Population estimate for yellow-eyed penguins (*Megadyptes antipodes*) in the subantarctic Auckland Islands, New Zealand

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ABSTRACT: Accurate long-term monitoring of a threatened species' population size and trend is important for conservation management. The endangered yellow-eyed penguin (*Megadyptes antipodes*) is a non-colonial breeder. Population monitoring of the subantarctic population has focused on beach counts rather than nesting birds. Here, we combined intensive nest-searching and counts of transiting penguins on Enderby Island, Auckland Islands, over 3 years to establish the relationship between count numbers and breeding birds. Morning beach counts of transiting penguins were extrapolated to estimate breeding population for the entire Auckland Island group from 2012 to 2017. Breeding numbers varied considerably between years, but overall did not appear to be declining in the short term. Breeding birds at the Auckland Islands averaged 577 pairs annually over the three ground-truthed breeding seasons, similar to the lower estimate of 520–680 pairs from the last survey in 1989, but less than the higher estimate of 650–1,009 pairs generated from that survey. Direct comparison of beach counts indicated a large decline, but these may be more prone to uncertainty. Large variations between years indicated variable breeding effort. The Auckland Islands (particularly Enderby Island) represent 37–49% of the total breeding population for yellow-eyed penguins, indicating the importance of the subantarctic populations for the species. We recommend ongoing monitoring, including mark-recapture methods, for future population estimates. At least 50% of the individuals in an area should be marked to reduce confidence intervals of estimates.

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Introduction

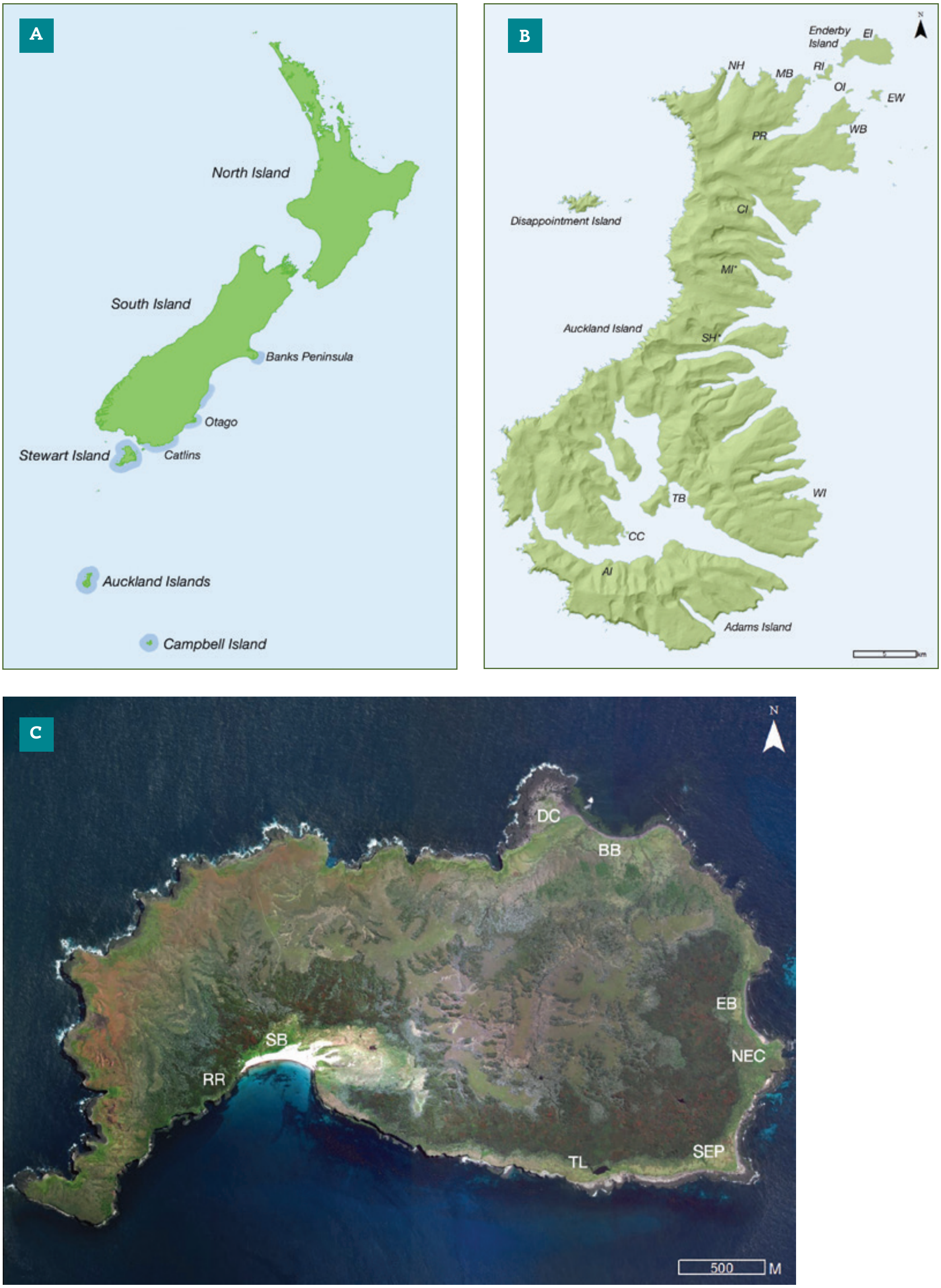
Accurate long-term monitoring of a breeding population is important to determine population trends and the effectiveness of conservation-management measures. Monitoring population numbers can reveal a species' resilience to threats (such as predation, mortality, disease, response to climate change, and effects on food supply), determine likelihood of decline, and help inform and measure management decisions (Purvis *et al.* 2000; Witmer 2005; Lindenmayer & Likens 2009). Population estimates for colonial-breeding seabird species are typically achieved using colony counts (Hutchinson 1980; Trathan 2004; Baker *et al.* 2017). These methods are used to survey colonial-breeding penguin species (Woehler & Croxall 1997), including western rockhopper (*Eudyptes chrysocome*) in the Falkland Islands (Baylis *et al.* 2013), and erect-crested penguins (*E. sclateri*) and eastern rockhopper penguins (*E. filholi*) in the New Zealand subantarctic (Hiscock & Chilvers 2014; Morrison *et al.* 2015).

FIGURE 1. Adult yellow-eyed penguin on a nest in rātā and *Dracophyllum* forest on Enderby Island. *Image: Chris Muller.*

FIGURE 2 (OPPOSITE). A. Location of yellow-eyed penguin breeding areas, including mainland New Zealand (primarily Otago and Catlins coast), Stewart Island (and outlying islands), and the subantarctic Campbell and Auckland Islands. **B.** Enlargement of the Auckland Islands archipelago, with observation sites listed from north to south: EI Enderby Island, RI Rose Island, MB Matheson Bay, NH North Harbour, OI Ocean Is, EW Ewing Island, PR Port Ross, WB Webling Bay, CI Chambres Inlet, MI Musgrave Inlet*, SH Smith Harbour*, WI Waterfall Inlet, TB Tagua Bay, CC Camp Cove, AI Adams Island. Sites marked with an asterisk (*) have been reported as possible sites of penguin activity (Beer 2010) but were not included in this survey. **C.** Enlargement of Enderby Island, with observation sites listed clockwise from the south-west: RR Rocky Ramp, DC Derry Castle, BB Bones Bay, EB East Bay, NEC North-east Cape, SEP South-east Point, TL Teal Lake, SB Sandy Bay.

