Year-round distribution, breeding cycle, and activity of white-headed petrels (*Pterodroma lessonii*) nesting on Adams Island, Auckland Islands

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ABSTRACT: Ten white-headed petrels (*Pterodroma lessonii*) from Adams Island, Auckland Islands, were tracked during 2011–14 using miniature geolocators, in the first study to examine the at-sea movements and key foraging areas of this pelagic seabird. Data revealed extensive migrations west to South Africa and east into the central South Pacific Ocean. The birds returned to colonies Aug–Oct. Median departure on pre-laying exodus was 24 Sep. Birds were away for up to 77 days during pre-laying and moved west towards the Indian Ocean. Laying occurred 24 Nov–10 Dec. The first major incubation shifts by males and females were *c*. 19 days in duration. The maximum foraging range during incubation was 5,230 km from the colony, the most distant recorded by any seabird during this breeding stage. After eggs hatched in January, some birds foraged off Antarctica in sea temperatures down to –1°C. Birds spent the inter-breeding period in disjunct areas (off South Africa, south of Australia, Tasman Sea, and South Pacific Ocean). This study revealed an unusual courtship behaviour not recorded previously in other seabird species. Females returned from distant oceans to spend just a few days ashore in the pre-laying period before leaving the breeding site until the following spring. The males also skipped breeding at the same time as their mates, but returned earlier in the season. The new knowledge gained about the breeding activity of this species will assist with future population assessments.

Introduction

The white-headed petrel (*Pterodroma lessonii*) (Fig. 1) is one of the four largest members of the genus *Pterodroma* (Murphy & Pennoyer 1952), along with three closely related winter-nesting species: Atlantic petrel (*Pt. incerta*), great-winged petrel (*Pt. macroptera*), and grey-faced petrel (*Pt. gouldi*) (Imber 1985; Wood *et al.* 2016). White-headed petrels (hereafter WHPs) nest in the summer and autumn on five subantarctic island groups (Auckland, Antipodes, Macquarie, Kerguelen, and Crozet Islands; Marchant & Higgins 1990). The largest populations (hundreds of thousands of pairs) occur in the New Zealand region, on Auckland and Antipodes Islands (Taylor 2000; Miskelly *et al.* 2019), with a smaller population (*c.* 10,000 pairs) present on Macquarie Island (Brothers 1984). There are 34 extant members of the genus *Pterodroma* and most are threatened with extinction (BirdLife International 2019). WHP is listed as Least Concern, based on its large population sizes and widespread breeding distribution, although some populations are declining (BirdLife International 2019). The major threat to WHPs is from invasive mammalian species at the breeding sites (Taylor 2013). Threats to WHP in the marine environment are poorly understood due to the limited knowledge of the nature and extent of their annual movements.

The breeding biology of WHP was studied by Warham (1967) and Brothers (1984) at Macquarie Island, and by Zotier (1990) and Chastel (1995) at the Kerguelen Islands. These studies gave valuable insight into the onshore activities of the species, including the discovery that WHP is a biennial breeder, something not recorded in other Procellariidae (Zotier 1990). However, the at-sea movements remained largely unknown, and many details about their breeding biology, especially in

FIGURE 1. White-headed petrel on Adams Island, February 2003. *Image: C. O'Donnell.*

the courtship and pre-laying period, are lacking (Marchant & Higgins 1990; Brooke 2004).

The availability of miniaturised tracking technology has revolutionised the study of migratory bird species and has been widely used on seabirds (Burger & Shaffer 2008; Block *et al.* 2011). Archival tags (also known as geo-locators, global location sensing, or GLS tags) weighing just a few grams can collect and store a range of data (light levels, sea-water immersion, and sea temperature) that permits detailed and remote study of bird species. The light data are used to estimate longitude and latitude at midday and midnight. The same light readings are also used to identify when burrow-nesting seabirds are spending time ashore by day, from recordings of continuous dark periods over 24 h. The sea-water immersion data provide details of when birds are landing on the sea when foraging, resting on the sea for long periods, or spending periods when the tag remains dry (either in continuous flight or when the bird is on land). Sea temperature data provide insight into the different water zones used by the birds throughout the annual cycle, and are used to calculate and verify latitude records by comparing with remote satellite sensing of the ocean surface temperature (Merkel *et al.* 2016).

Even from small samples of tagged birds it is now possible to provide an assessment of their movements at sea, and which ocean basins and water zones are used during different stages of the annual cycle. The precise dates birds are visiting the colony are captured on the tags through examination of activity and light logs. These have helped to collect information on onshore activity that was not available to earlier WHP researchers (e.g. Warham 1967; Zotier 1990).

This paper provides the first detailed examination of WHP at-sea movements and onshore breeding behaviour derived from GLS tag data. The study aims to provide more detailed information on the annual breeding cycle to help with refining future population censuses at breeding colonies. The results from the study can also be used to identify potential risks to the species in the marine environment (e.g. extent of overlap with known commercial fisheries, or whether climate change is likely to have impacts on their preferred foraging zones).

Materials and methods

Study area

Adams Island (50°53′S, 166°03′E) is a 9,693 ha island at the southern end of the Auckland Islands. The island rises to 705 m a.s.l. at Mt Dick, the highest point in the group. Adams Island is free of introduced mammalian predators and is probably the largest temperate land mass in the world to remain in a near-pristine state (Elliott *et al.* 2020 – Chapter 3 in this book). This research was an opportunistic project carried out as adjunct to a long-term project on Gibson's wandering albatross (*Diomedea antipodensis gibsoni*), and the WHP nests needed to be easy to monitor during travel to and from the open tops of Adams Island. WHP burrows were identified close to a marked route above Maclaren Bay on the central northern coast of Adams Island (Elliott *et al.* 2020 – Chapter 3). All the study nests were above the coastal zone of southern rātā (*Metrosideros umbellata*) forest, in a mixed shrubland and tussock plant community. Access to the nest chamber from the entrance was the main criteria for selection of study burrows. All suitable burrows were tagged and labelled, and the location was GPS-plotted.

Bird capture and tagging

British Antarctic Survey (BAS) Mark 15 (16 × 14 × 6 mm; 2.5 g) or Mark 18L (17 × 10 × 6.5 mm; 1.9 g) GLS tags were used in this project. Several days prior to bird handling, all GLS tags were turned on and the date and time in GMT was accurately recorded. The tags were left outside to calibrate light levels at a known location (the base hut at Maclaren Bay). The date and exact time of deployment was also recorded for each bird.

The birds were all captured in breeding burrows during the late incubation period between Jan 2011 and Jan 2014. All birds appeared to be on eggs when first captured. Where possible, both birds of a pair were captured over a 2-week period. On first capture, each bird had a uniquely numbered stainless-steel 7.5 mm internal diameter H-band applied to the tarsometatarsus. All birds were sexed by their subsequent behaviour associated with the laying period. Females departed quickly back to sea after laying, and males had very long first shifts as they do in all other closely related *Pterodroma*

FIGURE 2. Mark 15 GLS tag attached to plastic leg band on white-headed petrel on Adams Island, January 2013. *Image: C. O'Donnell.*

species (Imber 1976; Warham 1990; Brooke 1995; Taylor *et al*. 2012).

