

Seasonal movements, foraging activity, and breeding biology of black-winged petrel (*Pterodroma nigripennis*) from three New Zealand colonies

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Abstract: The black-winged petrel (*Pterodroma nigripennis*) is an abundant procellariiform seabird breeding on islands in the Southwest Pacific and Indian Oceans. The largest populations breed in the New Zealand region where at sea movements and breeding behaviour across the annual cycle remain poorly described. We used geolocators with saltwater immersion sensors to track movements and characterise breeding behaviour of *P. nigripennis* from three New Zealand breeding colonies (Raoul, Burgess, and Rangatira Islands) across a 1,600 km latitudinal gradient. Breeding extended from November to June and in Raoul Island birds pre-laying, incubation, and chick rearing periods lasted 36, 50, and 85 days respectively. During breeding, birds from all colonies foraged within waters of the subtropical convergence zone which for Raoul, required one-way foraging trips of over 1,500 km. During March–June birds migrated east, then north and northwest to core foraging zones predominantly within the North Pacific subtropical front, but a small number of birds also wintered south of Hawaii in equatorial waters. Birds were predominantly nocturnally active during breeding and non-breeding seasons indicating a dependence of nocturnally available prey. These data contribute to a growing understanding of the unprecedented movements and potential partitioning of habitat by Australasian *Pterodroma* petrels within the Pacific Ocean and we summarise and discuss available data.

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INTRODUCTION

The black-winged petrel (*Pterodroma nigripennis*) is one of ten small highly pelagic procellariiform seabirds often grouped within the subgenus

Cookilaria (Onley & Scofield 2007). Black-winged petrels are abundant, with a global population of 8–10 million individuals (Brooke 2004) they are considered Least Concern under IUCN criteria (BirdLife International 2023) and breed widely on tropical, subtropical, and temperate islands within the South Pacific and Indian Oceans (Marchant

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& Higgins 1990). In the New Zealand region, the largest breeding populations occur on Rangitāhua – the Kermadec Islands – with an estimated 2–3 million pairs on Macauley Island (282 ha) being the largest colony of this species (Taylor 2000). Significant colonies are also present on Curtis Island and the Meyer Islands, and the species is rapidly recolonising Raoul Island following pest eradication (Veitch 2004; Gaskin 2011). Over the past 40 years black-winged petrel populations have been expanding in range with prospecting birds observed at a number of sites around the northern North Island and Chatham Islands (Klapste 1981; Jenkins & Cheshire 1982; Tennyson 1991; Ismar *et al.* 2012). Small colonies (<1,000 birds) are now established on islands off the northeast coast of the North Island (Manawatāwhi – Three Kings Islands, Motuopao, Matapia, Simmonds, Motukokako, Poor Knights, Burgess, East, and Portland Islands) and on Rekohu – The Chatham Islands – on Rangatira, Mangere, and Little Mangere Islands (Taylor 2013).

The breeding biology of black-winged petrel was documented by Tennyson (1991) on Mangere Island, and Hutton & Priddel (2002) on Lord Howe Island. However, aspects of the species breeding biology remain poorly described including the duration of the pre-laying period and the degree of synchrony between colonies separated by broad geographic distance. Like many other small petrels the at-sea movements of black-winged petrel remain poorly described. Recent GPS tracking of breeding birds from Phillip Island (Norfolk Island Group) indicates a Tasman Sea distribution during chick rearing (Halpin *et al.* 2022), in accordance with earlier observational studies (Jenkins & Cheshire 1982). Ship-board observations and geolocation tracking suggests migration by this species to the waters of the equatorial and North Pacific Ocean during the austral winter (from July to October) (King 1970; Tanaka *et al.* 1985; Pitman 1986; O'Dwyer *et al.* 2022), although further understanding of the migration routes and population specific differences in migratory distribution are required.

The development of lightweight (<5 grams) combined geolocation and immersion geolocators (here after geolocators) has revolutionised the study of seabird biology and particularly for small petrels (Afanasyev 2004; Bridge *et al.* 2011). Attached to the bird's leg, a geocator collects light level and saltwater immersion data over long periods (>2 years). Upon retrieval of the device the light data, measured every minute and logged to its maximum intensity every 10 minutes, can be used to calculate twice daily latitude and longitudes for the animal at sea to an accuracy of several hundred kilometres (Phillips *et al.* 2004; Halpin *et al.* 2021). Such data are ideally suited for tracking the seasonal movements of wide-ranging migratory

animals such as seabirds. In addition, light data can be used to identify when burrow-nesting species are spending time ashore during the day during breeding, through identification of diurnal dark periods from time-stamped light data. Salt-water immersion data provide insight into the foraging activity of birds allowing description of periods of flight and resting activity, either at sea or on land (when the logger is continuously immersed or dry), and the duration and nature of flight bouts made by birds within and between seasons. With analyses of birds tagged from multiple colonies it is now possible to use geocator-based data to build a simple population-specific understanding of the intra- and inter-seasonal movements, and breeding and foraging behaviours of birds without extensive field studies that could occupy months, if not years, of researcher time.

In this study we used geolocators to provide an inter-seasonal analysis of the at-sea movements of black-winged petrel from three New Zealand colonies spanning a tropical to temperate latitudinal gradient of approximately 1,600 kilometres. Moreover, using a geolocation-based approach, we provide a description of the at-sea activity of birds using immersion data and the timing of breeding stages for New Zealand's northernmost breeding population, Raoul Island. Comparisons are made between the non-breeding distribution of black-winged petrel and other small *Pterodroma* species tracked within the tropical and subtropical Pacific Ocean.