The endangered yellow-eyed penguin (hōiho, *Megadyptes antipodes*, Fig. 1) is endemic to New Zealand (Gill *et al.* 2010). It is highly restricted in distribution, found only in the south-east of the South Island/Te Waipounamu, Stewart Island/Rakiura and adjacent islands, and the subantarctic Auckland Islands/Motu Maha and Campbell Island/Motu Ihupuku (Fig. 2A). Extant yellow-eyed penguins recolonised mainland New Zealand from the subantarctic after the mainland species (*M. waitaha*) became extinct (Boessenkool *et al.* 2009a; Collins *et al.* 2014), and there is currently less than 2% migration between the mainland and the subantarctic, meaning that these areas are identified as separate populations (Boessenkool *et al.* 2009b). The subantarctic breeding areas are an important stronghold, previously representing over 60% of the total population (Ellenberg & Mattern 2012). Despite this importance, the last population estimate for the Auckland Islands was in 1989 (Moore 1990). There is therefore a vital need to collect accurate and up-to-date population information for this area (Ellenberg & Mattern 2012). Concurrently, the Otago (Fig. 2A) portion of the mainland New Zealand yellow-eyed penguin population is undergoing a serious decline due to successive poor breeding seasons and ongoing high adult mortality (Couch-Lewis *et al.* 2016), making the need for a subantarctic survey even more important.

Yellow-eyed penguins breed in the austral spring and summer, laying one or two eggs in late-Sep. Chicks hatch in the subantarctic in late-Nov and fledge in Mar (Moore 1992a). Yellow-eyed penguins do not form colonies but nest in loose aggregations within coastal forest and scrub, with each breeding area associated with one or more access points to the sea. They prefer to nest out of sight of neighbouring birds, and nests are an average of 12–32 m and up to 78 m apart (Seddon & Davis 1989). The nests furthest from the sea may be up to 1 km inland, making them difficult to find (Darby *et al.* 1990). Direct colony counts are not possible for yellow-eyed penguins, and nesting birds must be individually located.


A
North Island
South Island
Banks Peninsula
Otago
Stewart Island
Catlins
Auckland Islands
Campbell Island
B
Enderby Island
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Disappointment Island
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Ground-searching is the main method of nest location around mainland New Zealand (Hegg *et al.* 2012), often requiring multiple search teams (and with a mean of 16 or fewer nests per breeding area) (Seddon & Davis 1989).

The Auckland Islands (50°44'S, 166°05'E, Fig. 2B) are located 465 km south of New Zealand's South Island. The main Auckland Island (45,889 ha) has three non-native mammalian predators: mice (*Mus musculus*), cats (*Felis catus*), and pigs (*Sus scrofa*) – with the latter two suspected of depredating yellow-eyed penguins and nests (Challies 1975; Moore 1990). Isolation and distance make the islands difficult and expensive to access, and large search teams are impractical. In the Auckland Islands, yellow-eyed penguins usually nest in thick coastal vegetation. This may include rātā (*Metrosideros umbellata*) forests, *Veronica elliptica* bushes, and *Myrsine divaricata* divaricating shrubs, which can form almost impenetrable thickets (Godley 1965; Taylor 1971; Peat 2006). The large area, combined with poor weather and terrain, make the New Zealand subantarctic islands a difficult environment in which to survey yellow-eyed penguins, and they can be reliably observed only when they are transiting from the forest to the sea, or vice versa.

Due to the difficulties of surveying in this environment, the manual ground-search method used for locating yellow-eyed penguin nests on mainland New Zealand is less practical in the subantarctic (Muller *et al.* 2019). Previous population surveys in the subantarctic have primarily utilised morning and evening beach counts of transiting penguins (Moore 1990, 1992a, b), and more recent count data have been collected at selected locations around the Auckland Islands (Beer 2010) and Enderby Island (Young 2009; Houston & Thomson 2013; Chilvers 2014). Houston & Thomson (2013) attempted validation of morning count data using remote cameras (still and video) combined with nest searches in a representative breeding area on Enderby Island (Rocky Ramp). However, this study was limited by a very short field season (7 days) to search for nests, resulting in only 25 active nests being found, and providing limited confidence that all nests were located. The authors also documented the limited success of the cameras, with battery life and detection issues a problem, especially at night. Results of this study identified that more comprehensive research is required, including improved technology.

There have been no comprehensive population surveys encompassing the wider Auckland Islands area since 1989, nor an accurate measure of the relationship between recent morning counts and breeding numbers. Moore carried out beach counts and population surveys on Campbell Island (Moore & Moffat 1991; Moore 1992a, b; Moore *et al.* 2001), including determining the number of banded nesting birds sighted during beach counts, a relationship that was used as part of an Auckland Islands population estimate. Moore (1990) carried out count surveys Oct–Dec, when breeding adults were incubating eggs or brooding young chicks, and so had a regular and predictable foraging schedule. Since each site around the Auckland Islands was counted on a different day, there was the possibility that daily variability in penguin numbers heading to sea may have been influenced by weather, sea conditions, and other factors, although this has not been measured. In addition, beach count data represent an unknown proportion of the total population, and since most yellow-eyed penguins remain in the same area year-round (Richdale 1957; Darby *et al.* 1990), the beach counts will also include an unknown proportion of non-breeding adults. Therefore, this method does not give a reliable breeding population estimate and can provide only an approximate indication of population trends (Chilvers 2014). To generate a reliable breeding population estimate, the survey must include direct counts of nests in at least one site (hereafter referred to as ground-truthing). The previous Auckland Islands survey by Moore (1990) used morning and evening counts with a correction factor from a previous ground-truthing survey on Campbell Island. This derived a relationship between morning count numbers and a known number of banded individuals to determine the proportion of the population sighted during counts (Moore 1992b), and also the relationship to nest numbers (Moore 1992a). From this, and an assumption that 60–70% of the population were breeders, 520–680 breeding pairs were estimated in the Auckland Islands in 1989, with the majority of these (260–360 pairs) estimated on Enderby Island (Moore 1990, 1992b; Fig. 2A, B). However, this probably underestimated breeding numbers, since the Campbell Island estimate of 490–600 pairs in 1988 (Moore 1992b) was re-evaluated as 610–890 pairs based on mark-recapture analysis (Moore *et al*. 2001).

The aims of this research were to: (1) determine relationships between the proportion of the yellow-eyed penguin population sighted in morning beach counts and the number of breeding adults; (2) estimate the number of breeders on Enderby Island and the total breeding population for the Auckland Islands; and (3) determine the ratio of breeders to non-breeders on Enderby Island, and estimate the total population for the Auckland Islands.

Methods

We surveyed the population of yellow-eyed penguins at the Auckland Islands (Fig. 2A) by using morning beach counts of penguins transiting to the sea at sites around the archipelago identified in previous publications. A population estimate was generated from the count data by using the proportion of the total population likely to have been seen in these counts. This proportion was estimated by conducting a detailed population study of one representative population, including a complete census of breeding birds at that site.

Beach counts

Morning beach counts on Enderby Island (50°30'S, 166°17'E, Fig. 2A, B) were conducted in November during three breeding seasons (2015–17) in conjunction with ground-truthing to identify breeding parameters, and three prior seasons with no ground-truthing (2012–14), as per Moore (1990; 1992b). To allow for comparisons between years, survey sites included major sites identified by Moore (1990) (Table 1, Fig. 2B, C). Estimates were made for sites not visited for logistical reasons (e.g. Ewing Island, Ocean Island, and Matheson Bay) (Table 1). It would have been ideal to repeat counts at all previously identified sites; however, for sites that were not surveyed in a given year, an estimate was made based on the average proportion of the total count found in previous years (Table 1). Additional sites were identified as access points to the sea by Beer (2010), but with low numbers of birds recorded these were not surveyed for logistics reasons (e.g. Musgrave Inlet and Smith Harbour). Counts for these sites could not be estimated.