Each bird had a GLS tag attached to a plastic leg band with a cable tie (Fig. 2). Ten tags were deployed in 2011, and eight tags in 2012 (including two repeat deployments). Any birds recaptured in 2012–14 with GLS tags present had these tags removed and the date of capture recorded. All tags were given a post-deployment calibration period of a few days at the base hut. Tags were initially downloaded in the field and then returned to the mainland for post-deployment processing.

Tag processing

All tag datasets are stored in compressed code. These files were initially decompressed using the software BasTrak (supplied by BAS; Fox 2010). The activity, sea temperature, and light data were used in the data analyses. Details about how these tags store archival data can be found in Fox (2010) and Cherel *et al*. (2016).

The tracking datasets were initially processed using standard methods (Phillips *et al*. 2004; Rayner *et al*. 2012). Briefly, the light data were run through the program TransEdit to check daily light transitions at sunrise and sunset, and to provide confidence intervals around the light curves (Fox 2010). The programs Birdtracker or Locater were used to generate twice-daily positions at midday and midnight using an astronomical algorithm; latitude is estimated from day/night length, and longitude from the absolute time of local midday/midnight (Fox 2010). Unreliable positions generated around equinox periods were excluded. Mean accuracy of positions is estimated at 186 ± 114 km in pelagic seabirds (Phillips *et al*. 2004). These initial visualisations of flight paths helped to define the bounding boxes used in the probGLS assessment.

Track processing in probGLS

All datasets from the WHP tags were analysed using the software probGLS (Merkel 2016). The locations from GLS tags were plotted using an iterative forward-step selection probability algorithm in the probGLS package (Merkel *et al*. 2016) in R (R Core Team 2015). The algorithm uses light, temperature, and activity data recorded by the loggers to predict the probable location of the birds. For this process, the twilight events were identified from raw light intensities using the twilightCalc function in the GeoLight package (Lisovski & Hahn 2012). A light threshold of 2 was used for all tracks, and the sun angle selection was set between –7° and –1°. For the temperature data, the daily median water temperature encountered by each bird was calculated from sea temperature data collected during sustained water contact by the loggers. The daily mean satellite-derived sea-surface temperature (SST) and mean SST error were extracted from the NOAA (National Oceanic and Atmospheric Administration) high-resolution dataset (0.25° × 0.25°, NOAA OI SST V2 High Resolution Dataset, http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.highres.html, accessed 20 Jun 2018). A maximum temperature difference of 2°C was allowed between recorded temperature and mean SST to calculate the locations for those tags that recorded temperature data. As the error in identifying latitude based on twilight events is

highest during equinoxes, the probability algorithm was allowed to assign random latitudes (with uniform distribution) based on the temperature (where available) and activity data to the locations obtained within 10 days of an equinox event.

To further increase the accuracy of locations, 20°E and 100°W longitudes were defined as the western- and eastern-most limits for WHP distribution (based on the original Locater mapped assessments) and the bounding latitudes were set at 25°S and 70°S for the known species distribution (Marchant & Higgins 1990). Additionally, a land mask (0.25° × 0.25°, NOAA OI SST V2 High Resolution Dataset, http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.highres.html, accessed 20 Jun 2018) was used to prevent the selection of points on land. A conservative maximum possible speed limit of 45 m/s (in flight) and 3 m/s (in water) was used to eliminate fixes that implied unrealistically high flying speeds (Pennycuick 1982; Catry *et al*. 2004). As the accuracy of the locations increases with the number of weighted particles calculated for each point cloud and with iterations (Merkel *et al*. 2016), 2,000 particles were generated for each possible location to create a track. This process was iterated 100 times to finally calculate the median geographical track (Merkel *et al*. 2016). The resulting location data were plotted in ArcMap 10.3.1 (ESRI 2011) and were projected using a conformal cylindrical projection.

All positions were uploaded as kml files onto Google Earth. The maximum distance each bird travelled away from the colony during each stage of the annual cycle was assessed using the measurement tool on Google Earth. This gave the great-circle distance from point to point (colony to the furthest location plotted at sea in each annual activity stage per bird). Point-to-point distances along a flight track (12-hour intervals) were measured using the same tool. Maximum distance measurements are given as mean (± *sd*).

Activity patterns ashore

WHPs tended to move longitudinally when foraging. This made it easier to identify dates when the birds were close to the longitude of the Auckland Islands and potentially visiting the colony. Assessment of light records identified

when the birds spent a 24-hour period ashore inside the burrow (continuous light readings of 0 = dark during daytime). Birds visiting the colony also had sea-water immersion records showing as continuously dry (= 0). The last sea-water immersion interval (1–200) showed when the bird was still at sea before returning to land, and the next sea-water immersion reading revealed when the birds returned to sea after being ashore at the colony.

Results

Tag recovery

Twelve of the 18 tags were recovered between 2012 and 2014. Extensive checking of the marked nests during 2012–15 failed to locate the six remaining tagged birds. It is likely that these birds shifted burrows, or their nests failed early in some of the monitored breeding seasons, and that they had departed the colony. Of the 12 tags recovered, two were from birds retagged in 2012. Of the ten individuals successfully tracked (six females and four males), three were tracked for a single year, five for two consecutive years and two birds for three consecutive years (19 bird-years in total). Tracks from these birds can be viewed on https://zoatrack.org.

