New Zealand penguins – current knowledge and research priorities

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Introduction

The New Zealand region is a hot spot for seabirds and hosts six of the world's eighteen penguin species; of these, four are endemic species that occur only in New Zealand. Despite this regional species richness and New Zealand's reputation for international leadership in conservation, very little is actually known about our penguins; compared to most other non-NZ penguin species, most New Zealand penguin species are poorly researched (Figure 1).

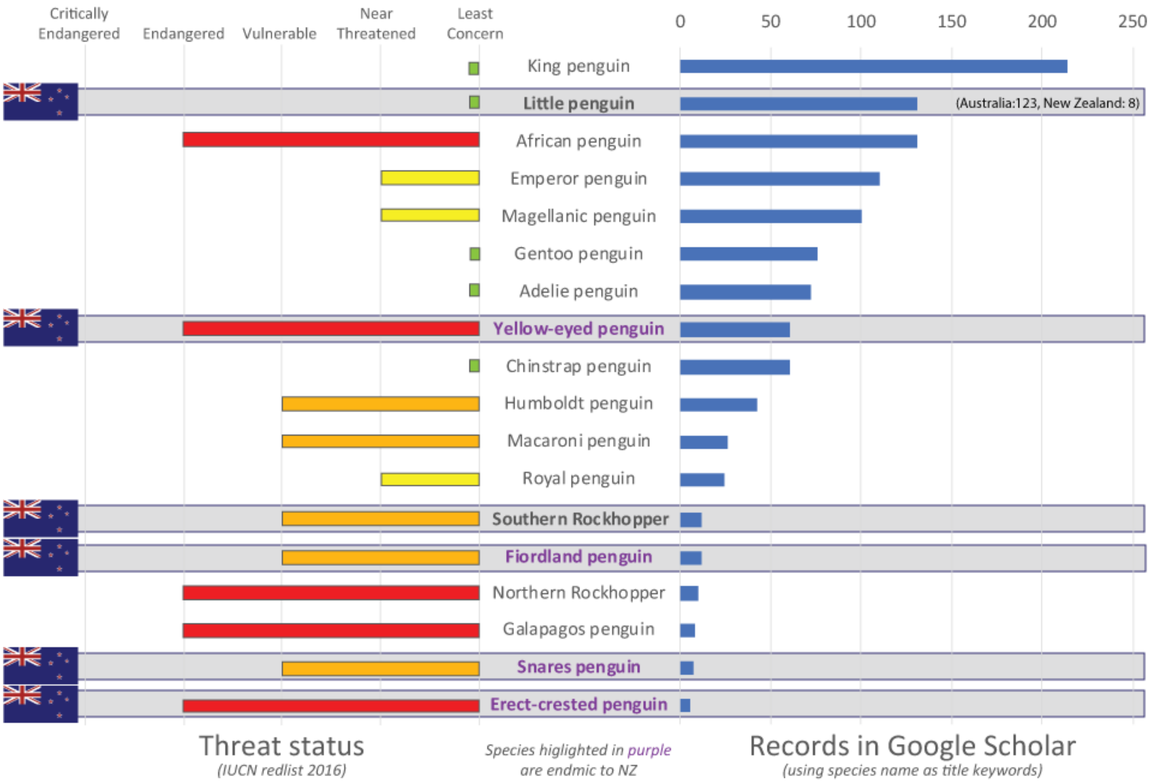

Figure 1. *Threat status and state of knowledge of the world's penguin species. New Zealand species rank highly (five out of six endangered or threatened) but are among the least researched. Note that the majority of research on Little penguins was conducted in Australia and it has recently been suggested that the Australian penguins are a different species to most little penguin populations in New Zealand. Similarly, almost all of the research conducted on yellow-eyed penguins occurred on the New Zealand mainland; there is very little knowledge about yellow-eyed penguin populations on the sub-Antarctic islands, which are generally considered the stronghold of the species.*

Five of our six penguin species are in decline. There is very little published literature for most New Zealand penguins, which means that the reasons for those population declines remain unknown. Consequently, current conservation actions principally revolve around occasional population counts and *ad hoc* research or conservation actions that may or may not address the real threats. With ever increasing pressure from anthropogenic factors, be it climate change, pollution, or fisheries interactions our penguins are in trouble. In order to prevent or reverse their population declines and to put in place evidence-based management, we first need to identify the actual rather than the perceived threats. For this research is essential.

In this report, we collate the information available on all six New Zealand penguin species. This includes published accounts (scientific papers, reports), grey literature (unpublished reports and data sets), and personal observations made by researchers that have worked with New Zealand penguins.

Based on our findings, we compile a list of research priorities that should aid closing many of the knowledge gaps that prevent effective evidence-based conservation management. In New Zealand, conservation management is too often of reactive rather than proactive. Hence, penguin populations often only become the focus of management when declines are well advanced.

Here, we follow the goals of the International Union for the Conservation of Nature which strives "to conserve the **integrity** and **diversity** of nature" (IUCN mission statement). In our opinion, this can only be achieved through a holistic approach where management actions are based on evidence-based strategies which necessitates at least a basic understanding of the species biology.

Penguins are considered ideal sentinels for the marine environment in that their population dynamics generally reflect the state of the ocean habitat they inhabit. However, this sentinel function can only be utilized if we have at least a basic understanding of their biology and population trends. With one third of the world's penguin populations living and breeding in New Zealand, utilizing this sentinel potential can be of international relevance in that it can highlight the effects of climate change on an important sector of the Southern Hemisphere. This report should be used in conjunction with Mattern & Wilson (2018) which lists conservation actions required for the immediate management of all six New Zealand Penguin species.

Research priorities identified here in are categorised into high, medium and low as indicated by prefixes H, M, and L, and are ordered by their level of priority.

References

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Yellow-eyed penguin / hoiho

(*Megadyptes antipodes*)

Thomas Mattern and Kerry-Jayne Wilson

Summary

The yellow-eyed penguin / hoiho (*Megadyptes antipodes*) is endemic to New Zealand. It occurs along the south-eastern coastline of the South Island, on Stewart Island and its outliers, as well as the sub-Antarctic Auckland and Campbell Islands. The species is now the world's second-rarest penguin species with an estimated 1,700 breeding pairs across its entire distributional range. The species is listed as 'endangered' by the IUCN red list and is considered 'nationally endangered' by the New Zealand Department of Conservation's threat ranking system.

The yellow-eyed penguin is one of the best-studied species in New Zealand with the first comprehensive population study conducted as early as the 1930s and a string of research projects that investigated various aspects of the species biology since the 1980s. Most of this research occurred on the New Zealand mainland, with very little information from the sub-Antarctic populations. A phylogenetic study found that there is very little gene flow between the mainland and sub-Antarctic populations, or between the two sub-Antarctic islands, so that the three subpopulations must be considered separate management units.

The species' mainland population has been undergoing a steady and significant decline since the mid-1990s, a trend that appears to continue; population projections predict local extinction on the mainland by 2060. While the sub-Antarctic islands are often considered to be the species' stronghold, because they were home to a large proportion of the population in the late 1980s and early 1990s, there is no recent data to show if this is still true. Climate change has been identified to be an important factor contributing to the yellow-eyed penguin decline on the mainland, and might have caused a shift in the penguins' prey from smaller fish (e.g. larval red cod, *Pseudophycis bachus*) consumed in the 1980s to large prey items (mainly juvenile and adult blue cod, *Parapercis colias*) since the 1990s. This may have consequences for reproductive success, with larger prey items unsuitable food for chicks, leading to starvation and facilitating disease outbreaks. However, climate change alone does not explain the population decline and it is suspected that fisheries interactions, pollution and human disturbance have all contributed to the species' dire status.

On the mainland, yellow-eyed penguins are predominantly benthic foragers that principally pursue demersal fish species. This makes them vulnerable to accidental bycatch in set nets with poor foraging on seafloor habitats degraded by bottom fishing activities such as

dredging and bottom trawls. Adult survival appears to be too low to sustain the population and may have led to an imbalance between the sexes with male penguins now outnumbering females. In recent decades, disease outbreaks have affected reproductive success, and several die-off events have reduced the breeding population further.

Previous reviews of Yellow-eyed penguin biology and priority lists

The first major review of the yellow-eyed penguins' breeding biology was compiled by Lance Richdale who studied the species between 1936 and 1954 (Richdale, 1949, 1951, 1957). A comprehensive review was later compiled by John Darby (Marchant & Higgins, 1990a).

Research and conservation priorities were listed by Taylor (2000). He proposed that habitat protection and restoration, and introduced predator control should be of highest priority, followed by advocacy to mitigate fisheries impacts, better control of dogs, and establishment of guidelines to manage visitor access to mainland colonies. These recommendations were developed further in the yellow-eyed penguin recovery plan (McKinlay, 2001). While habitat protection, restoration, and pest control efforts have improved since then (Webster, 2018), fisheries impacts have not been adequately addressed (Ellenberg & Mattern, 2012; Crawford et al., 2017). Likewise, predation by uncontrolled dogs (Melanie Young, pers. comm.), and unregulated visitor access at some mainland sites remain issues.

Taylor (2000) also recommended surveys be undertaken, with continued annual monitoring on the Otago Peninsula being a high priority as well as population counts on Stewart Island and the sub-Antarctic islands. While monitoring on the Otago Peninsula has continued (Mattern et al., 2017b) and a survey of Stewart Island was conducted in 1999/2000 (Massaro & Blair, 2003), there is no reliable recent information on population size for either of the sub-Antarctic populations (Seddon, Ellenberg & van Heezik, 2013). Some of the research priorities listed by Taylor (2000) have been addressed in the last two decades. These include phylogenetic studies across the species' distribution (Triggs & Darby, 1989; Boessenkool et al., 2009a,b; Rawlence et al., 2015), analysis of long-term survey data to estimate population sizes and trends (Moore, 2001; Darby, 2003; Mattern et al., 2017b), and tourism impacts (McClung et al., 2004; Ellenberg et al., 2007; Ellenberg, Mattern & Seddon, 2009, 2013). Some other recommendations currently being addressed, are factors affecting recruitment rates (Melanie Young, University of Otago) and some aspects of the species' biology on the Auckland Islands (Chris Muller, Massey University). Overall, priorities need to be revised in the light of the species' continued decline on the New Zealand mainland.

In 2012, a comprehensive review of yellow-eyed penguin biology and population trends on the mainland emphasised the importance of fisheries' impacts (Ellenberg & Mattern, 2012). This was followed up by a species review by Seddon *et al*. (2013). Most recently, a substantial literature review was published by the Yellow-eyed Penguin Trust which took a more system approach to management suggesting the management of factors extrinsic to the species

(Webster, 2018). All of the reviews include priority lists for research and conservation actions that reflect or expand on Taylor (2000).

Taxonomy

The yellow-eyed penguin is the single remaining representative of the genus *Megadyptes*. Genetic analysis using ancient DNA revealed that the New Zealand mainland was originally inhabited by a sister-taxon, the Waitaha penguin; *Megadyptes waitaha* (Boessenkool et al., 2009a), which is believed to have been hunted to extinction within a few hundred years of Maori settlement in New Zealand (Boessenkool et al., 2009a). The loss of *M. waitaha* allowed the yellow-eyed penguin to expand its range from the sub-Antarctic Islands from the 15th century onwards (Rawlence et al., 2015).

Despite this historic colonization of yellow-eyed penguins from the sub-Antarctic, there is apparently very little contemporary gene flow between the three main breeding locations of the species; the mainland, Auckland Islands and Campbell Island (Triggs & Darby, 1989; Boessenkool et al., 2009b). Both Triggs & Darby (1989) and Boessenkool *et al*. (2009b) recommended each of the three subpopulations be considered separate management units for conservation.

Conservation status

The Department of Conservation lists the Yellow-eyed penguin as ‘nationally endangered’ criteria C(1/1) (1000-5000 mature individuals, predicted decline 50-70%), qualifier EF (Extreme Fluctuations) (Robertson et al., 2017). The IUCN red list classifies the species as ‘endangered’ with selection criteria B2ab(ii,v)c(iv) (area of occupancy <5000 km², fragmented distribution, ongoing population decline and extreme fluctuations in the number of mature individuals (BirdLife International, 2016).

The Yellow-eyed penguin is the only penguin species in New Zealand with a dedicated recovery plan (McKinlay, 2001). A severe die-off in 1989 triggered years of intensive monitoring and research to understand that mechanisms that are contributing to the species’ apparent population decline (e.g. Efford, *et al* 1994, 1996; Moore *et al*., 1995; McKinlay, 1997; Edge, J*et al* , 1999). The recovery plan aimed to “manage the hoiho population by providing a framework for community and DOC initiatives to actively enhance hoiho numbers”. Nine objectives for the recovery of the species were outlined, seven of which focussed on terrestrial aspects of the species management, i.e. monitoring, protection and improvement of breeding habitat, predator control, management of tourism activities, and advocacy. The two other objectives were concerned with identifying the impact fisheries had on survival rates, and research that would assist the other objectives (McKinlay, 2001).

New research into the marine ecology of the species in the 2000s suggested that the species was facing serious threats at sea (Mattern et al., 2007, 2013; Mattern, Ellenberg & Davis, 2007; Browne et al., 2011). Examination of genetic diversity highlighted the need to consider the mainland and the sub-Antarctic populations as three separate management units (Boessenkool et al., 2009b).

To re-assess the objectives outlined in the recovery plan, a comprehensive stock take was conducted in 2015 (Couch-Lewis et al., 2016). This found that the “current [recovery] plan is no longer fit-for-purpose for the future, although many of the objectives and actions are still relevant”. That report lists a number of recommendations suggesting which directions a revised recovery plan should take but does not provide clear objectives. Therefore, for the time being, the original recovery plan remains the primary guideline for the recovery of the species. The recent review of the species’ management by Webster (2018) should provide additional guidance.

Distribution

Yellow-eyed penguins have probably only bred on the South Island for the last several hundred years. Ancient DNA analysis and radiocarbon dating show they expanded their range from sub-Antarctic New Zealand following extirpation of its sister taxa, *Megadyptes waitaha*. Bones of *M. waitaha* are relatively common in coastal dune deposits and archaeological midden sites (Worthy, 1997, 1998, 1999; Worthy & Holdaway, 2002; Boessenkool et al., 2009a; Cole et al., 2019). The rapid extinction of *M.* waitaha (Rawlence et al., 2015) is indicative of the vulnerability of these penguins; a salutary lesson for today’s penguin conservation workers. .

On the New Zealand mainland, the core breeding range of Yellow-eyed penguins is the Otago and Southland coastlines from Bushy Beach, Oamaru (-45.118°, 170.972°) south to Slope Point, Catlins (-46.670°,169.003°). There are a few breeding pairs on Banks Peninsula, but they exhibit poor breeding success and recruitment into the Banks Peninsula population comes from further south (Seddon, Ellenberg & van Heezik, 2013). Yellow-eyed penguins also breed on Stewart Island / Rakiura (-46.856°, 167.913°) and some of its satellite islands including Codfish Island / Whenua Hou (-46.772°, 167.624°) (Darby, 2003; Massaro & Blair, 2003).

One of the sub-Antarctic yellow-eyed penguin populations is on the Auckland Islands (-50.745°, 166.054°), some 500 km south of the New Zealand mainland. The majority of penguins apparently breed on Enderby Island at the northern end of the archipelago (-50.497°, 166.302°) (Moore, 1992a). Whether the species breeds at other places around the archipelago in significant numbers is unclear; a survey of the eastern coastline of the main island, as well as Carnley Harbour and Adams Island identified 306 potential Yellow-eyed penguin landing sites but could not assess penguin numbers (Beer, 2010). Based on the survey it appears as if Yellow-eyed penguins are clustered in the north (Enderby, Ewing and Frenchs Islands) and south (north-coast of Adams Island) of the Auckland archipelago.

The second sub-Antarctic population of yellow-eyed penguins is on Campbell Island (-52.539°, 169.148°) (Moore & Moffat, 1990; Moore, 1992a). The penguins predominately inhabit inlets and sheltered bays, including Northeast and Perseverance Harbours to the east and Southeast and Monument Harbours in the south. The largest concentration of birds occur in Northwest Bay on the western promontory of Campbell Island (Moore, 1992a,b).

Juvenile and non-breeding adults may range far beyond the breeding distribution. Fledglings satellite tracked in 2017 and 2018 ranged as far north as Kaikoura with one bird even making landfall in Clifford Bay at the northern tip of the South Island. Juvenile and non-breeding or moulting adult penguins have been seen as far north as Taranaki and Hawke's Bay (Department of Conservation, 2015).

Numbers and population trends

The current red list estimate of the yellow-eyed penguins' total population size of 1,700 breeding pairs (BirdLife International, 2016) is effectively pure speculation. The majority of these are believed to live on the two sub-Antarctic islands, with an estimated maximum of 600 pairs on Campbell Island and 570 pairs on the Auckland Islands (Moore, 1992a). However, population estimates for both islands date back to the late 1980s and early 1990s, a time when numbers of Yellow-eyed penguins on the mainland were considerably higher than now (Table 1). In 1996, a total of 635 nests were counted on the New Zealand mainland (excluding Stewart Island and its outliers); just 252 nests were found in 2017 (Department of Conservation, unpublished data). On the Otago Peninsula, the yellow-eyed penguin population has declined by as much as 75% in the past two decades (Mattern et al., 2017b).