Moore (1990) found that the main peak of morning penguin departures in early- to mid-Nov occurred 0500–0800 h NZST, but local sunrise was earlier and the peak of morning transit activity shifted to 0430–0700 h in late-Nov, and to 0400–0700 h in Dec. It would have been ideal to repeat this methodology to ensure that count data were directly comparable between studies; however, during the 6 years of data collection for this study, morning counts sometimes commenced at different times at some sites, due to weather and other factors. To ensure that the counts were comparable between different sites and years within this study, the count data were analysed over a standardised time period using the latest recorded start time (0530–0900 h). However, this means that morning count numbers will be an underestimate of the total morning activity peak, and should not be directly compared with counts collected using a different time period – an inherent issue with beach count data. Transit data from an automated microchip reader (see section on electronic monitoring below for details) indicated that a survey covering the 0530–0900 h time period would include around 89% of the peak morning transit numbers in the incubation phase. Count numbers were therefore increased by a 12% correction factor to make them comparable with counts from Moore (1990), which started at first light. However, due to the inherent issues with using beach counts as reliable indicators of population trends, comparison of population estimates is expected to be more accurate.

During 2015–17, morning count data from the Rocky Ramp (Enderby Island) reference population were collected every day for the duration of the survey undertaken elsewhere on the Auckland Islands, in order to measure daily variation in transiting penguin numbers (Fig. 3).

Reference population and ground-truthing

Ground-truthing field work was carried out on Enderby Island (Fig. 2B) for three breeding seasons: 2015 (Nov 2015–Feb 2016), 2016 (Nov 2016–Feb 2017), and 2017 (Nov 2017–Jan 2018). A detailed

TABLE 1. Results from yellow-eyed penguin morning beach counts conducted around the Auckland Islands, listed from north to south. Sites that were not counted in a particular year (shaded and italics) were adjusted for location based on the mean proportion of birds counted at these sites (shown at right), and applied to the total count from sites that were surveyed in that year. Counts from 2012 to 2017 were adjusted for survey time by incorporating a 12% increase to estimate the total morning commute, and to allow comparison with the 1989 survey. Surveyed sites include major sites identified by Moore (1990). Some additional sites identified as access points to the sea by Beer (2010) but with low numbers of birds recorded were not included for logistics reasons. Where no previous counts had been done, counts could not be estimated.

Location	1989	2012	2013	2014	2015	2016	2017	Average	Proportion
Enderby Island (total)	593	361	221	325	246	330	194	324	49.9%
Rose Island	41	28	27	33	34	114	26	43	6.7%
Matheson Bay	43	*34*	*21*	*27*	*25*	*37*	*21*	43	6.6%
North Harbour	88	50	*31*	*40*	54	*55*	*31*	64	9.9%
Ocean Island	2	*2*	*1*	*1*	*1*	*2*	*1*	2	0.3%
Ewing Island	61	*48*	*30*	*38*	*35*	*53*	*29*	61	9.4%
Terror/Erebus Cove (Port Ross)	13	*5*	*3*	*4*	3	*5*	3	6	1.0%
Webling Bay	26	*10*	*6*	*8*	*5*	16	4	13	2.0%
Chambres Inlet	*48*	*26*	*16*	*21*	4	67	29	33	5.1%
Waterfall Inlet	*34*	50	15	6	15	21	35	24	3.6%
Tagua Bay (Carnley Harbour)	3	*2*	*1*	*2*	*2*	*3*	*1*	3	0.5%
Camp Cove (Carnley Harbour)	*0*	*0*	*0*	*0*	0	*0*	1	0	0.0%
Adams Island	64	23	54	42	13	13	18	32	5.0%
Total – Raw counts	934	512	317	406	374	561	310	649	100%
Total – Adjusted for location	1016	639	427	547	437	716	393		
Total – Adjusted for survey time	1016	716	478	613	489	802	440		

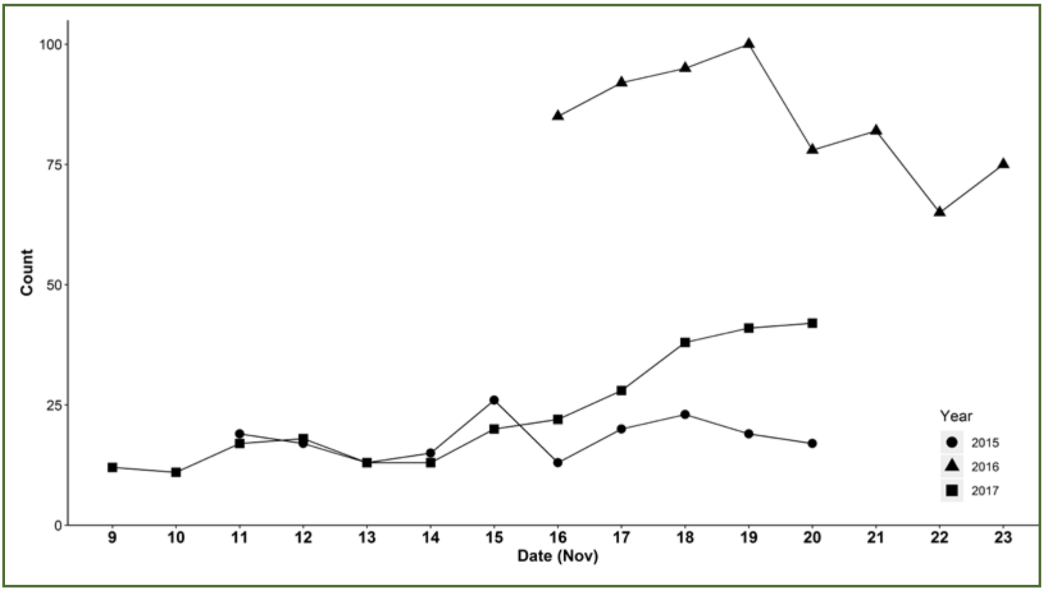

FIGURE 3. Number of adult yellow-eyed penguins counted during morning counts at Rocky Ramp (RR), 9–23 Nov, over three seasons (2015–17). The x-axis shows the date (in Nov) each year when counts were made.

population study of a reference population of breeding penguins was conducted at Rocky Ramp (Fig. 2C), including locating nests and identifying breeding and juvenile birds. These data were used to determine the proportion of the reference population seen during each morning count, as well as the proportion of breeders sighted. This correction factor for the morning counts was used to extrapolate a population estimate for the entire Auckland Islands archipelago.

Marking of birds

During 2015–17, all adult penguins using the landing site, nesting, or loafing in forest inland of Rocky Ramp were fitted with a 23 mm, TIRIS compatible, ISO standard Passive Integrated Transponder (PIT) microchip, (Allflex, Palmerston North, New Zealand). Penguins were captured by hand as they returned to the island in the evening following a foraging trip at sea. Microchips were injected subcutaneously at the back of the neck, as per Department of Conservation (DOC) protocol (Department of Conservation 2012). Microchipped penguins were also given a temporary individual mark on the chest using a Tag Pen stock marking pen (Allflex, Palmerston North, New Zealand) to allow visual recognition.

Nest searches

Nest searches were carried out over a 2-month period (Nov–Jan) to locate all the nests in the reference population at Rocky Ramp. This approximately 15 ha area was defined by the edge of the habitat (vegetation suitable for nesting) on its western and northern boundaries. The eastern boundary transitioned into the neighbouring breeding area (Sandy Bay), and there was some overlap of nests. The access point to the sea used by each breeding bird (and therefore the Rocky Ramp breeding population) was confirmed by electronic monitoring at the Rocky Ramp access point.

Nest searches utilised a variety of methods, including ground-searching (Hegg *et al.* 2012), and very high frequency (VHF) radio-tracking using transmitters attached to penguins, which significantly improved search efficiency. VHF tracking was carried out on foot and using a VHF-equipped drone, methods as per Muller *et al.* (2019). Ground-search teams used a handheld GPS (Garmin, USA) to record nest locations. GPS trail data of searchers' movements were analysed using mapping software (Garmin Mapsource and ESRI ArcGIS) to ensure that all likely breeding habitat in the reference population area was checked. Based on coverage of the area, and since both the cumulative number of nests located and the number of identified breeding birds reached an asymptote by the end of the season, we were confident that all nests in the area were located.

