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

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

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INTRODUCTION

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

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

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

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

While early visitors to the Bounty Island provide figures of '1 million' (Anonymous 1890a) to '3 million penguins' (Anonymous 1890b), the first scientific attempt at estimating erect-crested penguin population size was made in 1978. Robertson and van Tets (1982) estimated the total penguin population to be 115,000 breeding pairs. Almost two decades later, in 1997, a survey that included comprehensive ground counts on Proclamation and Depot Islands (*Totorore* Expedition; Clarke *et al.* 1998) put the Bounty Island erect-crested penguin population at 27,956 pairs (Taylor 2000). Both estimates used different approaches limiting the usefulness of a direct comparison (Taylor 2000; Wilson & Mattern 2019). However, a re-count on Proclamation Island in 2004 (*Mahalia* Expedition; De Roy & Amey, 2004) found no change in breeding pair numbers there suggesting that the population had remained stable between 1997 and 2004.

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

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

METHODS

Study site

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

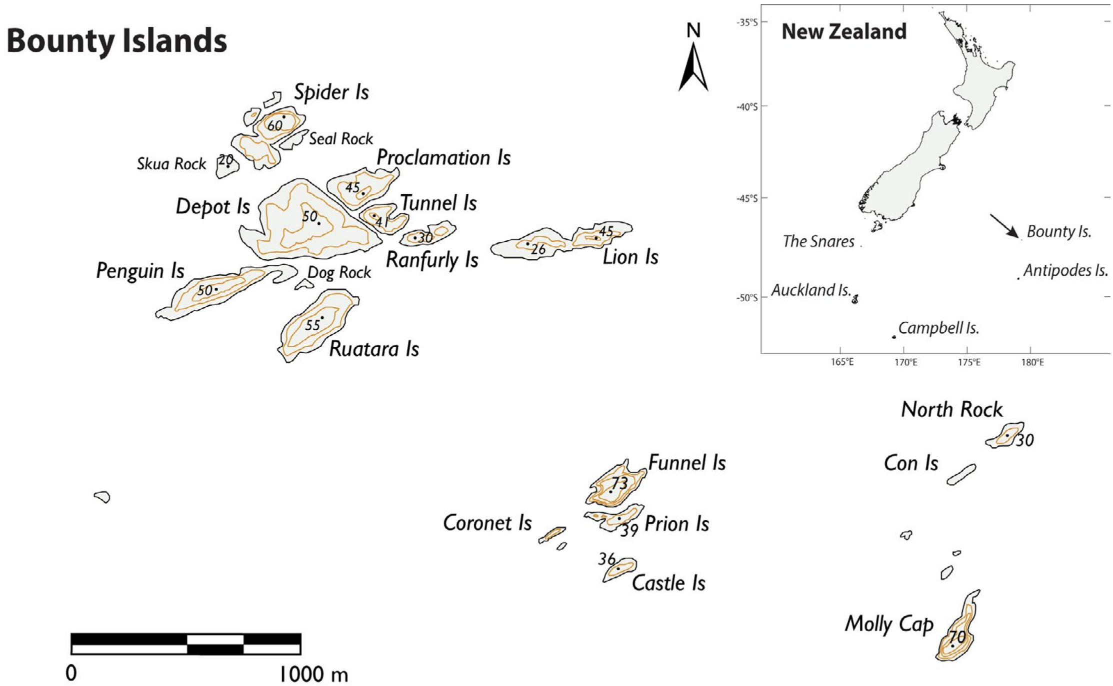

Figure 1. Map of the Bounty Island archipelago (based on LINZ Topo Map 25, 2011). Inset provides overview of New Zealand's subantarctic islands; arrow indicates location of the Bounty Islands.