***Table 1**. Population estimates of yellow-eyed penguins in New Zealand.*

Year of count	**Location**	**Number of breeding pairs**	**Reference**
1988-1989	South Island	300-320	Moore (1992a)
1996	South Island	635	DOC, unpublished data*
2011-2012	South Island	454	Seddon *et al*. (2013)
2017	South Island	252	DOC, unpublished data**
1988-1989	Stewart Island	470-600	Moore 1992a
1989-1990	Stewart Island	300-400	Marchant & Higgins (1990)
1934-1994	Stewart & Codfish Island	220-392	Darby (2003)
1999-2001	Stewart & Codfish Island	178	Massaro & Blair (2001)

2008-2009	Stewart & Codfish Island	153	Seddon *et al*. (2013)
1988-1989	Auckland Island	520-570	Moore (1992a)
1988-1989	Campbell Island	490-600	Moore (1992a)

* Extracted from 2015 version of the Yellow-eyed penguin database

** From the count spreadsheet maintained by Department of Conservation, Dave Houston, pers. comm.)

Current population trajectories on the New Zealand mainland point towards local extinction in the next two to four decades (Mattern et al., 2017b). While these predictions are based on monitoring data collected at Boulder Beach on the Otago Peninsula, subsequent data analysis found these trends to be hold across the mainland except for two intensively managed penguin populations, Katiki Point (-45.395°, 170.868°) and Barracouta Bay (-45.392°, 170.858°) (Houseman, 2018). Penguin numbers have declined on Stewart Island (King, 2008) and Codfish Island (Yellow-eyed penguin Trust, unpublished data).

There is evidence for population variation in the sub-Antarctic – at Campbell Island the population decreased by 41% between 1988 and 1992, with at least a partial recovery over the next six years (Moore, Fletcher & Amey, 2001). These data were based on whole island beach counts and mark-recapture analysis at study sites. Due to the lack of robust survey data since then, it is not possible to make any definitive inferences about population trends in the past 20 years. Beach counts conducted between 2001 and 2012 on Enderby Island, Auckland Islands, have suggested an increase in penguin numbers (Chilvers, 2014). However, the counts were conducted on a single day each year and then towards the end of the breeding season (i.e. February) when the nest attendance patterns and hence penguin movements are highly variable (Darby & Seddon, 1990). As a result, the beach count methodology employed does not provide a robust population trend assessment, particularly at that time of the year.

Boessenkool *et al.* (2010) used historic museum skins and contemporary blood samples to determine the effective population sizes of yellow-eyed penguins of the separate Management Units. They found very low effective population sizes (in the low hundreds), coupled with low immigration rates, supporting concern for the species, especially for the mainland population. Lopes & Boessenkool (2010) also applied a Bayesian coalescent approach using microsatellites and gene sequences derived from each management unit, suggesting that populations on sub-Antarctic islands have remained stable over the past 500 years. Genomic markers (such as whole genomes or Single Nucleotide Polymorphisms) from each management unit may also provide useful projections of past, present and future population sizes that cannot be detected from microsatellite loci alone and could contribute to understanding population trends.

The mainland population has been subject to several adult die-off events in the past three decades. The first major die-off event occurred in 1989 when penguin numbers on the Otago Peninsula declined by 62% (Gill & Darby, 1993) followed by a further die-off in 2001 (Mattern et al., 2017b). Another significant event occurred in February 2013, which resulted in a 41% drop in penguin numbers on the Otago Peninsula. To date, the cause of these die-offs remains unclear although the involvement of a toxic agent has been confirmed (Gartrell et al., 2016). Harmful algal blooms have been suggested as a potential toxin origin (e.g. Webster, 2018) yet plankton samples taken during the 2013 die-off found no trace of toxic algae in the marine environment (Mattern & Seddon, unpublished data).

Demography

Almost all yellow-eyed penguins breeding on Otago Peninsula have been banded and monitored for nearly 35 years, so there is a robust understanding of the species' main demographic parameters (Mattern et al., 2017b). Based on a Bayesian mark-recapture model, the median annual survival rate of adult yellow-eyed penguins on the New Zealand mainland is 87.4% (credible interval: 83.2%-90.4%). Since the mid-1990s, adult survival has been lower than the long-term average (determined from data dating back to the early 1980s). The low survival rates are to some extent associated with ocean warming (Mattern et al., 2017b). Since the mid-1990s, the mean age of first-time breeders has declined suggesting that the pool of birds available for recruitment into the breeding population has diminished in the past 20 years (Mattern et al., 2017b). It also appears as if the mainland population may have a gender imbalance, with male penguins outnumbering females (Melanie Young, pers. comm.)

Modelling showed the first-year survival rate of chicks to be very low, ranging between 7% and 19% (median: 12.4%) (Mattern et al., 2017b). Another study put the first year survival rate slightly higher at 17.2%, and found that only 10.2% of fledged chicks became successful breeders (Stein et al., 2017a).

There is no equivalent demography data available for the sub-Antarctic yellow-eyed penguin populations.

Breeding biology

Breeding biology is by far the best-studied aspect of yellow-eyed penguin biology. Lancelot Richdale provided first comprehensive insights into the species' breeding ecology (Richdale, 1949, 1951, 1957). Studies in the past 30 years have tackled various aspects of breeding behaviour, including nest site selection (Seddon & Davis, 1989; Darby & Seddon, 1990; Clark, Mathieu & Seddon, 2015), hormonal characteristics of breeding behaviour (Cockrem & Seddon, 1994; Setiawan et al., 2006), egg shell composition and incubation behaviour

(Moore, 1992b; Massaro et al., 2002; Massaro & Davis, 2004), mate choice and parental investment (Edge, Jamieson & Darby, 1999; Setiawan et al., 2005), and chick rearing strategies and feeding intervals (Seddon, 1989, 1990, 1991; Schuster & Darby, 2000).

A very comprehensive summary of the breeding biology has been published by Seddon, *et al*. (2013).

Yellow-eyed penguins breed in highly variable habitats that all share one characteristic: nests are visually isolated from other penguins (Seddon & Davis, 1989; Clark, Mathieu & Seddon, 2015). The species prefers to breed in dense vegetation such as *Hebe* groves, patches of New Zealand flax (*Phormium tena*x & *P. colensoi*) or mature coastal forests. On Campbell Island the majority of nests were under a canopy of *Dracophyllum*, *Myrsine* or *Coprosma* (Moore, 1992b). An important determinant for the presence of yellow-eyed penguin colonies is suitable landing sites, which can be sandy or pebble beaches or rocky platforms (Darby & Seddon, 1990). Nests are usually established in shallow excavations lined with twigs, grass and leaves under scrub, at the base of flax plants or under tree roots and windfalls (Seddon, Ellenberg & van Heezik, 2013).

Yellow-eyed penguins display high nest site fidelity in that adults tend to remain within a single breeding area (Darby & Seddon, 1990), usually establishing nets within 2-3 metres of previous nest sites; birds will defend territories of up to 10 m around their nest-sites (John Darby, pers. comm.). About three quarters of pairs remain together, but mate retention rates decline with the number of breeding seasons pairs stay together (Richdale, 1957). Death of one of the birds is the main cause of pair break-ups. Annual divorce rates not driven by mortality can range between 6-13% (Richdale, 1957; Setiawan et al., 2005).

Females enter the breeding population on average when 2.6 years old, while males start breeding at an average age of about 4.3 years (Richdale, 1957). Since the late 1990s, the age of first breeding has declined so that today a greater proportion of young birds make up the mainland breeding population (Mattern et al., 2017b).

On the Otago Peninsula, the mean egg laying date is 24 September (van Heezik, 1988). Further south egg laying can start later (Seddon, Ellenberg & van Heezik, 2013). On Campbell Island yellow-eyed penguins commenced breeding on average 9 days later than the mainland population (Moore, 1992b).

The two eggs of most clutches are laid 3-5 days apart, although young females may only lay one egg (Richdale, 1957; Darby & Seddon, 1990). Incubation starts after laying of the second egg; both parents share the incubation with incubation spells of around two days for both sexes (Seddon, 1989). Eggs are incubated for 39-51 days, which is the most variable incubation period among penguins (Richdale, 1957).

Hatching occurs synchronously in the first half of November (Richdale, 1957; Darby, 1989). 94% of two-egg clutches the eggs hatched within one day of each other (Darby & Seddon, 1990). The chick-rearing period has two phases: the chick-guard stage, during which the nest is constantly attended by one of the parents and lasts between 40 to 50 days, the post-guard stage during which chicks are left alone during the day while both parents forage to meet the increasing food demands of their offspring (Darby & Seddon, 1990; Seddon & Darby, 1990; Schuster & Darby, 2000). Chicks fledge about 106 days after hatching (Seddon, Ellenberg & van Heezik, 2013).

Moult

Moult takes place from late February to late March although it has extended into April in recent years (Seddon, Ellenberg & van Heezik, 2013). Shedding of old feathers and full growth of the new plumage takes about 24 days. Juveniles and non-breeding birds tend to moult earlier than breeding adults. Breeding penguins usually moult at or near their nest sites, while non-breeders and juveniles may moult as far north as Canterbury, Kaikoura and Cape Campbell.

Food and foraging

The marine ecology of Yellow-eyed penguins was first investigated in the 1980s and early 1990s (Seddon & van Heezik, 1990; van Heezik, 1990a,b; van Heezik & Davis, 1990; Moore & Wakelin, 1997; Moore, 1999), although these studies focussed principally on diet composition and foraging ranges. More sophisticated data logging technologies in the 2000s allowed reconstruction of at sea-movements in three-dimensions and highlighted the species affinity for benthic foraging (Mattern et al., 2007, 2013; Ellenberg & Mattern, 2012; Chilvers, Dobbins & Edmonds, 2014; Mattern & Ellenberg, 2018a). At the time this report was written, further studies of the pre-moult and winter movements of adult and fledgling penguins were being conducted (Melanie Young, unpubl. data). As with other aspects of the species' biology, most marine ecology studies have been conducted on the mainland, apart from a recent study of foraging behaviour at the Auckland Islands (Chris Muller, unpubl. data).

During the breeding season, mainland yellow-eyed penguins principally forage within 25 km from the coast (Moore, 1999; Mattern et al., 2007, 2013). While there is no marked difference in foraging ranges between incubation and chick rearing, the birds tend to stay at sea longer (14-65 hours, Moore, 1999) during incubation. During the chick rearing period, trip durations range from short evening trips (4 hours, Mattern *et al*., 2007) to full day-trips of 11 to 14 hours (Moore, 1999; Mattern et al., 2007, 2013). Outside the breeding period, penguins range further from their colony (Melanie Young, unpublished data) although their movements are still confined to the continental shelf where water depths do not exceed 160m. The deepest dive recorded so far is 161m, performed by a Yellow-eyed penguin from Campbell Island (Peter Moore, unpubl. data)

Of 46,948 dives recorded between 2003 and 2015 using GPS dive loggers on 71 yellow-eyed penguins from Oamaru, the Otago Peninsula, and Stewart and Codfish Islands during a total of 185 foraging trips, 54% were benthic dives (Mattern, unpubl. data). The majority of non-benthic dives occur during the home ward journey (Mattern et al., 2007). More recently the deployment of camera loggers on mainland yellow-eyed penguins revealed that pelagic foraging principally occurs if the environmental conditions are not conducive to bottom foraging (Mattern et al., 2017a). During periods with increased algal blooms water clarity is reduced so that visibility at the seafloor is close to zero, forcing the penguins to search for prey in the upper regions of the water column. Under such circumstances, the penguins primarily ate larval and juvenile fish that seek protection from larger jellyfish. As soon as water clarity improved birds resumed benthic foraging (Mattern et al., 2017a). The hypothesis that Yellow-eyed penguins may actually consume jellyfish (Thiebot et al., 2017) seems unlikely in the light of recent findings.

When benthic foraging, Yellow-eyed penguins predominantly prey on demersal fish species. The first comprehensive study of the diet of mainland yellow-eyed penguin in the 1980s identified the main prey species to be red cod (*Pseudyphycis bacchus*), opalfish (*Hemerocoetes monopterygius*) and, to a lesser extent, sprat (Sprattus antipodum), ahuru (*Auchenoceros punctatus*) and arrow squid (*Nototodarus sloani*) (van Heezik, 1990a; van Heezik & Davis, 1990). A change in the diet composition became apparent when red cod was replaced by blue cod and opalfish, with sprat and arrow squid again playing minor roles in terms of biomass brought ashore (Moore & Wakelin, 1997). Recent deployments of camera loggers found that at the Otago Peninsula, opal fish and blue cod are now the single most dominant species; larval fish and sprat were only targeted during the period of environmentally forced pelagic foraging (Mattern et al., 2017a, 2018b; Mattern & Ellenberg, 2018a).

There are regional differences in diet composition that may be related to the prevailing sediment structure of the seafloor within then Yellow-eyed penguins' home ranges (Mattern & Ellenberg, 2018a). Penguins with access to coarse substrate such as gravel and coarse sand predominantly feed on opalfish, while in regions with well-defined benthic structures such as horse mussel fields, bryozoans, oyster beds or reefs the penguins principally ate blue cod (*Parapercis colias*) and red-banded perch (*Hypoplectrodes huntii*) (Mattern & Ellenberg, 2018a; Seed et al., 2018). The same seems to be true for regions that are exposed to seafloor fisheries. The disturbance caused by bottom trawls appears to attract scavenging species such as blue cod, which makes foraging in the wake of bottom trawls attractive to yellow-eyed penguins (Mattern et al., 2013). Regional differences in diet may occur on very small spatial scales. Camera logger deployments on penguins from two breeding areas along Stewart Island's north-east coast (Rollers Beach -46.768°, 167.988°; Golden Beach -46.802°, 168.020°) found significant differences in prey composition even though these sites are only 5 km apart (Seed et al., 2018). Penguins from Golden Beach fed predominantly on red-banded perch and juvenile tarakihi (*Nemadactylus macropterus*) while birds from Rollers Beach principally consumed blue cod.

While the calorific value of blue cod makes it a suitable prey item for adult yellow-eyed penguins, their large body size renders it a suboptimal food for chicks (Mattern & Ellenberg, 2018a). The commercial oyster fishery in Foveaux Strait may have contributed to a change in benthic biodiversity benefitting blue cod and causing penguin prey to switch with a concomitant decline in breeding success (Browne et al., 2011).

Very little is known about diet composition and foraging ecology of yellow-eyed penguins on the sub-Antarctic islands. Underwater footage filmed at the Auckland Islands in 2016 shows five or six yellow-eyed penguins feeding on a dense school of bait fish (Mattern & Ellenberg, 2018a) suggesting that pelagic foraging could be more common there. GPS dive logger deployments of penguins on Enderby Island suggest that the birds forage within a 40-50 km radius east of the island; diving behaviour seems to consist of a mix of pelagic and benthic foraging (Chris Muller, unpubl. data). Dive recorder data from Campbell Island suggest a benthic foraging strategy (Peter Moore, unpubl. data).

Threats

The breeding distribution of yellow-eyed penguins means that the majority of the mainland population occurs in areas close to urban centres or locations readily accessible to humans (Seddon, Ellenberg & van Heezik, 2013). This exposes the penguins to a variety of anthropogenic threats.

Predators

Introduced terrestrial predators - major

On the mainland, Yellow-eyed penguins are exposed to an array of introduced terrestrial predators. Stoats (*Mustela erminea*) in particular prey on penguin eggs and chicks (Ratz & Murphy, 1999; pers. obs.). Ferrets (*M. furo*) and cats (*Felis catus*) are also thought to be yellow-eyed penguin predators (e.g. Darby & Seddon, 1990; Clapperton, 2001; Seddon, Ellenberg & van Heezik, 2013), although data on their true impact are lacking. Ratz & Murphy (1999) found that in comparison with stoats, the impact of cats and ferrets are minor. John Darby (pers. comm.) notes that trapping in the Boulder Beach complex in the 1980s resulted in 14 cats, 12 ferrets and two stoats being caught over a two-month period. Thereafter, stoats dominated the trap catch which could suggest that trapping may have changed the local predator guild benefitting stoats perhaps increasing predation on the penguins. A five-year study on Stewart Island investigating the impact of feral cats on the local yellow-eyed penguin populations found no conclusive evidence for any significant impact; instead starvation and disease were the dominant mortality factors (King et al., 2012). . Dogs (*Canis familiaris*) can kill adult penguins (Hocken 2005) and unrestrained dogs pose a significant threat to yellow-eyed penguins5). On the main Auckland Island, feral pigs (*Sus scrofa*) are believed to kill both adults and chicks (Taylor, 2000) perhaps explaining why few, if any yellow-eyed penguins still breed on the main island. A pig shot on Auckland Island contained the remains of a yellow-eyed penguin (Challies, 1975). However, whether this was the result of active predation or scavenging of a dead penguin is unclear.

Natural predators – medium (mainland)

Natural predators include sea lions (*Phocarctos hookeri*), sharks and, to a lesser, extent fur seals (*Arctocephalus forsteri*) (Hocken, 2005).Instances of sea lion predation have been recorded on Campbell Island (Moore & Moffat, 1990; Moore, Fletcher & Amey, 2001). Barracouta (*Thyrsites atun*) do occasionally inflict injuries to yellow-eyed penguins (Webster, 2018). However, claims that barracouta are 'main predators' (White, 2017) exaggerate their impact. Camera logger observations of yellow-eyed penguins encountering schools of barracouta showed that the birds did not react to their presence (Seed et al., 2018).