Electronic monitoring

Access to the sea from the Rocky Ramp area is via a narrow path down a cliff, allowing electronic monitoring of microchipped penguins and visual monitoring of all birds travelling to and from the landing site. A custom-built automatic PIT microchip reader (the 'autologger') was constructed from an ASR700 high-power reader (Agrident, Barsinghausen, Germany) and a modified radio frequency identification (RFID) logger (DOC Electronics, Wellington), and was used to record the identities of microchipped penguins passing by. The circular antenna, with a diameter of approximately 1.5 m, was oriented horizontally and spanned the path so that all transiting penguins would walk over it.

Using the autologger, a continuous record of all transiting penguins was collected at the Rocky Ramp access point to the sea, from Nov 2016 to Feb 2017 (n = 94 days). To determine daily movement patterns, transit times were analysed (using a Python 3.5.2 script, www.python.org, accessed 27 Jan 2019) by dividing the time of day into 10-min intervals, then determining the mean number of microchipped birds passing by during each time interval for each of the three main breeding phases:

- Incubation phase was defined from 17 Nov (the start of electronic monitoring) until 27 Nov (the mean hatch date for the reference area, determined by nest checks) (n = 11 days).
- Guard phase was defined from 28 Nov (the day after mean hatch date for the reference area) until 31 Dec (the estimated date when half the nests in the reference area showed evidence of non-continuous parental attendance, determined by nest visits) (n = 34 days).
- Post-guard phase was defined from 1 Jan 2017 (the day after mean non-continuous parental attendance) until 18 Feb (the end date of monitoring) (n = 49 days).

A Panoramic 150i or 180i game trail camera (Moultrie, USA) was set up with a field of view covering a section of the penguin trail adjacent to the autologger, to record a panoramic photo of transiting birds. The camera had three independent infrared movement sensors; movement detected by any of these as a penguin walked past would trigger a panoramic photograph, increasing the reliability of detections. Panoramic photos also allowed a single camera to record the chest area (where temporary marks were applied) of both arriving and departing birds. The camera and autologger were both powered from a 12 V battery and solar panel, and so could run continuously during the study.

A trial of morning beach count methods was conducted simultaneously at Rocky Ramp using a human observer, plus counts generated from the trail camera and autologger, to compare accuracy between the methods. Trials were conducted at the beginning of each season in 2015 (n = 8 counts), 2016, and 2017 (n = 3 counts each). Comparison data were analysed as part of the population estimate.

Population estimate

A population estimate was determined for the Rocky Ramp reference population using a mark-recapture method. This was conducted on a single day between 19 and 22 Nov each year, so that results would be comparable with the November counts elsewhere on the Auckland Islands. During the week prior to the survey date, birds were caught and marked with a microchip. The sample size increased each year, as birds marked the previous year that had returned to the area were included in the marked sample the following year. Marked birds were 'resighted' using the automatic PIT microchip reader (autologger). Counts used for the mark-recapture were independent of the morning beach count surveys, and so were taken at 0500–0900 h, when the majority of birds were heading to sea (Fig. 4; and Moore 1990), and to minimise the likelihood of double-counting birds if they returned later the same day. For the same time period, the total number of birds (marked and unmarked) was counted using photographs from the trail camera located adjacent to the autologger. Occasionally the species could not be identified from a photograph (particularly at night), and in some cases penguins did not always trigger the camera, although cameras with multiple sensors gave better results. Comparison with counts made by a human observer for a trial period at the beginning of each season demonstrated that detection rates for camera counts were 71% (with 150i single-sensor camera) in 2015, and 95% and 96% (both with 180i triple-sensor camera), respectively, in 2016 and 2017. A correction factor for the trail camera counts was determined from these data.

A Lincoln-Peterson index using the Chapman equation was used to estimate the total number of birds ($\hat{N}$) in the Rocky Ramp reference population by using the equation:

$$\hat{N} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1$$

Where n_1 = number of microchipped birds when the mark-recapture was undertaken, m_2 = number of microchipped birds recorded on the autologger, and n_2 = total number of birds counted on the trail camera. The Chapman equation was used since it is less biased at lower samples sizes than other methods (such as the Lincoln-Peterson; Chapman 1951). The variance and confidence interval were also calculated using methods described by Chapman (1951).

The population estimate for the reference population was then extrapolated to generate a population estimate for the Auckland Islands. This was determined by using the ratio of birds seen during morning counts (on the same day as the mark-recapture estimate) compared with the total population estimate for the reference population, and applying the same ratio to the total number of birds seen during morning counts around the Auckland Islands. Minimum and maximum estimates were derived using the corresponding values for the reference population from the mark-recapture study.

Morning count data during 2012–14 could not be extrapolated using the same method, since no ground-truth data were collected during these years. Therefore, the average ratio of morning counts to total population estimates was determined for 2015–17 and applied to the 2012–14 count data. The confidence interval for these years was estimated using the largest error (from 2015) to reflect the presumed much larger uncertainty associated with this method. A retrospective

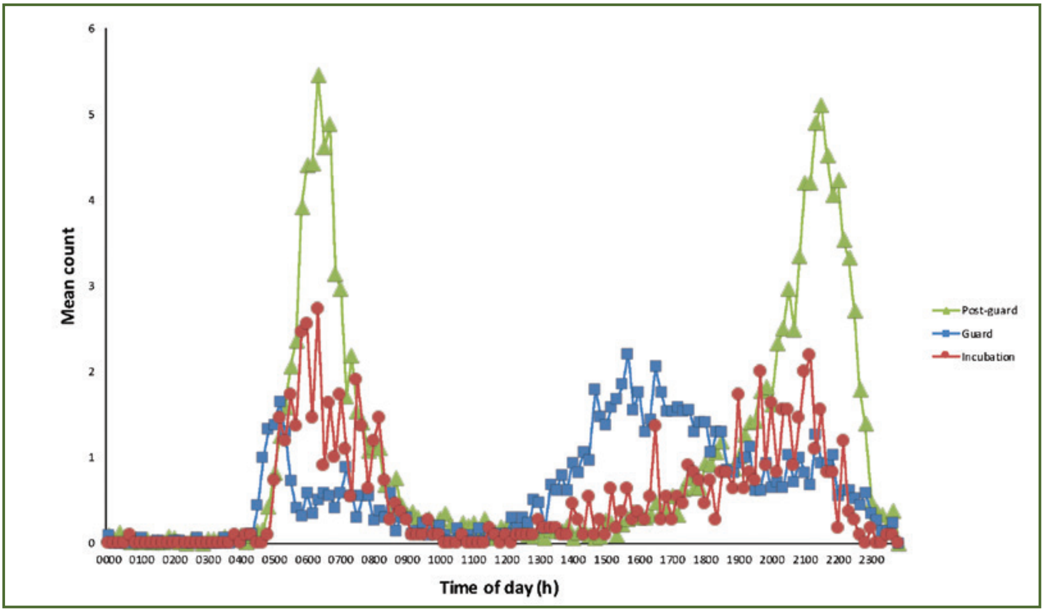

FIGURE 4. Daily activity patterns of nesting yellow-eyed penguins (2016-17 season) transiting to and from the sea during each breeding phase: Incubation (circles), Guard (squares), and Post-guard (triangles). Data were collected as microchipped birds passed by an automated reader, and represent the mean number of transits counted during each 10-min time block throughout the day, averaged per phase; Incubation (n = 11 days), Guard (n = 34 days), and Post-guard (n = 49 days).

TABLE 2. Mean and standard deviation (*sd*) of the number of adult yellow-eyed penguins counted during morning counts at the reference site on Enderby Island (Rocky Ramp) over three field seasons. Counts were initially conducted from 0500–0900 h for successive days in 2015 (n = 10 days), 2016 (n = 8 days) and 2017 (n = 12 days). The data shown were re-sampled from 0530–0900 h for comparison with morning beach counts collected around the remainder of the Auckland Islands (Table 4).