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

2019 Bounty Island Expedition

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

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

Ground counts of penguin nests

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

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

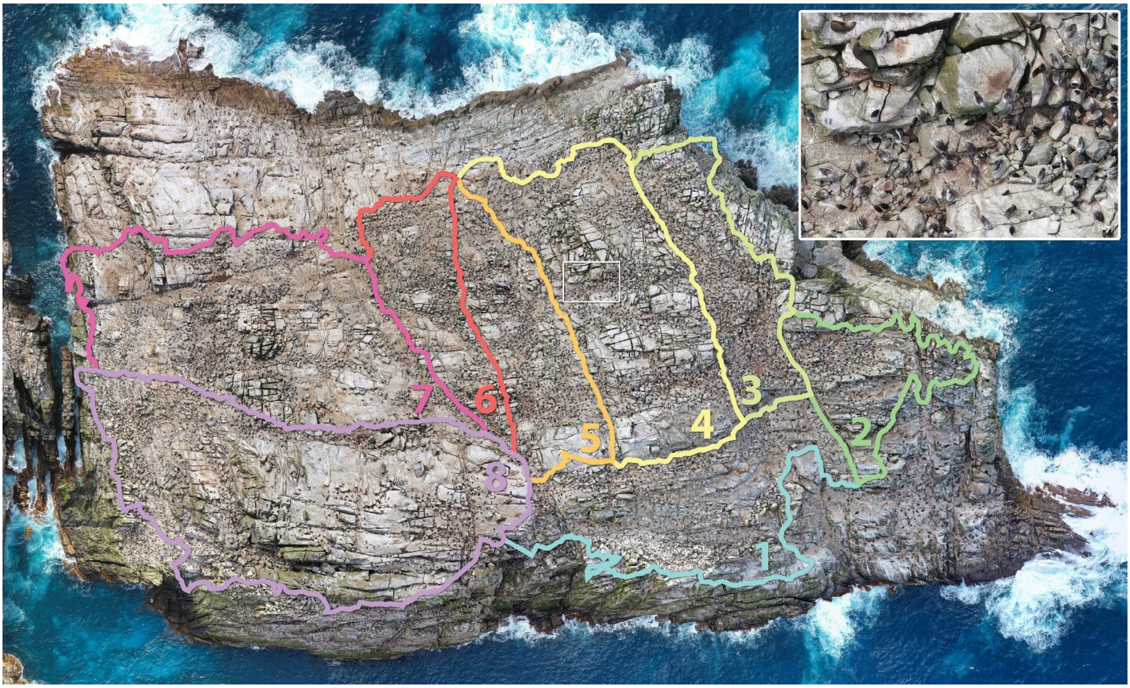

Figure 2. Composite image of Proclamation Island stitched from 799 individual images. Inset shows level of detail of the composite image; white rectangle indicates location of inset. Coloured polygons indicate the eight main counting blocks. Blocks were established during the 1997 *Totorore* Expedition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

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

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

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

Camera drone imagery

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

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

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

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

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

For each island, an image composite was created from respective photos using the software Image Composite Editor (Microsoft Corporation, Redwood, Washington, USA). The software automatically aligned photos, performed lens correction, and stitched the images using a transverse Mercator projection. Stitched images are accessible online (https://bit.ly/bounty-island-2019-data, see Table 1 for corresponding DOIs).

Composite image analysis

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

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

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

Spatial distribution and density analysis

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

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

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

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

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

Average densities for each surveyed island were determined by calculating raster statistics. For that, raster cells with values of individual densities of zero were omitted from the calculation to focus the statistics on breeding areas. Resulting density maps for all islands are accessible online (https://bit.ly/bounty-island-2019-data).

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

Penguin presence on other islands

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

RESULTS

Ground counts

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

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

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

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

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

Drone image counts

On 28 October 2019, conditions for the drone survey were ideal with moderate to low winds and a slightly overcast sky creating flat light with little to no shadows. On the drone composite image of Proclamation Island (28 October 2019, Fig. 2), a total of 5,468 penguins were counted (Table 3). About two thirds of these (3,588 birds, 65%) were present in pairs, the remaining 1,880 birds were single birds. 30 penguins were counted at or close to the main landing platforms and, thus, defined as commuting. Counts from drone images taken of the other islands were complicated by the higher flight altitude reducing the level of detail in the composite images. Moreover, clear weather and sunshine on the 29 October 2019 resulted in higher contrast and an increased amount of shadow. Thus, it was sometimes difficult to distinguish between single penguins and pairs; penguins located in shadowy areas were difficult to discern. Penguin counts for Spider, Tunnel and Ranfurly Islands were lower than on Proclamation Island (Table 3); pairs were in a minority and made up 43–50% of all penguins on the three islands.

