, G.M.; Butchart, S.H.; Dutson, G.; Pilgrim, J.D.; Steininger, M.K.; Bishop, K.D.; Mayaux, P. 2008. Using remote sensing to inform conservation status assessment: estimates of recent deforestation rates on New Britain and the impacts upon endemic birds. *Biological Conservation* 141: 56–66.
- Cerling, T.E.; Hart, J.A.; Hart, T.B. 2004. Stable isotope ecology in the Ituri Forest. *Oecologia* 138: 5–12.
- Dwyer, J.M.; Fensham, R.J.; Butler, D.W.; Buckley, Y.M. 2009. Carbon for conservation: Assessing the potential for win-win investment in an extensive Australian regrowth ecosystem. *Agriculture, Ecosystems & Environment* 134: 1–7.
- Flaherty, E.A.; Ben-David, M. 2010. Overlap and partitioning of the ecological and isotopic niches. *Oikos* 119: 1409–1416.
- Gill, B. 1983a. Brood-parasitism by the shining cuckoo *Chrysococcyx lucidus* at Kaikoura, New Zealand. *Ibis* 125: 40–55.
- Gill, B. 1983b. Morphology and migration of *Chrysococcyx lucidus*, an Australasian cuckoo. *New Zealand Journal of Zoology* 10: 371–381.
- Gill, B. 1998. Behavior and ecology of the shining cuckoo, *Chrysococcyx lucidus*. *Oxford Ornithology Series* 9: 143–151.
- Hahn, S.; Amrhein, V.; Zehtindijev, P.; Liechti, F. 2013. Strong migratory connectivity and seasonally shifting isotopic niches in geographically separated populations of a long-distance migrating songbird. *Oecologia* 173: 1217–1225.
- Hawke, D.J.; Cranney, O.R.; Horton, T.W.; Bury, S.J.; Brown, J.C.S.; Holdaway, R.N. 2017. Foliar and soil N and $\delta^{15}\text{N}$ as restoration metrics at Pūtaringamotu Riccarton Bush, Christchurch city. *Journal of the Royal Society of New Zealand* 47(4): 319–335.
- Hawke, D.J.; Holdaway, R.N. 2005. Avian assimilation and dispersal of carbon and nitrogen brought ashore by breeding Westland petrels (*Procellaria westlandica*): a stable isotope study. *Journal of Zoology* 266: 419–426.
- Hawke, D.J.; Holdaway, R.N. 2009. Nutrient sources for forest birds captured within an undisturbed petrel colony, and management implications. *Emu* 109: 163–169.
- Helama, S.; Arppe, L.; Uusitalo, J.; Holopainen, J.; Mäkelä, H.M.; Mäkinen, H.; Mielikäinen, K.; Nöjd, P.; Sutinen, R.; Taavitsainen, J.-P.; Timonen, M.; Oinonen, M. 2018. Volcanic dust veils from sixth century tree-ring isotopes linked to reduced irradiance, primary production and human health. *Scientific Reports* 8: 1339.
- Higgins, P.J. 1999. *Handbook of Australian, New Zealand & Antarctic birds*. Vol. 4. Parrots to dollarbird. Melbourne, Oxford University Press.
- Hobson, K.A.; Barnett-Johnson, R.; Cerling, T.E. 2010. Using isoscapes to track animal migration. pp. 273–298 In: West J.B., Bowen G.J., Dawson T.E., Tu, K.P. (eds) *Isoscapes: Understanding movement, pattern, and process on Earth through isotope mapping*. Dordrecht, Springer Science.

- Holdaway, R.N.; Rowe, R.J. 2020. Palaeoecological reconstructions depend on accurate species identification: examples from South Island, New Zealand, *Pachyornis* (Aves: Dinornithiformes). *Notornis* 67: 494–502.
- Holdaway, R.N.; Williams, M.J.; Hawke, D.J. 2013. A comparison of the pre-human and present isotopic niches of brown teal (*Anas chlorotis*): implications for conservation. *Notornis* 60: 233–244.
- Johnston, O.R. 2014. A comparison of the stable isotopic ecology of eastern, western, and pre-human forest ecosystems in the South Island of New Zealand. MSc thesis. School of Biological Sciences. Christchurch, Canterbury.
- Mayr, E. 1932. Birds collected during the Whitney South Sea Expedition. XIX. Notes on the bronze cuckoo *Chalcites lucidus* and its subspecies. *American Museum Novitates* 520: 1–9.
- McWethy, D.B.; Whitlock, C.; Wilmshurst, J.M.; McGlone, M.S.; Fromont, M.; Li, X.; Dieffenbacher-Krall, A.; Hobbs, W.O.; Fritz, S.C.; Cook, E.R. 2010. Rapid landscape transformation in South Island, New Zealand, following initial Polynesian settlement. *Proceedings of the National Academy of Sciences, USA* 107: 21343–21348.
- McWethy, D.B.; Wilmshurst, J.M.; Whitlock, C.; Wood, J.R.; McGlone, M.S. 2014. A high-resolution chronology of rapid forest transitions following Polynesian arrival in New Zealand. *PLoS One* 9: e111328.
- Newsome, S.D.; Martinez del Rio, C.; Bearhop, S.; Phillips, D.L. 2007. A niche for isotopic ecology. *Frontiers in Ecology and the Environment* 5: 429–436.
- Noske, R. 2019. New Zealand Shining Bronze-Cuckoos *Chalcites lucidus lucidus* are regular visitors to Southeast Queensland. *Sunbird* 48: 149–158.
- Paul, D.; Skrzyzypek, G.; Fórizs, I. 2007. Normalization of measured stable isotopic compositions to isotope reference scales – a review. *Rapid Communications in Mass Spectrometry* 21: 3006–3014.
- Robertson, C.J.R.; Hyvonen, P.; Fraser, M.J.; Pickard, C.R. 2007. Atlas of bird distribution in New Zealand 1999–2004. Wellington, Ornithological Society of New Zealand, Inc.
- Robertson, H.A.; Baird, K.; Dowding, J.E.; Elliott, G.P.; Hitchmough, R.A.; Miskelly, C.M.; McArthur, N.; O'Donnell, C.F.J.; Sagar, P.M.; Scofield, R.P.; Taylor, G.A. 2017. Conservation status of New Zealand birds, 2016. *New Zealand Threat Classification Series* 19: 1–23.
- Thomson, A.L. 1964. Cuckoo. pp. 169–171 In: Thomson A.L. A new dictionary of birds. London, Nelson.

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SHORT NOTE

Second record of Buller's shearwater breeding outside of the Poor Knights Islands

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Buller's shearwater (rako; *Puffinus bulleri*) was discovered in October 1884 when Walter L. Buller found a storm-tossed female on Waikanae Beach (Fig. 1), and in 1888, Osbert Salvin formally described the bird in honour of its initial finder (Salvin 1888; Harper 1983). More than thirty years passed before Robert A. Falla discovered the species breeding on the Poor Knights Islands in December 1923 (Falla 1924). Nearly a century later, Buller's shearwaters are reported to only breed with regularity on the Poor Knights Islands and outlying islets and rock stacks. The population increased significantly following the eradication of pigs from Aorangi Island in 1936 and has been estimated to stand at around 300,000–400,000 breeding pairs (Medway 2001; Clout & Russell 2006; Waugh *et al.* 2013). A recent survey of the Poor Knights Islands revealed the breeding population is lower than previously estimated and not yet at capacity,

with extensive areas of suitable burrowing habitat remaining (M. Friesen *pers. comm.*). Despite this, Buller's shearwater remains a common species, often seen feeding in large flocks close to numerous islands around eastern Northland, Hauraki Gulf and Bay of Plenty waters.

On 16 January 2019 we were conducting burrow transect counts and determining the contents of burrows on Lady Alice Island / Mauimua (Chickens / Marotere Islands; 35.89°S, 174.73°E). In total, we inspected 570 burrows in nine different seabird colonies across the island. One burrow checked contained a Buller's shearwater incubating an egg. The burrow was located in a highly burrowed area that is primarily a flesh-footed shearwater (*Pu. carneipes*) colony. The colony is interspersed with occasional Pycroft's petrel (*Pterodroma pycrofti*), sooty shearwater (*Pu. griseus*), and fluttering shearwater (*Pu. gavia*) burrows while grey-faced petrel (*Pt. macroptera*) and little shearwaters (*Pu. assimilis*) breed within the colony during the winter months. The burrow was approximately one metre long and the nesting chamber was accessible from

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Figure 1. Locations of Buller's shearwater recorded ashore in New Zealand and Australia. Stars represent breeding localities while triangles represent locations of Buller's shearwater recorded ashore but not breeding. Waikanae Beach (mentioned in text) is represented by a circle and is included for context.

the burrow mouth. The egg was aberrantly shaped, being of comparable width but well below the mean length, and even outside of the range, for Buller's shearwaters breeding on Aorangi Island (Table 1). Egg size often increases with female age in a variety of avian species and so an egg with the aforementioned dimensions could be indicative of a first- or early-breeding attempt by the female (Christians 2002). By 25 January 2019 the breeding attempt had failed with the entrance to the burrow covered by leaf litter and no bird or egg present inside the burrow. In January 2020 Buller's shearwaters were present and breeding in the same burrow. Travel restrictions due to the COVID-19 pandemic meant we were not able to revisit Lady Alice Island in April/May 2020 and determine if this breeding attempt was successful.

This is only the second reported record of Buller's shearwater attempting to breed outside of the Poor Knights Islands. The only other record of Buller's shearwater breeding outside of the Poor Knights Islands came from Motu Puruhi Island

Table 1. Comparison of the egg found in the Buller's shearwater burrow on Lady Alice Island, Hen and Chicken Islands, in 2019 and a sample of eggs measured on Aorangi, Poor Knights Islands, between 1963 and 1981 (Harper 1983).

	Lady Alice Island (<i>n</i> = 1)	Aorangi Island (<i>n</i> = 74)	
		Mean ± SE	Range
Length (mm)	57.4	65.4 ± 0.3	59.0–72.3
Width (mm)	42.4	43.0 ± 0.2	40.1–46.1

(Simmonds Islands; 34.76°S, 173.16°E) in the far north of New Zealand. It is reported by G.R. Parrish and B. Waddell in Taylor & Parrish (1991) that an adult and chick were found in a burrow on 25 January 1990. The Simmonds Islands are classified as a Nature Reserve and visits to the islands by the Department of Conservation (DOC) are infrequent.