At-sea distribution

WHPs from the Auckland Islands covered very large tracts of ocean during the annual cycle (Fig. 3). The birds were extremely pelagic, foraging over deep ocean basins with no discernible underwater features such as sea mounts at favoured hotspots. One bird had an annual cumulative point-to-point movement of 169,400 km, and another covered 318,700 km over 2 years. The lowest annual point-to-point movement recorded from the ten birds was 115,200 km. WHPs from Adams Island foraged mainly west of the Auckland Islands, travelling as far as the seas south-east of southern Africa (up to 9,500 km from the breeding colony; Fig. 4). The ten birds made extensive use of the seas south of Australia, in the southern Indian Ocean, and polar seas south of the Antarctic Convergence. Nine of the birds went south-west to the edge of the pack ice, with some individuals foraging 200–250 km north of the Antarctic
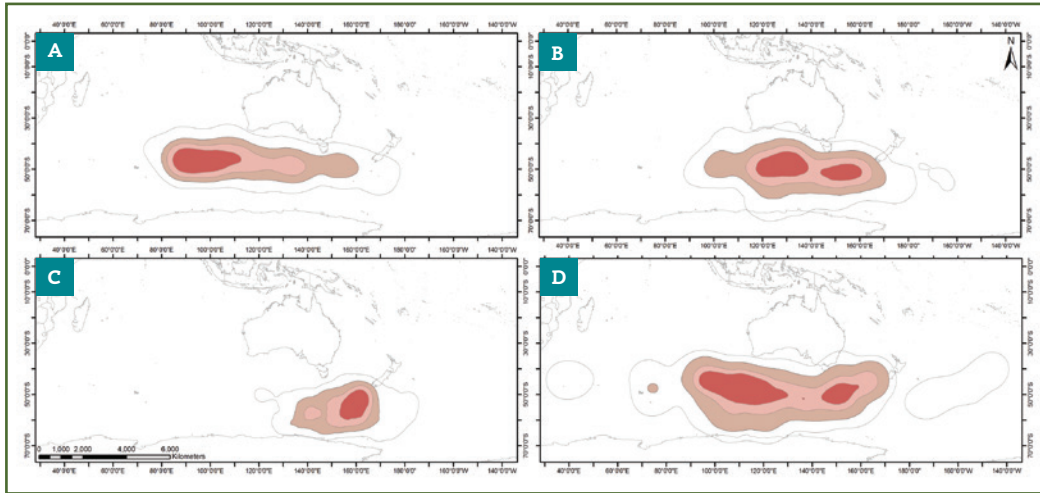
FIGURE 3. Kernel density distributions for white-headed petrels derived from geolocator/immersion-logger data ($n = 10$) during (**A**) pre-laying exodus, (**B**) incubation period, (**C**) chick-rearing period, and (**D**) non-breeding period. Coloured polygons represent the 25%, 50%, and 75% density contours, and the outer black line represents the 95% density contour.
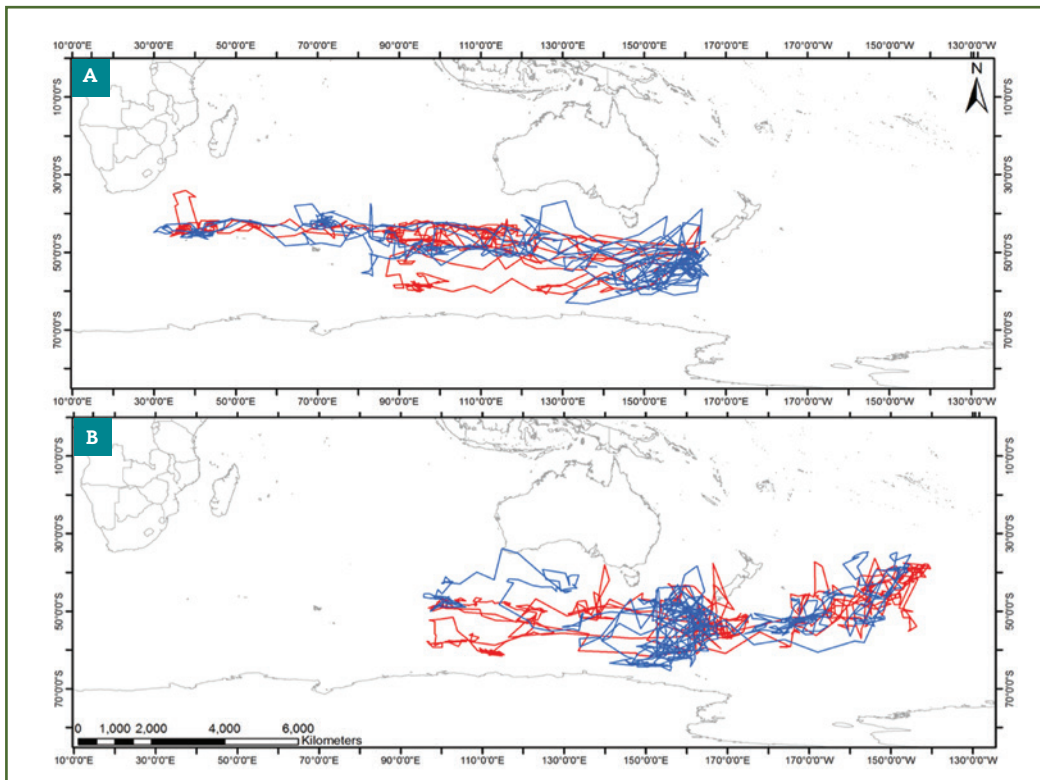
374

FIGURE 4. Migration routes of two white-headed petrels tracked with geolocator/immersion loggers for two consecutive years (2011–13) on Adams Island, New Zealand. The first year's track (2011–12) is shown in blue and the second year's track (2012–13) in red. The birds (both males) represent (**A**) the western-most, and (**B**) the eastern-most foraging areas for our study individuals ($n = 10$).
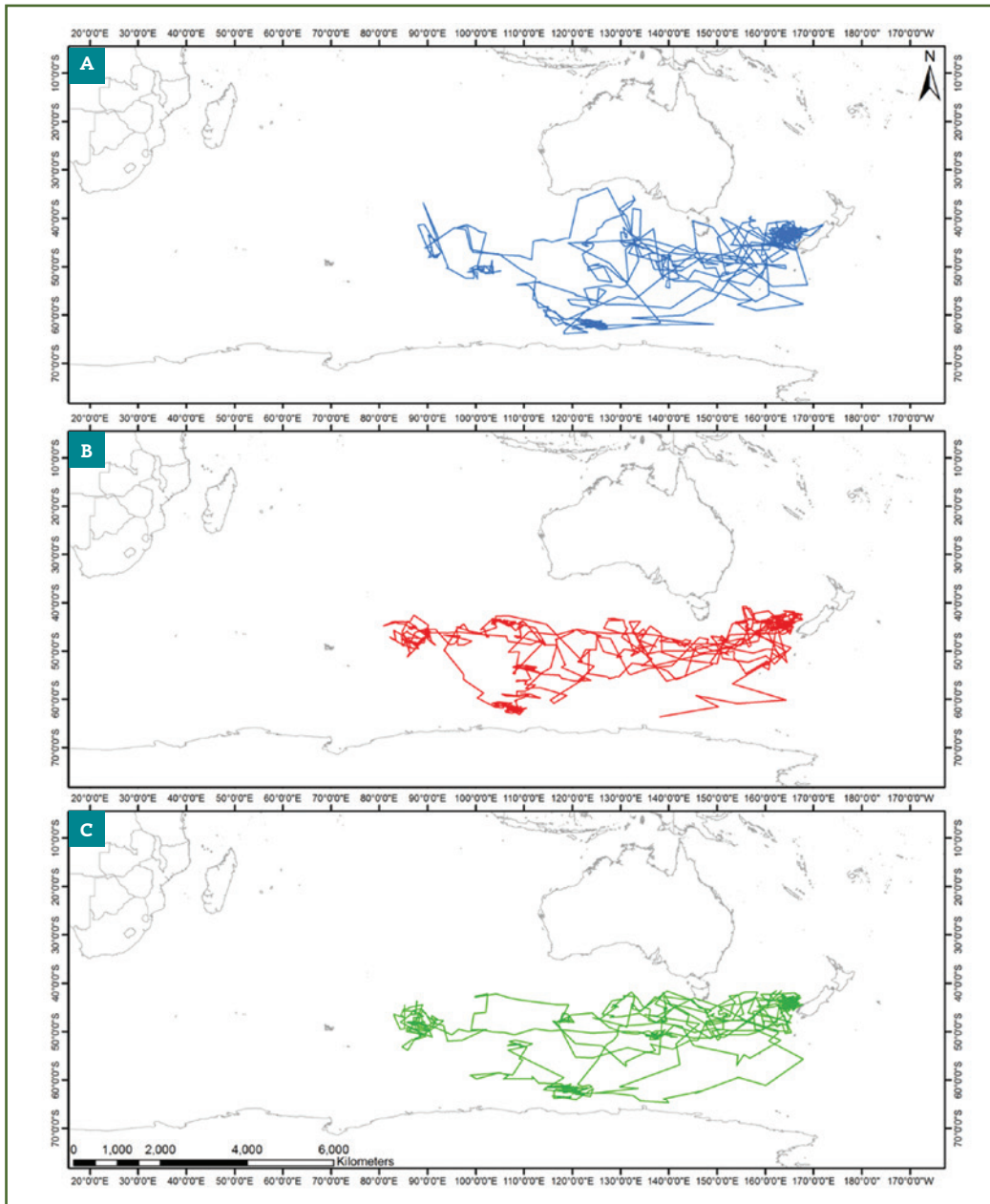
FIGURE 5. Migration routes of one female white-headed petrel (H-28516) tracked with a geolocator/immersion logger for three consecutive years (2011–14) from Adams Island, New Zealand. Migration route for individual years: (**A**) year 1 (2011–12) in blue, (**B**) year 2 (2012–13) in red, and (**C**) year 3 (2013–14) in green, showing consistent foraging and moulting areas over the 3-year period.