METHODS

Study sites

Geolocators (MK14 and MK18 tags, British Antarctic Survey) were deployed on adult black-winged petrels captured in breeding burrows at Raoul Island (Rangitāhua; The Kermadecs, 29°16'S, 177°55'W, n = 15) in February and March 2010, at Burgess Island (Mokohinau Islands, 35°50'S, 175°10'E, n = 11) in January and February 2011 and at Rangatira (Chatham Islands, 44°20'S, 176°10'W, n = 6) in February 2009 (Fig. 1). Geolocators were deployed on birds incubating eggs in all cases except for two birds tagged whilst courting in a burrow on Rangatira. Geolocators were retrieved at Raoul Island in January and March 2011, at Burgess Island in January and February 2012 and at Rangatira in February 2010 providing year-long datasets including the chick rearing period in the first year, non-breeding migration and the subsequent pre-laying, and in some cases incubation periods the following season. Geolocators were attached to birds with plastic leg bands, cable tie and superglue using the methods described by Rayner *et al.* (2008) and weighed <1% of the average body mass.

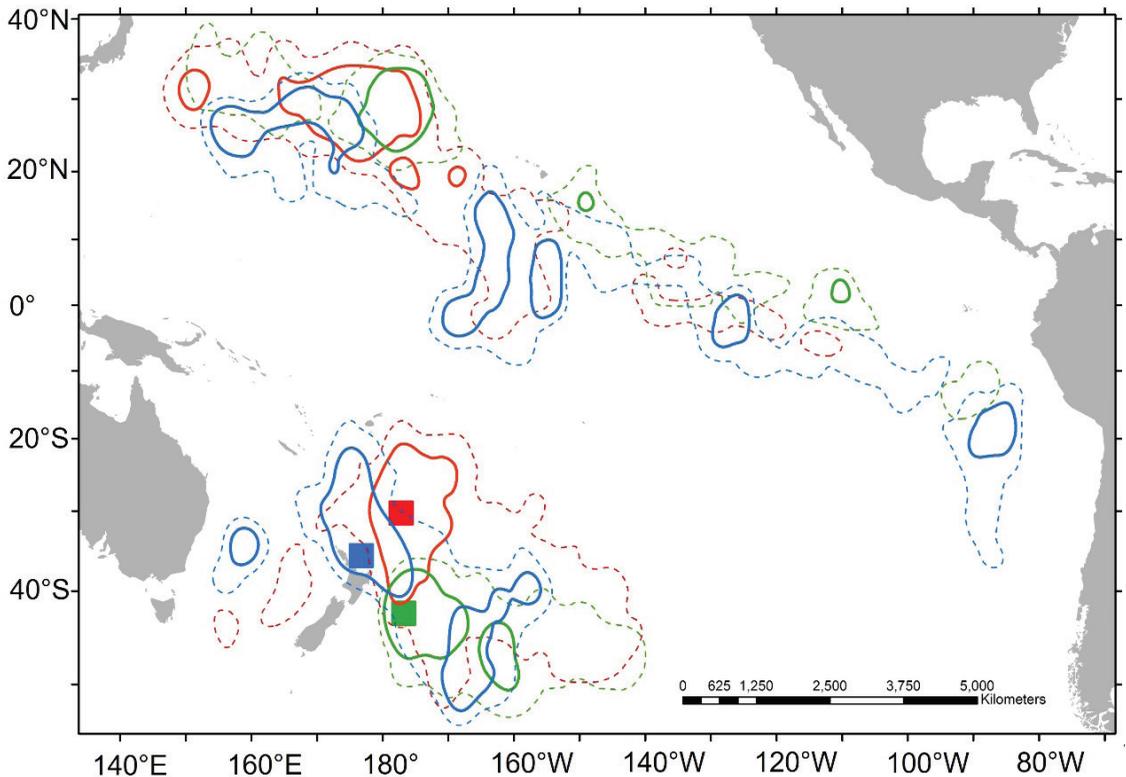


Figure 1. Year-round distribution of black-winged petrels (*Pterodroma nigripennis*) tracked from colonies on Raoul Island (red square), Burgess Island (blue square), and Rangatira (green square) between February 2009 and January 2012. Shown are the 50% (coloured lines) and 75% (hashed coloured lines) kernel contours of all locations for each population including Raoul (red lines; tracked from February 2010–March 2011), Burgess (blue lines, tracked from January 2011–January 2012), and Rangatira (green lines; tracked from February 2009–March 2010).

Tag and track processing

Light data from the geolocators were processed following the methods of Rayner *et al.* (2012). In brief, files downloaded from tags were decompressed using the software Bastrack (supplied by the British Antarctic Survey). The geolocators measured light level every minute and logged its maximum intensity every 10 minutes and the program Transedit was then used to establish sunrise and sunset transition times identified from light-curve thresholds and latitude calculated from length of day and night, and longitude from time of local midday or midnight relative to Greenwich Mean Time. Locations (2 per day) were assumed to have an accuracy of 300 ± 400 km (s.d.) (Phillips *et al.* 2004; Halpin *et al.* 2021); however, those occurring within three weeks of the equinoxes, during global sunlight uniformity, or involving unlikely movements $>1,600$ km day (Guilford *et al.* 2009) were excluded. Processed tracking datasets were analysed using the R programme ProbGLS (Merkel *et al.* 2016) to create an iterative smoothing

function for the tracks providing higher latitudinal accuracy closer to the equinox periods and in positions where birds are near the equator. The analysis followed the methods described by Taylor *et al.* (2020). Geolocators also test for saltwater immersion data every three seconds, with the data binned into 10-minute intervals, resulting in values ranging from 0 (dry) to 200 (immersed for the whole period). As described below, these data were used to calculate at-sea and colony-based activity for tracked birds.

Seasonal timing and foraging activity

Estimates of seasonal events during the breeding cycle were calculated based on screening of light, immersion, and location data from the geolocators. Mapping and geospatial processing of locations was conducted using ArcGIS v10.3 Spatial Analyst extension (ESRI). We first calculated kernel density maps for individual birds, with the 50% kernel contour used to define non-breeding ranges and

migration timing (Rayner *et al.* 2016). Subsequently population level distribution maps were created by developing kernel density estimates using combined datasets for each population. Both individual and population kernels density maps were calculated in a Lambert Equal-Area Azimuthal (South Pole) projection using a search radius of 200 km and cell size of 80 km (Phillips *et al.* 2005a; Phillips *et al.* 2007; Rayner *et al.* 2011).