Fisheries interactions

Resource competition - major

With the exception of blue cod and red cod, Yellow-eyed penguins principally prey on non-commercial fish species (Mattern & Ellenberg, 2018a). However, benthic habitats are subject to various bottom fisheries that in some areas have substantially altered the seafloor communities (Ellenberg & Mattern, 2012). This has the potential to reduce prey diversity and abundance, alter feeding strategies, and consequently affect penguin breeding success and population trajectories. Moreover, fisheries-related changes to the marine food web may have contributed to a deterioration of the quality of the penguins' diet.

Incidental bycatch - major

Yellow-eyed penguins are severely affected by set netting operations (Crawford et al., 2017). Their demersal foraging strategy makes them particularly prone to entanglement in set nets targeting rig and dogfish. The low-level of observer coverage for set net fishing vessels (Ramm, 2012; Richard & Abraham, 2015) and likely under-reporting from other vessels, means that it is impossible to adequately assess the true level of bycatch mortality of Otago and Southland penguins. In the 1990s, multiple captures of penguins in single nets were reported (Darby & Dawson, 2000). There is a four-nautical mile set net ban around the South Island's south-eastern coast line; however, Stewart Island and its outliers are exempt from this ban, so that nets may be set very close inshore and therefore across the main entry routes to penguin colonies. Conversely, a set net ban may result in set netting to occur further off shore where most yellow-eyed penguins forage.

Some yellow-eyed penguins have been caught in trawl nets (Webster, 2018) although trawl bycatch appears to be less likely than set-net bycatch.

Die-off events

Adult die-offs - major

The periodic die-off events over the past three decades have decimated the breeding population on the Otago Peninsula (Mattern et al., 2017b). Although dead yellow-eyed penguins with similar symptoms have been reported from other regions (Webster, 2018), it appears that the main impact has been around the Otago Peninsula. Harmful algal blooms seem an unlikely explanation as such phenomena usually also impact other species (Shumway, Allen & Boersma, 2003). Hence, climate-related or anthropogenic factors seem to be more likely to be the root cause of this problem. Possible causes could be accidental ingestion of toxic jellyfish (e.g. lion's mane *Cyanea capillata*) during periods of algal bloom or the introduction of toxic agents from rivers or sewage outfalls (Mattern et al., 2017b).

Disease

Diphtheritic stomatitis - major

Disease outbreaks in mainland yellow-eyed penguins have been reported since 2004 when chicks developed lesions in their oral cavity, which hampered food intake causing starvation, breathing difficulties, and occasional asphyxiation when lesions were inhaled. The disease has since been described as diphtheritic stomatitis and has occurred to varying extents since 2004 (Alley et al., 2017). The disease seems to be associated with the presence of *Corynabacterium amycolatum* but a primary viral pathogen is suspected. The means of transmission have not been established (Alley et al., 2017) although environmental stressors reducing the chicks' immune response (e.g. starvation) could also be responsible (Seddon, Ellenberg & van Heezik, 2013).

Avian malaria – potentially major

Plasmodium is commonly associated with the occurrence of avian malaria (Graczyk et al., 1995; Vanstreels, Braga & Catão-Dias, 2016; Grilo et al., 2016) but until recently was not thought to kill yellow-eyed penguins (Sturrock & Tompkins, 2007). The first cases of adult mortality due to avian malaria were reported from the Otago Peninsula during the 2017/18 breeding season, probably facilitated by an unusually high abundance of mosquitoes due to flood-related surface water and warm summer temperatures (Trudi Webster, pers. comm.).

Leucocytozoon – minor

Leucocytozoon have been reported from Yellow-eyed penguins throughout their entire range (Hill et al., 2010; Argilla et al., 2013) although it seldom is pathogenic (Vanstreels, Braga & Catão-Dias, 2016).

Climate change

Ocean warming - major

Recent population modelling has identified ocean warming to be a major driver of the current yellow-eyed penguin population decline (Mattern et al., 2017b). In periods with higher than normal sea surface temperature (SST), adult survival rates are below average. Higher adult mortality resulting in new pairings with less experienced birds could explain why in seasons following warm years fewer fledglings are produced (Peacock, Paulin & Darby, 2000). One third of variation in penguin numbers can be explained by ocean warming, which suggests other important, non-climatic factors are also involved.

Weather extremes (La Niña) – major

The El Niño weather phenomenon usually coincides with lower than normal sea surface temperatures, which enhance yellow-eyed penguin survival rates due to favourable foraging conditions (Mattern et al., 2017b). The opposite effect occurs during a La Niña events, which bring higher than normal SSTs and reduction in adult survival. Starvation events and avian malaria mortality have also been associated with La Niña conditions (Sturrock & Tompkins, 2007; Webster, 2018).

Human impacts

Disturbance - major

The impact of human disturbance, principally through unregulated tourism and other visitors in or close to penguin breeding areas, has been well documented (McClung et al., 2004; Ellenberg et al., 2006, 2007, Ellenberg, Mattern & Seddon, 2009, 2013; French et al., 2018). Yellow-eyed penguins are timid and easily disturbed by people even when the people are 100 m away (Ellenberg, Mattern & Seddon, 2013). People on a beach can prevent yellow-eyed penguins transiting between the ocean and their nest site (McClung et al., 2004; French et al., 2018). Camera phones and selfie-sticks have increased the likelihood that visitors will get too close to birds or their nests (Shawn McAvinue, 2017). Research and monitoring activities also contribute to elevated stress levels in penguins although their impact is generally mitigated if approved research protocols are followed (Ellenberg, Mattern & Seddon, 2009). A study investigating the impact of research activities on individual fitness and life-time reproductive success found no indication of long-term adverse effects by researchers (Stein et al., 2017b).

Pollution – potentially major

Marine pollution and its effect on penguins is extremely difficult to quantify with few attempts made to monitor this. Marine systems are dynamic so that continuous monitoring would be required to detect rapid changes in pollution levels. It has been suggested that yellow-eyed penguin die-off events may be related to temporally and spatially limited pollution events (Mattern et al., 2017b). However, the lack of data makes it impossible to verify such claims. The conversion from sheep to dairy farming has greatly increased pollution in many New Zealand's rivers (Davies-Colley, 2013), which will undoubtedly have flow-on effects for the coastal marine ecosystems yellow-eyed penguins rely upon.

Research Priorities

In the face of significant population declines, robust documentation of population trends and demographic variables are vital. Despite being the best studied of the New Zealand penguin species, there is still a substantial knowledge gap when it comes to the yellow-eyed penguins' marine ecology, especially how their foraging and subsequently breeding success is affected by changes in their marine environment. With the mainland population levels at their lowest and climate warming predicted for the coming decades, disease outbreaks may become an ever increasing but potentially manageable problem.

1. Population monitoring

R.1.H1 **Comprehensive surveys of sub-Antarctic populations.**
The assumption that the sub-Antarctic populations provide an insurance should the species disappear from the mainland is largely based on 30 year old information It is of utmost importance to investigate population size and trends on both sub-Antarctic island groups.

Investigate reliable automatic monitoring methods and repeat Moore's mark-recapture methods employed on Campbell & Auckland Islands in the 1980s and 1990s (Moore, Fletcher & Amey, 2001)*.*

R.1.H2 **Continue monitoring on the mainland.**
Maintaining the monitoring effort at sites with a long monitoring history (e.g. Boulder Beach) is essential. It is vital to identify as many of the breeding individuals each year to derive demographic parameters such as survival and recruitment rates, see Mattern *et al*. (2017c).

R.1.H3 **Investigate the viability of automated ID gateways**
Automatic monitoring solutions have proven to be reliable in determining demographic parameters and population trends in other penguin species (e.g. Gendner *et al*., 2005; Descamps *et al*., 2009). Transponder gates not only allow effective identification of breeding populations but also provide additional information about nest attendance patterns and foraging trip lengths. These are particularly in regions such as the Catlins and Stewart Island where there is limited monitoring effort. Automatic solutions could provide critical information about

population parameters that are currently principally extrapolated from monitored sites in Otago (Mattern et al., 2017b).

Trial the viability and reliability of transponder gates at suitable site, e.g. Penguin Bay and Hinahina Cove, Catlins.

R.1.H4 **Investigate the effects of diseases on key demographic parameters, especially adult survival and recruitment**.
While disease management is an important conservation tool that will likely increase in importance with a warming climate (Vanstreels, Braga & Catão-Dias, 2016; Grilo et al., 2016; Webster, 2018), the true impacts disease may have on yellow-eyed penguin populations remains unclear. Diphtheritic stomatitis is receiving management attention although it principally affects young chicks (Alley et al., 2017) while adult survival and recruitment are the two key demographic parameters that determine population trends (Mattern et al., 2017b). Consequently, the few adult deaths from avian malaria are probably of greater concern for the conservation of yellow-eyed penguins.

R.1.M5 **Investigate true impacts of predators**
While the impact of cats, ferrets and barracouta are often cited as significant, factual evidence for these claims is missing or seems to indicate the opposite is true (e.g. King, 2008). It is therefore vital to investigate the importance of the various species believed to prey on yellow-eyed penguins to ensure that conservation efforts target critical issues rather than over-emphasized claims. The influence the recovering sea lion populations have on survival rates of yellow-eyed penguins on the mainland requires consideration.

R.1.M6 **Examine viable methods to identify and subsequently control the cause of disease outbreaks, e.g. diet quality, climate change, disease vectors**
The prevention of disease outbreaks is critical (Wobeser, 2002). The causes of the frequent outbreaks of diphtheritic stomatitis are still unknown although it has been argued that it may be related to diet quality (Browne et al., 2011; Mattern & Ellenberg, 2018a). Regarding climate change, the abundance of disease vectors such as mosquitoes may become a serious problem for native wildlife in the future so that the development of methods for their control may become an essential management tool.

2. Marine ecology

R.2.H1 **Monitoring of marine ecology: foraging behaviour & diet composition**
Yellow-eyed penguins are primarily a marine species. Factors influencing their survival are likely marine-based. The decades focused on terrestrial conservation

efforts such as habitat regeneration and predator control have not resulted in recovery of the species on the New Zealand mainland (Mattern et al., 2017b). Currently there is an increasing focus on the development of reactive management of disease events. Yet compared to other penguin species that are of equal economic importance (i.e. Little penguins, African penguins; Sherley *et al*., 2013, 2017, 2018; Pelletier *et al*., 2014; Saraux *et al*., 2016), there is no concerted effort to investigate how marine-based factors may not only influence survival rates and population trends of yellow-eyed penguins, but also may provide new insights into mechanisms that potentially contribute or even be root causes of disease outbreaks (e.g. diet composition, food quality, pathogens).

Initiate a marine ecology monitoring programme that provides baseline information on foraging behaviour and foraging success (i.e. using GPS dive loggers) as well as diet composition (i.e. via faecal DNA analysis & animal-borne cameras) to supplement population monitoring and allow investigation of the importance of sea-based factors in causing poor breeding success, mortality events and disease outbreaks.

R.2.H2 **Quantify fisheries impacts on mainland population.**

The difficulties of assessing fisheries impacts on yellow-eyed penguins has already been highlighted (Mattern et al., 2017b). Quantifiable data on fisheries interactions is vital but can only be achieved through the implementation of better control mechanisms of the inshore fishing fleet. Video observation of set netting vessels is likely to help to quantify the true impact of bycatch mortality on penguin populations.

R.2.H3 **Investigate state of the benthic habitat**

Investigate state of the benthic habitat within the species' core foraging regions, perhaps by mapping seafloor biodiversity and quantify habitat degradation caused by fishing activity using animal-borne cameras and multi-beam survey).

R.2.H4 **Foraging behaviour of fledgling penguins**

Yellow-eyed penguins have one of the lowest first-year survival rates of all penguin species. It is therefore important to gain a better understanding of the at-sea behaviour, disttibutions and foraging success of penguins during their first year. Hence, the investigation of methods to study diving behaviour and diet composition during the crucial first year at sea is of considerable importance.

R.2.H5 **Foraging ecology of sub-Antarctic penguins**

Conduct a baseline study of the foraging ecology – foraging ranges, diving behaviour and diet composition – of breeding yellow-eyed penguins from the sub-Antarctic Islands, particularly Campbell Island where bathymetry does not seem conducive to a benthic foraging strategy. Investigate whether the species occupies different oceanic niches to mainland penguins, which may be key for the survival of the species in the face of climate change.

R.2.H6 **Conduct comprehensive studies on the critical pre-moult and winter movements of Yellow-eyed penguins throughout their entire range**.

3. Disease monitoring

R.3.H1 **Investigate potential ecological factors facilitating the occurrence of diphtheritic stomatitis in chicks, e.g. diet composition during egg formation and early chick rearing phase**.

R.3.H2 **Monitor the prevalence of avian malaria in the mainland population of Yellow-eyed penguins and investigate potential disease vectors and mitigation methods.**

R.3.M3 **Monitor for outbreaks of diphtheritic stomatitis and develop best-practice protocols for the treatment of infected chicks (e.g. debriding of lesions).**

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Little (blue) penguin / kororā

(*Eudyptula minor*)

Kerry-Jayne Wilson and Thomas Mattern

Summary

Little penguins are widely distributed around North, South, Stewart and Chatham Islands, their offshore islands as well as southern Australia and Tasmania. At about 1 kg it is the smallest of the world’s 18 species of penguins and is currently considered by the 2017 IUCN Red List Assessment and Department of Conservation to be ‘least concern’ or ‘at risk declining’ respectively. Their numbers are believed to be declining in some parts of their range, are assumed to be stable elsewhere while increasing at a few locations. This is one of the best studied genera of penguins, but most of the research has been carried out in Australia, and largely at a single site, Phillip Island where a team of researchers work on Little penguins full time as part of a long term coordinated strategic plan in collaboration with universities and other research groups.

The breeding season of the little penguin varies region to region with robust information on timing and breeding success available for just a few New Zealand localities. Little penguins in most New Zealand populations lay a single clutch of two eggs each year, although Otago birds can lay twice each year and fledge chicks from both clutches.

Their breeding distribution is well known in general terms in both Australia and New Zealand but actual colony locations, the population size and population trends are poorly documented from most New Zealand sites. Many New Zealand colonies are small, some <10 pairs, although there are a few colonies of about 1,000 breeding pairs (e.g. Taieri Island, Motunau Island, Pohatu/Flea Bay). There are no large colonies as are found in Australia.

There is robust, long-term data on marine ecology for Australian populations but limited data for New Zealand. There is virtually no information on at-sea movements between breeding seasons.

Unlike other penguins, little penguins are nocturnal on land, coming ashore after dark and departing before dawn. Little penguins breed in burrows, caves or crevices, sometimes close to settlements. Burrow nesting is an extra challenge to overcome when researching them; much of the best research has been undertaken in places where the birds use artificial nest boxes.

Despite the extensive and intensive research carried out in Australia, this is of limited use when it comes to addressing conservation needs in New Zealand. The little penguin is perhaps more plastic in its ecology than other penguin species. Demography, breeding

biology, timing of the annual cycle, fledgling success, foods and foraging ecology; all aspects of a species' biology that are important when it comes to conservation management, vary region to region and even year to year. Further research at multiple sites is required into all these aspects of their ecology.

During the breeding season little penguins generally feed within about 20 km of their colony although tracking studies show that at some sites penguins may fed much further offshore. It is assumed they travel further between breeding seasons, although there is no New Zealand data to confirm this. The penguins from Australian research sites forage in very different marine environments from those utilised by New Zealand penguins, and ashore are exposed to different predators and climates. Furthermore, the Australian birds perhaps belong to a different taxon than those inhabiting most of New Zealand.

Little penguins are subject to numerous threats both on land and at sea. Ashore the main threats include dogs (*Canis familiaris*), road-kill, introduced predators, coastal development and disturbance from people. Marine threats include entanglement in fishing nets, changes in food availability due to fishing, climate change and ocean warming. Threats vary from region to region, although most information available is anecdotal and there have been few attempts to quantify threats.

Conservation needs may differ region to region necessitating regional or population level management. Only a comprehensive, investigative approach will allow us to understand factors driving declines and identify and enact the management actions required to reverse declines of Little penguins in different parts of New Zealand.

In this report we review the current knowledge of this species in New Zealand, identify gaps in our knowledge and research priorities required to allow evidence-based conservation of the species. We use the name little penguin to refer to all members of the genus *Eudyptula* and present here information on all New Zealand *Eudyptula* populations. As the location of each study cited is given, it should be simple to assign information to a species/sub-species once the taxonomy is finally resolved and the geographical limits of the proposed Australian/Otago taxa determined.

Previous reviews of Little penguin biology and priority lists

There are numerous books on penguins catering for both the scientific and popular markets and most have sections devoted to little penguins (among the best are Davis & Renner 2003 and the three chapters on little penguins in De Roy *et al*. 2013); most use information from Australian studies with the implicit assumption that things will be similar in New Zealand. The account in Marchant & Higgins (1990) is the most encyclopaedic including snippets of information from all parts of their range. A concise summary of the status of the species and the basis for this appears in Birdlife (2017). The best recent review of current knowledge is by Peter Dann (2013), based mostly on his many years working with little penguins at Phillip Island in Australia. His account is Australian focused and, while an excellent overview, lacks the detail on New Zealand populations required here. In this review we focus on information obtained from New Zealand.