When they do occur, trips focus primarily on renewing toxins in bait stations and weed control (I. Petrove, DOC, *pers. comm.*). As such, it remains unclear whether this was a one-off record or if there is now an established breeding population on the island, but the former seems more likely.

A single Buller's shearwater had previously been observed at night-time on Lady Alice Island on 11 February 2017. This bird was found resting on the surface and was not observed exiting or entering a burrow. Another individual was observed resting on the surface at night-time on 6 Feb 2020. One individual was captured on a trail camera (Reconyx XP9 UltraFire, Reconyx USA) on 01 January 2020 set up to monitor fluttering shearwater activity on the island (Fig. 2). All of these observations were in separate locations to each other and not in the same immediate area as the breeding burrow. All of the observations were, however, within a 150 m radius and inside the defined boundary of the flesh-footed shearwater colony.



Figure 2. Buller's shearwater captured on a trail camera on Lady Alice Island in January 2020.

Elsewhere, a single Buller's shearwater was observed at night-time on Motumahanga/Saddleback Island (Ngā Motu/Sugar Loaf Islands, Taranaki 39.05°S, 174.02°E) on 17 January 2019. This bird was caught and banded but again was not observed prospecting existing burrows on the island (G. Taylor & M. Bell *pers. comm.*). Buller's Shearwater have been recorded prospecting on Manawatāwhi/Three Kings Islands (34.16°S, 172.13°E; Gill *et al.* 2010). Single Buller's shearwaters were caught during spotlighting on Burgess Island (Mokohinau Islands; 35.91°S, 175.11°E) on 31 January 2011 and Little Barrier Island/Te Hauturu-o-Toi (36.20°S, 175.08°E) on 3 March 2016 (C. Gaskin *pers. comm.*). In New South Wales, Australia, live birds have been observed ashore on Montague/Baranguba Island (36.25°S, 150.23°E) and Cabbage Tree Island/John Gould Nature Reserve (32.69°S, 152.22°E) multiple times since the 1960s (Serventy *et al.* 1971; Priddle

& Carlile 2004). These locations are summarised in Figure 1.

Procellariiform seabirds are generally considered highly philopatric and as such natural dispersal and colonisation or recolonisation of a new site has been regarded as unusual (Warham 1996). Procellariiformes will forage over thousands or even tens of thousands of kilometres yet remain indisposed to disperse and breed at sites mere tens or hundreds of kilometres away. This phenomenon was coined the "seabird paradox" by Milot *et al.* (2008) and was well exemplified in a study of two breeding colonies of Hawaiian petrels (*Pt. sandwichensis*; Wiley *et al.* 2012). In New Zealand, a review of recent seabird recolonisation events suggested that New Zealand seabird populations may have a greater capacity as colonisers of other islands (Buxton *et al.* 2014; Towns *et al.* 2016). Genetic analysis of grey-faced petrel colonies across New Zealand has shown no genetic structure in grey-faced petrel populations, suggesting high levels of gene flow between colonies (Lawrence *et al.* 2014).

The Hen and Chicken Islands lie 45 km due south of the Poor Knights Islands and are the nearest locality to the Poor Knights that support significant Procellariiform populations due to their predator-free status. The most influential factor in New Zealand seabird recolonisation events has been found to be having a nearby (most commonly ≤ 25 km) source population from the island being recolonised (Buxton *et al.* 2014). The attractiveness of an established seabird colony through calls and flight activity – even a heterospecific one – also makes it a much more likely candidate for recolonisation than nearby mainland sites such as Bream Head (Mönkkönen *et al.* 1999; Buxton & Jones 2012). As such, it seems logical that if Buller's shearwaters are indeed expanding in their breeding range that Lady Alice Island would be one of the first islands to become colonised. Multiple observations of Buller's shearwaters on the surface at night time may suggest that this species is primarily in the prospecting stage for a new breeding colony. A period of prospecting generally precedes a colonisation event and allows individuals to assess the quality and attributes of a potential new breeding location (Kharitonov & Siegel-Causey 1988; Oro & Ruxton 2001).

Buller's shearwaters have been characterised as "aggressive colonisers" and are believed to have displaced grey-faced petrels and fluttering shearwaters on Aorangi Island following the remarkable influx of Buller's shearwaters from neighbouring Tawhiti Rahi by 1981 (Harper 1983). If indeed our observations of Buller's shearwater breeding and prospecting on Lady Alice Island is a sign of a species expanding its breeding range, and not just a singular event, there is potential for

a resulting shift in the composition of the seabird community on the island in the future.

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LITERATURE CITED

- Buxton, R.T.; Jones, C.J. 2012. Experimental study of social attraction in two species of storm-petrel by acoustic and olfactory cues. *The Condor* 114: 733–743.
- Buxton, R.T.; Jones, C.J.; Moller, H.; Towns, D.R. 2014. Drivers of seabird population recovery on New Zealand islands after predator eradication. *Conservation Biology* 28: 333–344.
- Christians, J.K. 2002. Avian egg size: variation within species and inflexibility within individuals. *Biological Reviews of the Cambridge Philosophical Society* 77: 1–26.
- Clout, M.N.; Russell, J.C. 2006. The eradication of mammals from New Zealand islands. pp. 127–141 In: Koike, F.; Clout, M.N.; Kawamichi, M.; De Poorter, M.; Iwatsuki, K. (eds.) *Assessment and Control of Biological Invasion Risks*. Kyoto, Japan, Shoukadoh Book Sellers.
- Falla, R.A. 1924. Discovery of a breeding place of Buller's shearwater, Poor Knights Island, N.Z. *Emu* 24: 37–43.
- Gill, B.J. (Convenor); Bell, B.D.; Chambers, G.K.; Medway, D.G.; Palma, R.L.; Schofield, R.P.; Tennyson, A.J.D.; Worthy, T.H. 2010. *Checklist of the birds of New Zealand, Norfolk and Macquarie Islands and the Ross Dependency Ed. 4*. Wellington, Ornithological Society of New Zealand & Te Papa Press. 500 pp.
- Harper, P.C. 1983. Biology of the Buller's Shearwater (*Puffinus bulleri*) at the Poor Knights Islands, New Zealand. *Notornis* 30: 299–318.
- Kharitonov, S.P.; Siegel-Causey, D. 1988. Colony formation in seabirds. pp. 223–272 In: Johnston, R.F. (ed.) *Current Ornithology*, Vol. 5. New York, Plenum Press.
- Lawrence, H.A.; Lyver, P.O.B.; Gleeson, D.M. 2014. Genetic panmixia in New Zealand's Grey-faced Petrel: implications for conservation and restoration. *Emu* 114: 249–258.
- Medway, D.G. 2001. Pigs and petrels on the Poor Knights Islands. *New Zealand Natural Sciences* 26: 87–90.
- Milot, E.; Weimerskirch, H.; Bernatchez, L. 2008. The seabird paradox: dispersal, genetic structure and population dynamics in a highly mobile, but philopatric albatross species. *Molecular Ecology* 17: 1658–1673.
- Mönkkönen, M.; Härdling, R.; Forsman, J.T.; Tuomi, J. 1999. Evolution of heterospecific attraction: using other species as cues in habitat selection. *Evolutionary Ecology* 13: 93–106.
- Oro, D.; Ruxton, G.D. 2001. The formation and growth of seabird colonies: Audouin's gull as a case study. *Journal of Animal Ecology* 70: 527–535.
- Priddel, D.; Carlile, N. 2004. Seabird islands No. 22/1: Boondelbah Island, New South Wales. *Corella* 28: 104–106.
- Salvin, O. 1888. Critical notes on the Procellariidae. *Ibis* 6: 351–360.
- Serventy, D.L.; Serventy, V. & Warham, J. 1971. *The handbook of Australian sea-birds*. Sydney, A.H. & A.W. Reed.
- Taylor, G.A.; Parrish, G.R. 1991. Classified summarised notes, North Island 1 July 1989 to 30 June 1990. *Notornis* 38: 267–314.
- Towns, D.R.; Borrelle, S.B.; Thoresen, J.; Buxton, R.T.; Evans, A. 2016. Mercury Islands and their role in understanding seabird island restoration. *New Zealand Journal of Ecology* 40: 235–249.
- Warham, J. 1996. *The behaviour, population biology and physiology of the Petrels*. London, Academic Press.
- Wagh, S.M.; Tennyson, A.J.D. Taylor, G.; Wilson, K.J. 2013. Population sizes of shearwaters (*Puffinus* spp.) in New Zealand with recommendations for monitoring. *Tuhinga* 24: 159–204.
- Wiley, A.E.; Welch, A.J.; Ostrom, P.H.; James, H.F.; Stricker, C.A.; Fleischer, R.C.; Gandhi, H.; Adams, J.; Ainley, D.G.; Duvall, F.; Holmes, N.; Hu, D.; Judge, S.; Penniman, J.; Swindle, K.A. 2012. Foraging segregation and genetic divergence between geographically proximate colonies of a highly mobile seabird. *Oecologia* 168: 119–130.

Keywords: Buller's shearwater, *Puffinus bulleri*, breeding, Lady Alice Island, Hen and Chicken Islands

SHORT NOTE

Vessel survey observations confirm wintering dispersion of northern giant-petrel (*Macronectes halli*) juveniles in southern-central Perú; what is their origin?