Non-breeding migration timing was defined as time spent in the non-breeding core (based on the first and last locations inside or outside the non-breeding 50% kernel contour) and time spent in post- and pre-breeding transit to and from this core and a 1,000 km buffer around the respective breeding colony at the start or end of the breeding season (Rayner *et al.* 2016). During breeding, location data enabled screening of activity to dates when birds were close to their colony and could feasibly visit at night. Subsequently during those dates light data indicated extended periods when birds spent time ashore in dark burrows during the day (i.e. low light data during daylight hours during pre-laying and incubation).

Immersion data supported identification of longer visits to colonies (>12 hours) but also provided a record of when birds possibly made shorter visits to their burrows with immersion records showing as continuously dry for more than one hour. These data were particularly useful for identifying the change in behaviour associated with hatching and the subsequent shift in the behaviour of birds to more frequent short visits to feed their chicks. Quantifying the number of chick feeding visits by adults proved problematic in this species as the visits were typically of short duration (under an hour), occasionally diurnal on Raoul Island, and often with no obvious longitudinal movements back to colonies. These issues meant we could not reliably determine if the longer dry periods observed at night were time spent ashore with chicks or simply longer flight bouts near the colony (Rayner *et al.* 2012). We used the software Actave.net (Mattern *et al.* 2015) to provide temporal data on percent of time immersed, the number of flight bouts and their duration during daylight and darkness (based on the timing of civil twilight) across the year.

Data analysis

Following tests for normality, nonparametric ANOVA (Kruskal Wallis tests) were used to test for differences between range and activity parameters of the three populations during the non-breeding season and between breeding stages (non-breeding, pre-laying, incubation, and chick rearing) for Raoul birds for which tracking data were available.

Pairwise comparisons were conducted using Steel-Dwass-Critchlow-Fligner tests to protect error rate against multiple comparisons. Pairwise differences in time spent on the water between night and day across breeding stages were conducted using Wilcoxon rank-sum tests. Analyses were conducted with a threshold of significance at $\alpha = 0.05$ using JMP 11.2.0 (SAS Institute).

RESULTS

Geolocators were retrieved from black-winged petrels at Raoul Island in January and March 2011 ($n = 11/15$, 73%), at Burgess Island in January and February 2012 ($n = 6/11$, 55%) and at Rangatira in February 2010 ($n = 5/6$, 83%). Downloaded geolocators provided 6,432, 2,367, and 2,473 locations with activity data for Raoul, Burgess, and Rangatira respectively. Data for one logger on a Raoul Island bird was corrupted and could not be used.

Of birds tagged on Raoul Island during incubation, 82% (9/11 birds) indicated behaviour consistent with successfully rearing a chick in the 2010 breeding season (a schedule of short 1–3 hour mainly night-time visits to the burrow every 1–3 days from February to June) and all these birds were recaptured whilst incubating in January and March 2011.

On Burgess all six geolocators retrieved showed that birds tagged during incubation in January 2011 had abandoned breeding during February–April, and then left on migration. Activity data for three birds showed sporadic 1-day long visits to the burrow in February indicating nest failure during incubation. One of these birds was incubating an infertile egg at the time of logger attachment. For the other three individuals, data showed short (1–3 hours) visits to the burrow, indicative of chick rearing behaviour, until the early departure of these birds in March or April, suggesting the chick had died or was abandoned by its parents. All birds were recaptured in their burrows in late January 2012; however, only one was incubating an egg. One bird was found on the surface after being depredated by an Australasian Harrier (*Circus approximans*), fortunately with the geolocator attached to the remaining leg.

On Rangatira, the three birds tagged whilst incubating (two others were tagged courting in a burrow) in February had abandoned breeding attempts and left on migration during March–April. Activity data for two showed sporadic and longer 1-day visits to the burrow from early March indicating nest failure in late incubation. The other bird made frequent and short (1–3 hour) visits to the burrow, indicative of chick rearing, until the early departure of the bird on migration in late March

suggesting the chick had died or been abandoned. All three birds were recaptured incubating eggs in February 2010. The two birds tagged in one burrow without an egg made sporadic visits before migration departure in April. They were recaptured the following season with an infertile egg.

Seasonal distribution and timing

The three populations showed extensive overlap in their foraging habitats during the breeding season, predominantly east of New Zealand to waters approximately 45 degrees south in the Subtropical Convergence Zone (Fig. 1). Birds from Raoul and Burgess made a smaller number of trips into the Tasman Sea to 35–45 degrees south. During the season birds were active on their colonies the average maximum ranges from the colony of failed breeders from Burgess ($4,373 \pm 1,221$ km), Rangatira ($5,006 \pm 555$ km), and breeding birds from Raoul ($4,226 \pm 608$ km) were not significantly different from each other (Kruskal Wallis chi squared X^2 [DF = 2, N = 21] = 3.74, $P = 0.15$).