Forest and Bird reviewed the status of all New Zealand penguins and that document presents an overview of the status, research priorities and conservation of the little penguin (Baird 2016). Other descriptions of New Zealand little penguin populations such as Flemming (2013). were written primarily for the lay person and provide rather brief introductions to the species.

The most detailed list of research and management priorities is that by Graeme Taylor (2000a, b) who considered each of the five then recognised sub-species of little penguin that bred in New Zealand separately. Eighteen years later few of those priorities listed by Taylor have been addressed. Dann (2013) lists some research priorities, but, this is primarily Australian focused. Birdlife (2017) includes a short list of conservation actions required for little penguins relevant to both New Zealand and Australia.

Conservation status

The Department of Conservation lists the little penguin as 'at risk -declining' (Robertson et al., 2017) and the IUCN Red List as 'least concern' (BirdLife 2017). Both organisations recognise a single species with no sub-species. The status of the New Zealand taxon is likely to change if two species/sub-species were recognised.

Taxonomy

The taxonomy of the genus *Eudyptula* urgently needs to beresolved. Kinsky and Falla (1976) recognised six sub-species all within a single species. These were the northern blue penguin (*Eudyptula minor iredalei*) (North Island, north of Kawhia in the west and East Cape on the east coast); Cook Strait blue penguin (*E. m. variabilis*) (North Island; south of Cape Egmont and Hawke Bay, South Island; Nelson and Marlborough); southern blue penguin *(E.m.minor*) (South Island, West Coast, Southland , Stewart Island and Otago); white-flippered penguin (*E.m albosignata*), (Banks peninsula and Motunau Island); Chatham IslandbBlue penguin (*E.m. chathamensis*) (Chatham Islands) and the Australian blue penguin (*E. m novaehollandiae*) (New South Wales to Perth across southern Australia). These six subspecies were recognised by Davis & Renner (2003) and Taylor (2000a, b) despite the official checklist of New Zealand birds (OSNZ 1990) and Marchant & Higgins (1990) recognising just a single taxon. The current Ornithological Society checklist recognises a single species *Eudyptula minor* with no subspecies (Gill *et al*. 2010).

A study comparing mitochondrial DNA from all six putative sub-species found an unexpected pattern of molecular divergence (Banks *et al*. 2002). The molecular data showed the Australian and Otago birds to belong to a single clade (Australian little penguin), distinct from all other New Zealand birds (New Zealand little penguin). The separation of New Zealand and

Australian little penguins was further supported by Peucker *et al*. (2009) and Waugh (2016) using DNA barcodes, although Waugh did not include Otago birds. Variation within the New Zealand clade gave some support for the Kinsky and Falla (1976) classification, although this was equivocal (Banks *et al*. 2002) and not supported by Waugh (2016).

To test this unexpected divergence, vocalisations and morphological traits from four of the Kinsky & Falla sub-species were compared (Banks *et al*. 2002). Measurements showed that the Australian and Otago birds were similar to one another, and that while Southland, Stewart Island and West Coast birds were similar to one another, they differed from Otago penguins. Comparison of vocalisations provided some evidence to support the separation between Australian/Otago and New Zealand birds but it was not conclusive (Banks *et al*. 2002). A subsequent study found little variation in little penguins across southern Australia and in Otago, with further evidence to support this clade as distinct from those in the rest of New Zealand (Banks *et al*. 2008) with little gene flow (Overeem *et al*. 2008) between the two taxa.

More recently, Grosser *et al*. (2015, 2016, 2017) used morphological, behavioural and genetic data to provide further support for the distinction between the two taxa, albeit with low levels of interbreeding. They used mitochondrial control region, mitochondrial cytochrome oxidase 1 (COI) and microsatellite markers (Grosser and Waters, 2015), which are genetic markers commonly used to assess species-level distinctions and population structure in birds (Moritz & Cicero, 2004; Tavares & Baker, 2008). Grosser *et al*., (2015) genotyped little penguins from numerous sites across New Zealand and Australia. In Australia, only Australian genotypes were detected. Concordant with Banks *et al*. (2002), this Australian lineage was also detected on the Otago Peninsula and at Oamaru where a few New Zealand clade birds were also found. Elsewhere in New Zealand, including the Chatham Islands, the vast majority of individuals were the New Zealand clade, with just a few Australian-clade birds present, except in the Bay of Plenty and Auckland regions, where only the New Zealand clade was detected (Grosser *et al*. 2015). The divergence within the control region (10–14%) between the New Zealand and Australian lineages is similar to the divergence between *Spheniscus* penguins (8–10%), and for the COI gene is 3.8%, much higher than 0.8% between African (*Spheniscus demersus*) and Magellanic penguins (*S. magellanicus*), and 1.5% between southern (*Eudyptes chrysocome*) and northern (*E. moseleyi*) rockhopper penguins (Grosser *et al*. 2015). Cole *et al*. (2017) constructed a phylogenetic tree of all penguins using COI which also supported two distinct *Eudyptula* species. Grosser *et al*. (2015) cite further evidence for recognising two species, including plumage, vocalisation and behaviour. For example, only Australian and Otago penguins 'raft up' offshore and come ashore in groups, whereas New Zealand birds usually land singly. Moreover, only Australian and Otago birds relay after fledging young from their first clutch.

Grosser *et al*. (2017) made a total of 65 measurements of bones from little penguin skeletons collected from numerous sites around New Zealand and southern Australia. Little penguins from southern New Zealand were larger than those from northern New Zealand, and the authors suggest that body and bill sizes could be inversely correlated with sea surface temperature. However, little penguins in Australia inhabit warmer seas, yet have a larger body size than those in New Zealand (Dann 2013), even if it is only slight (Grosser *et al*. 2017). Despite this minor variation they detected consistent differences in the osteology between the New Zealand and Australian/Otago clades (Grosser *et al*. 2017). For most measurements Australian birds were slightly larger than New Zealand birds but very similar to those from Otago. Although they did not find any single element that was noticeably different between the two putative species, the sum of subtle differences between the Australian/Otago and New Zealand regions supported recognition of two species of *Eudyptula* penguins.

Grosser *et al*. (2015, 2016) suggested that the little penguins originally in Otago, which were of the New Zealand genotype, became locally extinct following Maori settlement, to be replaced by Australian little penguins sometime between AD 1500 and 1900, not during the late Pleistocene as suggested previously. Holocene fossil *Eudyptula* bones and those found in prehistoric middens were carbon dated and genotyped by Grosser *et al*. (2016) who found that all ancient bones thus sampled from Otago were of the New Zealand taxa, whereas almost all living and post AD1900 penguins sampled from Otago belonged to the Australian/Otago taxa. Little penguin bones occur in pre-historic middens dated between AD1280 and 1650, but are absent from midden sites accumulated since AD1650, indicative of local extinction about 1650 (Grosser *et al*. 2016).

The methods applied by Banks et al (2002), Overeem *et al*. (2008), Peucker *et al*. (2009), Grosser *et al*. (2015, 2016), Waugh (2016) and Cole *et al*. (2017) provide critical evidence for two clades of little penguins, yet these clades have not yet been formally recognised as distinct taxa. Grosser *et al*. (2015) recommended that the New Zealand and Australian/Otago little penguin clades be elevated to separate species, the New Zealand taxa as *Eudyptula minor* and the Australian/Otago clade as *E. novaehollandiae*.

The white-flippered penguin which is restricted to Banks Peninsula and Motunau Island is no longer recognised as a distinct taxon (Gill *et al*. 2010, Grosser *et al*. 2015). However, it is morphologically distinct from other little penguins and may warrant separate conservation management.

Tobias *et al*. (2010) use phenotypic and ecological differences for their definition of species, omitting molecular data arguing that there is no consistent correlation between genetics and phenotype, and it is the Tobias score that is favoured by Birdlife International and the IUCN in determing species status. To ultimately address the taxonomic status of the *Eudyptula* taxa a comprehensive study of the phenotypic characteristics differentiating the various little penguin populations is required to assess whether molecular differences described above reflect ecological differences.

Distribution

Little penguins occur around most of New Zealand (Robertson *et al*. 2007) but systematic surveys of their distribution and abundance have been carried out for few parts of this country. A comprehensive list of all known Little penguin colonies in New Zealand will be compiled by K-JW during 2019. Unless otherwise cited, the information in this section and the following section comes from that provisional colony list held by K-JW.

Little penguin colonies occur around much of Stewart Island but there have been no comprehensive surveys in the Stewart/Foveaux Region. There are about 1,000 Little penguins on Codfish Island/Whenua Hou (T. Mattern unpublished). Little penguins occur in southern Fiordland but colonies there have not been mapped or counted.

In Otago, the coast from the Waitaki River south to Nugget Point was searched on foot between October 1991 and February 1992 and counts made at all the little penguin colonies located (Dann 1994). In all, a total of 2073 breeding pairs were counted from 20 different colonies; most colonies were small, only four, Oamaru (218 pairs), Taiaroa Head (128 pairs), Green Island (223 pairs) and Taieri Island (1,338 pairs) supported more than 100 pairs. Between them these four colonies accounted for 97% of the total number of pairs found (Dann 1994). The survey has not been repeated although those colonies in and near Oamaru and those on Otago Peninsula have been revisited.

A survey of Little penguin colonies on Banks Peninsula between 2000 and 2002 located 68 colonies of which 51 contained 5-20 active nests and just five had >50 active nests; the largest at Pohatu/Flea Bay with 717 nests (Challies & Burleigh 2004). Forty other sites had fewer than five nests. Penguin colonies were found around the entire Peninsula with 72% of colonies located along the Peninsula's eastern coast. Challies & Burleigh (2004) estimated the total Banks Peninsula population to be 2,112 active nests, four times that of a previous estimate, although the difference is almost certain to reflect survey effort rather than any increase in numbers. Coupled with the estimated 1,650 nests on Motunau Island this makes a total of about 10,460 birds of the white-flippered form of the little penguin (Challies & Burleigh 2004). Only Pohatu/Flea Bay and Stony Bay have been resurveyed since, both these colonies have increased (F. Helps unpublished) although this is unlikely to be typical of other Banks Peninsula colonies.

The West Coast Penguin Trust has surveyed Little penguin colonies along much of the South Island West Coast (Blyth *et al*. 2006, 2008). The initial survey consisted of observers walking along about 400 km of coast between the Heaphy River and Jackson Head noting any sign of penguin presence. This was followed up by intensive searches of those areas where penguins appeared most common. The initial walk through survey proved more accurate than might be expected; some colonies were missed but the overview of penguin distribution it gave has proven useful. The West Coast Penguin Trust continues to survey or revisit sections of the coast as land development, new threats, coastal erosion or other circumstances require. Data accumulated since 2008 are on file but not published. On the West Coast, penguin presence is discontinuous with large areas of suitable habitat apparently not used (Blyth *et al*. 2008). Most colonies are small, the largest only 30-40 pairs. The main concentrations appear to be in the Buller Region (Buller River to Punakaiki) and near Okarito with colonies on the urban fringes of both Hokitika and Greymouth (Blyth *et al*. 2008, Braidwood *et al*. 2011, WCPT unpublished). Little penguins appear to be scarce south of the Waiho River (Franz Josef).

Little penguins breed on islands and in some mainland localities in Nelson and Marlborough but there has been no systematic mapping of their distribution and few colonies have been censused.

There appear to have been few systematic surveys of little penguin distribution on the North Island, although many colonies are known and at a few numbers have been estimated. Most known colonies are in the Northland, Hauraki Gulf and Coromandel areas with fewer recorded colonies in the Bay of Plenty, Hawkes Bay and Wellington. On the West Coast of the North Island there are small colonies in Taranaki but few elsewhere. Little penguin colonies in the Mount Maunganui area have been surveyed by Winter (2000).

On the Chatham Islands Little penguins are known to nest on Chatham, Pitt, Rangatira, Mangere, Star Keys, Houruakopara and Kokope Islands but there are no estimates of numbers for any of these islands.

Numbers and population trends

The total number of little penguins including both New Zealand and Australian birds is estimated to be around 470,000 mature individuals with perhaps about 64,700 of those in New Zealand; previous estimates based on anecdotal information had suggested about 1 million individuals (BirdLife 2017). Based on a comparison of colony counts made prior to and since 2000, an increase in numbers was suggested (Birdlife 2017). However, for New Zealand this apparent increase is more likely to reflect increased survey effort rather than an increase in penguin numbers. For instance, on the West Coast, the Birdlife assessment includes 2,420 penguins counted since 2000 whereas only 1530 were counted prior to that date, yet colony monitoring in that region indicates a slow decline with some small colonies lost in the last decade (Blyth *et al*. 2008, R. Lane and K-J. Wilson, unpublished data). Some regional estimates used in the Birdlife estimate are simply wrong, for instance, at the Chatham Islands, the pre-2000 number was just 350, whereas the post-2000 estimate used was 20,350. In reality there were more than 350 but far fewer than 20,350; Aikman & Miskelly (2004) estimate there to be 5,000-10,000 pairs, with the lower end of this range perhaps being most likely (D. Houston pers. comm.).

In New Zealand Little penguins are thought to be in decline but there is little robust data on population trends. A survey of Little penguin distribution in 1991-92 failed to find penguins at seven sites in Otago where Little penguins had bred prior to 1990 and found far fewer little penguins on Otago Peninsula than comments by Lance Richdale suggested were present in the 1930s (Dann 1994). Numbers on Green Island had declined from an estimated 1,500 pairs in 1983-84 to an actual count of 223 pairs in 1991-92, noting though that the earlier estimate was less accurate than the later count (Dann 1994). On Otago peninsula 11 of the 29 breeding sites found in the 1970s had been extirpated by 1994, although the total number of penguins breeding on the Peninsula increased; numbers rebounding in those colonies with predator control, with the greatest increases in colonies where nest boxes were also provided (Perriman & Steen 2000).

In those Oamaru colonies protected from dogs and other predators, penguin numbers have increased. At the Oamaru Blue Penguin Colony numbers of breeding pairs increased from 33 in 1993 (Perriman *et al*. 2000) to 160 in 2010, dropping back to 145 in 2011 (Agnew 2014).

Little penguins were very common on Banks Peninsula in the late 19th and early 20th centuries but since then numbers have declined markedly (Challies 2015, Challies & Burleigh 2004). Penguins disappeared from the heads of most bays, particularly those with human habitation, by the 1950s or early 1960s, and from most other colonies accessible to predators during the 1980s and 1990s (Challies 2015). Numbers in monitored colonies on Banks Peninsula declined by 83% between 1981 and 2000, except in areas where feral cats (*Felis catus*) were the dominant predators (Challies 2015, Challies & Burleigh 2004). The declines in the 1980s coincided with an increase in ferret (*Mustela furo*) and rabbit (*Oryctolagus cuniculus*) numbers following changes in rabbit control during the 1970's. Ferret numbers on Banks Peninsula declined after 2000 allowing some recovery in the penguin population (Challies 2015).

Population demographic modelling may provide important insights into the effective population sizes, and provide a window to understand past, present and future population trends of little penguins under different scenarios. Population genomic information may also be important for identifying which management units (Palsbøll 2007) within little penguin populations, may require particular conservation management.

Two papers (Gales 1988, Renner & Davis 1999) provide information on how to sex Little penguins from external measurements.

Demography

Age at first breeding

Little penguins first breed when 2-3 years old (Dann 2013). On Otago Peninsula four of 42 known-age birds first attempted to breed when only one year old and 25 when two years old (Perriman & Steen 2000). They do not tell if those first attempts were successful.

Survival

Annual survival can only be calculated during long-term studies with marked birds. Over 19 years adult little penguins in Oamaru had an annual survival of 0.86 (SE = 0.02), first year birds 0.42 (SE = 0.03) and second years 0.82 (SE=0.03, Agnew *et al*. 2016). Annual survival of breeding penguins was not affected by age although breeding birds had a higher survival rate than pre-breeders of the same age (Agnew *et al*. 2016). A study following banded birds month by month found that the eight-week survival during moult, post-moult and midwinter was significantly lower than that during the breeding season, with the lowest survival rate occurring during the post-moult period (eight-week survival probability 0.88) (Johannesen *et al*. 2002b).

Cause of death

In the only systematic study of mortality factors for little penguins in New Zealand Hocken (2000) necropsied 213 Little penguins found dead in Otago between 1994-1998 (Table 1). In that paper he describes in detail the diagnostic features used when attributing the cause of death and any one undertaking a similar study should consult that paper.

Table 1. *The likely cause of death of little penguins in Otago and the West Coast from Hocken (2000) and West Coast Penguin Trust (unpublished).*

Cause of death	**Otago (Hocken 2000)**	**West Coast**
Unknown	32 (15%)	62 (20%)
Starvation/beach stranding	34 (15.9%)	31 (10%)
Road kill	22 (10.3%)	168 (54%)
Railway kill	8 (3.75%)	
Unspecified trauma	20 (9.4%)	
Predation by dog	30 (14%)	41 (13%)
Predation by cat		1 (0.3%)
Predation by mustelid	20 (9.4%)	3 (1%)
Predation by shark/other fish	8 (3.75%)	
Unspecified predation	5 (2.3%)	
Drowned	10 (4.7%)	
Killed by human	10 (4.7%)	1 (0.3%)
Killed in predator traps	3 (1.4%)	
Killed by fur seal		3 (1%)
Coastal development		1 (0.3%)

In Hocken's (2000) study the only species of mustelid known to prey on penguins was the ferret; stoats (*Mustela erminea*) were present though rare in his study area. Mustelids posed a greater threat to penguins in Otago than on the West Coast where ferrets were absent. He assumed those birds that drowned were caught in fishing nets, then thrown overboard before washing up in Oamaru.