Penguin and seal densities

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

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

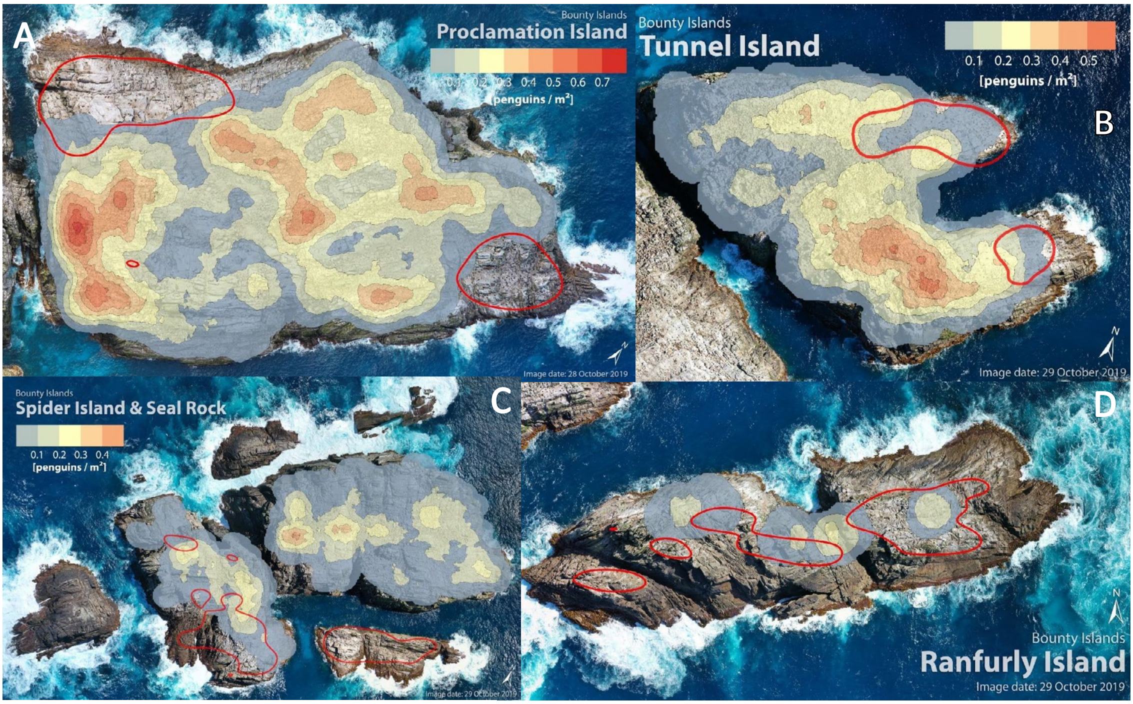

Figure 3. Point density (shaded polygons) of erect-crested penguins on four islands of the Bounty Island archipelago surveyed with camera drone on 28 & 29 October 2019. Red line features indicate 50% kernel density distribution of New Zealand fur seals.

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

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

Penguin presence on other islands of the group

Besides the four surveyed islands, erect-crested penguins were recorded on six other islands in the archipelago; on four of these they were recorded as 'abundant' (Depot, Penguin, Prion Islands, and North Rock). Few penguins were recorded on Ruatara and Funnel Islands. The ship-based survey recorded penguin presence on Seal Rock; however, no penguins were visible on the drone imagery of this rock. Erect-crested penguins were therefore present on 10 of 18 named islands of the Bounty archipelago.