continent in seas as cold as –1°C. Just five (50%) of the tracked birds moved east of the Auckland Islands at various times. One female foraged south-east of the Antipodes Islands during incubation and chick-rearing, and one male moved extensively into the South Pacific Ocean after breeding (Fig. 4). A female spent three successive winters in the south Tasman Sea in much the same region just west of Fiordland (Fig. 5).

WHPs are capable of rapid movements into distant foraging zones. The 12-hourly point-to-point movement averaged 217 km (*sd* 25.3 km, range 173–251 km). Trips often involved moving west or north-west over several thousand kilometres to reach the seas south and south-west of Australia, before returning rapidly downwind to the Auckland Islands. In this zone of strong to gale-force winds, the birds covered distances of up to 1,500 km in a day while still landing periodically to feed. WHPs mainly used the very cold Antarctic waters in late summer and early autumn (Jan–Mar). After breeding, they moved further north into subantarctic seas, but in general they stayed in cooler water with very little time spent in sea temperatures above 15°C.

The long pre-laying period in this species (Table 1) allowed birds to fly substantial distances from the colony during this phase of the annual cycle. All ten birds tracked across 15 pre-laying flights flew west of the Auckland Islands. The maximum distance reached away from the colony was 7,550 km (Table 1). This bird and another individual flew north of the Kerguelen Islands, almost reaching Amsterdam Island in the southern Indian Ocean. Six of the birds travelled to the Indian Ocean (west or south-west of Australia), while the other four moved westwards but remained to the south of Australia. None went close to Antarctica in spring.

WHPs mainly foraged west or south-west of the Auckland Islands during the incubation period (Fig. 4). Most trips went south of Australia, but some trips in January started to go much further south towards Antarctica. Just two birds headed south-east of Adams Island during Dec–Jan. The maximum distance reached away from the colony during the incubation period was 5,230 km by a female that flew well into the Indian Ocean while her mate was sitting on the egg. The total point-to-point (12-hour interval) distance of this 22-day

flight was 16,165 km. The average maximum distance away from the colony of these ten birds was 3,846 ± 968 km (Table 1).

During the chick-rearing period, the birds mainly foraged to the south-west of the Auckland Islands towards the polar seas (Fig. 3). The area used was west of the Ross Sea and north of the Adelie and Clarie coasts. However, some individuals foraged in all directions away from the island, including towards the Antipodes Islands. The maximum distance away from the colony that any bird travelled while feeding their chick was 4,403 km. Long foraging trips were not abnormal, and the average maximum distance away from the colony of the eight birds on trips gathering food for chicks was 2,801 ± 766 km (Table 1).

After the breeding season was over (whether successful, a failure, or the birds skipped breeding altogether), they all departed rapidly away from the Auckland Islands and never returned within 500 km of the colony until the following breeding season (Fig. 3). Apart from two birds that stayed in the south Tasman Sea (near Tasmania and near Fiordland), seven birds moved much further west. Just one bird went east into the South Pacific Ocean, wintering east of the Louisville Ridge seamount chain (Fig. 4). The birds going west mainly went towards the seas south or south-west of Western Australia and east of the Kerguelen Islands, although one male went as far as 9,500 km west of the colony, ending up close to Marion Island in 2012, and less than 600 km from South Africa in 2011 (Fig. 4). The mean maximum distance each bird reached away from the colony during the winter moult period was 5,623 ± 1,727 km (Table 1).

Foraging activity

The at-sea foraging activity will be examined in detail in a separate paper. Briefly, the sea-water immersion sensors showed that WHP are active by both day and night throughout the year. There are regular landings on the sea throughout the 24-hour period. Tags often revealed extensive flying periods during the day, with only occasional sea-water contacts for periods <10 min. Long sustained periods of sitting on the water was observed by both day and night, but this mainly occurred during the winter months when the birds are presumably in feather moult. The coldest sea temperatures recorded were in water of –1°C,

TABLE 1. Summary of different stages of the annual cycle and foraging range (mean ± std) of white-headed petrels (*Pterodroma lessonii*) from Adams Island, New Zealand, as derived from global location sensing tags.

Annual cycle stage	Bird-years (*n*)	Range	Distance covered	
			Mean maximum (km)	Range (km)
Pre-laying	15	Mid-Sep to late-Nov	5,563 ± 1,288	2,500–7,550
Incubation	15	Late-Nov to late-Jan	3,846 ± 968	1,640–5,230
Chick-rearing	8	Late-Jan to mid-May	2,801 ± 766	2,028–4,403
Inter-breeding	19	Mid-May to mid-Sep (if breeding) Late-Oct to mid-Sep (if skipped breeding)	5,623 ± 1,727	2,590–9,500

indicating that the birds were close to sea-ice or icebergs. Immersion in sea temperatures above 15°C was uncommon during the breeding season, but there were visits into sea temperatures up to 20°C during the inter-breeding period.

Breeding activity

Courtship period: WHPs begin returning to the colony at Adams Island as early as 14 Aug. Some individuals of both sexes returned in August, but return dates varied widely, extending from 14 Aug to 26 Oct (median date 18 Sep). The number of visits to the colony in the courtship period varied from one to seven (*n* = 19), with females usually having a single visit (range 1–3 visits) and spending between 1 and 8 days ashore. In contrast, males spent much longer attending the colony early in the season, with multiple burrow visits (range 1–7) and 7–33 days spent ashore by day during those visits. The longest continuous time ashore during the courtship phase was 14 days by one male. WHP that bred successfully in the previous season and that were to breed again in successive seasons returned 26 Sep–6 Oct. Failed breeders from previous years came back earlier.