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The northern giant petrel (NGP) (*Macronectes halli*) is a circumpolar seabird breeding in three main groups of subantarctic islands (ACAP 2016a; Howell & Zufelt 2019). South Georgia (54°00'S, 38°36'W) in the South Atlantic is the largest colony with 15,398 breeding pairs (bp), encompassing more than 70% of the world population (Ponce *et al.* 2020). In the southwest Pacific, main breeding areas are located in the Forty Fours islets (44°00'S, 176°67'E) in the Chatham Islands Archipelago, New Zealand (~1,977 bp, Bell *et al.* 2017), and Macquaire Island, Australia (~1,793 bp, ACAP 2016a). Other representative main breeding areas in the southern Indian Ocean are Iles Kerguelen (49°09'S, 69°16'E) and Crozet (46°26'S, 51°47'E), with 1,400 and 1,263 bp, respectively (ACAP 2016a). Minor breeding areas in New Zealand are located in the Auckland islands with 340 bp (Parket *et al.* 2020); Antipodes island with 233 bp (Wiltshire and Hamilton, 2003);

Campbell islands with 234 bp (Wiltshire & Scofield, 2000), and The Sisters (Chatham Islands) with 156 bp (Bell *et al.* 2018). Finally, in the south-west Indian Ocean in the Prince Edward Islands, 464 bp were counted (Ryan *et al.* 2003; ACAP 2016). Immature and juveniles NGP tend to disperse great distances from their breeding colonies, often showing an eastward movement from the south western Pacific in Macquaire island towards South America due to the prevailing westerly winds (Woehler & Johnstone, 1988; Trebilco *et al.* 2008).

There are records of the presence of juvenile NGP in the western coasts of South America (Ayala 2007; Zavalaga *et al.* 2009; Fibla *et al.* 2010, Van Den Hoff, 2011). In the austral winter 2004, juveniles loafing on Peruvian inshore waters were sighted at San Juan de Marcona (15°20'S, 75°10'W), Ilo (17°42'S, 71°22'W) and La Vieja island (14°16'S, 76°11'W) off Bahía Independencia (Ayala 2007). Between the winter-spring 2002 and 2007, 11 juvenile NGP were recorded >60 km off Callao (~12°S), the northernmost location of its post-breeding distribution known to date (Zavalaga *et al.*

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2009). There is more recent evidence from the eBird web site (<https://ebird.org/home>) of the presence of juveniles NGP in offshore waters of central-southern Perú during the winter and spring.

Four banded fledglings of NGP from the Kerguelen and Crozet archipelagos in the southern Indian Ocean that were recovered as juveniles in Chile revealed that these birds can travel great distances (Voisin 1990). Two band recoveries of dead juvenile NGP in northern Chile, one captured in a longline in June 2002 at 21°50'S, 72°28'W, approximately 150 km offshore Tocopilla (Zavalaga *et al.* 2009), and another found dead in March 2007 at Papudo beach (32°26'S, 71°25'W), 75 km north of Valparaiso (Fiblia *et al.* 2010), showed that these birds travelled from Macquarie Is. These findings were confirmed by Van Den Hoff (2011) who reported 34 banded fledglings and seven banded second-year *Macronectes* spp. from Macquarie Is. sighted from Arica (18°S) to Puerto Aysen (45°S) in the coast of Chile between 1955 and 2006. Although it was not possible to separate northern from southern giant petrels (*M. giganteus*) in this study because the majority of the band deployments occurred before the two species were separated by Bourne & Warham (1966), it is likely that a proportion of these birds corresponded to NGP (Van Den Hoff 2011; ACAP 2016 a,b). Thus, these and earlier findings confirmed that birds from Macquarie Is. travelled outbound distances between 12,000–13,000 km to visit the western coasts of South America (Woehler & Johnstone, 1988; Trebilco *et al.* 2008, Zavalaga *et al.* 2009; Fiblia *et al.* 2010). The recurrent visits of NGP to Chile is also reported by the Fisheries Development Institute (IFOP) in Chile. Between 2014 and 2017, 66 and seven unbanded NGP were incidentally captured in central and southern Chile (39°S–57°S) by the trawl and longline fisheries, respectively (Richard & Adasme 2019). Because NGP are not banded in New Zealand, it is also possible that a proportion of unbanded NGP reported as by-catch in Chile may come from Auckland, Antipodes, Campbell, Forty Fours, and The Sisters colonies.

Although valuable, all sightings and records of NGP in the eastern South Pacific have been opportunistic (Ayala 2007; Zavalaga *et al.* 2009; Fiblia *et al.* 2010), and therefore there are limitations to explain the recurrent presence of NGP in Perú and Chile and if these birds are present farther north from Callao. Unlike previous reports, in this study we undertook systematic vessel-based survey observations of NGP occurrence along the Peruvian coast. We were particularly interested in the distribution of birds at sea, records of age classes other than juveniles, the seasonality of their presence in Peruvian waters and the association of NGP sightings to some oceanographic features.

Thirty five at-sea surveys were conducted

between 1998 and 2020 (12 in austral summer, seven in autumn, six in winter and 10 in spring) onboard the BIC *Humboldt* and *Jose Olaya*, both research vessels of the Peruvian Marine Research Institute (IMARPE). The surveys were part of the biannual Pelagic Anchovy Surveys and covered a long latitudinal range for almost the entire Peruvian coast from 03°30'S to 18°20'S, except in the autumn 2019 (from 06°57'S to 18°20'S). Offshore distance ranged from 3.5 km to 180 km (100 nm) offshore (Fig. 1), completing 45 parallel transects, each separated by 15 nautical miles (nm). Birds were sighted with the aid of 10 x 50 binoculars within a 300 m strip-transect by two observers on both sides of the bridge. Observations were continuous from civil dawn to dusk (approximate 0530 h – 1830 h local time, GMT – 0500 h) while the ship was underway. Transects were partitioned every 6 minutes or 1 nm, since the vessels cruise speed was 10 knots. During these surveys, we counted NGP in Peruvian waters and categorized the habitat where birds were encountered: coastal waters (0–15 m); continental shelf (15–200 m); continental slope (201–4,500 m); Perú-Chile Trench (>4,500 m) and pelagic abyssal plain (offshore, beyond the Perú-Chile Trench). Sea surface temperature were obtained from a submerged probe recording continuously during the surveys. Likewise, for each sighting we observed birds behaviour as follows: flying, resting on the water, feeding or scavenging, and associated species. Age classes were determined using Shirihai (2008), Howell & Schmitt (2018), and Howell & Zufelt (2019) (Fig. 2). In addition, 20 seabird sightings were also carried out by IMARPE in the artisanal commercial fleet targeting jumbo squid (*Dosidicus gigas*), between Lomas (15°34'S) and Mollendo (17°) up to 210 km offshore.

A total of 11,500 observation hours and a distance of 175,000 km surveyed were completed in the 35 research cruises. A total of 34 NGP were sighted from 09°S to 18°S and between 20 to 199 km offshore (Fig. 1). Most of the NGP sightings (84%) occurred in winter-spring, and the remaining in late autumn. No birds were observed in the austral summer (February – March) despite the majority of cruises were undertaken during this season (n=12). In autumn, birds occurred between 14°20'S and 17°59'S, 35–116 km offshore. In winter, birds were sighted between 10°36'S and 14°27'S, 20–199 km offshore. In spring, birds were recorded between 09°S to 18°05'S, 28 to 183 km offshore (Fig. 1). Most of the sightings (94.2%) in all cruises were located in pelagic waters in the 12°S–18°S range, and the remaining (5.8%) in waters over the continental shelf (Fig 1). The range of Sea Surface Temperatures (SST) at the locations of this study's sightings ranged between 15°C and 20°C, with 64% of the measurements between 18°C and 20°C.

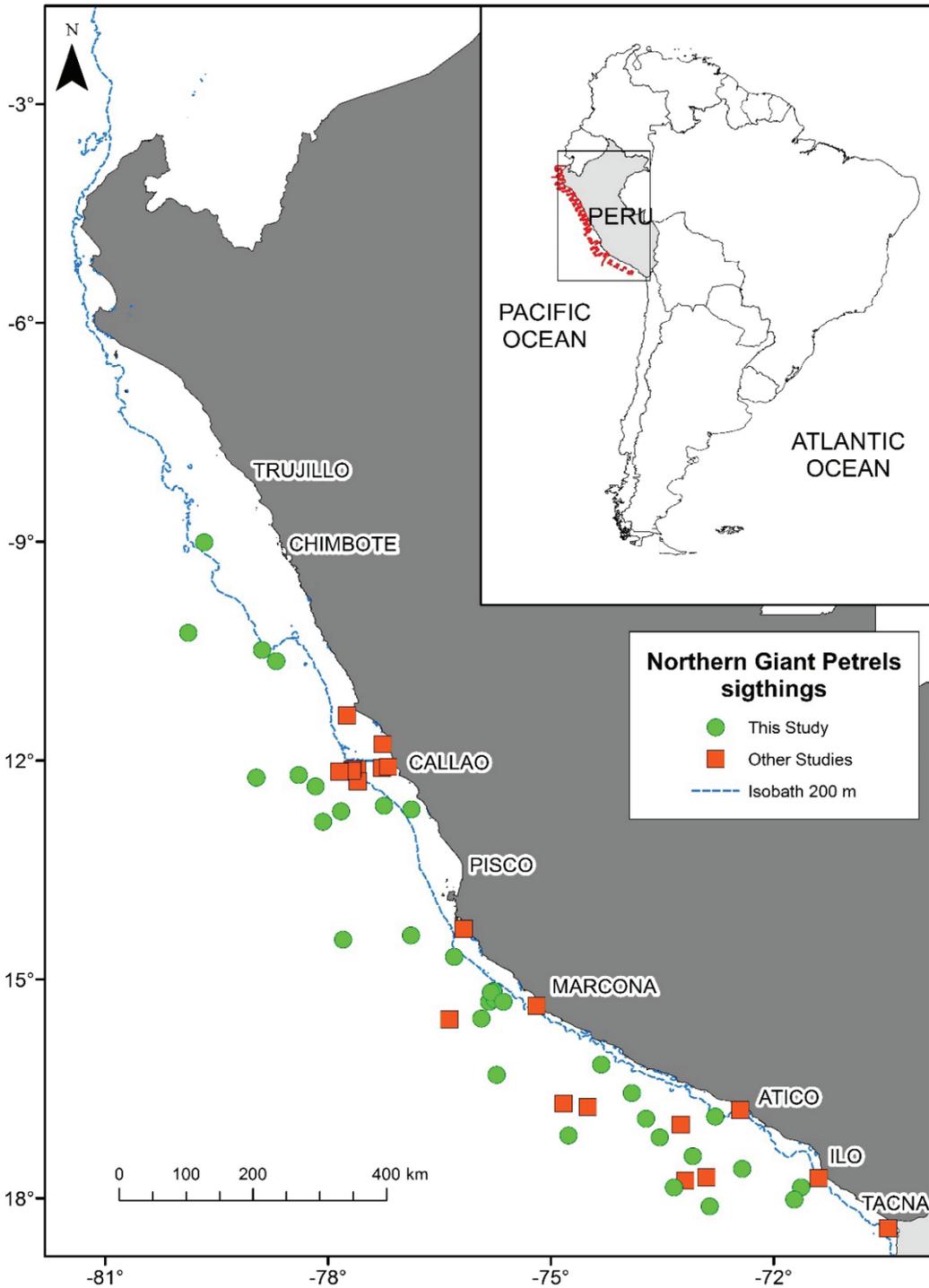


Figure 1. Sighting of juvenile northern giant petrels (*Macronectes halli*) in Peruvian waters recorded in this study from research vessel cruises between 1998 and 2020 are depicted in green circles. Additional historical records from other studies, i.e. Ayala (2007); Zavalaga *et al.* (2009); eBird (2009–2019,) are shown in orange squares. The inset shows the extent of the transects undertaken during vessel.