DISCUSSION

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

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

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

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

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

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

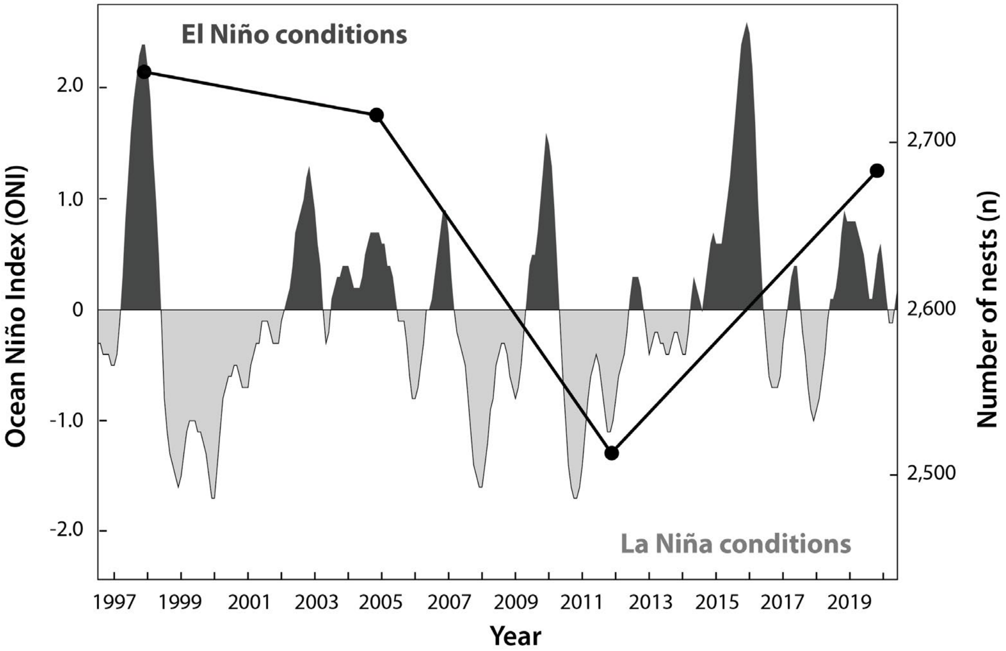

Figure 4. Ocean Niño Index (ONI*) over the time-period of the four comprehensive ground counts of erect-crested penguins on Proclamation Island (1997–2019). The ONI is a measure of the departure from normal sea surface temperatures in the east-central Pacific; positive values indicate El Niño conditions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

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

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

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

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

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

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

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

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

Shifting of nests between counting blocks?

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

Distribution and density of penguins and fur seals

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

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

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

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

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

Validity of the 1978 population estimates

Erect-crested penguins are ranked 'endangered'

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

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

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

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

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

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

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

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

While the reports of 'millions of penguins' (e.g. Anonymous 1890a) likely exaggerate the true numbers of penguins in the late 1800s, some historic photography (e.g. Ref: 1/2-056479-F. Alexander Turnbull Library, Wellington, New Zealand, https://natlib.govt.nz/records/23196041) seem to suggest a higher density of penguins on the Bounty Islands than what we observed during this survey. However, bear in mind that many of the historic photos were taken in February, i.e. during the moult when most of the erect-crested penguins would be confined to land (Wilson & Mattern 2019). At this stage, all breeding birds plus non-breeders are present on the island which more than doubles the numbers ashore compared to our survey which occurred when many breeders were at sea. Nevertheless, analysis of historic photos may allow it to determine if erect-crested penguins used to be more numerous on the Bounty Islands in the past. Photos taken by William Dougall in February 1888 (held by Te Papa, https://collections.tepapa.govt.nz/agent/6043) and Rollo Beck in February 1926 (held by the American Museum of Natural History) provide clearly identifiable vantage points on Depot and Proclamation Islands that allow reproduction of their photos and subsequent comparative bird counts. Both visited the islands during the late breeding/early moulting season so that penguin numbers visible are not comparable to census data presented here. Therefore, to adequately investigate historic trends using this method it would be necessary to reproduce historic photos in February/March.

CONCLUSIONS

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

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