Pre-laying exodus: The pre-laying exodus starts immediately after courtship. Most of our birds ventured far out to the west into the Indian Ocean. The exodus period started as early as 13 Sep and the last bird departed on 14 Oct (median date = 24 Sep, *n* = 15) (Table 1). The duration of the pre-laying exodus was 40–77 days. The median duration was 68 days (*n* = 15), with pre-laying

exodus durations for females (51–77 days) tending to be longer than for males (40–68 days).

Biennial breeding: WHPs exhibited an unusual behaviour around biennial breeding. The birds that skipped breeding attempts returned to the colony just briefly at the start of the breeding season that they were about to skip, and then departed after just one or several visits, long before other birds had returned to lay their eggs. Two females that skipped breeding both returned to their burrow after mid-Oct, but the two males that skipped breeding returned earlier (Aug–Sep). Birds that skipped breeding attempts never came back to the Auckland Islands after these early-season visits until the following spring.

Skipping of breeding attempts was observed on four occasions. One female reared a chick two seasons in a row, then skipped a breeding season. Two birds skipped breeding after a successful breeding attempt in the previous summer. One bird skipped breeding the following season even though it failed as early as the previous January.

In one burrow both partners had a GLS tag (Table 2). The male first returned on 25 Sep 2011 and visited the burrow on five occasions up to 7 Nov, spending days ashore on each visit. His partner first returned on 23 Oct and the pair presumably met at the burrow on 8 Nov. Both birds spent 9 Nov ashore by day, then departed to sea on 10 Nov and went separate ways until the next breeding season (Table 2). Another female returned on 26 Oct 2012, spent 1 day ashore and then departed for the season on 28 Oct. This bird had flown all the way back from the Indian Ocean

TABLE 2. Activity and dates of one pair of white-headed petrels (*Pterodroma lessonii*) tracked with GLS tags 2011–13. **Bold dates** highlight times when both birds were together at the nest.

Date	Male H28513	Female H28522
Jan 2011	28 Jan – back to sea	31 Jan in burrow
Feb 2011	Chick fed 8, 11, 22, 26 Feb	1 Feb – back to sea, chick fed 2, 16, 25 Feb
Mar 2011	Chick fed 7, **11**, **20**, 28 Mar	Chick fed 1, 2, **11**, 18, 19, **20**, 24 Mar
Apr 2011	Chick fed 3, **16**, 24, 26, 28, 29 Apr	Chick fed 1, 6, 13, **16**, 20, 22, 25 Apr
May 2011	Chick fed 7, **9** May; departs for season 10 May	Chick fed 3, **9** May; departs for season 10 May
Jun–Aug 2011	Moults in South Pacific Ocean	Moults in Indian Ocean
Sep 2011	First return 25 Sep, back to sea 29 Sep	At sea
Oct 2011	Visits burrow 6–7, 11–12, 27–28 Oct	First return 23 Oct, back to sea 26 Oct
Nov 2011	Visits burrow 7–**9** Nov; skips breeding 10 Nov	Visits burrow 1–2, 8–**9** Nov; skips breeding 10 Nov
Dec 2011–Mar 2012	Australia to Antarctica	Australia to Antarctica
Apr–Jul 2012	Crosses dateline 6 Apr, moults in South Pacific Ocean	Moults in Indian Ocean
Aug 2012	First return 20 Aug, back to sea 25 Aug, visits burrow 28 Aug–3 Sep	Furthest west 11 Aug
Sept 2012	Visits burrow [from Aug, then] 5–6, 9–10, **12–18**, 26–27 Sep	First return **13–21** Sep; departs on pre-laying exodus 22 Sep
Oct 2012	Visits burrow 1–2 Oct; departs on pre-laying exodus 3 Oct, Tasmania to Auckland Islands	South of Australia
Nov 2012	Returns to burrow **28** Nov (57 days at sea)	Returns to burrow **28** Nov (68 days at sea), lays egg and stays ashore with male for 2 days
Dec 2012	Departs to sea **16** Dec (17 days ashore)	Departs to sea 1 Dec, returns **15** Dec (15 days at sea)
Jan 2013	Returns to burrow **3** Jan; tag removed	Departs to sea **4** Jan (19 days ashore), returns 18 Jan (15 days at sea); tag removed

near the Kerguelen Islands to spend just 1 day ashore before flying all the way back again to the Indian Ocean. All four birds returned and bred in the same burrow the year after they skipped breeding.

Incubation period: Egg-laying extended over 2 weeks. The first return from the pre-laying exodus was a male on 22 Nov. The first female was back on 24 Nov. The last apparent date for an egg to be laid was 10 Dec. The median laying date for females (assuming the egg is laid on the night of return) was 28 Nov (*n* = 10). On six occasions the female returned from exodus, laid the egg on the same night, and immediately departed to sea. The shortest possible time to have laid the egg was

less than 3.5 hours (based on the longest gap in sea-water immersion recorded on the same night), but most birds apparently laid during less than 6 hours ashore. One female spent 2 days ashore after laying, although her partner was already back on the same night she laid. Two females spent up to 6 days ashore after laying, presumably waiting for their (untagged) mates to return. One female was very consistent in her laying dates across three seasons, laying on 26 Nov 2011, 26 Nov 2012, and 25 Nov 2013. A female that skipped breeding for one season laid a week earlier in the year after she skipped.

After laying, females headed back to sea on long foraging trips mainly to the west of the colony. These trips were 15–22 days (median 19 days, *n* =

10), while males were sitting ashore in burrows incubating the egg for shifts of 16–21 days (*n* = 5). The females returned from sea from mid-Dec to early-Jan to relieve their mates. They then spent 16–21 days ashore (*n* = 7) while the males stayed at sea for 18–20 days (*n* = 5). Due to tag removals occurring in January, there were no completed second shifts by males recorded on the tags, but the females spent 11–15 days at sea during the same period (*n* = 8).

It is not possible to determine the exact dates of hatching of eggs, or the full length of the incubation period using GLS tags. Based on successful hatchings (chick-rearing activity observed) and days spent ashore during the incubation period, incubation length is likely to be 53–62 days. This could also include some time spent brooding and guarding the newly hatched chicks. Hatching appears to be mainly in the second half of January, and typically the last week of January.

Chick-rearing period: One female bred 3 years in a row and failed in January each year. Only six chicks were fully reared by the study birds during the period of observation, although some chicks may have hatched after tags were removed in Jan 2012–14. Two nests failed during the chick-rearing period. In the year tags were first deployed on birds (only the birds subsequently recovered with GLS tags), four nests were successful (40%) and six failed (60%). In the seasons when birds were not handled, two nests were successful (40%) and three failed (60%). Most nest failures happened around hatching time, but one nest failed in mid-March during chick-rearing.

There was less certainty with identifying the number of chick-feeding visits using GLS tags than there was identifying visits to the burrow during other stages of the breeding season. No bird stayed ashore by day during chick-rearing. The only clear way to determine that a chick was being reared was repeated longitudinal movements of birds back and forth to the longitude of the Auckland Islands. On the nights that the longitude was close to that of Auckland Islands, we looked for evidence that a dry period of at least 1 hour was present on the tag (similar to the minimum time taken by Chatham Island taiko (*Pterodroma magentae*) to feed their chick – authors, *pers. obs.*) and allowing time to fly in

from the sea and then back out to sea again (10 min each). On most nights it was more obvious, with extended dry periods of 6 or more hours recorded, but some potential visits were less apparent from the data captured by the tags. Last visits by adults feeding chicks ranged from 24 Apr to 15 May (*n* = 8).