When historical NGP records and the sightings in the jumbo squid fleet were added to our observations, a total of 63 bird sightings allowed some insight into any preferences of marine habitats. Birds were observed over the continental slope (55.6%, $n=35$), followed by the continental shelf (15.9%, $n=10$), Perú trench (11.1%, $n=7$), coastal areas (9.5%, $n=6$), and finally the abyssal plain (7.9%, $n=5$). Regarding the age class composition, 96.8% of the birds ($n=61$) were juveniles with uniform dark plumage. Only two sub-adult (3.2%) were observed, based on the presence of some white feathers in the head and chest area, both of them were in the vicinity of the guano islands (Fig. 2). Fifty-eight percent ($n=36$) of the birds were observed flying, 32% ($n=17$) were on the water surface, 8% ($n=5$)

were feeding and one individual was registered hooked in a longline (2%). Two juvenile NGP were observed foraging in offshore pelagic water off the Chala – Mollendo area (16°S–17°S), one of them was not photographed. However, we recorded another NGP associated with three white chinned petrels (*Procellaria aequinoctialis*) feeding in pelagic areas over the continental slope at 30 km offshore Chala (~16°S) (Fig. 2).

In the more systematic vessel surveys ($n=35$) in a 21-year time series (1998–2020) along the entire Peruvian coast up to 180 km in offshore and during the four seasons confirmed several patterns of the presence of NGP in Peruvian waters. First, almost all individuals sighted were juveniles (only two sub-adults). Second, NGP were absent north of 09°S.



Figure 2. Juvenile northern giant petrels (*Macronectes halli*) flying (A) and feeding (B) in pelagic oceanic waters off Atico (~16°S) in Southern Perú. Some white chinned petrels (*Procellaria aequinoctialis*) (C) also present. And finally, a sub-adult NGP in isla Mazorca (11°23'S; 77°44'W) (D). Photographs A-C by Javier Quiñones (IMARPE); photograph D by Melchor Llica (AGRORURAL).

Table 1. Sighting of northern giant petrels (*Macronectes halli*) along the southern and central coast of Perú.

Date of sighting	Latitude	Longitude	Number of birds	Distance to the coast (km)	Bathymetry at sighting (m)	Habitat	Source
Autumn season							
07 April 2017	-16.7012	-74.8293	1	117.3	5,994	Abyssal plain	Andrey Moreno
13 June 2019	-17.8476	-71.6274	1	35.6	877	Slope	This study
13 June 2019	-18.0143	-71.7217	1	52.8	1,123	Slope	This study
16 June 2019	-17.1634	-73.5337	1	86.9	4,810	Perú trench	This study
19 June 2019	-16.3059	-75.7276	1	116.7	4,264	Abyssal plain	This study
20 June 2019	-15.3031	-75.6372	1	34.6	1,293	Slope	This study
20 June 2019	-15.5326	-75.933	1	74.8	5,056	Perú trench	This study
21 June 2019	-14.3942	-76.882	1	70.7	3,635	Slope	This study
Winter season							
06 July 2004	-15.3587	-75.1923	3	0.4	15	Coastal	Ayala (2007)
12 July 2004	-17.7214	-71.3943	3	2	135	Cont. Shelf	Ayala (2007)
04 August 2004	-17.7583	-73.19	1	75	1,650	Perú trench	Zavalaga <i>et al.</i> (2009)
07 August 2004	-14.3084	-76.1716	1	8	12	Coastal	Ayala (2007)
27 August 2005	-12.1133	-77.6083	2	50	186	Shelf	Zavalaga <i>et al.</i> (2009)
02 August 2007	-12.2833	-77.6	3	55	397	Slope	Zavalaga <i>et al.</i> (2009)
16 September 2007	-12.0825	-77.1916	1	5.8	37	Cont. Shelf	Zavalaga <i>et al.</i> (2009)
25 August 2008	-14.4512	-77.7964	1	170.8	4,316	Abyssal plain	This study
28 August 2008	-12.6654	-76.8764	1	20.4	130	Cont. Shelf	This study
28 August 2008	-12.6159	-77.2448	1	56	370	Slope	This study
29 August 2008	-12.8353	-78.0682	1	134.2	3,509	Slope	This study
29 August 2008	-12.6915	-77.8232	1	103.7	2,051	Slope	This study
26 November 2008	-9.00533	-79.6675	1	111.4	120	Cont. Shelf	This study
29 November 2008	-10.4817	-78.8875	2	90.2	562	Slope	This study
08 August 2009	-12.1019	-77.2723	1	13	38	Cont. Shelf	D. Lane (eBird)
25 July 2010	-12.1494	-77.8436	1	75	1,650	Slope	N.D., Perrins (eBird)
13 September 2013	-10.6343	-78.6972	1	80.4	720	Slope	This study
17 September 2013	-12.3501	-78.1672	1	123.3	2,556	Slope	This study
18 September 2013	-12.1948	-78.3946	1	146.3	3,066	Slope	This study
18 September 2013	-12.2297	-78.9658	1	198.7	5,556	Perú trench	This study
18 July 2015	-11.7742	-77.2644	1	9	10	Coastal	C. Calvo (eBird)

Table 1. continued

Date of sighting	Latitude	Longitude	Number of birds	Distance to the coast (km)	Bathymetry at sighting (m)	Habitat	Source
Spring Season							
29 September 2002	-12.1133	-77.6683	2	50	475	Slope	Zavalaga <i>et al.</i> (2009)
05 October 2002	-16.9069	-73.7192	1	76.7	4,050	Slope	This study
05 October 2002	-16.5538	-73.9102	1	43.3	2,689	Slope	This study
12 October 2002	-15.3051	-75.8299	1	53.9	2,686	Slope	This study
12 October 2002	-15.2676	-75.7548	1	45.6	1,750	Slope	This study
25 October 2002	-10.2459	-79.8828	1	182.5	4,306	Slope	This study
December 2004	-17.7116	-72.9033	1	115	4,640	Perú trench	Zavalaga <i>et al.</i> (2009)
17 November 2007	-12.1366	-77.6766	1	58	742	Slope	Zavalaga <i>et al.</i> (2009)
25 October 2015	-16.791	-72.4503	1	7.4	543	Shelf	Andrey Moreno
17 November 2015	-16.9904	-73.2501	2	59.9	3,150	Shelf	Andrey Moreno
02 November 2016	-16.749	-74.5041	1	98.6	6,537	Abyssal plain	Andrey Moreno
27 September 2017	-11.3812	-77.7456	1	13.7	0	On Island	Melchor Llica
27 October 2017	-15.5493	-76.3649	1	130	3,710	Perú trench	R. Tizard (eBird)
28 October 2017	-14.6864	-76.3	1	41.7	1,364	Slope	This study
29 October 2017	-15.1531	-75.7714	1	37.2	1,109	Slope	This study
29 October 2017	-15.1729	-75.806	1	41.2	1,428	Slope	This study
05 November 2019	-16.1638	-74.3216	1	33	1,746	Slope	This study
05 November 2019	-17.1358	-74.7635	1	148.9	4,717	Abyssal plain	This study
08 November 2019	-17.8485	-73.3415	1	27.6	603	Slope	This study
08 November 2019	-17.421	-73.0896	1	95.4	4,086	Slope	This study
08 November 2019	-16.8767	-72.7868	1	137	5,535	Perú trench	This study
08 November 2019	-18.4105	-70.4565	1	10	92	Cont. Shelf	G. Riley (eBird)
09 November 2019	-18.1085	-72.8602	1	72.8	1,999	Slope	This study
09 November 2019	-17.5951	-72.4234	1	149.8	6,260	Perú trench	This study

Third, NGP were not recorded in Peruvian waters during the austral summer. Fourth, birds fed both at inshore and offshore waters. And fifth, they are found at different realms of marine habitats from coastal highly productive cold waters to warm, deep oceanic waters. In addition, during the systematic surveys we did not identify NGP associated with fishing vessels; however, during the sightings in the artisanal fishery targeting giant squid, we did identify four juvenile NGP approaching to the vessel when offal was discarded.

The occurrence of juvenile NGP in central and southern Perú constitutes one of the farthest recorded movements from their main nesting areas, ~7,000 km from South Georgia; ~11,000 km from the Forty Fours in the Chatham Islands, ~13,000 km from Macquaire island, finally ~19,500 and 21,000 km from Kerguelen and Crozet islands respectively. It is known that NGP disperse mainly between 30°S–64°S (Voisin 1988). Juveniles and sub-adults tend to disperse great distances from their breeding colonies, often with an eastward movement likely due to prevailing westerly winds (Weimerskirch *et al.* 1985; Woehler & Johnstone 1988; Voisin 1990). However, according to tracking data from their breeding colonies, they disperse to different geographical areas during their non-breeding period. For instance, breeding birds tracked from South Georgia disperse towards the Argentinian shelf-break areas up to 30°S–35°S (BirdLife International 2004; Gonzales-Solis *et al.* 2007). Satellite tracked NGP fledglings (n=5) from Macquaire disperse eastward reaching the east coast of South America up to 45°S (Trebilco *et al.* 2008). Another five NGP fledglings were tracked in Crozet and Kerguelen in the Southern Indian Ocean, dispersed eastward from their colonies, and performed at least one, and for some individuals several circumpolar trips during the first year after fledging (Thiers *et al.* 2014). There is no information of fledging dispersals from New Zealand off shore islands such as The Forty Fours, Auckland, Campell, Antipodes, and The Sisters islands. However, other tracked species in The Forty Fours, like the northern royal albatross (*Diomedea epomophora sanfordi*) and the northern Buller's albatross (*Thalassarche bulleri platei*), reached the South American Pacific coasts (Deppe 2012).