Breeding black-winged petrel from Raoul showed significant changes in foraging distribution across the season in 2010 and 2011 (Table 1; Fig. 2). There was a significant difference in the maximum range of birds between pre-laying, incubation, and chick rearing (Kruskal Wallis chi squared X^2 [DF = 2, N = 21] = 6.20, $P < 0.05$). Following pre-breeding migration and mating, birds conducted a pre-laying exodus of 36 ± 3 days, foraging south in subtropical convergence waters of the Tasman Sea and South Pacific Ocean up to $3,591 \pm 1,127$ km from the colony. Egg laying occurred late-December to early-January. During incubation foraging range contracted significantly compared to pre-laying ($2,424 \pm 1,063$ km; Steel-Dwass $Z = -2.14$, $P < 0.05$) with birds ranging south and southwest to the subtropical convergence over 14 ± 5 -day trips (based upon average incubation shift lengths). The total incubation period was 50 ± 8 days. Hatching occurred in mid-February to mid-March with no significant change in chick rearing maximum foraging range in comparison with incubation ($2,764 \pm 1,014$ km, Steel-Dwass $Z = 0.37$, $P = 0.93$),

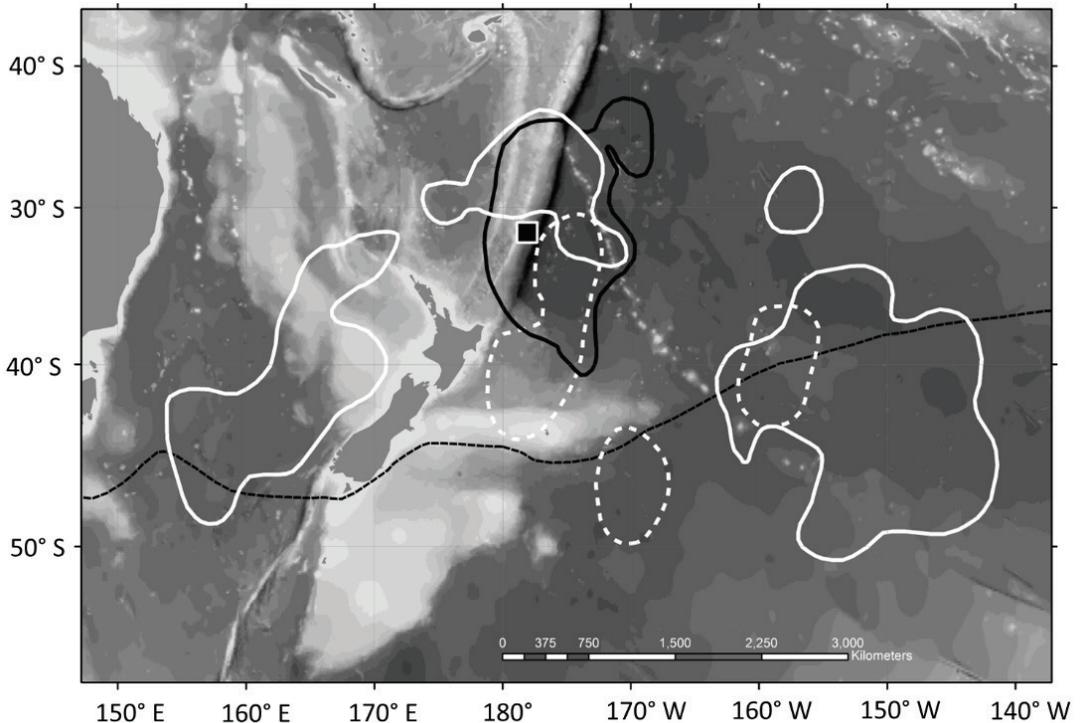


Figure 2. Distribution of breeding black-winged petrel (*Pterodroma nigripennis*) from Raoul Island (black square) as shown by 50% kernel contours during pre-laying exodus ($n = 10$; solid white lines), incubation ($n = 6$; hashed white lines) and chick rearing ($n = 6$; solid black line). Approximate location of Southern Ocean subtropical convergence shown by black hashed line adapted from Harris & Orsi (2001).

Table 1. Summary of annual cycle stages and maximum distance (mean \pm SD; range in parentheses) from the colony for breeding black-winged petrel (*Pterodroma nigripennis*) on Raoul Island and non-breeding birds on Mokohinau and Rangatira. *Calculated from hatch and laying dates for birds in successive years (2009 and 2010) see methods. Superscript numbers in each sample stage represent sample size of individuals.

| Seasonal Stage | | Max distance from colony (km) |
|---|---|--------------------------------|
| Raoul pre-laying ¹⁰ | First arrival: 7 Nov–5 Dec Pre-laying exodus duration: 36 \pm 3 days (range 31–39 days) | 3,956 \pm 541 (3,425–4,816) |
| Raoul incubation ⁶ | Laying dates: 31 Dec–15 Jan Incubation period: 50 \pm 8 days (range 43–61 days) * Shift length: 14 \pm 5 days (range 6–19 days) | 3,067 \pm 643 (2,059–3,900) |
| Raoul chick rearing ⁶ | Hatch date: 15 Feb – 16 Mar Chick rearing period: 85 \pm 6 (range 79–94 days) | 2,798 \pm 929 (1,745–3,503) |
| Raoul migration ⁹ | Departure: 4 May–15 Jun Post-breeding transit: 50 \pm 11 days (range 32–62 days) Non-breeding core: 1 Jun–11 Aug until 3 Sept–15 Nov Pre-breeding transit: 42 \pm 31 days (range 10–92 days) | 8,869 \pm 770 (7,475–9,688) |
| Burgess ⁵ & Rangatira ⁵ migration | Departure: 3 Mar–17 Apr Post-breeding transit: 57 \pm 19 days (range 37–89 days) Non-breeding core: 21 Apr–25 Jun till 9 Sept–9 Nov Pre-breeding transit: 30 \pm 21 days (range 17–77 days) | 9,869 \pm 716 (8,490–10,861) |

although with apparent clustering of foraging locations closer to Raoul as based on the kernel 50% contour. The chick rearing period was 85 \pm 6 (range 79–94 days).

Breeding birds from Raoul commenced migration during May and June. Failed breeders from Burgess and Rangatira departed earlier in March and April (Table 1). All birds followed a similar post-breeding migration pathway moving eastwards across the South Pacific Ocean, then northeast to the equatorial waters of the eastern tropical Pacific Ocean. From here the birds tracked west and northwest to reach core non-breeding habitats between 0 and 30 degrees north after approximately 50 days (range 32–89 days; Table 1; Fig. 1 & 3). There was no significant difference in post-breeding migration duration between populations. However, failed breeding birds from Burgess and Rangatira arrived earlier (April–June) than birds from Raoul (June – August) reflecting their earlier departure times. Birds from all three colonies departed southward on pre-breeding migration between early September and mid-November. Most birds flew eastwards before heading south and southwest towards New Zealand. The return migration took approximately 50 days (range 10–92 days) for birds to reach their breeding colonies, which was not significantly different between these populations (Table 1).