The West Coast Penguin Trust in collaboration with DOC maintains a penguin mortality data base on which is recorded the date, location and if possible the cause of death of all little penguins reported dead on the West Coast. Between August 2000 and April 2018, 311lLittle penguins were found dead and the likely cause of death is shown in Table 3. Road kill was the major cause of penguin deaths on the West Coast with most kills on just a few kilometres of coastal highway. Penguin-proof fences were built along the 3.3 km of highway where most deaths occurred. There have been no road kills in areas thus protected, although road kill remains an issue elsewhere. Dogs are the other major cause of little penguin deaths on the West Coast and Otago as they are in other urban and rural locations around New Zealand.

These studies of mortality factors are highly biased. The probability of a road-killed penguin being reported is much higher than one drowned in a fishing net; one killed by a dog more likely to be reported than a penguin killed by a shark or ferret, and those in urban areas more likely to be reported than any killed in rural areas let alone those from remote colonies.

There are periodic wrecks when large numbers of little penguins are found washed up on beaches but there have been few attempts to assign a cause of death to beach-cast birds. Wrecks may occur anywhere around New Zealand but seem to be particularly frequent with larger numbers killed in Auckland/Northland than elsewhere (Powlesland 1984). The cause of death of some of the 1,648 penguins found on Northland Beaches in July, August and December 1973, and 3,649 found between January and July 1974 was reported by Crockett & Kearns (1975). All birds examined were young with more females than males being found. All showed wasted musculature, deplenished fat reserves, empty intestines and high parasite loads (Crockett & Kearns 1975). The cause of death appeared to be exhaustion and starvation, accentuated by high parasite loads and rough seas (Crockett & Kearns (1975). Those birds tested had insignificant levels of heavy metals, organochlorines or polychlorinated biphenols.

Colony, nest site and mate fidelity

Little penguins generally return to breed at their natal colony. There are few estimates of the percentage that breed in colonies other than those in which they were born, or for those birds the distance between natal and breeding colonies. Of 3,970 fledglings banded in the Oamaru Blue Penguin Colony, 19 subsequently bred at the Oamaru Creek Colony 1 km away (Agnew *et al*. 2016). Thirty-one penguins (19 females, 12 males) had been banded elsewhere in Otago but bred at the Oamaru Blue Penguin Colony; 28 of which were banded at other Oamaru colonies and three at Taiaroa Head 80 km distant (Agnew *et al*. 2016).

Little penguins tend to retain their pair bond and nest in the same burrow year after year. There is good data spanning multiple years from Phillip Island in Australia where 76% of female penguins and 79% of males returned to the nest they used the previous year (Reilly & Cullen 1981). In Australia divorce rates varied from 0-40% each year with pair bonds lasting 1-13 years with little penguins having on average 1.8 mates during their life time (Reilly & Cullen 1981). Those that bred successfully had a higher probability of nest and mate fidelity than those that failed to raise chicks.

The data from New Zealand are less robust. At Taiaroa Head, Otago Peninsula, little penguins were monitored for five consecutive years in two colonies either side of the headland (1 km apart as the penguin swims) (Johannesen *et al*. 2002a). None of the 187 penguins in their analysis moved from one colony to the other. Nest fidelity from one year to the next was 72% (69-79%) and pair fidelity 82%, differing between the two colonies and between nest boxes and natural burrows (Johannesen *et al*. 2002a). Nest fidelity was higher for pairs that bred successfully the previous year and for those that retained the same partner. The probability of moving from one nest to another was higher than that of changing partners, with females just as likely as males to return to the same nest (Johannesen *et al*. 2002a).

During a two-year study on Matiu/Somes Island, Wellington, of 29 pairs banded in 1995, the pair bond is known to have remained intact for 12 pairs, but only eight pairs used the same nest a year later (Bull 2000a). In only two of those 29 burrows was one bird known to breed with a different partner in 1996 than in 1995, for the remaining burrows the 1996 partner was not identified, or the pairs not located (Bull 2000a). Of the 74 nests located in that study only 15 were used both seasons (Bull 2000a).

Breeding Biology

Little penguins usually breed in colonies with the distance between nests determined by terrain and substrate. A few pairs nest solitarily which may be the last survivors of once larger colonies. Colony size varies from less than 10 pairs to over 1000 pairs.

Terrain and substrate include sand dunes, talus slopes, coastal forest and rocky coasts, the only requirement appearing to be substrate which allows burrows to be dug, or the presence of natural crevices, tree roots or caves which allow the penguins to find a dark place to nest. The penguins will nest on breakwaters, under buildings, in culverts, or beneath other structures. Little penguins breed in some urban areas including harbour-side suburbs in Wellington city and Oamaru.

Little penguins will breed in artificial nest boxes particularly where natural sites are limiting. The standard nest box (http://www.doc.govt.nz/Documents/conservation/native-animals/birds/nest-box-design.pdf) needs to have an entrance tunnel at least 50 cm long in areas where weka (*Gallirallus australis*) are present. Concrete nest boxes have been used in public areas to prevent interference by people.

Nests are a collection of sticks, twigs, leaves and other material including plastic and other debris found close to the burrow entrance.

Nest density and nest type has seldom been quantified in New Zealand and probably reflects substrate and terrain more so than penguin preference. On the West Coast, nest density of both available and occupied nest sites was higher in the Buller Region (0.25-0.45/100m^2 and 0.13-0.21 /100m^2 respectively) than in South Westland (0.003-0.01 /100m^2, 0.002-0.006/100m^2) with density tending to be greater <25 m from the shore than >25 m from it (Braidwood *et al*. 2011). In South Westland the penguins nested in scrub and low forest spread along the length of sandy beaches, whereas in the Buller penguins nested on rocky coasts where colonies were bounded by cliffs, rivers and roads (Braidwood *et al*. 2011).

As with all seabirds bi-parental care is required to incubate eggs and raise chicks. A good concise account of the breeding cycle appears in Dann (2013) and an introduction to the challenges facing little penguins while breeding by Chiaradia (2013). Breeding biology has been studied in greater detail in Australia than in New Zealand, here we only review those studies carried out in New Zealand. The most detailed account of the little penguin breeding cycle and chick development in New Zealand is by Kinsky (1960) which contains details from very frequent inspections at all stages of the annual cycle. Both parents spend about five days together in the nest about a month before egg laying. For the next month both are at sea, the male returning a day or two before, or on the same day as the female, and they remain together at the nest until the first egg is laid. The mean interval between laying first and second eggs is 2.8 days (Davis & Renner 2003). During incubation the parents alternate with stints of 1-10 days where one is ashore incubating the eggs while the other is feeding at sea.

The date first eggs were laid at Oamaru during 19 breeding seasons ranged from 2 May in 1996 to 30 September in 1999, with a median date of 17 July, the first pair to lay often laying a month before any others (Agnew *et al*. 2014). One or other parent remains with the chicks for the first two to three weeks after hatching (Davis & Renner 2003); the length of this guard stage being variable, reflecting foraging success. After that chicks are left alone in the nest, both parents returning to feed them every 1-2 days, less often when food is scarce. Breeding success varies year to year; in good years some pairs can fledge both chicks, whereas in poor years few pairs manage to raise even a single chick to independence.

Little penguins usually lay two eggs per clutch, about a quarter of clutches comprised a single egg and of 167 clutches observed, three contained three eggs (Kinsky 1960). The three egg clutches probably a result of two females laying in the same nest. Australian little penguins and at least some of the Otago population can lay two clutches per year and successfully rear chicks from both (double brooding) (Dann 2013, Agnew *et al*. 2014). On Otago Peninsula 48% of pairs laid a second clutch after successfully fledging at least one chick in 1993, whereas none did in 1998 when breeding began much later in the year (Perriman & Steen 2000). In Oamaru double brooding occurred in >10% of pairs during 12 of the 19 study years, double brooding being more likely in seasons when breeding began early in the year, and only by those pairs that laid their first clutch prior to mid-September (Agnew *et al*. 2014). Experienced breeders were more likely to lay early thus, lay second clutches.

Double brooding regularly occurs only with Australian and Otago penguins, suggesting double clutching is characteristic of the Australian/Otago clade. Rare instances of double brooding have been reported from New Zealand clade birds in Oamaru, (P. Agnew pers. comm.), at Kaikoura (L. Rowe pers. comm) and at Pohatu/Flea Bay, Banks Peninsula (F. Helps pers. comm.).

Elsewhere in New Zealand Little penguins lay a single clutch (Bull 2000b, Heber *et al*. 2008, Braidwood *et al*. 2011, O'Brien 1940). On Matiu/Somes Island, Wellington, about 10-11% of failed breeders re-nested after their first clutch was lost, but never after chicks had fledged successfully (Kinsky 1958, 1960, Bull 2000a). In those Wellington studies the date of laying had no effect on breeding success (Bull 2000b).

The incubation period is 35-39 days (Table 2) but can be as long as 43 days if the eggs were left unincubated for several days (Kinsky 1960).

During incubation feeding trips, thus incubation spells, were about twice as long at Motuara Island (outer Marlborough Sounds) than Oamaru (Numata *et al*. 2000), although most feeding trips during the guard stage were one day, seldom two days, at both places (Numata *et al*. 2004). The guard stage lasted longer at Oamaru than at Motuara Island and was longer for single chick broods than for pairs with two chicks to feed. Parents with two chicks lost more body condition than those with a single chick (Numata *et al*. 2004).

Table 2. *Incubation and nestling periods for little penguins in New Zealand*

Location	**Incubation period, days**	**Nestling period, days**	**Reference**
Otago	36 (33-39)	54 (48-59)	Marchant & Higgins 1990
Banks Peninsula	38		O'Brien 1940
Charleston West Coast, South Is	34 (30-38))	58 (48-64)	Heber *et al*. 2008
Wellington	35-38	49-60	Kinsky 1958

Table 3. *Breeding success for little penguins in studies carried out in New Zealand. *Hatching success was defined as the proportion of eggs that hatched relative to the number of eggs laid. Fledging success is the proportion of chicks that fledged relative to the number of chicks that hatched. Breeding success was defined as the number of chicks that fledged relative to the number of eggs laid. **Some pairs in these populations laid two clutches per year. Means, ranges and SD are included where these appear in the papers cited.*

Location	**Year(s)**	**Hatching success* %**	**Fledging success* %**	**Breeding success* %**	**Chicks fledged /pair**	**No. seasons**	**Reference**
Taiaroa Head, Otago Peninsula	1992-1998	40-81	58-95	23-78		7	Perriman & Steen 2000
Taiaroa Head, Otago Peninsula	1993-1997				Colony A, 1.64 range (1.09-1.87) colony C, 1.12 (range 0.94-1.18)**	5	Johannesen *et al*. 2002a
Oamaru	2000	79	82	64		1	Mattern 2001
Oamaru	1994-2012	75	92	69	1.89** (1.29-2.48)	19	Agnew *et al*. 2014
Otago	1982	63	75	47	1.6	1	Gales 1985
South Westland	2008			78.8		1	Braidwood *et al*. 2011
Charleston West Coast, South Is	2006	78.9	83.9	66.2	1.8	1	Heber *et al*. 2008

Charleston	2008			63.4		1	Braidwood *et al*. 2011
Pohatu/Flea Bay, Banks Peninsula	1996-2009	75 (+/- 8.4%) (58-83)	85 (+/- 9.0) (68-97)	64 (7.9%) (53-80)	1.29 (+/- 0.84)	13	Allen *et al*. 2011
Motuara Island	1999			36		1	*Numata et al. 2000*
Motuara Island	2000	76	45	34		1	Mattern 2001
Wellington	1954, 1956-1957	54 and 59		50 and 51	0.8-and 0.9	3	Kinsky 1958, 1960
Wellington	1995-1996	57	83	47	0.94	2	Bull 2000a

Breeding success at Taiaroa Head varied greatly year to year and from one part of the Headland to another (Table 3), the lowest recorded breeding success (23%) was in one small sub-colony where one season some nests were flooded (Perriman & Steen 2000).

The ways environmental factors affect breeding success in Little penguins and how the birds cope with environmental variability has been studied in much greater detail in Australia than in New Zealand; see Chiaradia (2013) and Saraux *et al*. (2011) for introductions into the Australian research. In New Zealand a study of factors affecting breeding success was conducted over 13 years at Pohatu/Flea Bay where breeding success was measured relative to 21 variables spanning biological, climatic, predator abundance and nest factors (Allen *et al*. 2011). They found that breeding success was significantly greater when the guard period was longest, average pair bond length shorter, and lay date later (Allen *et al*. 2011), the effect of the latter two variables being counter to some other studies. The length of the guard period was the strongest predictor of breeding success, both presumably influenced by food availability. Lay date was the only variable that was significantly related to hatching success and none of the variables examined predicted fledgling success (Allen *et al*. 2011).

There have been few attempts in New Zealand to relate breeding success to climatic factors. Over a five-year study in Otago, Perriman *et al*. (2000) found that when La Niña conditions prevailed (warmer than average ocean temperatures), penguins started breeding later, leaving insufficient time for most pairs to lay a second clutch, than in El Niño (cooler waters) and normal years. The probability of a newly hatched chick fledging was influenced by these large-scale climatic conditions, whereas hatching success was not correlated with climate perturbations (Perriman *et al*. 2000).

The timing of the breeding season of little penguins is highly variable both year to year and within New Zealand region to region. At Oamaru the breeding season can range from May to January but in most parts of the country laying generally occurs in August and September (Agnew *et al*. 2014, Heber *et al*. 2008, Kinsky 1960, Bull 2000b).

Gales (1987) studied the growth of chicks on Otago Peninsula and compared Otago chicks with chicks elsewhere. That paper includes growth curves that allow chicks to be aged. Other sources of information on chick growth are Mattern (2001) and Numata *et al*. (2004).

Moult

The annual moult is the most stressful and energy demanding time in a penguins' year, yet there is little data on the timing and duration of moult in New Zealand little penguins. The most detailed description of moult is by Kinsky (1960).

In New Zealand little penguins moult between December and March (Kinsky 1960). In Wellington the duration of moult was on average 15.5 days (12-18) with the loss of 40-50% of their pre-moult weight (Kinsky 1958). In Otago moult lasted on average 16.2 days (15-18) (Gales 1984 in Marchant & Higgins 1990).

Non-breeders and failed breeders usually moult before penguins that bred successfully, many birds moulting in the colony in which they bred. On Matiu/Somes Island 20% of banded birds moulted in the burrow in which they bred, several birds moulted in the same burrow, sometimes even simultaneously, and that the sites best suited for breeding were not always those preferred for moult (Kinsky 1960).

Food and foraging

Diet composition

Little penguins have a generalist diet mostly taking small nearshore pelagic, schooling fish with lesser reliance on cephalopods and krill (Australian data reviewed by Dann (2013), for New Zealand see Fraser & Lalas (2004), Flemming *et al*. (2013)). Their diet varies regionally and seasonally presumably reflecting prey availability.

Table 4. *The composition of the diet of little penguins at four locations in New Zealand.*

Location	**Fish**		**Cephalopods**		**Crustaceans**		**Year**	**Reference**
	Prey mass	Prey No.	Prey mass	Prey No.	Prey mass	Prey No.		
Oamaru	90%	97%	10%	0.5%	0.1%	2.5%	1994-1995	Fraser & Lalas 2004

Oamaru	95.2	95.5%	4.8%	4.5%	0	0	2010	Flemming *et al*. 2013
Codfish Island/Whenua Hou	97	98	3	1	0	0	1984	Van Heezik 1990
Stewart Island	21.4%	9.6%	73.1%	4.6%	5.5%	85.7%	2010	Flemming *et al*. 2013
Banks Peninsula	85.4%	83.2%	14.6%	16.8%	0	0	2010	Flemming *et al*. 2013

Table 5*. Prey species known to be taken by little penguins in New Zealand. *** prey species that comprised >50% of prey biomass, **10-50% of prey biomass, * <10% prey biomass, r recorded but insignificant by mass. This table is derived from information in Fraser & Lalas (2004) (Oamaru 1994-95), Flemming et al. (2013) (Oamaru, Stewart Island and Banks Peninsula 2010) and Van Heezik (1990) (Codfish Island/Whenua Hou 1990).*

	Stewart Is 2010	**Codfish Island/ Whenua Hou 1990**	**0amaru 1994-95**	**Oamaru 2010**	**Banks Peninsula 2010**
Fish					
Slender Sprat (*Sprattus antipodum*)	*		***	*	**
Graham's Gudgeon (*Grahamichthys radiata*)	r		*	***	r
Southern Pigfish (*Congiopodus leucopaecilus*)			*		
Common Smelt (*Retropinna retropinna*)			*		
Whitebait (*Galaxias* sp.)			r		
Pearlside (*Maurolicus muelleri*)			r		

Ahuru (*Auchenoceros punctatus*)	r	**			**
Red Cod (*Pseudophycis bachus*)	*	*	r		**
Hoki (*Macruronus novaezelandiae*)		r	r		
Lantern fish (*Electrona sp*)		r	r		
Seahorse	r				r
Pipefish (*Leptonotus* sp)	r		*		r
Sea Perch (*Helicolenus* sp			r		
Opalfish *Hemerocoetes* sp)			r		
Barracouta (*Thyrsites atun*)				r	r
Estuary Stargazer (*Leptoscopus macropygus*)				r	
Cephalopods					
Arrow Squid (*Nototodantarus sloanii*)	***	***	*	*	**
Warty Squid (*Moroteuthopsis ingens*),		*			
Octopus (*Octopus maorum*)		*			
Crustaceans					
Planktonic copepod (*Neocalanus tonsus*)			r		
Mantis Shrimp (*Heteosquilla tricarinata*)			r		
unidentified Mysid krill			r		
Euphausid krill (Nyctiphanes australis)			r		

Unidentified planktonic amphipod			r		
Unidentified ectoparasites			r		
Stromatopod larvae	*				

The most detailed study of little penguin diet in New Zealand is a year-long study at Oamaru which identified a total of 22 prey species (Table 5) (Fraser & Lalas 2004). Fish dominated, occurring in 89 of the 90 penguins sampled, accounting for 90% of the estimated prey mass (Table 4). (Fraser & Lalas 2004). Cephalopods occurred in only 21 samples and made up about 10% of the prey mass; the few crustaceans found included fish ectoparasites, presumably ingested along with their hosts (Fraser & Lalas 2004). The most commonly taken prey species was slender sprat which was recorded in all 10 months when samples were obtained, and over the course of the study comprised 75% of prey biomass. Of the 22 prey species (Table 5), just four others were commonly eaten, these being; Graham's Gudgeon, arrow squid, southern pigfish and common smelt (Fraser & Lalas 2004). Most prey were estimated to be 15-100 mm in length.