The northern limit of the NGP juvenile distribution may be the result of inter-specific competition with more numerous waved albatross (*Phoebastria irrorata*) and Salvin's mollymawks (*Thalassarche salvini*), both species regularly use Peruvian waters as wintering grounds. Adult and immatures *P. irrorata* and *T. salvini* frequent the northern offshore waters off Perú, just close to the northernmost limit distribution of the NGP (Anderson *et al.* 2003; Awkerman *et al.* 2006;

Quiñones *et al. in prep.*). *Thalassarche salvini* are even more robust and larger (mean 4.1 kg; Brooke 2004) than NGP juveniles (3.6 kg; Carlos & Voisin 2008) and may outcompete them during feeding opportunities. The lack of experience of juvenile NGP in agonistic encounters with more abundant and larger, adult albatrosses may exclude them from northern waters. The wide extent of NGP distribution in southern Peruvian waters (from coastal to offshore), with a contrasting bathymetry (from 15 to 6,260 m deep) and SST ranging from 15–20°C during the study period, would not limit their presence in the north.

The influence of winds on albatrosses and petrel movements is well documented (Weimerskirch *et al.* 2000; Suryan *et al.* 2008), and the start of the long westerly migration was likely caused by the seasonally predictable prevailing westerly winds that dominate the Southern Ocean between 30°S and 60°S. (Weimerskirch *et al.* 2000). The great majority of our sightings (84%) were in the winter-spring seasons, and the remaining 16% in late autumn (13–20 June); this coincides with the formation of the Subtropical Jet Stream (SJT) during winter and spring in the South Pacific (Nakamura & Shimpo 2004). On the other hand, in summer-autumn the SJT is absent, coincidentally during summer cruises (February – April) no NGP were reported. Consequently, we hypothesize that most of the NGP in central and southern Perú come from the New Zealand offshore islands and Macquaire island in the far west South Pacific, and Crozet and Kerguelen in the Southern Indian Ocean. Nineteen (19) NGP fledglings band recoveries from Macquaire (1967–1986) registered in Chile by Woehler & Johnstone (1988) and subsequently by Van Den Hoff (2011) supports our hypothesis. However, we do not rule out that some birds could travel from South Georgia, since there are some band recoveries (n=6) from this UK island registered in the 1960s and 1970s on the Pacific coast of South America (Hunter 1984). We could conclude that the presence of juvenile NGP in Perú come from both areas; however, due to the strong seasonal presence of the SJT the possibilities of an origin from the west (New Zealand offshore islands, Macquaire and South Indian Ocean islands) are greater than those from the South Atlantic (South Georgia), despite that breeding pairs of NGP in the latter are almost one order of magnitude greater.

The presence of NGP in a wide bathymetric range reflects that the foraging behaviour of juveniles is versatile and adaptive during their wintering dispersion. Giant petrels often showed a flexible foraging strategy, switching from coastal to pelagic habits, probably governed by spatial-temporal changes in carrion availability (Gonzales-Solis *et al.* 2007), related mainly to penguin and seal

carcasses availability during the austral winter in their colonies (Johnstone 1979; Bruyn & Cooper 2005). The majority of the observations were made at distance, and therefore, it was difficult to discriminate males from females and determine any sex-specific migration pattern, particularly because there is clear spatial separation between sexes in their forage zones (Hunter & Brooke, 1992; Gonzales-Solis 2004).

In southern Perú, we noted several small artisanal boats targeting giant squid using hand-line, and blue sharks (*Prionace glauca*) and shortfin mako sharks (*Isurus oxyrinchus*) using artisanal long-lines. Both artisanal fisheries are very common in oceanic waters in southern Perú (Adams *et al.* 2016; Csirke *et al.* 2018). In both artisanal fisheries there was interaction with NGP, which gradually approach the boat when offal discards of giant squid and sharks occur (Andrey Moreno & Christian Jimenez, *pers. comm.*). Moreover, NGP was also registered close to inshore guano islands and headlands, probably looking for fledglings of seabird species or carrion close to the colonies. Humboldt penguin (*Spheniscus humboldti*) in Perú fledges from July to December (Zavalaga & Paredes 1997) and Peruvian diving-petrels (*Pelecanoides garnotii*) chicks leave their nests colonies almost year-round (Jahncke & Goya 1998) and are present <30 km offshore (Figuroa *et al.* 2011). We could infer that NGP in the coastal areas were males, since switching from coastal to pelagic habits, probably governed by spatio-temporal changes in carrion availability, in contrast females remains in pelagic waters (Gonzalez-Solis *et al.* 2007). The provided information demonstrates the importance of the Northern Humboldt Current for juveniles NGP during their wintering season, and give new insights to take measures for the proper management of this highly migratory species.

LITERATURE CITED

- ACAP. 2016a. Northern Giant Petrel Species Profile. <http://www.acap.aq>. Accessed: 15 June 2020.
- ACAP. 2016b. Southern Giant Petrel Species Profile. <http://www.acap.aq>. Accessed: 04 September 2020.
- Adams, G.D.; Flores, D.; Flores, O.G.; Aarestrup, K.; Svendsen, J.C. 2016. Spatial ecology of blue shark and shortfin mako in southern Perú: local abundance, habitat preferences and implications for conservation. *Endangered Species Research* 31: 19–32.
- Anderson, D.J.; Huyvaert, K.P.; Wood, D.R.; Gillikin, C.L.; Frost, B.J.; Mouritsen, H. 2003. At-sea distribution of waved albatrosses and the Galapagos Marine Reserve. *Biological Conservation* 110: 367–373.
- Awkerman, J.A.; Huyvaert, K.P.; Mangel, J.; Alfaro-Shigueto, J.; Anderson, D.J. 2006. Incidental and intentional catch threatens Galapagos waved albatross. *Biological Conservation* 133: 483–489.
- Ayala, L. 2007. Records of juvenile northern giant petrels (*Macronectes halli*) in Peruvian seas. *Notornis* 54: 234–236.
- Bell, M.D.; Bell, D.J.; Boyle, D.P.; Tuanui-Chisholm, H. 2017. *Motuhara seabird research: December 2016*. Technical report to the Department of Conservation, Wellington, New Zealand. Wildlife Management International Ltd, Blenheim, New Zealand. 14 pp.
- Bell, M.D.; Bell, D.J.; Boyle, D.P.; Tuanui-Chisholm, H. 2018. *Rangitahi Seabird research: December 2017*. Technical report to the Department of Conservation. Wildlife Management International Ltd, Blenheim, New Zealand. 27 pp.
- BirdLife International. 2004. Tracking ocean wanderers: the global distribution of albatrosses and petrels. Results from the Global Procellariiform Tracking Workshop, 1–5 September, 2003, Gordon's Bay, South Africa. Cambridge, UK: BirdLife. http://www.birdlife.org/sites/default/files/attachments/tracking_ocean_wanderers.pdf Accessed: 16 June 2020.
- Bourne, W.R.P.; Warham, J. 1966. Geographical variation in the giant petrels of the genus *Macronectes*. *Ardea* 54: 45–67.
- Brooke, M. 2004. *Albatrosses and petrels across the world*. Oxford University Press. 499 pp.
- De Bruyn, P.J.N.; Cooper, J. 2005. Who's the boss? Giant petrel arrival times and interspecific interactions at a seal carcass at sub-Antarctic Marion Island. *Polar Biology* 28: 571–573.
- Carlos, C.J.; Voisin, J.F. 2008. Identifying giant petrels, *Macronectes giganteus* and *M. halli*, in the field and in the hand. *Seabird* 21: 1–15.
- Csirke, J.; Argüelles Torres, J.; Alegre Norza Sior, A.R.P.; Ayón Dejo, P.; Bouchon Corrales, M.; Castillo Mendoza, G.; Mariátegui Rosales, L. 2018. Biología, estructura poblacional y pesquería de pota o calamar gigante (*Dosidicus gigas*) en el Perú. *Boletín Instituto del Mar del Perú* 33: 302–364 <http://biblioimarpe.imarpe.gob.pe/handle/123456789/3239>. Accessed: 16 June 2020.
- Deppe, L. 2012. Spatial and temporal patterns of at-sea distribution and habitat use of New Zealand albatrosses. PhD Thesis in Ecology, School of Biological Sciences, University of Canterbury, Christchurch, New Zealand, 140 pp.
- eBird. 2020. eBird: An online database of bird distribution and abundance [web application]. eBird, Cornell Lab of Ornithology, Ithaca, New York. Available: <https://ebird.org/peru/species/parpet1/PE> Accessed: 16 June 2020.
- Fibla, P.; Sallaberry-Pincheira, N.; Sallaberry, M. 2010. Conteo de aves marinas muertas en la