Activity

Flight activity of black-winged petrel changed consistently across the annual cycle with birds from

all three populations spending less time in flight and conducting fewer flight bouts during the non-breeding season than the breeding season (Table 2; Fig. 4 & 5). Within the non-breeding season there were no significant differences in daylight and night-time flight activity, foraging trip number and foraging trip duration between the three populations (Kruskal Wallis tests $P > 0.05$).

Birds from all populations spent significantly more time on the water during the day (combined population average 51 \pm 8% (range 34–64) than at night (combined population average 24 \pm 6% (range 13–37) (combined all population Kruskal Wallis chi squared X^2 [DF = 2, N = 18] = 14.28, $P < 0.001$; Fig. 4). There were significant differences in flight activity between breeding stages for birds tracked from Raoul. Time on the water during the day was significantly different between seasons (Kruskal Wallis chi squared X^2 [DF = 2, N = 24] = 29.14, $P < 0.0001$) with birds spending more time on the water during pre-laying than during incubation and chick rearing (Steel-Dwass tests $P < 0.01$) which were not significantly different from each other. Time on the water at night was significantly different between seasons (Kruskal Wallis chi squared X^2 [DF = 2, N = 24] = 13.70, $P < 0.001$) with birds spending more time on the water during pre-laying than during incubation and chick rearing (Steel-Dwass tests $P < 0.05$ and $P < 0.01$ respectively) which were not significantly different from each other. The number of flight bouts differed between seasons (Kruskal Wallis chi squared X^2 [DF = 2, N = 24] = 10.67, $P < 0.01$) with bouts being significantly longer during

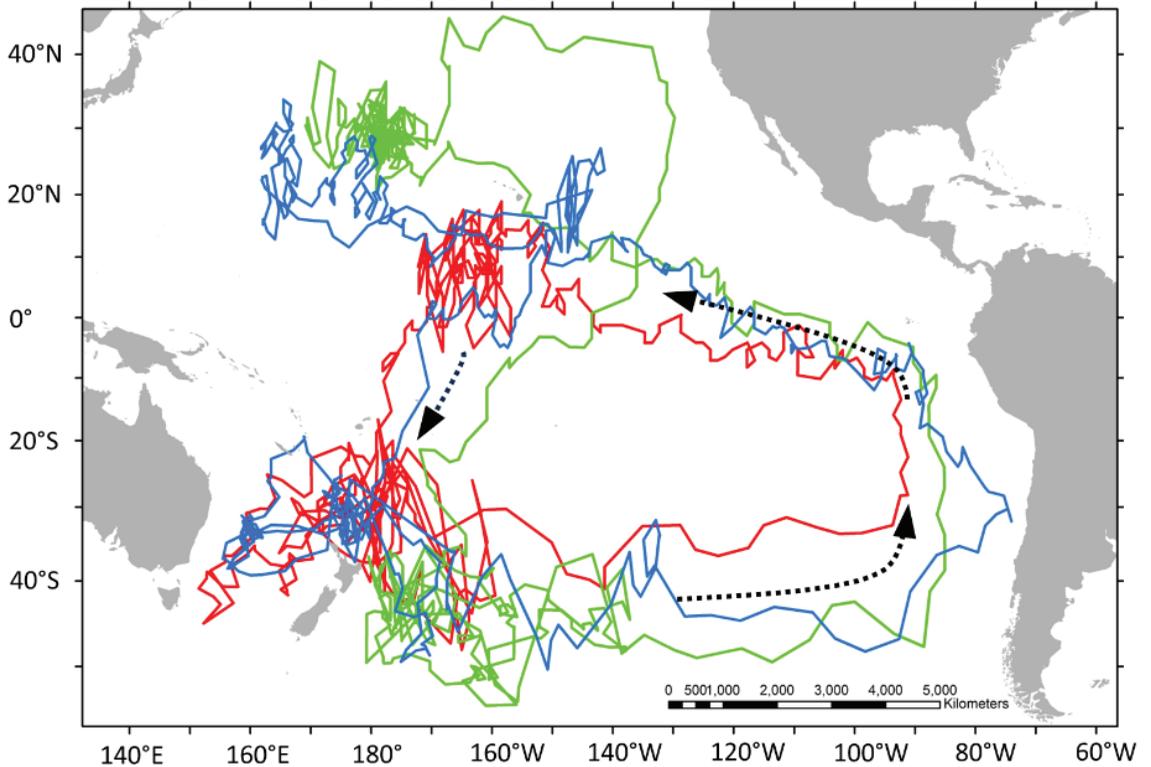


Figure 3. Representative annual tracks of three black-winged petrels (*Pterodroma nigripennis*) from Raoul (red line), Burgess (blue line), and Rangatira (green line) showing migration routes taken between breeding habitat around the New Zealand archipelago and non-breeding habitat in the equatorial and North Pacific Ocean. General patterns of movement shown by black arrows.

incubation and chick rearing in comparison with pre-laying (Steel-Dwass tests $P < 0.01$ and $P < 0.01$ respectively; Table 2) but not significantly different from each other. There was no significant difference in flight bout duration between breeding stages.

Birds spent significantly more time sitting

on the water during the day than night across all stages: pre-laying (day 24%, night 9%, Wilcoxon test $Z = 3.74$, $P < 0.001$), incubation (day 10%, night 5%, Wilcoxon test $Z = -2.51$, $P < 0.05$), and chick rearing (day 11%, night 3%, Wilcoxon test $Z = -3.53$, $P < 0.001$) (Table 2; Fig. 5).