Van Heezik (1990) studied the diet of little penguins at Codfish Island/Whenua Hou in October 1984 and compared their diet with that of tawaki (*Eudyptes pachyrhynchus*) and yellow-eyed penguins (*Megadyptes antipodes*) on the same Island. Arrow squid made up 58% of little penguin diet by weight but comprised only 2% of the individuals caught. Ahuru was the most commonly recorded prey (88% of prey items) but comprised only 37% by weight of food taken. The other species recorded (Table 5) were rare constituents of the diet (van Heezik 1990). Fish taken by little penguins were generally post-larval and juveniles, <50mm long, the squid being <10 gm. Most of the food taken in this study were pelagic macro-zooplankton (van Heezik 1990).

In November-December 2010 little penguins were sampled at Banks Peninsula, Oamaru and Stewart Island (Flemming *et al*. 2013). They identified 12 prey species (Table 5). Arrow squid were present in about 90% of samples at all three sites; being the most important prey at Stewart Island where they made up 73.1% of the food by mass, compared with 14.6% on Banks Peninsula and just 4.8% at Oamaru (Table 4). Of the 10 fish species found (Table 5), Graham's Gudgeon was the most important at Oamaru (present in all samples and over 91% of diet by both number taken and prey mass) and ahuru the most important at Banks Peninsula (in 75% of samples, 59.3% by number and 37.4% by mass). At Stewart Island, red cod and slender sprat occurred in over half of the samples but made up just 8.8% and 10.4% respectively of prey mass (Flemming *et al*. 2013). The other fish species were uncommon prey (Table 5). Tiny stomatopod larvae were only found in Stewart Island samples; although they were found in over half of the 22 samples obtained there, they made up just 5.5% by mass but 85% of the prey items recorded from Stewart Island (Flemming *et al*. 2013). Excluding the stomatopod larvae, mean prey length varied from 62 mm for red cod at

Stewart Island to 169 mm for slender sprat at Oamaru, and mean prey mass 3 g for red cod at Stewart Island to about 60 g for slender sprat at Oamaru and Banks Peninsula (Flemming *et al*. 2013).

Stomach flushing, the method used in all of the above studies provides a biased snapshot of diet, reflecting the food taken in the previous days. Furthermore, some foods are digested faster than others. For example, cephalopod beaks are likely to be retained in the stomach longer than many fish otoliths. Stable isotope ratio analysis (SIA) of carbon and nitrogen in feathers and blood provide information on diet over longer periods. SIA can provide information on the trophic level targeted and whether fish, cephalopods or crustaceans, were eaten, but do not generally distinguish between actual species. SIA is based on the predictable and quantifiable ways that tissue nitrogen (δ15N) and carbon (δ13C) isotopes change at different trophic levels in the food chain. Isotope levels in blood reflect the food taken during the last 28 days, whereas those of feathers indicate food obtained prior to the moult.

Flemming & van Heezik (2014) compared the diet of little penguins as determined using SIA with that estimated by stomach flushing (Flemming *et al*. 2013, see above) using the same penguins at the same sites. Feathers from little penguins on Stewart Island had lower δ15N than those at either Oamaru or Banks Peninsula. Feathers from Oamaru penguins had lower δ13C than those from either Banks Peninsula or Stewart Island, with no significant differences found between feathers from Stewart Island and Banks Peninsula penguins (Flemming & van Heezik 2014). Isotopic mixing models for feathers, indicated that fish made up the major part of the diet for birds that later bred at Oamaru (46.4%) and Stewart Island (62.3%), but to a lesser extent those that subsequently bred at Banks Peninsula (35.4%). Cephalopods comprised a third to a half of the pre-moult diet of penguins from all three sites (Flemming & van Heezik 2014).

Isotopic mixing models for blood estimated that cephalopods and fish made up 49.9% and 33.8% respectively of diet at Oamaru, at Banks Peninsula fish (46.3%) and cephalopods (46.8%) were taken in approximately equal amounts, whereas at Stewart Island, crustaceans (77.2%) dominated the diet (Flemming & van Heezik 2014).

SIA when compared with stomach flushing indicated that stomach content analysis underestimated the importance of squid and crustaceans and overestimated the proportion of fish in the diet (Flemming & van Heezik 2014). SIA of blood suggested that little penguins from Oamaru and Banks Peninsula fed at higher trophic levels than penguins at Stewart Island, where field observations show little penguins feeding very close inshore (T. Mattern unpublished). SIA of feathers indicated that Stewart Island penguins were feeding at a lower trophic level during the pre-moult period than penguins further north, and those from Oamaru feeding further offshore than little penguins at Stewart Island or Banks Peninsula (Flemming & van Heezik 2014).

Stable isotope ratios of little penguins breeding on Motuara Island, outer Marlborough Sounds, indicated that during incubation penguins fed on a broader range of offshore-dominated prey compared with birds rearing chicks which took a narrower range of prey from higher trophic levels; reflecting the longer duration feeding trips made during incubation than during chick rearing (Poupart *et al.* 2017).

Genetic information derived from scat samples can provide information of the diets of penguins (Deagle *et al*., 2010), that may be overlooked by more conventional approaches. This is non-invasive, and a single sample can provide information about the individual, including genotype, sex, bacterial communities, pathogens and parasites. Any study wishing to use this method will need to ensure a genetic database (such as GenBank's BLAST; https://blast.ncbi.nlm.nih.gov/Blast.cgi) of all potential prey items is available to compare sequence data to, as a reduced database will limit the power of the analysis, and 'miss' potential food species.

At-sea movements during the breeding season

There have been extensive studies of the foraging ecology of little penguins in Australia with fewer studies in New Zealand. The most thorough study of foraging ecology in New Zealand was conducted in Oamaru by Agnew (2014) who during 2010, 2011 and 2012 deployed GPS units a total of 241 times on 22 different individuals and conducted 135 successful deployments of time depth recorders (TDR) on 26 individual penguins. Deployments occurred during all stages of the breeding cycle for birds with both first and second clutches. Dive depth tended to decrease with each subsequent stage in the breeding season, whereas the number of dives per day tended to increase (Agnew 2014). Mean dive depth was greatest (12.67, SE 0.45, m) while feeding their first brood of chicks in 2010, and least (5.06, SE 0.28, m) while rearing their second brood in 2012 (Agnew 2014). The number of dives per day peaked at 1264 (SE 151) when rearing the second brood of chicks in 2010. Dive depths were shallowest, averaging just 5-7 m, in December and January (Mattern 2001, Agnew 2014).

Oamaru little penguins generally fed in waters <50 m deep and <20 km from shore, and on single day trips usually remained within 20 km of their colony (Agnew 2014, see also Chiaradia *et a*l. 2007). Penguins travelled further during incubation than during chick rearing; all two-day trips occurred during incubation and mostly to places north of the Waitaki River (Agnew 2014). While breeding the furthest point from the colony reached by an Oamaru penguin on a single day trip was 35.2 km north of the colony by a penguin rearing a second brood. Penguins tended to travel further and stay at sea longer during stormy weather (Agnew 2014).

A multi season, multi-site study using GPS in central New Zealand (Poupart *et al.* 2017) bought together tracks made during the breeding season in Wellington Harbour (2011, 2012, 2014), Motuara Island, outer Marlborough Sounds, (2014, 2015) and the Buller Region, (2013, 2015, 2016). All three sites are within a single latitudinal band with contrasting offshore marine environments. There was considerable variation between sites. Wellington penguins mostly remained within the harbour feeding within 12 km of their colony; only two of the 22 birds tracked left the harbour reaching a maximum distance of 36 km from their colony. For Wellington penguins there was no difference in range, distance travelled or trip duration between incubation and chick rearing periods (Poupart *et al.* 2017). Of the three sites, those from Motuara Island showed the greatest variation between breeding stages and between individual birds. During incubation Motuara penguins foraged within 102±69 km of their colony (1 - 214 km) and their trips lasted 7±4 days (1-16 days). Three birds remained within 10 km of the colony; three undertook medium-distance trips 40–75 km from the colony into Cook Strait or the Marlborough Sounds, while eight crossed Cook Strait to feed 93–214 km north of the Island, some reaching the Taranaki Bight (Poupart *et al.* 2017). During chick rearing, Motuara penguins either made 1-day trips remaining 6-10 km of the Island or 2-day trips into Cook Strait reaching 36–43 km from the colony (Poupart *et al.* 2017). Buller birds also travelled further on longer duration trips during incubation (up to 5 days) than chick rearing (1 day), feeding west or north-west of their colonies. Wellington and Buller birds showed little year to year variation in areas used, unlike the Motuara penguins where there was marked variation between years (Poupart *et al.* 2017). This study suggested that penguins breeding far from a major river mouth travelled further to find food than those nesting close to a river mouth.

Previous studies at Motuara Island also showed this to be a poor site for little penguins, the birds there diving more often than little penguins from Oamaru (mean number of dives per trip: 1,165 versus 809), deeper (mean depth: 10.1 versus 6.0 m) and longer (mean dive duration: 29.5 versus 22.4 seconds) (Mattern *et al.* 2004), with lower body condition, and poorer breeding success (0.71 chicks/pair) than those at Oamaru (1.44 chicks/pair) (Mattern *et al.*2001, Numata *et al*. 2000; 2004). Incubation spells, thus foraging trips, were about twice as long at Motuara than Oamaru (Numata *et al*. 2000). On predator-free Motuara Island breeding failure was generally due to chick starvation or adult desertion, whereas at Oamaru, predation was the main mortality factor (Mattern *et al.*2001, Numata *et al*. 2004). The guard stage was shorter at Motuara Island than at Oamaru, and chicks fledged at a lower body mass, again indicative of less favourable foraging conditions (Numata *et al*. 2004).

A study comparing foraging ecology across the entire range of the little penguin showed that at sites with high fledgling success such as Oamaru and Penguin Island (Western Australia) the penguins made shallower dives with lower diving effort than at sites with lower fledgling success such as Motuara Island and Phillip Island (Victoria) (Chiaradia *et al*. 2007). They conclude that availability of seas <50 m deep close to the colony is one important factor influencing breeding success.

Movements between breeding seasons

There is only fragmentary information on the movements of adult little penguins between breeding seasons in New Zealand with no information on dispersal of juveniles. Wellington little penguins appear to remain in the harbour year-round returning to their colony frequently, with only three of the 435 adult penguins banded on Matiu-Somes Island between 1954 and 1958 seen outside Wellington Harbour (Kinsky 1958, 1960).

Of 168 banded little penguins captured at Pilots Beach, Otago Peninsula between September 1999 and December 2000, nine were banded at Oamaru 80 km away, one at Penguin Beach 2 km away, the rest from Pilots Beach or adjacent Taiaroa Head (Johannesen *et al*. 2002b).

In both studies penguins were far more likely to be resighted at the point of banding where regular searches were made than elsewhere, thus movements away from their breeding colony will occur more often than suggested by these results.

Threats

Anthropogenic factors

In New Zealand the major land-based threats to little penguins appear to be loss or modification of breeding habitat through land-development or erosion, deaths due to dogs, road kill, introduced predators and disturbance by people. The relative intensity of these threats varies regionally.

Little penguins are long-lived and strongly philopatric thus, loss or modification of breeding habitat, even if no birds are killed, can have long-lasting effects on breeding productivity and inbreeding may be of concern in the small colonies that are now typical of some parts of New Zealand.

Road kill poses a significant threat to little penguins wherever they nest near roads. This was the major land-based cause of death in the Buller Region until penguin-proof fences were built in those areas where most road- kills occurred to prevent the penguins straying onto the highway (http://www.bluepenguin.org.nz/pahautane-penguin-fence/). At the Oamaru Blue Penguin Colony, tunnels were installed under the access road to avoid road kills by tourist traffic.

Changes in the density and composition of vegetation have been found to influence the breeding success of little penguins (Bull 2000b). Fire is a risk in drier parts of their range such as Banks Peninsula and Chatham Islands (Taylor 2000a, b).

Trampling of burrows by cattle and sheep can occur where birds nest on farmland, or by feral goats or even deer elsewhere (Taylor 2000a, b), but trampling of burrows is probably rare. Possums and rabbits could potentially compete with penguins for burrows but there appear to be no verified records of this happening.

Disturbance by people is likely to be problematic at some well-known unprotected sites such as the Oamaru Creek colony and those in Wellington city.

Predators

Uncontrolled dogs are one of the major threats to little penguins (Taylor 2000b, Dann 1994), the penguins being particularly vulnerable at night when moving between the sea and their burrows. Dogs are capable of digging penguins out from their burrows although we do not know of any verified reports of that. In February 2001, 116 penguins from the Oamaru Creek Colony were killed by two dogs over the course of just two nights (Mattern, pers. obs.). At Cape Foulwind on the West Coast, 15 adult little penguins were killed, probably by a single dog on a single night, and several small colonies at Punakaiki have been extirpated probably by dogs (West Coast Penguin Trust unpublished).

Predation by mustelids requires further research although the information available suggests that ferrets pose more of a threat than stoats. The most conclusive study of mustelid predation is that by Challies (2015) at Harris Bay, Banks Peninsula. Those colonies that were accessible to predators, remained stable during the 1970's, but declined suddenly after 1981; two colonies were extirpated and 42 of the 47 penguins found dead had wounds typical of those inflicted by mustelids (Challies 2015). Of the 47 mustelids trapped between 1981 and 1995, 43 were ferrets, three were stoats and one a weasel (*Mustela nivalis*). Sixteen of the penguin kills could be attributed to ferrets but both ferrets and stoats were present when three other penguins were killed (Challies 2015). Predation affected the surviving birds indirectly by breaking pair bonds and skewing the sex ratio as females were killed more often than males (Challies 2015).

Penguins disappeared from most Banks Peninsula colonies accessible to predators during the 1980s and 1990s except in areas where feral cats were the dominant predators (Challies 2015, Challies & Burleigh 2004). The declines in the 1980s coincided with an increase in ferret and rabbit numbers following changes in rabbit control during the 1970's. No penguins were preyed upon between September and January when rabbits were most numerous; most penguins being taken in Autumn and Winter when mammal prey was scarce (Challies 2015). Ferret numbers on Banks Peninsula declined after 2000 following the introduction of rabbit haemorrhagic disease, allowing some recovery in the penguin population (Challies 2015).

Ferrets were the only species of mustelid known to prey on little penguins in the Oamaru area (Hocken 2000) where in December 1999 they killed about a third of eggs and chicks but did not kill any adult penguins (Agnew *et al*. 2014).

On the West Coast breeding success and survival of eggs, chicks and adults were not significantly different in penguin colonies with, or with no predator control and mustelids appeared to constitute a very minor threat to little penguins (R. Lane and K-J. Wilson unpublished). At those West Coast colonies stoats were common, weasels rare but ferrets absent.

In Otago, most extant colonies are on islands or sites where predators were absent or were protected from predators by physical barriers or trapping (Dann 1994, Perriman & Steen 2000). Mustelids were the main predators recorded at Taiaroa Head, Otago Peninsula, although Norway rats (*Rattus norvegicus*) preyed on little penguin eggs during one season, even then in just one of the three sub-colonies studied (Perriman & Steen 2000).

The impact of feral cats (*Felis catus*) on little penguins is uncertain. Taylor (2000a) lists cats as predators of little penguins on Banks Peninsula citing an early report by Chris Challies, although in a recent paper Challies (2015) states that while penguin numbers declined in most colonies accessible to ferrets 'the main exceptions being those in areas where feral cats remained the dominant predator'. Penguin feathers have been found in cat scats on the Chatham Islands (Taylor 2000b) and one probable instance of predation by a cat has been recorded on the West Coast (Table 3). Cats were a significant threat to little penguins in Tasmania (Dann 2013).

Weka are probably capable of taking penguin eggs and chicks but we know of no verified account of this happening. Feral pigs (*Sus scrofa*) can root out and kill little penguins (Taylor 2000b).