The best chick-rearing data was from one pair of birds that both had a GLS tag and presumably raised a chick (Table 2). The chick appeared to hatch around the end of January and was apparently fed 16 times by the male and 19 times by the female (total 35 feeds). The pair was ashore together with the chick on four different nights. At times the male was away from the nest for up to 13 days and female for up to 14 days. The longest gap between meals for this chick was 7 days. The male and female were both present ashore on 9 May, which was the last visit to the nest that season. Immediately after the last feed, the adults flew to remote foraging areas well away from the colony (the male to the South Pacific Ocean and the female to the Indian Ocean). There is no information on when the chick departed, but it was likely to be after 9 May (at least 100 days after probable hatching in late-January).

Inter-breeding and moult period: The length of the inter-breeding period in WHPs is extremely variable due to the species' biennial breeding behaviour. The shortest period away from the colony between seasons was 139 days for a male (about 4.5 months). The longest break away from the colony was by a female that skipped breeding, departing on 28 Oct 2012 and returning to the colony on 19 Sep 2013 (11 months later). All birds moved well away from the colony during the inter-breeding period. The tracking data show a high level of consistency in areas used for moulting by each bird (Figs 4, 5).

Discussion

The 12 GLS tags recovered from just ten different birds provided a remarkable amount of data on the annual cycle, breeding activity, and at-sea movements of this species. This has expanded our knowledge of the behaviour of this rarely studied oceanic seabird.

At-sea distribution

WHPs exhibit a pelagic lifestyle, ranging far from land during each stage of the annual cycle. The remarkable point-to-point distances travelled (averaging 217 km every 12 h) over the course of a year produced the longest annual movements (over 169,000 km) by any member of the family Procellariidae, and possibly all seabird species unless some circumpolar-ranging albatrosses exceed this feat. By comparison, the tracked movements of trans-equatorial migrating sooty shearwaters (*Ardenna grisea*) average 64,037 ± 9,779 km during their 198 ± 17 days northern migration (Shaffer *et al.* 2006) and this species stays closer to New Zealand during the breeding season than WHP. The Arctic tern (*Sterna paradisaea*) is widely considered to have the longest recorded animal migration (Egevang *et al.* 2010). Tracking tags have revealed that these birds travel an average of 70,900 km (range 59,500–81,600 km) over the 10-month period that they move between northern and southern hemispheres (Egevang *et al.* 2010), which is less than half the distance observed in the annual movements of some WHPs.

The distant foraging behaviour of WHPs may be a response to avoiding competition with the large number of seabirds that breed in southern New Zealand. For example, there are huge colonies (millions of pairs) of sooty shearwaters breeding at the Snares Islands and on islands off Stewart Island (Taylor 2000). An estimated 184,000 pairs of white-chinned petrels (*Procellaria aequinoctialis*) breed at the Auckland Islands (Rexer-Huber *et al.* 2020 – Chapter 15 in this book) and there are large albatross colonies (>100,000 pairs) nesting in the region (Taylor 2000). Pelagic foraging well west of the colony in the deep ocean basins south of Australia would reduce competition with these other large and aggressive seabird species that feed on similar prey species such as squid, fish, and krill (Warham 1990).

Foraging by New Zealand-breeding WHPs in the Indian Ocean was not expected prior to this study. There are large colonies of WHPs on islands in the Kerguelen archipelago (Weimerskirch *et al.* 1989) and they also occur on the Crozet Islands (Brooke 2004). It was expected that competition with these Indian Ocean-breeding WHPs would keep the New Zealand birds closer to home. For example, Wakefield *et al.* (2013) found that northern gannets

(*Morus bassanus*) from 12 monitored colonies established mutually exclusive foraging areas, presumably as a way of reducing intraspecific competition for food resources. Foraging in large groups in this species also allowed information transfer between birds, to enhance foraging opportunities on patchy prey across large spatial distances. In contrast, the pelagic foraging range and solitary feeding behaviour of *Pterodroma* petrels (Warham 1990, 1996) may explain why these birds are able to forage closer to other large colonies.

The tracking data revealed long-distance movements to previously visited foraging zones across consecutive years by some birds, indicating a strong fidelity to favoured regions far from the colony, and sometimes in different ocean basins. For example, one male repeatedly used seas off Marion Island (Fig. 4). The male WHP that migrated eastwards after breeding and headed into the South Pacific Ocean (Fig. 4) further exemplifies the diversity of foraging zones used by WHPs breeding at Adams Island. With the similarly large population of WHP breeding at Antipodes Islands (Miskelly *et al.* 2019), eastward movement into the Pacific Ocean was not expected due to potential competition with conspecifics. Gibson's wandering albatrosses from Adams Island, for example, remain in the seas south of Australia, the Tasman Sea, and just east of New Zealand during their inter-breeding season, whereas Antipodean albatrosses (*Diomedea antipodensis antipodensis*) breeding at Antipodes Island forage much further east than their close relative, with some reaching the Humboldt Current off Chile (Nicholls *et al.* 2002; Walker & Elliott 2006). The wintering area east of the Chatham Rise favoured by this male WHP was also visited by Murphy's petrels (*Pterodroma ultima*) from the Pitcairn Islands during their pre-laying exodus in May (Clay *et al.* 2017).

The observations that WHPs forage well to the south into cold Antarctic waters supports prior sightings in Antarctic seas in summer and autumn (Marchant & Higgins 1990; Brooke 2004). The species has been recorded foraging just north of the pack-ice (Marchant & Higgins 1990). Some birds went far enough south in January to be in continuous daylight for several days. From the tracking data it seems that the Antarctic sector west of the Ross Sea is a favoured area used by

WHPs from Adams Island in late summer and autumn (Jan–Mar). This area is also favoured by most short-tailed shearwaters (*Ardenna tenuirostris*) from Tasmania (Cleeland *et al.* 2014) and a portion of the sooty shearwater population from New Zealand (Shaffer *et al.* 2006). The polar seas are rich in Antarctic krill (*Euphausia superba*), which breed under the ice-floes and become exposed as the pack-ice retreats in late summer (Cleeland *et al.* 2014). This is presumably the major reason that WHPs forage this far west and south in late summer.