Year	Mean	*sd*
2015	18	3.9
2016	84	10.8
2017	23	11.1

population estimate was not possible for counts collected in 2009 by Beer (2010), as methods and sites differed from those of our survey.

Proportion of breeders

For conservation management purposes, it is important to know the number of breeders, as they represent the ability of a population to reproduce and produce future generations (Baasch *et al.* 2015). All birds caught at the Rocky Ramp reference population were microchipped, and when a nest was located it was revisited until both partners were scanned on the nest and thereby identified as breeders. All microchipped birds located loafing in the forest and/or never found on a nest during nest searches were assumed to be non-breeders. The Rocky Ramp breeding population was confirmed using electronic monitoring, as described in the section on nest searches, above.

Mean daily detection rates for breeding birds recorded on the autologger were determined by averaging the number of detections per day for all known breeding birds from the Rocky Ramp reference population. The proportion of breeders was calculated based on the average number of breeders detected by the autologger, compared with the total number of birds detected by the trail camera per day during the same period. The estimated proportion of breeders was then applied to data from other surveyed sites around the Auckland Islands to determine the total breeding population (assuming that the proportion of breeders was similar across all sites).

Results

Electronic monitoring

Analysis of the mean number of microchip detections recorded by the autologger during 10-minute intervals throughout the day identified morning and evening peaks in transiting activity during the Incubation phase (Fig. 4). During the Guard phase the morning activity peak was smaller and occurred earlier in the morning, whereas during the Post-guard phase both morning and evening activity peaks were much larger.

Analysis of the number of microchip detections during the Incubation phase indicated that a count period of 0530–0900 h included 89% of the transits recorded during a count period of 0430–0900 h.

Morning counts

A generalised linear model showed that counts at Rocky Ramp in 2016 were significantly higher than the other two years (Fig. 3, Z = 18.30 and 18.15, $P < 0.01$). There was a smaller difference in counts between 2015 and 2017, but this was still significant (Z = –2.41, $P < 0.02$). The variability between days was more pronounced in 2016 and 2017, as shown by the standard deviations (Table 2).

Enderby Island was the largest population centre, accounting for an average of 50% of the total Auckland Islands counts (Table 1). Morning count numbers from around the Auckland Islands also varied between years and showed an increase in 2016, similar to that observed on Enderby Island in the same year (Table 1). As not all sites were surveyed each year, corrected results incorporate estimates for unsurveyed areas (Fig. 5).

Population and breeding estimates

Population estimates for the reference area (Table 3) and the Auckland Islands (Table 4) showed a similar trend to the number of nests found in the reference area (Table 5). Population estimates varied between years and included a large uncertainty. This uncertainty was more pronounced for counts extrapolated from 2012–14 that were not ground-truthed, and for 2015 where the number of marked birds was lower than subsequent years (Fig. 6).

The proportion of breeders was estimated for the Incubation phase (when morning counts were

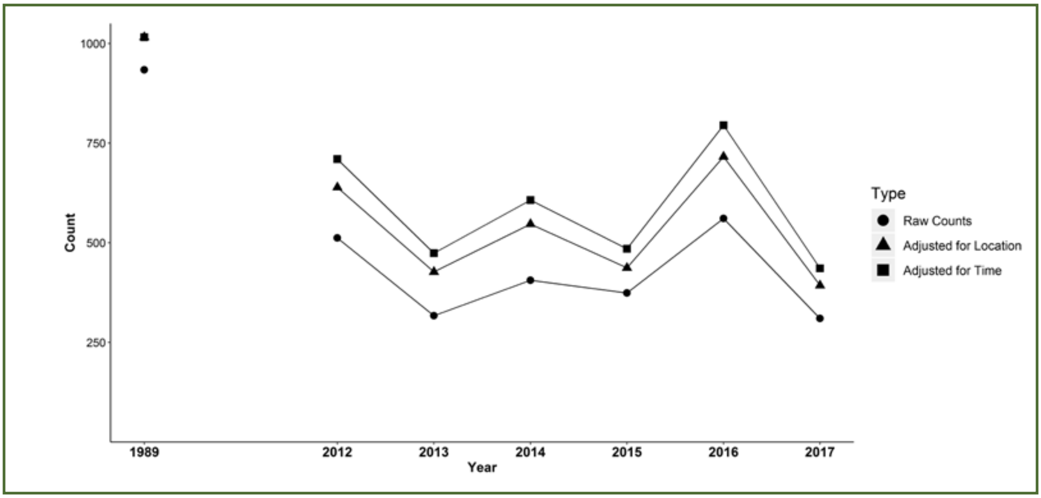

FIGURE 5. Morning count data for yellow-eyed penguins at the Auckland Islands, including total raw counts (circles) that omitted some sites in some years, and adjusted counts including estimates for areas that were missed in a particular year, as per Table 1 (triangles), as well as a 12% increase to account for a shorter time period for counts (0530–0900 h) (squares). Totals from Moore's survey in 1989 are shown for reference (Moore 1990). The 1989 counts were made from first light (0430–0900 h) and so should be comparable to the time-adjusted counts, but any direct comparisons between beach counts should be made with caution.

conducted), based on data collected during the Post-guard phase (after microchipping was completed; Table 6). The proportion of non-breeders ranged from 0.34 to 0.46 at Enderby Island across the 3 years, averaging 0.42 (*sd* = 0.06). A lower proportion of breeders was evident in 2015 compared with subsequent years, although numbers of breeders also appeared to fluctuate about a mean (Fig. 7).

Linear regressions of the estimated population (Fig. 6) and number of breeders (Fig. 7) both show no trend during 2012–17, indicating that on average the population also appeared to be fluctuating around a mean during this time. The most recent season (2017), which had the smallest confidence interval, had an estimated total of 887–1,105 breeders, or 444–553 pairs, for the Auckland Islands, although the estimate for the previous season (2016) was much higher at 580–922 pairs.

Discussion

Our results showed that despite large annual fluctuations, the overall population trajectory of yellow-eyed penguins at the Auckland Islands appears to have been relatively steady during 2012–17 (Fig. 6). Similarly, the estimated number of breeders varied considerably between years, but overall the trajectory was stable (Fig. 7). The number of breeding yellow-eyed penguins in the Auckland Islands averaged 1,154 individuals (or 577 pairs) over the three ground-truthed breeding seasons. The actual population would be expected to be higher than this, since not all known breeding areas were surveyed. However, the population may have declined since 1989, when comparable areas were surveyed.

Population estimate

Our estimate of 577 pairs in the Auckland Islands is similar to the 520–680 pairs estimated for the entire archipelago in 1989 (Moore 1990). However, Moore's estimate of breeding pairs on the Auckland Islands may have been an under-estimate (Moore 1990, 1992b) since some breeding areas were not surveyed (e.g. Chambres Inlet and Waterfall Inlet). In addition, the population estimate was based on ground-truthing from Campbell Island survey data, which were adjusted to a total population size based on the proportion of banded breeders known to be alive at a study site, the proportion

TABLE 3. Population estimates of yellow-eyed penguins for the reference area on Enderby Island determined using mark-recapture studies. n_1 = number of microchipped birds when the mark-recapture was undertaken (after the first week), m_2 = total number of microchipped birds recorded on the autologger, n_2 = total number of birds counted on the trail camera. The confidence intervals (CIs) are also shown.

Date	Total number chipped (n_1)	Number chipped in count (m_2)	Total counted (n_2)	Reference population estimate	CI
19 Nov 2015	21	4	20	91.4	56.7
22 Nov 2016	101	27	59	217.6	49.5
19 Nov 2017	120	33	39	141.4	15.5

TABLE 4. Population estimates of yellow-eyed penguins for the Auckland Islands determined from the ratio of count to population estimate in the Enderby Island reference area applied to the total count from the Auckland Islands. 'Breeders estimate' was generated using the proportion of breeders from Table 6.