Table 2. Seasonal activity for breeding black-winged petrel (*Pterodroma nigripennis*) from Raoul Island. Superscript numbers in each sample stage represent sample size of individuals.

| Seasonal Stage | Time spent wet (%) | | Number of flight bouts | Duration of flight bouts (min) |
|----------------------------|--------------------|------------|------------------------|--------------------------------|
| | Day | Night | | |
| Non-breeding ¹⁰ | 55.0 ± 5.1 | 22.5 ± 4.5 | 15.2 ± 1.1 | 37.2 ± 2.9 |
| Pre-laying ¹⁰ | 23.7 ± 8.2 | 8.2 ± 3.1 | 20.5 ± 6.9 | 32.2 ± 5.0 |
| Incubation ⁶ | 9.8 ± 1.7 | 4.7 ± 1.4 | 26.8 ± 2.2 | 33.7 ± 6.1 |
| Chick rearing ⁹ | 11.1 ± 2.0 | 3.7 ± 0.9 | 25.8 ± 1.4 | 37.1 ± 3.1 |

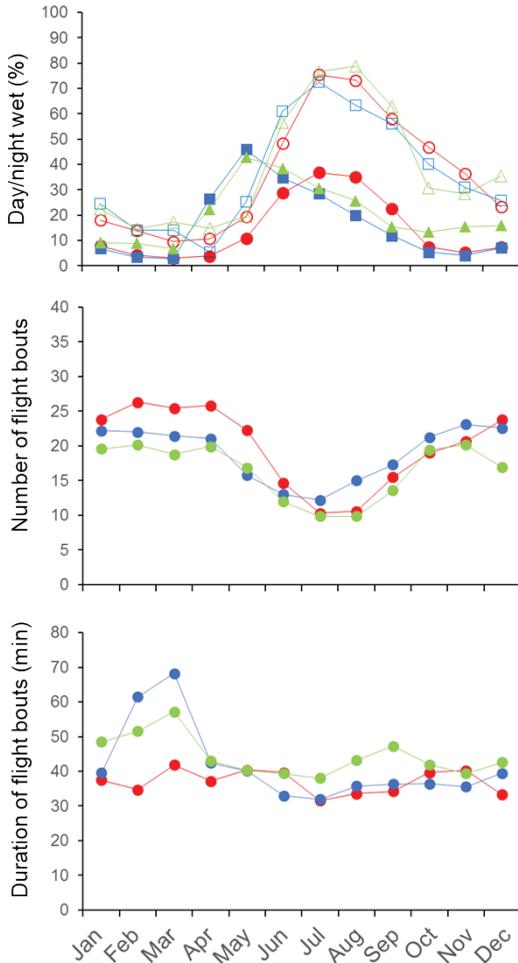


Figure 4. Mean monthly activity metrics for black-winged petrels (*Pterodroma nigripennis*) tracked from Raoul (red symbols), Burgess (blue symbols), and Rangatira (green symbols) including A) percent of time spent on the water during day (unfilled circles) and night (filled circles); B) number of flight bouts and C) duration of flight bouts.

DISCUSSION

The results of this study add to historic and contemporary data demonstrating the extreme, “ocean scale” habitat use of small *Pterodroma* petrels within the Pacific Ocean (King 1970; Bartle *et al.* 1990; Spear *et al.* 2007; Rayner *et al.* 2011, 2016). Black-winged petrels breeding on Raoul, Burgess, and Rangatira made extensive use of the waters of the Tasman Sea and South Pacific Ocean during the breeding season, consistent with previous ship-board observations and tracking studies in the Tasman Sea (Halpin *et al.*

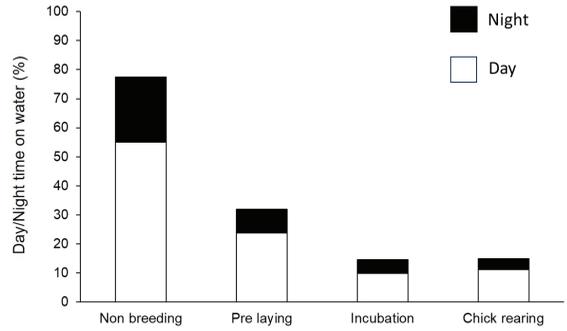


Figure 5. Proportion (%) of time at sea spent on the water during day and night for black-winged petrels (*Pterodroma nigripennis*) from Raoul during the non-breeding, pre-laying, incubation, and chick rearing seasons.

2022). There was extensive overlap in the range of birds from the three colonies, particularly in the waters of the subtropical convergence zone east of New Zealand (Fig. 6). Birds made regular long trips to, and within, this productive frontal region. The New Zealand section of the subtropical convergence is an important foraging habitat for many breeding seabirds including Chatham petrel (*P. axillaris*) (Rayner *et al.* 2012), Cook’s petrel (*P. cookii*) (Rayner *et al.* 2008), Buller’s albatross (*Thalassarche bulleri*) (Stahl & Sagar 2000), northern royal albatross (*Diomedea sanfordi*), and Antipodean albatross (*D. antipodensis*) (Nicholls *et al.* 2002).

The breeding behaviour of black-winged petrel from Raoul Island observed in this study is consistent with our understanding of the breeding biology of small (160–200 g) *Pterodroma* petrels in general. Features of the breeding cycle in this genus include an extended pre-laying exodus from the colony following mating, long incubation shifts, and a long chick rearing period (Marchant & Higgins 1990; Tennyson 1991; Hutton & Priddell 2002; Brooke 2004; Rayner *et al.* 2012). The pre-laying exodus in black-winged petrels in our study (36 days) was similar to the Chatham petrel (34 days) (Rayner *et al.* 2012) and the incubation and chick rearing periods (50 and 85 days) were similar to black-winged petrels from Lord Howe Island (45 and 85 days; Hutton and Priddell (2002), Cook’s petrel (47 and 87 days; Imber *et al.* (2003), Bonin petrel (*P. hypoleuca*) (49 and 82 days; Pettit *et al.* (1982), and Pycroft’s petrel (*P. pycrofti*) (45 and 80 days; Marchant and Higgins (1990). Incubation shift length in this study (14.5 days) was similar to the species discussed above.