Sex segregation was observed in the monomorphic Murphy's petrel during the pre-laying period but not during other stages of the annual cycle (Clay *et al.* 2017). The sample size in our study was too small to determine whether sex segregation during foraging also occurs with WHP, which is also monomorphic (Marchant & Higgins 1990). There was no apparent difference from the mapped positions, with all birds heading west during pre-laying and most heading into the Indian Ocean between the Subantarctic and Subtropical Fronts. Clay *et al.* (2017) speculated that male *Pterodroma* petrels disperse further during the pre-laying exodus to reach more productive zones, as has been recorded for Chatham petrel (*Pt. axillaris*) and Barau's petrel (*Pt. baraui*) (Rayner *et al.* 2012; Pinet *et al.* 2012). However, WHPs seem to deviate from this pattern, as the three shortest maximum distances from the colony during the pre-laying exodus (2,500, 3,753, and 4,350 km) were all observed from males. These males had pre-laying exodus trips of shorter duration than those typically observed in females, as they returned to the colony for a brief burrow visit 1–2 weeks after the female had departed. However, the most distant recorded trip during the pre-laying exodus was also by a male, reaching 7,550 km away from the colony, and almost as far as Amsterdam Island in the Indian Ocean. This is apparently the longest recorded distance travelled by any bird species from its nest between mating and egg-laying.

The long incubation shifts of these seabirds allow them to cover huge distances while their mates sit on eggs. Clay *et al.* (2017) reported that one Murphy's petrel travelled as far as 4,898 km away from the colony during an incubation foraging trip, and considered this to be the longest distance travelled by any seabird during the breeding period. The 5,232 km reached by one WHP female during an incubation-period foraging trip is now the furthest for this stage of the breeding season. Two other birds (a male and a female) also travelled more than 5,000 km away from the colony during the same period.

WHPs are capable of foraging well west of the colony and then returning rapidly downwind when they are ready to swap over at the nest. For example, one female departed the core area used during her foraging trip (south-west of Western Australia and 4,400 km from Adams Island) and returned to her burrow in just 4 days (a minimum distance of 1,100 km per day if travelling on a great-circle route). The point-to-point path (12-hourly intervals) on the 4-day trip was 5,955 km, an average of 1,489 km travelled per day. Such sustained rapid downwind flights have been observed in a grey-headed albatross (*Thalassarche chrysostoma*) tracked with a GPS tag during an Antarctic storm. This albatross was travelling at speeds >110 kph over 9 h, and also stopped to feed during the storm event (Catry *et al.* 2004).

Breeding cycle – courtship and pre-laying exodus

WHPs have a more extended breeding season than the closely related Chatham Island taiko. This is probably due to the biennial breeding behaviour observed in WHP compared with annual breeding only in Chatham Island taiko (Taylor *et al.* 2012). The latter species starts to return to nests only from late-September (Taylor *et al.* 2012) compared with mid-August in the much smaller sample of WHP nests used in this study. The early-returning WHPs were mainly those that skipped breeding attempts in the previous summer. The first return dates of WHPs to Adams Island in August were similar to those recorded at other breeding sites of this species (Table 3).

The pre-laying period observed in WHP in this study is among the longest ever reported in any procellariiform species (Warham 1990), and probably the longest confirmed by data loggers for any bird species. How the male's sperm is stored by the female WHP after mating and stays viable for so long (up to 77 days) remains a mystery. In a previous study, Warham (1967) did not identify a major pre-laying exodus for this species. Interference with his study burrows by rabbits

TABLE 3. Comparison of dates and activity patterns for different stages of the breeding cycle at three colonies of white-headed petrel (*Pterodroma lessonii*; WHP); [1] this study, [2] Warham (1967), [3] Brothers (1984), [4] Zotier (1990), and with the summer-nesting Chatham Island taiko (*Pterodroma magentae*) (Taylor *et al.* 2012; G. Taylor *unpubl. data*).

Annual cycle	Stages	WHP, Adams Island[1]	WHP, Macquarie Island[2]	WHP, Macquarie Island[3]	WHP, Kerguelen Islands[4]	CI taiko, Chatham Islands
Courting and pre-laying exodus	First return date	14 Aug	21 Aug	2 Aug	21 Aug	21 Sept
	Burrow occupancy during courtship	Aug–Oct	Aug–Oct	Aug–Oct	Mid-Sep to early-Oct	Late-Sep to late-Oct
	Pre-laying exodus departure	13 Sep–14 Oct	Not monitored	Not monitored	Mid-Oct	25 Sep–8 Nov
Egg-laying and Incubation	Egg-laying dates	24 Nov–10 Dec	24 Nov–16 Dec	c. 19 Nov–c. 13 Dec	29 Nov–12 Dec	22 Nov–13 Dec
	Incubation period	<62 days	c. 60 days	Not recorded	c. 61 days	<54 days
	Main incubation shift lengths	11–21 days	Not recorded	Not recorded	10–24 days	11–19 days
Chick-rearing	Hatching	Late-Jan	Late-Jan	16 Jan–2 Feb	Late-Jan	22 Jan–4 Feb
	Chick-rearing period	Late-Jan to mid-May	Late-Jan to mid-May	Late-Jan to late-May	Late-Jan to late-May	Late-Jan to May
	Last record of bird ashore (adult or chick)	15 May	3 Jun	26 May	12 Jun	2 Jun

(*Oryctolagus cuniculus*) and weka (*Gallirallus australis*) made it difficult to monitor bird activity patterns. Also, non-breeding birds flying around in November gave the impression that birds were still actively visiting the colony. Zotier (1990) reported a pre-laying exodus of only a month at the Kerguelen Islands (lasting from mid-Oct to mid-Nov). Imber (1976) suggested that some grey-faced petrels can be away on exodus for 80 days, but GLS tracking of this species has not revealed any pre-laying exodus of this duration across a larger sample of birds (>100 individuals; G.A. Taylor, *unpubl. data*). Imber (1976) likely missed some additional visits of his study pairs after his early-season field trips concluded.

Breeding cycle – incubation and chick-rearing

Eggs are laid between late-Nov and mid-Dec at all the WHP colonies studied (Table 3). None of the study birds at the Kerguelen Islands laid eggs and returned to sea on the same night. Those females spent a mean of 7 days ashore immediately after laying (range 2–15 days; Zotier 1990). In contrast, females of the Adams Island population seem quicker to depart for sea from the colony when compared with the other populations studied. The incubation shifts at other WHP colonies are of similar duration to those recorded on Adams Island (Table 3). The incubation shifts of WHP are some of the longest recorded for any seabird. Brooke (1995) and Clay *et al.* (2017) also observed extremely long first incubation shifts (averaging 20 ± 5 days and 18 ± 4 days, for males and females, respectively) for Murphy's petrel.

Warham (1967) considered the incubation period of WHP to be about 60 days, while Zotier (1990) found it lasted 61 days at Kerguelen Island. These figures are similar to the estimates derived in this study. Hatching at all three islands occurs around the end of January (Table 3).

The WHP chick-rearing period and departure

of adults from Adams Island is similar to that recorded at other colonies (Table 3). Warham (1967) noted that calling from adult WHPs at Macquarie Island stopped around the end of April, and his sole remaining study chick fledged around 10 May, aged about 102 days. Brothers (1984) found that most of his WHP study chicks disappeared in the month after hatching (from predation). Just three chicks survived, and two of these were still present in the nest on 18 May. At the Kerguelen Islands, WHP chicks fledged from 2 May to 12 Jun, with a mean date of 21 May ± 9 days (Weimerskirch *et al.* 1989; Zotier 1990). Chicks of the summer-nesting Chatham Island taiko fledge late-Apr to early-Jun, similar to WHP (Taylor *et al.* 2012; G.A. Taylor, *unpubl. data*).