Re-sight date	Reference area count (0530–0900 h)	Reference area est. total	Auckland Is count (adjusted for location) (0530–0900 h)	Auckland Is population estimate	Auckland Is breeders estimate
19 Nov 2015	19	91	437	2093	1381
22 Nov 2016	55	218	716	2838	1589
19 Nov 2017	29	141	393	1911	1032

TABLE 5. Number of nests in the reference area (Rocky Ramp). 'Nests identified' values represent the number of active nests during the incubation period when the survey was undertaken. Successful nests included one or more fledged chicks.

Year	Nests identified	Nests successful	Breeding success
2015	51	42	82.4%
2016	69	60	87.0%
2017	51	30	58.8%

TABLE 6. Calculation of the estimated proportion of breeding yellow-eyed penguins in count data during the incubation phase. Total bird numbers were counted using the trail camera, and microchipped breeders were counted using the autologger. 'Daily rate' is the mean number of detections per day for microchipped breeders. (This includes the morning and evening peak commutes to and from the sea. Some birds may have returned on the same day – hence why mean daily detection rates are greater than 1 at certain times, especially in the Post-guard breeding phase). The proportion of confirmed breeders out of the number of birds transiting was determined during the Post-guard phase (when the maximum number of birds had been microchipped), and used to estimate the proportion of breeders during the Incubation phase when morning counts were conducted (but before the majority of breeders had been microchipped).

Year	Daily rate (Post-guard)	Total breeders (Post-guard)	Total birds (Post-guard)	Daily rate (Incubation)	Total birds (Incubation)	Est. proportion of breeders (Incubation)
2015–16	0.8	61	74	0.25	29	0.66
2016–17	1.19	132	176	0.73	146	0.56
2017–18	1.49	140	271	0.43	76	0.54

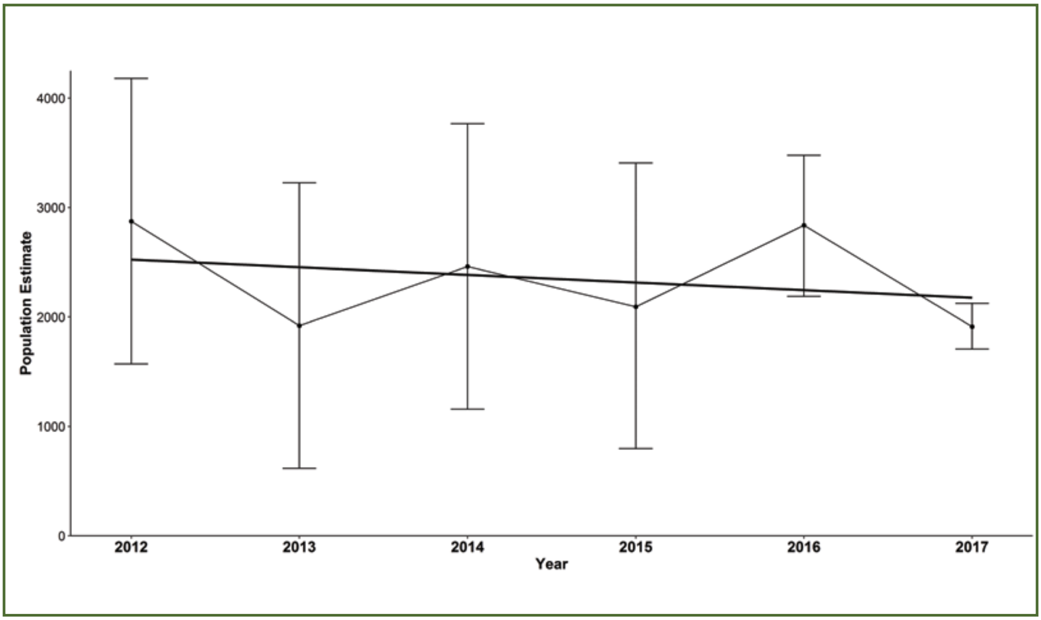

FIGURE 6. Population estimates for yellow-eyed penguins in the Auckland Islands, including error bars and linear regression model. Ground-truthed years (2015–17) are right of the dotted line – estimated from the ratio of birds seen during morning counts of the population in a reference area determined from a mark-recapture study. Also shown are population estimates (2012–14) left of the dotted line – extrapolated from birds seen using data from the ground-truthed years.

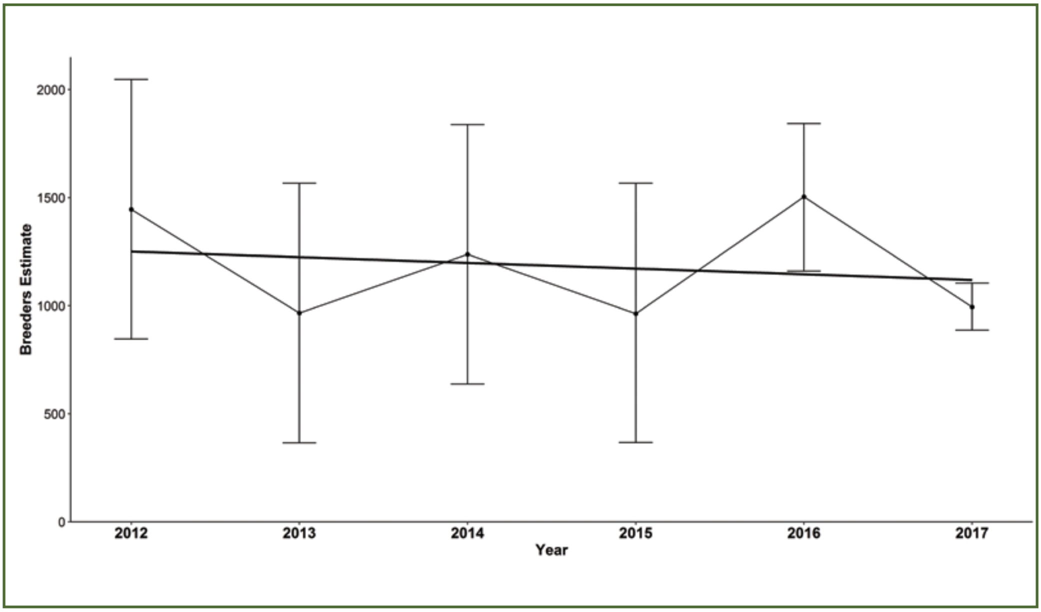

FIGURE 7. Estimate of the number of breeding yellow-eyed penguins in the Auckland Islands, including error bars (as per Table 4) and linear regression model for ground-truthed years (2015–17), right of the dotted line, and extrapolated estimations (2012–14), left of the dotted line.

of banded birds in the beach counts at the study site, and an assumption that 60–70% of the total population were breeders. When count data were re-analysed using mark-recapture analysis, while still assuming that 60–70% of birds were breeders, then the total estimate for Campbell Island went from 490–600 pairs to 610–890 pairs (Moore *et al.* 2001), an increase of 25–48%. When applied to the Auckland Islands count data, a similar method could give an upper estimate of 650–1,009 pairs for 1989.

Based on the comparison between population estimates in 1989 and 2012–17, there may have been a population decrease, since counts of individual sites also decreased in most cases (Table 1). Moore *et al.* (2001) also found substantial annual variation on Campbell Island, with a 41% population decrease and a 19% decrease in the number of landing sites between 1988 and 1992. Index counts over the next 6 years showed that the population partially recovered during 1994–98, but the recovery was markedly different between areas (Moore *et al.* 2001).