Parasites and disease

A review of the information available on parasites and diseases in New Zealand penguins is given by Duignan (2001). Pulmonary infection due to Aspergillosis has been recorded in emaciated beach-cast, juvenile little penguins. Fleas, ticks, mites and lice occur on most penguin species with three species of ticks *Ixodes kohlsi*, *I. auritulus* and *I. eudyptidus* recorded from little penguins. Endoparasitic cestodes, nematodes, trematodes, and acanthocephalans have been found in little penguins but neither these nor the ectoparasites appear to have much effect on the health of well-fed birds but can accentuate the impact of starvation (Duignan 2001). High seroprevalence of avian malaria has been found in little penguins from Codfish Island/Whenua Hou; deaths due to avian malaria have not been reported from New Zealand but have occurred in Australia (Duignan 2001).

Climate change

With their wide latitudinal span from warm temperate Northland to cool Stewart Island, little penguins may at first glance appear sufficiently adaptable to cope with climate change, but such a complacent view is ill advised. A recent assessment of the impact climate change is likely to have on Australian birds showed seabirds to be particularly vulnerable (Garnett & Franklin 2014). While climate warming may directly contribute to the death of penguins through overheating, as has happened in Australia, it is the, associated changes such as ocean warming and increased storm frequency and intensity that are more likely to affect seabirds. Research on other species suggests that extreme climatic events are more likely to impact penguins than long-term averages (Boersma & Rebstock 2014).

The seas surrounding New Zealand, the Tasman Sea and southern and eastern Australia comprise one of the world's major marine biodiversity hotspots which, through climate change, is likely to experience reductions in primary productivity and trophic shifts (Ramírez, *et al.* 2017) that will affect seabirds including little penguins. A major concern is that an increase in intensity and frequency of sea surface temperature (SST) anomalies will affect breeding onset and trigger a mismatch between marine productivity and peak breeding (Ramírez, *et al.* 2017).

The ways in which various marine parameters affect little penguins and the responses of the birds to these have been subject to intensive research in Australia (for example see Pelletier *et al*. 2012, 2014, Ropert-Coudert *et al*. 2009, Saraux *et al*. 2016). Research on how variations in marine parameters affect little penguins in New Zealand is much more limited.

At Oamaru, high marine productivity (estimated by chlorophyll-a) correlated positively with early breeding, higher breeding success and better survival of breeding penguins, the effect being most marked when chlorophyll-a was high in the months preceding the breeding season (Agnew *et al*. 2015). Breeding was delayed in years when seas were warmer (Perriman *et al*. 2000), so on that basis we might expect ocean warming to negatively affect breeding success. During prolonged periods of rough weather Oamaru penguin parents returned less frequently, increasing the likelihood of egg desertion when the foraging bird failed to return before the incubating bird's reserves become exhausted, or chicks that were fed less frequently died or fledged at lower weights (Agnew *et al*. 2015). Wrecks, when large numbers of little penguins wash up dead on beaches, occur more often following prolonged bouts of stormy weather (Crockett & Kearns 1975, Powlesland 1984), but may also be a result of low prey abundance or harmful algal blooms (Taylor 2000b). Wrecks appear to be a particular issue in Northland (Crockett & Kearns 1975).

Fisheries bycatch

Fisheries bycatch is a major threat to penguins worldwide with 14 of the 18 species recorded as bycatch, with set-nets and trawls posing the greatest threat to penguins with rare captures on longlines (Crawford *et al*. 2017).

In New Zealand, little penguins are caught and drowned in inshore set-nets, drag-nets and possibly also in trawl, purse-seine and long-line fisheries but the numbers killed and locations where kills occur are very poorly documented (Crawford *et al*. 2017). In 2016 eight Little penguins were caught in a single net set for butterfish (*Odax pullus*) in the Stewart−Snares area (Crawford *et al*. 2017). Little penguins are known to be caught in set nets around Motunau Island and drag-nets at Timaru (Baird 2016). The commercial fisheries most likely to cause penguin by-kill are small inshore vessels which are not required to carry observers and we suspect few penguins killed are reported. Penguins are less likely to be caught by larger vessels that use trawls or long-lines, the commercial fisheries where observer coverage is best. The extent of bycatch from recreational fishers is unknown.

Other marine-based threats

There is little if any evidence to suggest over fishing has reduced prey abundance for penguins (Taylor 2000a, Dann 2013). Little penguins have died on mass after a viral disease decimated their pilchard prey in both Australia and the North Island (Chiaradia et al. 2003, 2010).

Penguins are especially vulnerable to oil pollution with particular risk around major ports such as Whangerei, Auckland, Tauranga, Wellington and Lyttelton; all busy ports with little penguin colonies close by. Eighty-nine Little penguins were found dead and 383 live birds found contaminated with oil following the wreck of the container ship 'Rena' on Astrolabe Reef near Tauranga on 5 October 2011. An oil spill of this magnitude would have had an even greater impact on seabirds had it not been for the proximity of the wreck to a major city with all the infrastructure required to find, rescue and rehabilitate seabirds.

Little penguins breeding on Motuara Island foraged as far away as the Taranaki Bight during incubation (Poupart *et al*. 2017), the very place where Trans-Tasman Resources Limited (TTR) have a permit that allows them to extract iron ore from up to 50 million tonnes of sea-bottom sand each year (https://www.ttrl.co.nz/projects/south-taranaki-bight/). Ninety percent of the sand will be returned to the sea bed. Such at-sea sand mining is likely to increase turbidity and disrupt the food chain, but the impact of this and the continuous presence of a large 335 m long ore processing ship working in the area will have on penguins is unknown but potentially severe. Australian little penguins avoided turbid water when foraging even when those turbid waters had higher productivity than the preferred less turbid waters nearby (Kowalczyk *et al*. 2015). They suggest that the visual hunting penguins are less successful in catching prey in turbid water. TTR have a prospecting permit for the South Island West Coast extending from Ross in the south, to north of Karamea, from one kilometre offshore out to the 12 nautical mile territorial limit (https://www.ttrl.co.nz/projects/westland-sands/), coinciding with areas where Buller little penguins forage (Poupart *et al*. 2017).

Plastic ingestion is a growing threat to most seabirds (Wilcox *et al*. 2015) although penguins are perhaps less vulnerable that many other species. Chemical contaminants pose an ongoing but up to now minor threat to penguins in New Zealand. Organochlorines and heavy metals are found in Australian little penguins but whether these occur at detrimental levels was not determined (Dann 2013).

Sharks are reputed to prey on little penguins and barracouta (*Thyrsites atun*) reputed to attack penguins but the numbers taken, if indeed sharks or barracouta are even implicated are unknown. Thousands of sharks caught in Australia whose stomach contents were inspected did not contain penguin remains (A. Chiaradia pers. comm.) There are two published records of New Zealand fur seals (*Arctocephalus forsteri*) attacking little penguins at sea (Notman 1985, Clemens *et al*. 2011) with three records of predation by seals on the West Coast (Table 3). Penguin feathers have occasionally been found in fur seal scats.

There are anecdotal reports of little penguins killed or injured by boat strike in the Hauraki Gulf and as the number of recreational boats is increasing this threat is likely to grow.

Research priorities

Much of the best research published on little penguins in New Zealand has been undertaken at Oamaru or Otago Peninsula where the penguins are potentially a different taxon than penguins elsewhere in New Zealand. This bias toward Otago based research is particularly marked for population trends, breeding biology, mate, nest site and colony fidelity, foods, foraging ecology, and weather/climate impacts on breeding; all aspects of biology critical to an understanding of conservation requirements. Regardless of taxonomy, due to regional differences in ecology and environment, New Zealand little penguins need to be managed at the population (or regional) level.

1. Taxonomy

R.1.H1 In order to clarify the taxonomic standing of the two putative taxa use the Tobias criteria (Tobias *et al*. 2010) to compare the behavioural, biological and ecological differences between the New Zealand and the Australian/Otago taxa.

R.1.L2 Determine when the taxa diverged from one another.

R.1.L3 Analyse large genomic datasets to test historical and/or contemporary gene flow between the two taxa.

2. Population monitoring & demography

In order to understand the population trends of New Zealand little penguins which, due to differing marine environments, food availability and threats, are likely to vary region to region it is necessary to monitor changes in population size and breeding success at different parts of New Zealand. With scientific guidance much of this could be done by community groups or volunteers.

While we know the overall distribution around New Zealand moderately well, there is robust data on little penguin distribution and abundance for just a few parts of the country. A colony database listing all known little penguin colonies together with estimates of numbers (where available) will be compiled by K-J. Wilson during 2019.

Conservation management requires an understanding of demography (in human terms births deaths and marriages) which in turn affects breeding success and population trends. Demography of little penguins has not been well researched in New Zealand, although analysis of Chris Challies long-term studies may provide much of the required data.

R.2.H1 Distribution and abundance of little penguins in selected areas throughout New Zealand, of particular concern is Northland where major wrecks have occurred and pressure from people and development is greatest.

R.2.H2 To determine population trends and breeding success, annual monitoring at selected colonies at the Chatham Islands and for mainland and offshore island sites throughout New Zealand.

R.2.H3 Population dynamics including data on age of first breeding, annual productivity, first year survival, and annual survival of adults; a comprehensive analysis of Chris Challies' data set could provide much of the required data.

R.2.H4 Develop monitoring protocols suitable for use by researchers, community groups and individuals.

R.2.M5 Compile a list of all little penguin colonies where annual monitoring is undertaken or where annual monitoring has occurred in the past.

R.2.M6 Select those colonies in R.2.M5 where annual monitoring should be continued or resurrected and provide the support required to ensure annual monitoring in those selected colonies continues, preferably using standardised methodology.

R.2.M7 Colonies where we know annual monitoring has/does occur are; Otago Peninsula, Oamaru, Flea Bay and Harris Bay (30 years) (Banks Peninsula), Motunau Island (30 years), Charleston (12 years) and Okarito (West Coast), Wellington city, Matiu/Somes Island (7 years) (Wellington), Mt Maunganui (Bay of Plenty). We recommend monitoring be continued at these sites.

R.2.M8 Identify and attempt to fill major geographical gaps in monitoring coverage. Gaps include; Chatham Islands, Stewart/Foveaux, Nelson/Marlborough, Hawkes Bay, Taranaki, Hauraki Gulf and Northland.

R.2.M9 Estimate current population size in those areas, or for those colonies where population estimates were made >10 years ago using comparable methodology.

R.2.M10 Document recruitment into the breeding population.

R.2.M11 Analyse and publish Chris Challies long-term demographic study on Motunau Island and Harris Bay, Banks Peninsula. Similarly, analyse data from transponder trials on Somes Island (Mike Rumble).

R.2.L12 Determine emigration rates and distance between natal and breeding colonies.

3. Marine ecology

Little penguins obtain all their food at sea and spend most of their lives at sea, circumstantial evidence suggests that some of the declines in their numbers observed are the result of marine rather than terrestrial threats. Conservation management requires much more robust knowledge of their marine ecology than we have at present.

Little penguins experience regional differences in the marine environments thus the foods available to them. Further knowledge of regional and seasonal variation in diet could help explain differences in foraging effort, breeding success and the timing of egg laying.

R.3.H1 Foraging range using GPS devices during the breeding season at representative colonies throughout their New Zealand range. Ideally multi-year studies during all stages of the breeding cycle, but most crucial are those during chick rearing.

R.3.M2 Satellite/GLS tracking of breeding penguins from representative colonies throughout their New Zealand range during the pre-moult period.

R.3.M3 Satellite/GLS tracking of breeding penguins from representative colonies throughout their New Zealand range and, if feasible fledglings, to find out where they go between moult and breeding.

R.3.M4 Climate change and sea surface warming will impact on Little penguins. Modelling may help predict and manage impacts.

R.3.M5 Diet studies throughout their New Zealand range.

R.3.M6 Collect blood and feathers for stable isotope studies

R.3.M7 Use non-invasive molecular methods to directly obtain data on diet using faecal samples

4. Breeding biology

Breeding biology has been studied in detail in Australia and in moderate detail in New Zealand. The main gaps in our knowledge are around the timing of breeding and breeding success which appear to vary regionally. The influence of offshore marine conditions and climate on breeding success could provide useful insights into ways in which climate change is likely to affect the penguins in future.

R.4.M1 Timing of the breeding cycle and breeding success of Little penguins at the Chatham Islands and at selected locations on mainland New Zealand in regions where no previous studies have been undertaken.

R.4.M2 For colonies experiencing different offshore marine conditions and climates, determine the way annual variation in prevailing environmental conditions affect timing of the breeding season and breeding success.

R.4.L3 Obtain further data on nest site, mate and colony fidelity.

5. Threats

The research priorities above all contribute to our understanding of the ways different aspects of their ecology influence the threat status of little penguins in New Zealand. In this final section we list research topics that directly concern threats to the birds.

R.5.H1 Determine the impact introduced predators have on little penguins. The impact appears to vary region by region

R.5.H2 Record the cause of death for penguins at monitored sites.

R.5.H3 Study the cause of periodic die-offs of little penguins, the northern North Island being of particular concern.

R.5.M4 Determine what role, if any, recreational and commercial vessels play in little penguin mortality in the Hauraki Gulf and other penguin foraging areas with high marine traffic.

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Fiordland penguin / tawaki

(*Eudyptes pachyrhynchus*)

Thomas Mattern and Kerry-Jayne Wilson

Summary

The Fiordland penguin or tawaki (*Eudyptes pachyrhynchus*) is the only crested penguin species to breed on the New Zealand mainland and, therefore, the only crested species in the world that lives in relative proximity to human settlements. Although only breeding in remote parts of the mainland and satellite islands in South Westland, Fiordland and Stewart Island that are mostly difficult of access tawaki are exposed to many anthropogenic influences including inshore fisheries, unregulated tourism, and pollution, that other crested penguins are not. The species is believed to have undergone a significant decline in recent decades, although it is unclear whether this trend continues. Currently, the official population estimates for the species range between 5,500 and 7,000 mature individuals (BirdLife International, 2018), although recent surveys suggest that tawaki are more common than generally thought. Until recently little was known about the species marine ecology; diet studies carried out in the 1980s found that the penguins fed predominantly on cephalopods and krill in an open coast environment, while fish dominated the diet in the Foveaux Strait region. Studies conducted since 2014 have significantly expanded our knowledge about the species.

Previous reviews of Tawaki biology and priority lists

The first detailed account of tawaki was published by John Warham (1974) which primarily focussed on terrestrial aspects of species biology. A comprehensive, encyclopaedic review was compiled by Marchant & Higgins (1990) which cites several sources that cannot be accessed today. A report summarised the results of the Department of Conservation’s monitoring programme and identified several issues related to survey design (McLellan, 2009). More recently a review of available knowledge largely based on unpublished reports was compiled by Mattern (2013); that chapter serves as basis for this review.

Research and conservation priorities for tawaki have been listed in Taylor (2000) and Mattern (2013). Both stress the urgent need for a better understanding of the species’ demography and marine ecology in order to improve conservation outcomes.

Here, we focus on aspects of the species' biology that are deemed most important for conservation. Below we list topics and relevant publications that will not be discussed in detail in this review.

- Genetic & Social monogamy (McLean et al., 2000)
- Vocalisation (Studholme, 1994)
- Egg formation (Grau, 1982) & reproductive endocrinology (McQueen, Davis & Young, 1998)
- Brood reduction (McLean, 1990; St Clair, 1992)

Conservation status

The Department of Conservation lists tawaki as 'Nationally Vulnerable' (criteria D, 5,000-20,000 mature individuals, predicted decline 10-50%; Robertson et al. 2017). The IUCN red list classified the species as 'Vulnerable' due to the species' small population that underwent 'rapid decline over the last three generations' (Birdlife International 2017).

Taxonomy

Fiordland penguins have only recently been recognised as distinct from the Snares penguins (*Eudyptes robustus*). In the 1970s, the Checklist of New Zealand Birds considered Snares, Fiordland (and even Erect-crested (*E sclateri*)) penguins as conspecifics (Kinsky, 1970). This was disputed due to morphological and ecological differences between each taxa (Stonehouse, 1971; Falla, Warham & Fleming, 1974; Warham, 1974a). In more recent decades, studies that examined relationships using morphology, protein data, and mitochondrial and nuclear DNA have all supported the recognition of three separate species (Davis & Renner, 2003; Baker et al., 2006; Ksepka, Bertelli & Giannini, 2006; Cole et al., 2019). Nevertheless, a review of the taxonomic status in 2008 still considered Fiordland and Snares penguins as conspecific (Christidis & Boles, 2008). Consultations by Birdlife International in 2014 led to the calculation of the Tobias score (Tobias et al., 2010), which demonstrated that tawaki and Snares penguins should be considered separate species (https://docs.google.com/spreadsheets/d/1f_19T94NhYfrqZCONBMEoqQ_IMZn8DSGKb6wqQMiiUk/edit?usp=sharing).

Distribution

Tawaki have been recovered from a number of natural fossil deposits and archaeological middens throughout coastal New Zealand, and there are numerous publications that summarise findings (e.g. Worthy 1997, Holdaway et al. 2001). Although difficult to distinguish from other crested penguins (and even *Megadyptes* penguins), most prehistoric specimens found to date on the New Zealand mainland were tawaki (Cole et al., 2019). The large number of bones excavated from many sites in coastal New Zealand indicate that tawaki have probably inhabited New Zealand at least since sea level stabilised, 6000 years ago.