The WHP chicks at Adams Island appeared to be fed on average every 3 days over the rearing period. There is more uncertainty over timing of feeding visits, but the number of potential visits recorded will be a maximum, as on other nights the birds were either too far east or west of the colony to return, or the sea temperatures recorded at night showed that they were not close to the island. One pair of WHP fed their chick on 35 occasions. This is comparable to Chatham Island taiko, where a pair monitored by data loggers at the nest were recorded feeding their chick on 33 occasions (Taylor *et al.* 2012).

Records from one burrow in our study area suggested that the chick was fed more frequently as it got closer to adult size (Table 2). Zotier (1990) by contrast considered the feeding rate to be even throughout the chick-rearing period. By measuring chick weight changes, Zotier (1990) concluded that chicks <75 days old were fed on 37.9 ± 7% of nights (although the range of 16.7–37.5% given in the paper suggests that the feeding rate was lower than the reported mean). The mean feeding rate later in the chick-rearing period was 42.7 ± 18.2% for chicks aged 85–93 days old, and 36.8 ± 9.9% for those aged over 93 days (Zotier 1990). Allowing for the apparent error in his Table 2, it seems that lower feeding rates early in chick-rearing may be normal for this species. There are at least two potential explanations. First, adults are going south to Antarctica early in the chick-rearing period (Feb to mid-Mar) and the long-distance trips limit the frequency of visits back to the nest. Second, it is possible that food supplies for WHPs increase during the autumn months, allowing the birds to stay closer to the colony and return more frequently to feed the growing chick. More work is needed to test these hypotheses.

The poor breeding success identified in this study of WHP (only 40% of pairs rearing a chick each breeding attempt) was not expected from an island that is free of introduced predators. On Macquarie Island, both Warham (1967) and Brothers (1984) experienced high nest losses due to burrow interference from rabbits and to chick predation by ship rats (*Rattus rattus*), feral cats (*Felis catus*), and weka. None of these species occur on Adams Island. Invasive species are considered to be the main threat to WHP (Taylor 2013; BirdLife International 2019). There were several nest failures around hatching or early in the chick-rearing period on mammal-free Adams Island. Potential causes could include nest interference from conspecifics or other burrow-nesting species, as happens with Chatham petrels (Gummer *et al.* 2015). The cause of early nest failures would be worth further investigation.

Biennial breeding

Zotier (1990) was the first to report biennial breeding by WHP. Birds mainly returned to breed in consecutive seasons if they failed early in the previous breeding season. Just one pair in his study (*n* = 70 nests) bred and raised chicks 2 years in a row. However, one of only ten birds tracked on Adams Island reared chicks 2 years in a row, then skipped breeding in the third season.

Biennial breeding normally occurs in albatrosses and petrels when the full annual cycle of breeding activity and feather moult cannot fit within a 12-month period (Warham 1990, 1996). WHP probably evolved a biennial breeding pattern as the duration of its breeding season can extend up to 10 months (Aug–May) and feather moult normally takes several months to be completed (Imber 1976; Warham 1996). By staying in cold subantarctic waters over the winter, these birds remain in an area of lower primary productivity during the moult period. In contrast, another summer-nesting species from Adams Island, the annual breeding sooty shearwater, migrates to the North Pacific Ocean during the austral winter to moult in highly productive up-welling zones during the boreal summer (Shaffer *et al.* 2006).

The behaviour of the two female WHPs that returned from distant foraging areas to spend just a day or so ashore during the courtship period, then departed again to sea to take a season off, appears to be novel among seabirds studied so far. Males returned earlier in the season, spending more time ashore in Aug–Oct, presumably to guard their nest and stop other pairs using it, even if they subsequently skipped breeding after the female returned. The date on which the female returns seems to determine whether or not a breeding attempt will take place that year. If the female first returns after the other pairs have already gone on their pre-laying exodus, then the pair skip breeding that season. It can only be speculated why the pair return at all to the colony, but it seems that the female comes back for a fleeting visit to meet up with her partner, presumably to reaffirm the pair bond, before they leave the colony and head away to distant seas (Table 2).

Zotier (1990) found lots of empty burrows in his study area, and assumed that they were vacant for the entire season. It is possible that fleeting early-season visits, as recorded at Adams Island, by birds that subsequently skipped breeding were overlooked. The biennial breeding pattern does seem more prevalent at Kerguelen Islands than at Adams Island. In a follow-up study, Chastel (1995) checked WHP nests and found that only 13% of successful breeders returned to nest 2 years in a row. An average of 87% of successful breeders returned two or more years later, whereas 86% of failed breeders returned the following year.

Due to the high number of empty nests found each season, Zotier (1990) concluded that intraspecific competition was limited in WHP. This conclusion may oversimplify the picture. The early returns of the birds at Adams Island by both breeding and non-breeding WHP males that subsequently skipped breeding suggests that retaining a burrow is important for this species. WHP are extremely wary over land, and do not spend much time on the surface at night or call from the surface like other *Pterodroma* petrels (Taylor 2013). Pairing occurs during elaborate aerial chases over the colony (Warham 1967; Zotier 1990). Maintaining a burrow in open tussock or shrubland communities and retaining a partner is critical for bird survival, as it reduces the risk of predation by subantarctic skuas (*Catharacta*

antarctica lonnbergi) and New Zealand falcon (*Falco novaeseelandiae*) (Miskelly *et al.* 2020 – Chapter 2 in this book; Elliott *et al.* 2020 – Chapter 3). In contrast, prospecting birds landing on the surface at night to search for vacant burrows, and those digging new burrows, would be at much higher risk of predation without a familiar burrow to retreat into.

Conclusions

While this study was an opportunistic look at a tiny subset of the hundreds of thousands of WHPs breeding at the Auckland Islands (Miskelly *et al.* 2019), a surprising amount of variability in the at-sea behaviour was revealed from just ten birds. Prior to this study there was no information available about the extent of movements of WHPs from any breeding colony, how these movements varied between different stages of the breeding cycle, and the consistency or otherwise of their inter-annual movements. GLS tracking has revealed that WHPs from Adams Island can migrate as far west as Africa in the Indian Ocean and east into the central South Pacific, and from seas off Antarctica in late summer to subtropical seas of 15–20°C in winter. The birds showed remarkable consistency in their inter-annual behaviour both on land and at sea, especially in the choice of winter moulting zones. The data collected will be used to inform risk assessment models for New Zealand breeding seabirds, especially in relation to increasing pressures from high-seas fisheries and climate change.

While WHPs had been recorded breeding in a biennial pattern at the Kerguelen Islands (Zotier 1990), their brief return to the colony in the year that they subsequently skipped breeding was not recorded in earlier studies. This new information about the onshore activity patterns of WHP will inform conservation management of the species, especially when planning population assessments at breeding colonies. Our study has highlighted the importance of quantifying used but vacant burrows in the colony in addition to those occupied by birds on eggs, to get a more accurate picture of the total breeding population of WHP.

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