Extrapolation of the 2012–14 data suggests that the number of breeders on the Auckland Islands also varied annually for successive years. The percentage of breeders present in each season suggests that the number of birds attempting to breed in 2017 was similar to 2015. Breeding success on Enderby Island was poor in 2017, with substantial egg failure early in incubation (CGM, *unpubl. data*). The 2016 season included larger numbers of breeders, although the proportion of breeders did not increase as much due to a larger increase in the number of non-breeders. The margin of error for population estimates reduced during the 3 years of ground-truthing (2015–17), primarily due to an increasing proportion of microchipped birds (up to *c.* 85% of the estimated total population in the reference area in 2017), which provided a better sample size for the mark-recapture estimate. Considering the two most recent seasons where the confidence intervals were more accurate, the 2017 estimate of 444–553 pairs for the Auckland Islands is less than the original estimate of 520–680 pairs for 1989 (Moore 1990), but is considerably less than the revised estimate of 650–1,009 pairs. However, the 2016 estimate of 580–922 pairs is more similar, making it difficult to determine trend over the longer time period.

The proportion of yellow-eyed penguins breeding in the subantarctic (Auckland and Campbell Islands) was previously estimated at around 60% of the population (Ellenberg & Mattern 2012). However, subsequent population surveys on the mainland have shown a significant decline in the number of pairs breeding there in recent years (Mattern & Wilson 2018; Department of Conservation 2019), including Stewart and Codfish Islands (Seddon *et al.* 2013). The most recent Campbell Island estimate from 1992 (Moore *et al.* 2001) also indicates a population decline, but likely needs updating. Using these estimates, the mainland updated numbers, and taking our possible range of 444–922 pairs for the Auckland Islands, this gives a revised estimate of 68–79% of the population breeding in the subantarctic, with 38–50% of the total population breeding at the Auckland Islands. The Auckland Islands (particularly Enderby Island) therefore represent a significant proportion of the total breeding population, indicating the importance of the subantarctic populations for the species.

Yellow-eyed penguins begin to breed around 2–3 years old for females, and 2–5 years old for males (Marchant & Higgins 1990). It can therefore be surmised that a large proportion of non-breeders are young birds that are yet to breed. An increase in the proportion of non-breeders in some years, as occurred in 2016 on Enderby Island (Tables 4, 6), may therefore be due to the presence of cohorts from previous highly successful breeding seasons, and/or higher than usual juvenile survival rates. Non-breeding birds from nearby areas may also visit Enderby Island, affecting counts. Overall, the average proportion of non-breeders across the 3-year study of 0.42 on Enderby Island is consistent with the range of 0.34–0.47 reported on mainland New Zealand (Richdale 1957; McKinlay 2001).

Variable breeding success has been documented in mainland yellow-eyed penguins, and could indicate that both populations are affected by similar processes, such as the effects of climate change and food availability (van Heezik 1990; Moore & Wakelin 1997; Moore 1999; Mattern *et al.* 2017). However, some population crashes observed on mainland New Zealand are thought to be the result of mass adult mortality events, possibly due to disease (Seddon *et al.* 2013; Couch-Lewis *et al.* 2016). Such die-offs have not been observed in the subantarctic, although this may reflect infrequent monitoring. Avian malaria is present in the yellow-eyed penguin population (Graczyk & Cockrem 1995), and birds carry ticks that could transmit viruses and blood parasites. Tourism has been implicated in declines in nesting success, fledging condition, and juvenile survival for some mainland yellow-eyed penguin areas (McClung *et al.* 2004; Ellenberg *et al.* 2007). While human disturbance has been shown to affect yellow-eyed penguin behaviour in the subantarctic (Young 2009; French *et al.* 2019), tourism is not believed to be a factor affecting breeding success on Enderby Island (French 2018). Banding of penguins has been implicated in poor breeding success in some studies (e.g. Culik *et al.* 1993); however, this is not currently a factor in subantarctic yellow-eyed penguin populations since no banding is allowed by DOC.

A biennial breeding cycle could result in a pattern of alternating variability in individual breeding success, as occurs in southern royal albatross (*Diomedea epomophora*) and Gibson's wandering albatross (*D. antipodensis gibsoni*), which also breed in the Auckland Islands (Robertson 1972; Walker & Elliott 2001; Childerhouse *et al.* 2003). However, while individuals of these species breed in alternate years, this does not result in a variable breeding rate between years for the population, as a similar proportion of adults still breed each year (Walker & Elliott 2001; Childerhouse *et al.* 2003). Furthermore, a breeding 'sabbatical' is not likely for yellow-eyed penguins in the subantarctic. The species has an annual breeding cycle on the mainland (Richdale 1949; Darby *et al.* 1990), and failure to breed annually is more likely due to partner loss (Setiawan *et al.* 2005). Known birds were observed breeding in successive years on Enderby Island (CGM, *unpubl. data*), and so a biennial breeding cycle is unlikely to be the reason for the high counts in 2016. Deferred breeding after years of poor breeding success and/or abnormal feeding conditions might occur occasionally. Moore *et al.* (2001) found evidence for deferred breeding on Campbell Island – after poor adult survival and breeding success in 1991-92, only 68% of surviving breeders at the study site bred the following year.

Counts (and by assumption breeding attempts) on Adams Island have decreased over the past 3 years (Table 1). Being a large, predator-free island, it would be expected that Adams Island would be an important breeding location. It is possible that birds previously seen there may have moved to new, unmonitored locations, although due to high nest-site fidelity in yellow-eyed penguins this is unlikely (Darby *et al.* 1990; Seddon *et al.* 2013). Factors such as climatic effects on food supply or disease outbreaks would result in wider-scale declines, but a localised decline could occur if penguins from different breeding areas were foraging in different locations and subject to localised effects. Fisheries by-catch and indirect competition have been shown to cause declines in some mainland populations (Ellenberg & Mattern 2012), and therefore it would be useful to know where Adams Island breeders concentrate their foraging effort. Conversely, over the past 2 years morning count numbers appear to have increased at Chambres Inlet on Auckland Island (Table 1), where predators such as pigs, cats, and mice are present). However, there is some evidence that cliffs may limit ground access by large predators to most of the nesting area at this site (CGM, *pers. obs.*), which may explain why this area appears more successful than other locations on Auckland Island. Terrestrial predation has been shown to be a significant cause of population decline for mainland yellow-eyed penguin populations (Couch-Lewis *et al.* 2016). It would therefore be expected that control of mammalian predators on Auckland Island would provide more suitable breeding locations for yellow-eyed penguins.

Predation by New Zealand sea lions (*Phocarctos hookeri*) was implicated in at least localised population declines of yellow-eyed penguins on Campbell Island (Moore & Moffat 1992; Moore *et al.* 2001). Evidence of predation was observed on Enderby Island during the 1990s (Moore *et al.* 2001) and in 2015–17 (CGM, *unpubl. data*), which indicates that predation by sea lions may also be a factor.

Variability in the number of breeders observed each year is cause for concern, as is an apparent decline since 1989. While the population appears stable over recent years, a further decline could occur if the factors contributing to a sub-optimal breeding season intensified, or continued for successive years. Our results show that there are some differences in the ratio between breeders and the total population estimates between years. This suggests that while some factors may be influencing the population as a whole, in some years the proportion of breeders altered. This may indicate greater or lesser pressure on different cohorts within the population. Variability in the proportion of non-breeders could indicate variability in the numbers of juvenile birds returning to their natal areas, and therefore to recruitment of breeders. Recruitment is an important factor affecting long-term population survival; however, little is known about juvenile yellow-eyed penguin movements and survival in the subantarctic. Moore (1992a) reported that 15% of chicks banded on Campbell Island were subsequently resighted as juveniles or adults. It has been determined that disturbance (McClung *et al.* 2004) and lower-quality diet (van Heezik & Davis 1990) can contribute to poorer survival for juveniles, but there is no corresponding research for the subantarctic. In addition, loss of a partner may result in the surviving partner not breeding in subsequent years (Richdale 1957; Setiawan *et al.* 2005), which could also affect breeding proportions.