- playa La Rinconada, Antofagasta y comentario acerca de la distribución de *Macronectes halli* en Chile. *Boletín Chileno de Ornitología* 16: 37–41.
- Figueroa, J.; Suazo, E.; Santillán, L. 2011. Registros actuales e históricos del potoyunco peruano *Pelecanoides garnotii* (Lesson, 1828) (Procellariiformes, Pelecanoididae) en el Perú. *The Biologist* 9: 19–37.
- Gonzales-Solis, J. 2004. Sexual size dimorphism in northern giant petrels: Ecological correlates and scaling. *Oikos* 105: 247–254.
- Gonzalez-Solis, J.; Croxall, J.P.; Afanasyev, V. 2007. Offshore spatial segregation in giant petrels *Macronectes* spp.: differences between species, sexes and seasons. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 17: S22–S36.
- Howell, S.N.; Schmitt, F. 2018. *Birds of Chile: A Photo Guide*. Princeton, Princeton University Press. 240 pp.
- Howell, S.; Zufelt, K. 2019. *Oceanic birds of the world: a photo guide*. Princeton, New Jersey, USA, Princeton University Press. 358 pp.
- Hunter, S. 1984. Movements of giant petrels *Macronectes* spp. ringed at South Georgia. *Ringed and Migration* 5: 105–112.
- Hunter, S.; Brooke, M.D.L. 1992. The diet of giant petrels *Macronectes* spp. at Marion Island, southern Indian Ocean. *Colonial Waterbirds* 15: 56–65.
- Jahncke, J.; Goya, E. 1998. The status of the Peruvian diving-petrel population at its main breeding areas along the coast of Perú. *Colonial Waterbirds* 21: 94–97.
- Johnstone, G.W. 1979. Agonistic behaviour of the giant-petrels *Macronectes giganteus* and *M. halli* feeding at seal carcasses. *Emu* 79: 129–132.
- Nakamura, H.; Shimpo, A. 2004. Seasonal variations in the Southern Hemisphere storm tracks and jet streams as revealed in a reanalysis dataset. *Journal of Climate* 17: 1828–1844.
- Parker, G.C.; French, R.K.; Muller, C.G.; Taylor, G.A.; Rexer-Huber, K. 2020. First northern giant petrel (*Macronectes halli*) breeding population survey and estimate for the Auckland Islands, New Zealand. *Notornis* 67: 357–368.
- Ponce, S.; Wolfaardt, A.C.; Barbraud, C.; Reyes-Arriagada, R.; Black, A.; Powell, R.B.; Phillips, R.A. 2020. The distribution, abundance, status and global importance of giant petrels (*Macronectes giganteus* and *M. halli*) breeding at South Georgia. *Polar Biology* 43: 17–34.
- Richard, Y.; Adasme, L. 2019. Assessment of the risk of trawl and longline fisheries to ACAP-listed seabirds in Chile. ACAP Ninth Meeting of the Seabird Bycatch Working Group, Florianopolis, Brazil May 2019. 23 pp. [https://www.acap.aq/es/documentos/grupos-de-trabajo/english/working-groups/seabird-bycatch-working-](https://www.acap.aq/es/documentos/grupos-de-trabajo/english/working-groups/seabird-bycatch-working-group/seabird-bycatch-wg-meeting-9/sbwg9-information-papers/3363-sbwg9-inf-08-assessment-of-the-risk-of-trawl-and-longline-fisheries-to-acap-listed-seabirds-in-chile/file)
- group/seabird-bycatch-wg-meeting-9/sbwg9-information-papers/3363-sbwg9-inf-08-assessment-of-the-risk-of-trawl-and-longline-fisheries-to-acap-listed-seabirds-in-chile/file
- Accessed: 01 September 2020.
- Ryan, P.; Dyer, J.C.; Underhill, B. L.; Crawford, R. 2003. Counts of surface-nesting seabirds breeding at sub-Antarctic Prince Edward Island, summer 2001/02. *African Journal of Marine Science* 25: 441–451.
- Shirihai, H. 2008. *The complete guide to Antarctic wildlife, birds and marine mammals of the Antarctic continent and the southern ocean*, 2nd Edition. Princeton University Press, 544 pp.
- Suryan, R.; Anderson, D.J.; Shaffer, S.A.; Roby, D.D.; Tremblay, Y.; Costa, D.P.; Sievert, P.R.; Sato, F.; Ozaki, K.; Balogh, G.R.; Nakamura, N. 2008. Wind, waves, and wing loading: morphological specialization may limit range expansion of endangered albatrosses. *PLoS ONE* 3: e4016. doi: 10.1371/journal.pone.0004016
- Thiers, L.; Delord, K.; Barbraud, C.; Phillips, R.A.; Pinaud, D.; Weimerskirch, H. 2014. Foraging zones of the two sibling species of giant petrels in the Indian Ocean throughout the annual cycle: implication for their conservation. *Marine Ecology Progress Series* 499: 233–248.
- Trebilco, R.; Gales, R.; Baker, G.B.; Terauds, A.; Sumner, M.D. 2008. At sea movement of Macquarie Island giant petrels: relationships with marine protected areas and regional fisheries management organizations. *Biological Conservation* 141: 2942–2958.
- Van den Hoff, J. 2011. Recoveries of juvenile Giant Petrels in regions of ocean productivity: potential implications for population change. *Ecosphere* 2: 1–13.
- Voisin, J.F. 1988. Breeding biology of the northern giant petrel *Macronectes halli* and the southern giant petrel *M. giganteus* at Île de la Possession, Îles Crozet, 1966–1980. *Marine Ornithology* 16: 65–97.
- Voisin, J.F. 1990. Movements of giant petrels *Macronectes* spp. banded as chicks at Îles Crozet and Kerguelen. *Marine Ornithology* 18: 27–36.
- Weimerskirch, H.; Jouventin, P.; Mougín, J.L.; Stahl, J.C.; Van, B.M. 1985. Banding recoveries and the dispersal of seabirds breeding in French Austral and Antarctic Territories. *Emu* 85: 22–33.
- Weimerskirch, H.; Guionnet, T.; Martin, J.; Shaffer, S.A.; Costa, D.P. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 267: 1869–1874.
- Wiltshire, A.J.; Scofield, R.P. 2000. Population estimate of breeding Northern Giant Petrels *Macronectes halli* on Campbell Island, New Zealand. *Emu* 100: 186–191.

- Wiltshire, A.; Hamilton, S. 2003. Population estimate for northern giant petrels (*Macronectes halli*) on Antipodes Island, New Zealand. *Notornis* 50: 128–132.
- Woehler, E.; Johnstone, G.W. 1988. Banding studies of giant petrels, *Macronectes* spp, at Macquarie Island. *Papers and Proceedings of the Royal Society of Tasmania* 122(1): 143–152.
- Zavalaga, C.B.; Paredes, R. 1997. Sex determination of adult Humboldt Penguins using morphometric characters (Determinación del sexo en adultos de *Spheniscus humboldti* utilizando características morfométricas). *Journal of Field Ornithology*: 66: 102–112.
- Zavalaga, C.B.; Engblom, G.; Alfaro-Shigueto, J.; Mangel, J. 2009. Immature Northern Giant Petrels *Macronectes halli* visiting the coast of Perú. *Marine Ornithology* 37: 237–240.

Keywords: northern giant-petrel, *Macronectes halli*, Perú, circumpolar seabird, dispersal

SHORT NOTE

Longevity records for Chatham Island pigeon (*Hemiphaga chathamensis*) and New Zealand pigeon (*H. novaeseelandiae*)

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The New Zealand avifauna evolved in the absence of predatory land mammals and is characterized by a high level of endemism and a large number of flightless species (Bell 1991). Compared with the temperate Northern Hemisphere, birds in the tropics and the temperate zone of the Southern Hemisphere, including New Zealand, are characterised by having smaller clutches, multiple nesting attempts, extended parental care, delayed maturation, and high adult survival (e.g. Ricklefs 2000; Russell 2000; Franklin & Wilson 2003).

Pigeons and doves (Columbidae) breed at a young age and generally have a long breeding season during which multiple clutches of 1–2 small eggs are laid. Some clutches are overlapped, incubation and fledging periods are short, nestling growth rates are high, and chicks often leave the nest well below adult weight (Robertson 1988). Smaller bird species tend to live shorter lives than larger ones, and short-lived species mature early, have short breeding cycles and have large clutches (Newton 1998). Pigeons and doves have most of the characteristics of short-lived species, except for their small clutches, and because many species are

legally hunted around the world for food or sport, their lifespan is often curtailed. The two native pigeons in New Zealand, the Chatham Island pigeon (parea; *Hemiphaga chathamensis*) and New Zealand pigeon (kereru; *Hemiphaga novaeseelandiae*), are both relatively large fruit pigeons (mean weights 800 g and 650 g, respectively; Heather & Robertson 2015) which are absolutely protected, and so they might be expected to be longer-lived than most pigeons and doves.

Grant *et al.* (1997) calculated an annual survival rate of parea of 96%, and a life expectancy of 24.5 years based on one apparent death in 22.4 bird years of resightings of 19 colour-marked parea. Clout *et al.* (1995) calculated that the mean life expectancy of 75 radio-tagged kereru at Pelorus Bridge, northern South Island, was 5.4 years, and suggested that at least some individuals should live for more than 10 years.

Here we report on new longevity records for the two native New Zealand species of pigeon from band recoveries reported through the New Zealand National Bird Banding Scheme.

Chatham Island pigeon/parea

The parea is a fruit pigeon endemic to the Chatham Islands. Its conservation status was classified as

'Nationally Critical' (Miskelly *et al.* 2008), but they have increased in abundance in response to habitat protection and control of their predators, and so since 2012 they have been classified as 'Nationally Vulnerable' (Robertson *et al.* 2013, 2017).

In July 1990, we visited Chatham Island to conduct a survey of parea and to capture some individual birds for banding and radio-tagging (Clout & Robertson 1991). Our conclusion was that there were probably only *c.* 40 individuals remaining, all of them in the southern part of Chatham Island. We considered that the remaining birds were threatened by habitat degradation and predation. We therefore recommended fencing of key forest remnants to exclude sheep (*Ovis aries*), cattle (*Bos taurus*), and feral pigs (*Sus scrofa*), and intensive control of feral cats (*Felis catus*) and brushtail possums (*Trichosurus vulpecula*).

We mist-netted, banded, marked with a coloured plastic leg jess, and released three parea, two of them in the Awatotara Valley on 10 July 1990 and one in the Tuku-a-tamatea Valley on 14 July 1990.

Over the past 30 years, pest control and protection of key forest remnants have resulted in a strong recovery of parea on Chatham Island, to the extent that in 2009, the population was estimated to be *c.* 600 birds (Grant *et al.* 1997; Powlesland *et al.* 1997; Dilks *et al.* 2010). This recovery is undoubtedly partly due to ongoing trapping of feral cats which, despite efforts to exclude parea by using bird scaring models and hazing at traps, unfortunately results in a few accidental deaths of parea each year (Graeme Taylor, *pers. comm.*).

On 24 April 2018, a parea (K-8152) which we had banded in the Awatotara Valley (44°02'S, 176°38'W) was found to have been caught in a cat trap, still in the Awatotara Valley. The bird was badly injured and had to be euthanised. On examination, by Kailash Willis, it was found to be a female. It was caught 27 years 9 months and 14 days after it had been banded on 10 July 1990. It was already a large adult bird when we caught it in 1990, weighing 895 g. This individual was therefore probably at least 29 years old when it died.