Changes in the at-sea distribution of seabirds across the breeding season reflects the energetic demands of breeding duties as well as seasonal shifts

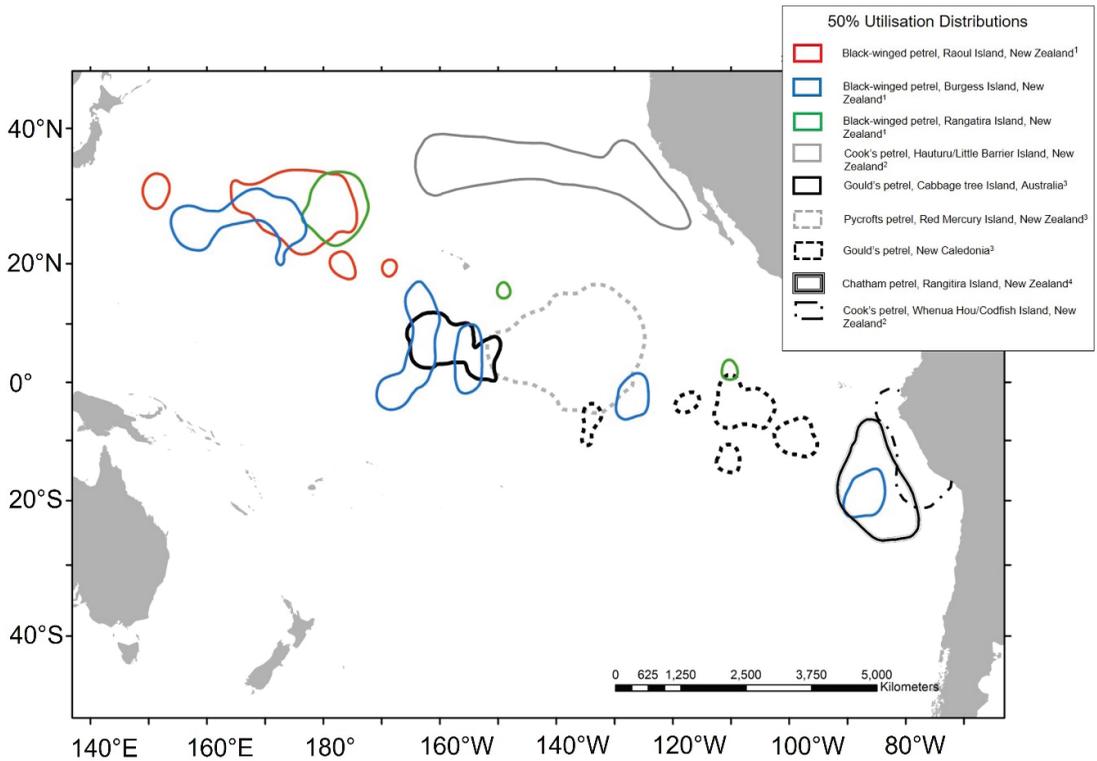


Figure 6. Core kernel utilisation distributions (50%) for non-breeding small *Pterodroma* petrels tracked from Australasian colonies between 2007 and 2011. Data sourced from current the study, Rayner *et al.* (2011), Rayner *et al.* (2012), and Rayner *et al.* (2016).

in oceanographic productivity with time (Phillips *et al.* 2005b; Gonzalez-Solis *et al.* 2007; Weimerskirch 2007; Peron *et al.* 2010). In breeding black-winged petrels from Raoul Island, reduced foraging range sizes between pre-laying, incubation, and chick rearing likely reflects the reduced time available between colony visits as a necessity of incubation shifts, and then chick provisioning duties. Though there was no difference between maximum ranges of birds during incubation and chick rearing, the concentration of the 50% kernel around Raoul during chick provisioning suggests birds can meet the needs of chicks by foraging, in part, in subtropical waters nearer to their colony. Similarly, Halpin *et al.* (2022) found that during chick rearing, GPS tracked black-winged petrels from Phillip Island alternated between short trips, closer to the colony, and longer trips southwards of several thousand kilometres presumably for maintenance of parental body condition. Future GPS-based studies of breeding birds from Raoul and other sites would help clarify the effects of breeding stages on the energetic budgets of these populations.

Breeding failure of black-winged petrel on Burgess and Rangitira during our study was concerning, but unlikely attributed to tag attachment methods as these same methods were applied successfully on the Raoul birds. Moreover, our work on *Pterodroma* petrels that breed in New Zealand has shown little impact of geolocator deployments on breeding success and or migration return rates including Cook's petrel (Rayner *et al.* 2007, 2008, 2011), Chatham petrel (Rayner *et al.* 2012), and white-headed petrel (*P. lessonii*) (Taylor *et al.* 2020). These observations are also consistent with international studies examining the impact of lightweight geolocators on procellariiform and charadriiform seabirds (Kürten *et al.* 2019; Nicoll *et al.* 2022). Other colony-specific factors including competitor and predator disturbance are likely more influential. On Burgess Island, black-winged petrels have recently established a small population (Ismar *et al.* 2012) but, with little shrub or tree cover, appear susceptible to predation by Australasian harrier when arriving at breeding sites before dark. During our field work on this island predated birds

of multiple species, including one black-winged petrel tagged with a geolocator, were found. Some of the black-winged petrel nests were on the surface under dense grasses and downy chicks may have been visible to harriers flying low over the colony. Harriers are also present on Rangatira; however, a more likely factor in poor breeding success at this site is nest disturbance by large numbers of broad-billed prion (*Pachyptila vitatta*), a major cause of nest failure in the endangered Chatham petrel on this island at unmanaged sites (Gummer *et al.* 2015).