Changes in climate and ocean environment have been shown to affect the proportion of breeders and breeding success in emperor penguins (*Aptenodytes forsteri*), and are thought to be contributing to declines in chinstrap penguins (*Pygoscelis antarctica*) and Adélie penguins (*P. adeliae*) (Jenouvrier *et al.* 2009; Trivelpiece *et al.* 2011). Decreases in adult survival can have a large impact on population growth rate, which has led to a population crash in emperor penguins and other Antarctic seabirds (Barbraud & Weimerskirch 2001; Jenouvrier *et al.* 2005). Changes in breeding success may also contribute to population fluctuations, especially if breeding success is more variable than adult survival (Jenouvrier *et al.* 2005).

As in other penguin species, yellow-eyed penguins are central-place foragers, and on the mainland their breeding success is dependent on foraging within 20 km of the breeding site (Moore 1999; Mattern *et al.* 2007). The density and distribution of prey species can be affected by warming water, which can reduce the available food or move it further away, making it energetically inefficient for provisioning chicks. El Niño conditions have been associated with declines in breeding success in Galapagos penguins (*Spheniscus mendiculus*) (Boersma 1998; Vargas *et al.* 2006) and Humboldt penguins (*S. humboldti*) (Hays 1986). Warmer water coincided with declines in rockhopper penguins on subantarctic Campbell Island (Cunningham & Moors 1994), and in yellow-eyed penguins on the mainland (Peacock *et al.* 2000). The 2015 breeding season was one of the strongest El Niño years reported, associated with warmer conditions in the Pacific (Jacox *et al.* 2016; Null 2018). In contrast, the 2016 and 2017 seasons were mild La Niña years with cooler conditions. The 2015 El Niño corresponded with a lower breeding population of yellow-eyed penguins on Enderby Island, although similar breeding results in 2017 corresponded with La Niña conditions, indicating a more complex relationship with climate. A link between population decline and El Niño oscillations has not been demonstrated for mainland yellow-eyed penguins, where longer-term climate changes may be more relevant (Peacock *et al.* 2000).

Limitations of morning counts

Conducting morning counts in mid-November during the Incubation phase was supported by the timing of peak morning transits evident in the autologger data (Fig. 4). These data also showed that during the Guard phase fewer transits were detected per day, as adults spent more time on the nest brooding young chicks, and activity began much earlier in the day. While there were more transits recorded during the Post-guard phase in January and February, many birds were conducting daily foraging trips. While this would increase the proportion of transiting birds from the population available to be counted each day, both partners may have gone to sea at the same time, making it more difficult to determine the proportion of breeders, and birds returning on the same day would appear in both morning and evening counts, requiring unique identifiers to avoid double-counting. Additionally, any beach counts conducted later in the season would be biased towards successful nests, as a proportion of nests fail during each breeding phase.

Morning count data for the Auckland Islands during 2012–17 show that total numbers of birds counted (Table 1) were less than the 934 counted in 1989 (Moore 1990). However, count totals depended on which areas were surveyed, and so required a correction factor. In addition, counts for the present study were analysed from 0530 h to 0900 h, which was a shorter time period than Moore's, and so our raw counts would be expected to be lower. Increasing morning counts by 12% to approximate a longer data collection period from first light (0430–0900 h) would still result in lower counts than in 1989, which would imply a decline in the population. However, beach counts are difficult to compare unless all of the same areas were surveyed under identical conditions, which is difficult to achieve due to weather and other effects. Large daily variation in beach counts has also been demonstrated (Fig. 3). It is therefore more accurate to compare population estimates derived from beach counts using an appropriate ground-truthing method. Morning counts may be useful as an interim monitoring method between population surveys (Moore 1992a), but ideally should not be used as a sole means of comparison.

In addition, morning count data collected over multiple days on Enderby Island showed daily variation in counts and also a progressive change over time, indicating that using a single daily count at other locations could introduce a margin of error (Fig. 3). The Auckland Islands are around 50 km long, with the potential for weather systems to affect different areas at different times. Enderby Island is in the north-east and has a more benign climate, with greater sunshine hours and less rainfall than other areas in the archipelago (Higham 1991), and so trends here may not be representative of other locations. Nevertheless, since only a single count was taken at each site around the Auckland Islands, it was considered to be more appropriate to adjust counts using Enderby Island count data from the same day, when conditions were relatively similar, rather than use weekly averages of Enderby Island data, which might introduce more variability. A more accurate population estimate could be achieved with multiple counts at each site, as well as conducting a mark-recapture study at each site (or at selected sites across the region), although this would be logistically difficult.

Using a mark-recapture estimate provided a more reliable population estimate than a simple ratio between beach counts and nest numbers, which does not take into account the proportion of breeders counted. Mark-recapture theory utilises the ratio of marked to unmarked individuals so that the whole population does not need to be counted. However, mark-recapture models assume that all members of the population have an equal chance of being resighted, which is not necessarily true for transiting penguins. Only one bird from each nest will commence a foraging trip on a given morning during incubation, and if partners do not swap every day then an even smaller proportion of breeders will be transiting. This effectively reduces the proportion of marked birds available to be resighted in the sample. If birds are marked when returning to their nests following a foraging trip, then the re-sighting survey should be conducted after a suitable time period to prevent bias towards their potentially unmarked partners. Our results showed that the confidence interval surrounding population estimates reduced markedly between years as progressively more of the population was marked.

Conclusion and recommendations

Based on the reduction in confidence interval we observed between ground-truthed years (2015–17) as more of the population became marked (Figs 6, 7), the recommended method for future population estimates would be a mark-recapture study at as many of the sites as possible, where at least 50% and preferably over 75% of the expected population in that area is marked – although a compromise with logistics may be needed due to the difficult terrain and weather conditions that can affect research in the subantarctic. Beach counts in all areas would also be needed to derive a total population estimate and determine population trends.

Our estimate of the total number of breeding birds for the Auckland Islands assumed that the proportion of breeders was similar across all sites, which is an untested assumption. The proportion of breeders is similar at most mainland colonies (Richdale 1957; McKinlay 2001) but this could vary in small colonies, or if predation and other factors influence breeders and non-breeders unequally. A more detailed population census at selected sites around the Auckland Islands would determine the variation in the proportion of breeders, which would improve the accuracy of the resulting population estimate. Some breeding sites surveyed by Moore were not included in this survey due to time constraints, or difficult or dangerous access (including Matheson Bay, Ewing Island, and Tagua Bay in Carnley Harbour). In addition, other possible breeding areas (including Musgrave Inlet and Smith Harbour; Fig. 2B) were identified by Beer (2010) but were not included in this survey. Breeding numbers in these areas are expected to be low, but are largely unknown and so cannot be estimated based on previous data. Therefore the Auckland Islands population estimates should be regarded as a minimum estimate, and future surveys should ideally also include these additional areas where penguins may be breeding.

It is evident that there is some variability between years, not only in the numbers of birds attempting to breed but also in their ability to successfully incubate and hatch eggs, and raise chicks to fledging (CGM, *unpubl. data*). Morning beach counts are conducted near the beginning of the breeding season, which does not give any indication of breeding success. It would therefore be valuable to conduct breeding success studies to determine hatch rates, fledging rates, and nest-predation rates. The large main Auckland Island provides potential habitat for breeding to increase, and therefore eradication of mammalian pests would be expected to benefit yellow-eyed penguin population numbers. Detailed population surveys before and after any planned eradication would be useful to measure changes.

We recommend that long-term monitoring of yellow-eyed penguin populations in the subantarctic continues, including measures of breeding success as well as juvenile survival and recruitment, particularly considering population declines recently observed on the mainland. We have demonstrated that the subantarctic still has a large proportion of the population, and the larger population centres, such as Enderby Island, are likely to become more important for the survival of the species if populations on the mainland continue to decline. Continued monitoring and regulation of threats to subantarctic yellow-eyed penguins is therefore important, including protection of habitat, eliminating introduced predators, and minimising negative interactions with fisheries and tourism. Ongoing monitoring is also needed to determine longer-term effects of changes in climate on food availability, as well as potentially catastrophic natural and unnatural events, including disease epidemics, tsunamis, and oil spills from fishing or tourist vessels.

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