New Zealand pigeon/kereru

The kereru is a fruit pigeon endemic to mainland New Zealand and its offshore Islands, and it was on Raoul Island, Kermadecs, until the mid-1800s (Heather & Robertson 2015). Its conservation status was once classified as 'Nationally Vulnerable' (Miskelly *et al.* 2008), but it has increased in abundance as a result of predator control, and so since 2012 it has been classified as 'Not Threatened' (Robertson *et al.* 2013, 2017).

During a study of the ecology of kereru at three sites on the mainland of New Zealand between 1983 and 1990 (Clout *et al.* 1995), we mist-netted

121 kereru. These birds were banded, marked with a coloured plastic leg jess and 102 of them had a radio-transmitter attached as a "backpack" with a specially designed harness incorporating a weak-link so the harness would break if snagged by vegetation, or would eventually break and shed the transmitter if the bird could not be recaptured (Karl & Clout 1987).

Of the 17 birds caught at Mohi Bush, eastern Hawke's Bay (39°51'S, 176°42'E), one (K-7518) was banded, leg-jessed and radio-tagged on 5 October 1988. It was found freshly dead on 28 March 2012, 23 years 5 months and 23 days after banding. This individual was therefore at least 24 years old when it died. The bird, minus its leg jess and radio-tag, died after apparently colliding with a deckchair on a lawn less than 100 m from its original capture site. A study skin of the male is preserved in the National Museum Te Papa Tongarewa collection (NMNZ OR.029558).

Comparison with other longevity records of pigeons

The five oldest longevity records for wild pigeons and doves (Family Columbidae) we could find in the literature were: a Cape turtle-dove (*Streptopelia capicola*) in South Africa that lived 34 years 7 months (SAFRING data in Birds4Africa 2020), two mourning doves (*Zenaida macroura*) that were shot 30 years 4 months and 27 years 3 months after banding (USGS 2019), a white-winged dove (*Zenaida asiatica*) shot 21 years, 9 months after banding (USGS 2019), and a bar-shouldered dove (*Geopelia humeralis*) released alive in Western Australia 20 years 2 months after first capture (ABBBS 2020). For comparison, the longevity records for pigeons and doves banded in Europe are a woodpigeon (*Columba palumbus*) and a collared dove (*Streptopelia decaocto*), both of which were recovered 17 years 8 months after banding (Euring 2017).

The two pigeon recoveries we are reporting on, that died 27 years and 9 months and 23 years and 6 months after banding, appear to be the third oldest and the fifth oldest free-living pigeons that we know of. What makes these New Zealand longevity records even more remarkable is that relatively small numbers of birds of these two species have been banded and recovered or reported resighted compared with many overseas species. A total of 103 parea have been banded and only three have ever been recovered or reported resighted, and 734 kereru have been banded (including birds in captivity) and 91 have been recovered or reported resighted (Michelle Bradshaw, NZ National Bird Banding Scheme, *pers. comm.*). For most of the other long-lived pigeons noted above, tens of thousands of birds have been banded and thousands have been recovered or resighted. This suggests that

both parea and kereru have relatively long potential life spans, and that both of these new records will eventually be broken.

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LITERATURE CITED

- ABBBS 2020. Australian Bird and Bat Banding Scheme Database Search: *Geopelia humeralis* (Bar-shouldered Dove). https://www.environment.gov.au/cgi-bin/biodiversity/abbbs/abbbs-search.pl?taxon_id=784 Accessed: 17 July 2020.
- Bell, B.D. 1991. Recent avifaunal changes and the history of ornithology in New Zealand. *Proceedings of the International Ornithological Congress XX*: 195–230.
- Birds4Africa. 2020. Longevities. <https://birds4africa.org/bird-ringing/longevities/> Accessed: 17 July 2020.
- Clout, M.N.; Karl, B.J.; Pierce, R.J.; Robertson, H.A. 1995. Breeding and survival of New Zealand pigeons *Hemiphaga novaeseelandiae*. *Ibis* 137: 264–271.
- Clout, M.N.; Robertson, H.A. 1991. Chatham Island pigeon recovery prospects: report on a visit to Chatham Island in July 1990. *Science & Research Internal Report 95*. Wellington, Department of Conservation. 9 pp.
- Dilks, P.J.; Powlesland, R.G.; Adams, L.K.; Flux, I.A. 2010. Changes in abundance of parea (Chatham Islands pigeon, *Hemiphaga chathamensis*), 1994–2009. *Notornis* 57: 156–161.
- Euring. 2017. European longevity records – 2017-04-05. <https://euring.org/data-and-codes/longevity-list> Accessed: 17 July 2020.
- Franklin, D.C.; Wilson, K-J. 2003. Are low reproductive rates characteristic of New Zealand's native terrestrial birds? Evidence from the allometry of nesting parameters in altricial species. *New Zealand Journal of Zoology* 30: 185–204.
- Grant, A.D.; Powlesland, R.G.; Dilks, P.J.; Flux, I.A.; Tisdall, C.J. 1997. Mortality, distribution, numbers and conservation of the Chatham Island pigeon (*Hemiphaga novaeseelandiae chathamensis*). *Notornis* 44: 65–77.
- Heather, B.D.; Robertson, H.A. 2015. *The field guide to the birds of New Zealand*. Auckland, Penguin. 464 pp.
- Karl, B.J.; Clout, M.N. 1987. An improved radio transmitter harness with a weak link to prevent snagging. *Journal of Field Ornithology* 58: 73–77.
- Miskelly, C.M.; Dowding, J.E.; Elliott, G.P.; Hitchmough, R.A.; Powlesland, R.G.; Robertson, H.A.; Sagar, P.M.; Scofield, R.P.; Taylor, G.A. 2008. Conservation status of New Zealand birds, 2008. *Notornis* 55: 117–135.
- Newton, I. 1998. *Population limitation in birds*. London, Academic Press. 597 pp.
- Powlesland, R.G.; Dilks, P.J.; Flux, I.A.; Grant, A.D.; Tisdall, C.J. 1997. Impact of food abundance, diet and food quality on the breeding of the fruit pigeon, parea *Hemiphaga novaeseelandiae chathamensis*, on Chatham Island, New Zealand. *Ibis* 139: 353–365.
- Ricklefs, R.E. 2000. Density dependence, evolutionary optimization, and the diversification of avian life histories. *Condor* 102: 9–22.
- Robertson, H.A. 1988. Relationships between body weight, egg weight, and clutch size in pigeons and doves (Aves: Columbiformes). *Journal of Zoology (London)* 215: 217–229.
- Robertson, H.A.; Dowding, J.E.; Elliott, G.P.; Hitchmough, R.A.; Miskelly, C.M.; Powlesland, R.G.; Sagar, P.M.; Scofield, R.P.; Taylor, G.A. 2013. Conservation status of New Zealand birds, 2012. *New Zealand Threat Classification Series 4*. Wellington, Department of Conservation. 22 pp.
- Robertson, H.A.; Baird, K.; Dowding, J.E.; Elliott, G.P.; Hitchmough, R.A.; Miskelly, C.M.; McArthur, N.; O'Donnell, C.F.J.; Sagar, P.M.; Scofield, R.P.; Taylor, G.A. 2017. Conservation status of New Zealand birds, 2016. *New Zealand Threat Classification Series 19*. Wellington, Department of Conservation. 23 pp.
- Russell, E.M. 2000. Avian life histories: is extended parental care a southern secret? *Emu* 100: 377–399.
- USGS 2019. Longevity records of North American birds. https://www.pwrc.usgs.gov/BBL/longevity/Longevity_main.cfm Accessed 17 July 2020.

Key words: Chatham Island pigeon, *Hemiphaga chathamensis*, New Zealand pigeon, *Hemiphaga novaeseelandiae*, longevity, banding

SHORT NOTE

First description of the egg of the enigmatic pied cuckoo-dove, with a literature review on the breeding biology of the congeneric crested and great cuckoo-dove

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The poorly known genus *Reinwardtoena* comprises three taxa of Old World Columbiformes with a distribution range restricted to the central Indo-Pacific region around the main and offshore islands of New Guinea, including several islands within the Bismarck, Moluccas, and Solomon Archipelagos (Gibbs *et al.* 2001; del Hoyo & Collar 2014). The widely distributed great cuckoo-dove (*R. reinwardtii*) is the only polytypic member of this genus with three subspecies ranging from the nominate of the Moluccas to Biak (*brevis*) and New Guinea (*griseotincta*), with the largest subpopulation known to occur on the main island of New Guinea. The pied cuckoo-dove (*R. brownii*) and crested cuckoo-dove (*R. crassirostris*) are two allopatric congeners that are geographically confined to some islands in the Northern Melanesia region. The crested cuckoo-dove is native only to the islands of the Solomon Archipelago (Gibbs *et al.* 2001; del Hoyo & Collar 2014).

The pied cuckoo-dove is endemic to the Bismarck Archipelago and found on various islands; inter alia on New Britain, Duke of York, Djaul, New Ireland, New Hanover, Lihir, Lolobau, Tabar, Umboi, Bipi,

and Watom (del Hoyo & Collar 2014; Dippo & Cowton 2016). Furthermore, the species also occurs on the Admiralty Island group (Manus, Rambutyo, and Nauna), which geographically belong to Papua New Guinea (BirdLife International 2020). This presumably frugivorous species inhabits the primary lowland and hill forest up to 1,000 m (BirdLife International 2020).

The pied cuckoo-dove is considered globally Near-Threatened (NT), with the global population estimated to consist of 15,000–30,000 individuals (BirdLife International 2020). This species is threatened by the ongoing loss of suitable habitat and hunting pressure (BirdLife International 2020). It is suspected to be undergoing a moderate decline in some areas due to the excessive logging of the lowland forest, while remaining common in areas with suitable habitats (BirdLife International 2020). A recent survey indicates that the species is more tolerant of degraded forest, but avoids severely degraded forest areas (Davis *et al.* 2018). Based on these observations Davis (*et al.* 2018) recommended to recategorizing the species status to Least Concern (LC). Courtship displays were observed during July on Djaul, between March–May on New Hanover, and August on New Britain (Leavesley & Leavesley 2000; Gibbs *et al.* 2001). Nothing else has been

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published about the breeding biology, with eggs and nest remaining undescribed.