The migratory movements of black-winged petrel from New Zealand populations were similar in terms of timing, pathway and non-breeding distribution to birds tracked from Lord Howe and Phillip Island in 2017 and 2021 (O'Dwyer *et al.* 2022) allowing for general conclusions on the migratory behaviour of the species. Overall, black-winged petrels breeding in Australasia migrate first eastwards across the South Pacific Ocean, then northeast towards the equator, and then west and northwest into the subtropical North Pacific Ocean during April–November. Post-breeding movements in this species are protracted (up to 90 days) with most birds reaching core non-breeding grounds between 22 and 33 degrees north on the southern side of the North Pacific Current, a warm water current flowing west-to-east between 30 and 50 degrees north forming the northern boundary of the North Pacific Subtropical Convergence (Howell *et al.* 2012). Interestingly, in the case of the New Zealand tracked populations, a small number of individuals occupied non-breeding core ranges south of Hawaii in the central North Pacific between 0 and 15 degrees north (Howell *et al.* 2012) (Burgess (2/6 birds, 33%), Rangatira (1/5 birds, 20%), (Raoul (1/11 birds, 9%)). Observed differences in non-breeding core distributions may reflect habitat flexibility in this species or be mediated by breeding failures and or life history characteristics. For example, failed breeding birds from Burgess and Rangatira initiated their migrations earlier than Raoul birds thus encountering differing seasonal productivity which could have influenced habitat selection. Possibly these birds also represent a younger, less experienced cohort, still establishing migratory core choices as observed in other species (Clay *et al.* 2018; Powers *et al.* 2022).

Broad-scale segregation is an important component of resource partitioning by procellariiform seabirds at high latitudes (Navarro *et al.* 2015; Quillfeldt *et al.* 2015) and our study supports growing geolocator-based data indicating such segregation of non-breeding habitats is also prevalent in small *Pterodroma* petrels in the tropical and subtropical Pacific Ocean (Fig. 6). In the North Pacific black-winged petrels from Australasia (O'Dwyer *et al.* 2022; this study) occupy a different

region of the subtropical gyre than northern Cook's petrel (*Pterodroma cookii cookii*) tracked to the eastern section of this frontal system during 2007–2009 (Rayner *et al.* 2011). Southwards in the eastern equatorial Pacific Ocean Rayner *et al.* (2016) demonstrated spatial and habitat segregation between three taxa tracked between 2010 and 2011: Gould's or white-winged petrel (*P. leucoptera leucoptera*) occupying the North Equatorial Counter Current south of Hawaii (10°N–5°S, 150–165°W), *P. leucoptera caledonica* 3,000–6,000 km southeast over the East Pacific Rise in the South Equatorial Current (0–15°S, 135–100°W), and Pycroft's petrel occupying a region between *P. l. leucoptera* and *P. l. caledonica* also in the North Equatorial Counter Current (0–10°N, 140–135°W). In the South Pacific Ocean, Chatham petrels tracked during 2009 and 2010 occupied waters centred at 20°S, 84°W within the Humboldt Current (Rayner *et al.* 2012) whereas southern Cook's petrel *P. cookii orientalis*, tracked during 2007–2009 were distributed further east towards the coast of South America (Rayner *et al.* 2011). Clearly seasonal differences in productivity could explain different habitats selected by these species as not all were tracked across in the same years. However, several lines of enquiry suggest that species-specific non-breeding distributions may be an interannual feature across this massive oceanic region: first, work combining tracking and isotope data from contemporary and historic specimens of Cook's petrel suggest long-term, population specific, stability in core migratory destination over century-long time-spans (Rayner *et al.* 2011), and second, modelling of species distributions within the same year (i.e. Rayner *et al.* 2016) indicates population-specific habitat niches based on responses to environmental parameters such as thermocline depth, sea surface temperature and bathymetry. Future research combining new high-resolution lightweight tracking technologies across multiple species within the same season will provide fascinating insights within this new frontier of avian habitat selection.

Our analysis of geolocator immersion data from black-winged petrel across the annual cycle showed an activity pattern similar to previous migratory seabirds with decreased time resting on the surface, and more frequent and longer flight bouts during the breeding season than during the non-breeding period (Rayner *et al.* 2012; Ramirez *et al.* 2013). This reduced flying activity outside of breeding is expected during a time when birds moult most of their main body and flight feathers (Warham 1996). For breeding birds from Raoul Island more time was spent on the water during pre-laying than during incubation and chick rearing reflecting the well-known energetic demands of these latter stages. Comparisons of night and day

activity data supports previous work showing that black-winged petrel is predominantly a nocturnal forager during the non-breeding season with less time sitting on the water and more time in flight, during which they surface seize and make short plunge dives to capture prey (Bonnet-Lebrun *et al.* 2021). However, our data also indicate that, during breeding, birds are more active at night across all breeding stages and although they almost certainly forage opportunistically during the day, targeting nocturnal prey appears their primary foraging strategy. In the tropical Pacific the diet of black-winged petrel is dominated by small mesopelagic fishes which migrate vertically at night to surface waters and make up over 85% of the diet (Spear *et al.* 2007). It is likely that such taxa form at least part of the diet of breeding birds, but further studies are required.

In conclusion, the results of our geolocator-based study of three populations of black-winged petrel in New Zealand show that during breeding birds regularly forage south of their colonies within waters of the Subtropical Convergence Zone which for some colonies, i.e. Raoul, require long foraging trips over 1,000 km one way. During the non-breeding season birds occupied wintering core foraging zones predominantly within the North Pacific subtropical front, as observed in other Australasian populations. However, a small number of birds also wintered south of Hawaii in equatorial waters. The timing of migration and breeding was consistent between breeding populations with the species showing similar breeding traits to other small *Pterodroma* petrels studied to date. Geolocator immersion data indicate that throughout the year black-winged petrel forage extensively by night, most likely on vertically migrating prey.

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