Our descriptions are based on a single preserved egg set that is deposited in the American Museum of Natural History (AMNH). A single-egg clutch of *R. browni* was collected by W.F. Coultas on New Britain during the Whitney South Sea Expedition (see Figure 1). The active nest was discovered on the 30 May 1930 at a locality known at that time under the name of “Katomic”. The coordinates and current name of the original locality are not known and not given in the original label.

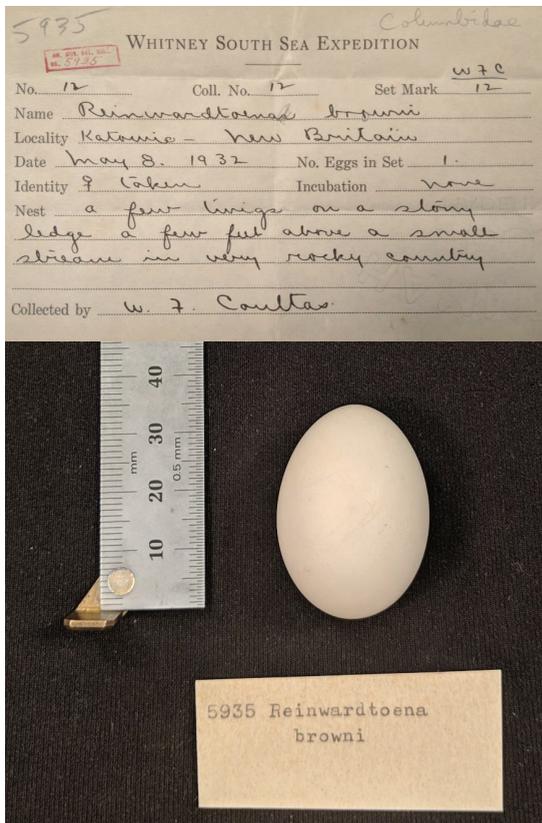


Figure 1. Original data card associated with the pied cuckoo-dove egg set in the American Museum of Natural History (catalog number: AMNH EN 5935), and egg of the pied cuckoo-dove deposited in the American Museum of Natural History (catalog number: AMNH EN 5935). Photographs: Bentley Bird © AMNH.

The egg was presumably collected during an early incubation stage, as no visible development was noted by W. F. Coultas. The species identity was confirmed by the nest attendance of the incubating female, which was also collected. The nest was

briefly described as a simple structure composed of a few twigs, which was placed on a ledge a few feet above a stream in a rocky country. The egg is uniform white and elongated-oval shaped (see Figure 1). The size is 34.71×25.03 mm (B. Bird *pers. comm.*).

Details on the nest site, egg, and clutch size are consistent with the available, published descriptions for the congeneric great cuckoo-dove and crested cuckoo-dove. The breeding biology of the widespread great cuckoo-dove is reasonably well known, with several nests documented in the wild (Baptista *et al.* 2020). Nests with single-egg clutches were reported from Boneno (Mt. Simpson, in E Papua New Guinea) in late December (Coates 1985). Two other nests were recorded in the Chimbu Province in mid-August and on Karkar Island, containing a single egg, in late May or late June, respectively (Coates 1985). Recent records include a nest with a single egg, discovered on the 26 July 1990 in a *Pandanus* tree c. 12 m above the ground (Mack 1994). A further three nests were found between April and June, all placed on a cliff ledge and containing either a single egg or single nestling (Symes & Marsden 2005). The nest of the great cuckoo-dove is described in general as a flat or slightly bowl-shaped platform composed in majority of sticks or occasionally moss, roots, sticks, and ferns, lined with fine plant material (Baptista *et al.* 2020). The nest is built usually in a bush or tree 1.2–12 m above the ground or occasionally on a rocky ledge at 2.4–12 m height (Gibbs *et al.* 2001; Baptista *et al.* 2020). The clutch size consists of a single, uniform white egg (Coates 1985; Baptista *et al.* 2020). The egg size range is reported as $37.1\text{--}40.0 \times 25.0\text{--}26.8$ mm (Harrison & Frith 1970; Coates 1985; Müntst & Wolters 1999). The incubation period at one observed nest site lasted 22 days (Chmel *et al.* 2018). In captivity, the species is recorded to lay multiple clutches if the egg failed to hatch (Müntst & Wolters 1999). According to the world first captive breeding of the species, a chick hatched successfully after an incubation period of 16 days. Brooding was documented until a post-natal age of 13 days and the chick left the nest after a total nestling period of 25 days (Müntst & Wolters 1999). After 35 days the fledgling started to pick on food items by itself (Müntst & Wolters 1999).

By contrast data on the breeding biology of the crested cuckoo-dove is very limited, with only a single nest description published to date (Gibbs *et al.* 2001). The nest was discovered in November 1995 on the Choiseul Island c. 20 m up at an inaccessible river cliff. The nest was composed mainly of twigs, and both adults attended whilst the contents were not accessible (Gibbs *et al.* 2001). The species is reported to have a single-egg clutch (French 1957) but nothing else is known about the breeding biology (Gibbs *et al.* 2001).

A single-egg clutch is likely characteristic for this genus. Apart from that, basic details on the breeding biology remain inadequately known and further research is needed on both ecology and breeding biology, with an emphasis on the general biology of the rather poorly known crested and pied cuckoo-dove. Furthermore, an assessment of the population is essential to re-evaluate the current status of the crested cuckoo-dove and establish a long-term conservation plan for this insular species.

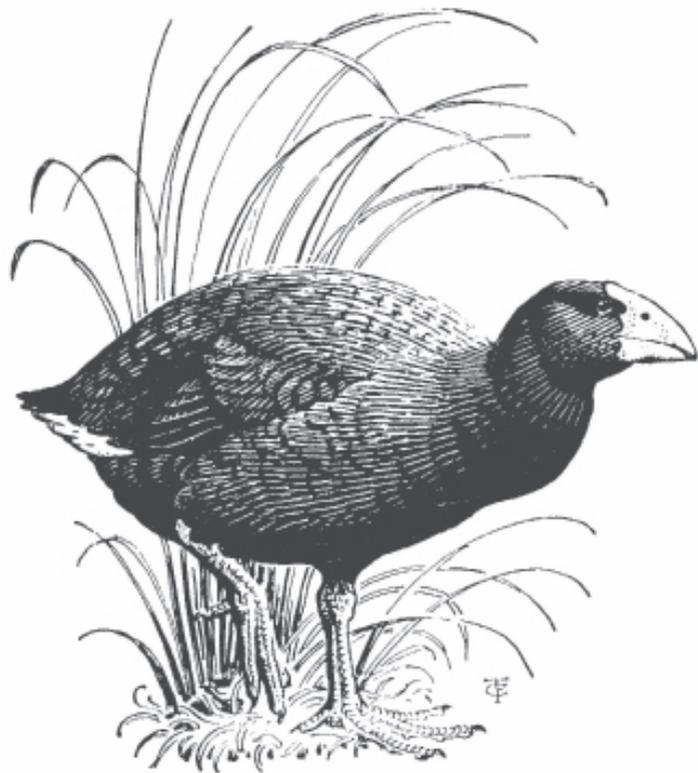
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LITERATURE CITED

- Baptista, L.F.; Trail, P.W.; Horblit, H.M.; Boesman, P.F.D.; Garcia, E.F.J. 2020. Pied Cuckoo-Dove (*Reinwardtoena browni*), version 1.0. In: del Hoyo, J.; Elliott, A.; Sargatal, J.; Christie, D.A.; de Juana, E. (Eds). Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA. doi: 10.2173/bow.picdov1.01
- Baptista, L.F.; Trail, P.W.; Horblit, H.M.; Kirwan, G.M. 2020. Great Cuckoo-Dove (*Reinwardtoena reinwardti*), version 1.0. In: del Hoyo, J.; Elliott, A.; Sargatal, J.; Christie, D.A.; de Juana, E. (Eds) Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA. doi: 10.2173/bow.grcdov2.01
- BirdLife International 2020. Species factsheet: *Reinwardtoena browni*. Downloaded from <http://www.birdlife.org> on 22 August 2020.
- Chmel, K.; Riegert, J.; Paul, L.; Mulau, M.; Sam, K.; Novotny, V. 2018. Predation on artificial and natural nests in the lowland rainforest of Papua New Guinea. *Bird Study* 65(1): 114–122.
- Coates, B.J. 1985. *The Birds of Papua New Guinea. Vol. 1. Non-passerines*. Alderley, Australia, Dove Publications.
- Davis, R.A.; Dutson, G.; Szabo, J.K. 2018. Conservation status of threatened and endemic birds of New Britain, Papua New Guinea. *Bird Conservation International* 28(3): 439–450.
- del Hoyo, J.; Collar, N.J. 2014. *HBW and BirdLife International illustrated checklist of the birds of the world. Volume 1: Non-passerines*. Lynx Edicions and BirdLife International, Barcelona, Spain and Cambridge, UK.
- Dippo, C.; Cowton, K. 2016. Bipi Island eBird checklist <http://ebird.org/ebird/view/checklist/S32330389> Accessed: 26 August 2020.
- French, W. 1957. Birds of the Solomon Islands. *Ibis* 99: 126–127.
- Gibbs, D.; Barnes, E.; Cox, J. 2001. *Pigeons and doves: a guide to the pigeons and doves of the world*. London, A & C Black.
- Harrison, C.J.O.; Frith, C.B. 1970. Nests and eggs of some New Guinea birds. *Emu* 70(4): 173–178.
- Leavesley A.; Leavesley M. 2000. New Hanover bird report, March–May 1999. *Muruk* 8(2): 63–73.
- Mack, A.L. 1994. Notes on the nests and eggs of some birds at the Crater Mountain Research Station, Papua New Guinea. *Bulletin of the British Ornithologists' Club* 114: 176–181.
- Münst, A.; Wolters, J. 1999. *Tauben: die Arten der Wildtauben. 2nd edition*. Bottrop, Verlag Karin Wolters.
- Symes, C.T.; Marsden, S.J. 2005. Notes on breeding of Salvadori's Teal *Anas waigiensis* and other birds in Crater Mountain Wildlife Management Area, Papua New Guinea. *Bulletin of the British Ornithologists' Club* 125: 11–27.

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