It has been suggested that historically tawaki had a wider distribution with breeding sites in the north of the South Island and potentially even the lower North Island (Mattern, 2013a). However, recent studies seem to contradict this idea. A study looking at genetic information in prehistoric bones, museum skins and blood samples found that the genetic diversity of tawaki does not suggest any substantial range restriction over the last thousand years (Cole et al., 2019). Moreover, while historic samples were obtained from adult penguins found as far north as the North Cape, no juvenile bones or eggshells were excavated from the upper South Island or lower North Island. This may indicate that bones from these northern sites originate from vagrants rather than resident breeders. This hypothesis is further supported by a recent examination of the pre-moult dispersal in tawaki (Mattern et al., 2018c). The authors argue that genetic predisposition may drive the penguins to travel to the sub-Antarctic front some 2,000 km south of New Zealand and that the current range of the species likely represents the geographic extremes at which this strategy is viable.

Mattern (2013) provides an extensive list of tawaki breeding sites that have been surveyed in the past. Penguin numbers at 43 colonies have been estimated sometime between 1991 and 2009. On the mainland, tawaki range from Heretaniwha Point near Bruce Bay, South Westland (S43.59, E169.55) to Coal Island in southern Fiordland (S46.12, E166.63). In Foveaux Strait, the penguins breed on Solander Island/Hautere, Codfish Island/Whenua Hou, Stewart Island/Rakiura and its outliers (Mattern, 2013a).

Outside the breeding season, recent satellite tracking data suggests that tawaki spend most of the time prior to their moult in sub-Antarctic waters between 1,500 and 2,500 km south-east of the South Island (Mattern et al., 2018c). Outside the breeding season, tawaki (mostly moulting birds) have been observed around most of the South Island, but also on the Snares/Tini Heke, Auckland, Campbell and Macquarie Islands. They are common visitors to Tasmanian shores and are occasionally reported from southern West Australia all the way to New South Wales; there is one unconfirmed report of a tawaki on the Falkland Islands (Marchant & Higgins 1990). Where tawaki go after completing the moult is currently being investigated; it appears that birds tend to show similar dispersal movements to the pre-moult period (Mattern, unpublished data).

Numbers and population trends

A series of distribution surveys were carried out between 1990 and 1995 that covered most of the species' current breeding distribution (McLean & Russ, 1991; Russ, McLean & Studholm, 1992; McLean, Studholm & Russ, 1993; Studholm, Russ & McLean, 1994; McLean et al., 1997). To date these surveys represent the only attempt at an estimate of tawaki numbers. The authors concluded that there were 2,500-3,000 breeding pairs (McLean et al., 1997). However, methodology and scope of these surveys made undercounting of penguins highly likely (Mattern, 2013a). Using accounts published prior to 2016, a review of Fiordland penguins for the IUCN Red List concluded that there are between 2,500 and 9,999 mature individuals (BirdLife International, 2018).

However, more recently, nest counts carried out in Fiordland (Mattern & Long 2017) and South Westland (Long, 2017) found considerably more penguins than reported by the survey 20 years earlier. A ground survey conducted in Milford Sound/Piopiotahi in the spring of 2016 found 77 nests and resulted in an estimate of between 130 and 150 breeding pairs in this fjord (Mattern & Long, 2017), a stark contrast to the 9 nests found in the 1990s (McLean & Russ, 1991). Similarly, nest searches carried out in the spring of 2014 between Cascade River and Martins Bay found a total of 835 nests (Long, 2017); the previous estimate for that region was just 150 nests (McLean et al., 1997).

The estimates from the 1990s and recent surveys either indicate significant undercounts in the earlier surveys or suggest an increase in tawaki numbers in the past 20 years. McLean et al. (1997) themselves caution readers to consider their counts to be “a minimum estimate” due to the logistic constraints of their survey. So, undercounting certainly contributes to the apparent differences in penguin numbers between the 1990s and the recent surveys.

Most recent estimates of tawaki numbers (Long, 2017; Mattern & Long, 2017) can be used to adjust counts from the 1990s surveys. Along the southern West Coast Long (2017) counted 850 breeding pairs while McLean et al (1997) only recorded 150 pairs in the early 1990s suggesting a population increase (or previous underestimation) of approximately 566%. Similarly, the recent nest counts provided for the Milford Sound population of 77 breeding pairs (Mattern & Long, 2017) compared to 9 breeding pairs recorded there in 1990s would represent 770% increase in numbers. Assuming that much higher penguin numbers apply to the species’ entire breeding range and applying a conservative adjustment factor of 500% to the IUCN numbers, the current population size of tawaki could range between 12,500 and 50,000 mature individuals.

Yet, a recent paper analysing tawaki population trends using data from DOC’s monitoring programme that operated from 1990 to 2010 concludes that the tawaki population is still in decline (Otley et al., 2018), in line with the assessments in Taylor (2000) and the IUCN red list (BirdLife International, 2018).

However, other observations seem to suggest numbers have actually increased:

- Beach counts (n=1270 counts) of tawaki commuting between the sea and their breeding colonies at a beach north of Haast conducted over the past 20 years showed an increase in penguin numbers from an average 8 birds per observation in 1996 to 12 birds in 2017 (Gerry McSweeney, unpubl. data)

- Other credible observers have noted an increase in tawaki numbers in recent decades. Several tourist boat skippers operating in Milford Sound during the past two decades believe that penguin numbers have increased; as do some fishermen operating in Dusky Sound. Tawaki were seldom seen along the north-east coast of Stewart Island in the 1970s (K.-J. Wilson, pers. obs.), where in 2005 and 2014, they seemed to be omnipresent, both at sea as well as on land (Mattern, pers. obs., see http://www.tawaki-project.org/2014/11/07/little-cave-men/).
- Recently tawaki have attempted to breed in the Catlins which may suggest a range expansion for the species (Young, Pullar & McKinlay, 2015).
- Genetic analyses of 72 historic and recent tawaki samples found no evidence for significant changes in population size for tawaki over last thousand years (Cole et al., in review).

The assumption by Taylor (2000) that numbers were in decline was based on observations from a single site, Open Bay Islands. Between 1988 and 1995 the tawaki population on the island reportedly declined by 33% (St. Clair, 1998). However, during that period research that involved handling of eggs shortly after laying and daily nest checks was undertaken on the island (St Clair, 1992). As tawaki are perhaps the most timid of all crested penguin species (Ellenberg et al., 2015), that intensive research may have contributed to this apparent decline.

In this light it seems doubtful that negative population trends observed at Open Bay Islands are representative across the species' entire range. The information available does not allow us to determine population trends with any degree of certainty.

The diverse breeding and foraging habitats occupied by tawaki are reflected in notable differences in their ecology and demographic parameters. For example, while the breeding success and number of breeding tawaki from Jackson Head, West Coast was significantly impacted first by a strong El Niño in 2015 and then by an invasion of stoats (*Mustela erminea*) in 2016, the situation in Milford Sound was diametrically different with above average breeding success and stable nest numbers (Mattern & Ellenberg, 2016, 2017). Similarly, breeding success was found to be high and penguin numbers stable at Codfish Island/Whenua Hou in both 2016 and 2017 (Mattern & Ellenberg 2017; Mattern et al, unpubl. data). At some sites, terrestrial predators can have serious impacts on breeding success while at other sites these predators are absent (Mattern & Ellenberg, 2017). Predation by stoats varies season to season and site to site. At Jackson Head no predation events were recorded during the 2014, 2015 and 2017 seasons, yet all breeding attempts failed in 2016 with stoat predation being the likely main cause; at the same time no predation events were recorded at their Gorge River study site 45 km away (Wilson & Long 2018).

Tawaki are notoriously difficult to monitor. They mostly breed in inaccessible places such as in thick kiekie (*Freycinetia banksia*) vegetation, narrow rock crevices or labyrinthine caves making it very difficult to conduct reliable counts (e.g. Mattern 2013; Mattern & Long 2017, https://youtu.be/Z2Qc6SrGDjc). Observer experience and endurance is of utmost importance to achieve reproducible monitoring results and can significantly affect the reliability of ground counts. For example, on three consecutive surveys an increasing number of nests were found in previously overlooked areas even though the observers were highly experienced and knew the terrain extremely well (Long et al., 2009; Long, Long & Stewart, 2011; Long, 2017).

Overall, it is unlikely valid conclusions about population trends can be drawn from ground counts. The penguins' cryptic breeding habits and often impenetrable breeding habitat effectively prevents the application of traditional nest searches to obtain reliable information on population trends. Instead, a focus on determining key demographic parameters (i.e. survival rates, fecundity) from mark-recapture studies across their varied habitat should be used to assess population trajectories.

Demography

Between 1990 and 2010 the Department of Conservation conducted annual nest counts at various sites ranging from Codfish Island/Whenua Hou, Foveaux Strait to Monro Beach, South Westland, (Otley et al., 2018). More recently, double counts (the count repeated by a second team two days later) at selected sites were employed to minimize the potentially substantial observer error from the single counts prior to 2010; this indeed delivered more reliable population estimates (Ellenberg et al., 2015). However, limited resources have since led to a cessation of the DOC monitoring programme.

Based on the monitoring data, Otley et al. (2017) determined core demographic variables for the species. Survival probabilities were calculated to be around 89% for adult penguins, with juvenile survival – defined as survival until first breeding – estimated at 77%. Combined with a mean breeding success of 0.61±0.02 chicks per pair, tawaki core demographic variables appear to be higher than for most other crested penguin species (e.g. Guinard et al. 1998, Dehnhard et al. 2014, Morrison et al. 2015).

The Tawaki Project has researched the marine ecology of tawaki at three sites – Jackson Head, Milford Sound and Codfish Island/Whenua Hou – and in conjunction with this work has monitored breeding success. While breeding success at Jackson Head varied due to the aforementioned impacts of El Niño and stoat invasion between 0.12 and 0.94 chicks per pair (2014-2017), reproductive efforts of tawaki from Harrison Cove, Milford Sound were consistently high (0.8 – 1.1 chicks per pair, 2015-2017); breeding success was similarly high at least until crèching on Codfish Island/Whenua Hou (Mattern et al. unpubl. data). However, as with ground counts, determination of breeding success is difficult as chick survival can only be determined with certainty until the crèching stage during which chicks are highly mobile and often impossible to locate.

Breeding biology

Except for a few open nests, tawaki are cryptic breeders that prefer to nest in inaccessible locations. Along open coast sites like Jackson Head, the penguins tend to breed in dense, impenetrable kiekie shrub often in small clusters of nests (Warham 1974; Mattern, pers. obs.). At Gorge River, the penguins breed in a more open forest setting, primarily under tree roots or fallen trees, in amongst kiekie or tangles of supplejack (*Ripogonum scandens*) (Long 2017; Mattern, pers. obs.). In Harrison Cove, Milford Sound less than a third of all nests are under rock overhangs or upturned tree roots. Most of the nests are in rock crevices or in cavities and caves under rock falls. At Sinbad Gully, Milford Sound, the penguins occupy a steep slope that is dominated by windfall of rimu (*Dacrydium cupressinum*) and other large trees; a few kilometres up the fjord, the majority of the penguins nest in an extensive warren under remnants of a glacial moraine (Mattern & Long, 2017). On Codfish Island/Whenua Hou, the penguins breed in dense tree fern groves, mainly in dug out, deep burrows in the soft peaty soil or in deep hollows under tree roots, while along the north-east coast of Stewart Island the penguins breed in sea caves and fissures in cliffs only accessible from the sea (Mattern, pers. obs.).

Nests usually consist of shallow bowls lined with twigs and stones.

John Warham (1974) published the first and seminal account of tawaki breeding biology, although his observations were largely limited to a single site, Jackson Head. In the late 1980s and early 1990s, St Clair (1992, 1999) focussed on site fidelity and incubation behaviour in an effort to decipher the crested penguins' obligate brood reduction. Some aspects of the breeding biology of tawaki are also touched on by Ellenberg *et al*. (2015).

Mattern (2013) provides a detailed summary of the species breeding biology thus only a condensed account is presented here.

Tawaki return from three months at sea to their breeding colonies in mid-June, with the majority of penguins returning to the nest sites they used in the previous year; about two-thirds of the penguins reunite with their previous partner (Warham, 1974b; St Clair, 1999). Egg laying occurs over a 10-day period in late July and early August, the clutch size is two with the eggs being laid 3-6 days apart. As with other crested penguins, the first laid A egg is smaller than the second laid B egg, although the size difference is less marked than in other crested penguins (Warham, 1975). While largely synchronized within colonies, the timing of egg laying seems to vary between sites by as much as 2-3 weeks (Ellenberg et al., 2015).

In tawaki, the roles during incubation are the reverse of that in other crested penguins. The pair spends the first 5-10 days after the B-egg is laid together at the nest, the female then leaves on a two week long foraging trip (Warham, 1974b); in all other crested penguins it is the male that makes the first foraging trip (Warham, 1975). After the females return, the male penguins leave for up to two weeks usually returning a few days prior to egg hatching. Like all other crested penguins, tawaki are considered obligate brood reducers that generally only raise one chick. However, McLean *et al*. (2000) noted that in years when food is abundant, up to 12% of tawaki pairs can fledge both chicks. Some tawaki breeding in Milford Sound/Piopiotahi and on Codfish Island/Whenua Hou can also fledge both chicks (Mattern & Ellenberg, 2016, 2017, 2018b).

Eggs hatch throughout September, 31-36 days after the B-egg is laid (Warham, 1974b; St Clair, 1992). In nests where only one chick is raised, the smaller chick that hatched from the A-egg usually dies within a week after hatching, severely disadvantaged by smaller body size compared to its sibling. Both Marchant & Higgins (1990) and St Clair (1992) state that 50-60% of nests only hatch one egg; the rate of egg loss was lower during recent studies (Mattern & Ellenberg, 2015, 2016, 2017, 2018b). The male penguins guard the chicks for up to three weeks, while the female is the sole provider of food to her offspring (Warham, 1974b).

From early October, chicks may form small crèches that are often guarded by one male penguin. Mostly, however, both male and female undertake foraging trips at this stage. It is mainly the female that feeds the chicks, although males increase their food contribution closer to fledging (Warham, 1974b). Chicks fledge between mid-November and early December. The parents leave on their pre-moult foraging trips shortly after the chicks have fledged.

Moult

Satellite tracking of adult tawaki from Gorge River, South Westland during the pre-moult dispersal November 2016 to February 2017 found that the penguins travelled extraordinary distances compared to other crested penguins at this stage of the annual cycle (Mattern et al., 2018c). The birds left their colonies between mid-November and early December with those birds departing earlier travelling towards the subtropical front some 800-1000 km south of Tasmania, while penguins leaving in December ventured further south to the sub-Antarctic front southeast of Macquarie Island. Return journeys ranged from 3,500 – 6,800 km during the 8-10 week sojourn at sea before returning to the mainland to moult. Of the five birds that could be tracked for the entire trip, three penguins returned to their breeding colony at Gorge River to moult. The remaining two birds moulted at Dusky Sound and Sutherland Sound, respectively. Warham (1974) states that penguins generally return in mid-January and early February to moult. The satellite tracking study found that some birds may return as late as the end of February (Mattern et al., 2018c).

Although it has been stated that tawaki generally return to their breeding colonies to moult (Warham, 1974b), this seems to vary between sites. For example, tawaki colonies on the western side of Jackson Head were found to be virtually devoid of moulting penguins or sign that penguins had recently completed moulted there in February and March 2014-2018 (Mattern, pers. obs.). Instead, moulting tawaki are commonly seen in the nearby settlement of Neils Beach and along the coastal road to Jackson Bay (Geoff Robson, Greenstone Helicopters, pers. comm.). In Harrison Cove, Milford Sound/Piopiotahi, on the other hand, there seem to be more penguins moulting there than are present during the breeding period. On Codfish Island/Whenua Hou, the colonies seem to be largely occupied by moulters that had bred there months earlier (Mattern, pers. obs.).

Replacement of feathers takes roughly three weeks; the penguins then depart on their winter sojourns (Warham, 1974b).

Food and foraging

Until recently the only information available on the marine ecology of tawaki was derived from two studies of their diet in the early 1980s (van Heezik, 1989, 1990b). Prey taken varied between regions with arrow squid (*Nototodarus sloani*) (relative biomass contribution: 85%) and krill (13%) dominating the diet of tawaki from Martins Bay, Fiordland (van Heezik, 1989), while fish (85%), especially larval stages, were most important for penguins from Codfish Island/Whenua Hou, where cephalopods and crustaceans were minor constituents of their diet (van Heezik, 1990b). More recently, the prey composition of penguins from Jackson Head was investigated by identifying prey DNA in penguin scats (Julie McInnes *et al.*, unpubl. data). Fish were the most common prey category (frequency of occurrence: 75%) followed by cephalopods (15%) and krill (10%). Interestingly, jellyfish DNA was found in several of the samples which could indicate that, like yellow-eyed penguins (Mattern et al., in press), tawaki may feed on fish larvae associated with jellyfish.

Since the 2014 breeding season, The Tawaki Project has studied the foraging behaviour of chick rearing tawaki at sites representative of the species' varied marine habitat, i.e. Jackson Head, South Westland (continental shelf); Harrison Cove, Milford Sound/Piopiotahi (fjord); and Codfish Island/Whenua Hou, Foveaux Strait (shallow, coastal). The at-sea movements and diving behaviour differed significantly between these sites.

At Jackson Head, the penguins generally foraged between 10 and 50 km offshore, mostly north-west of the colony. Foraging ranges and trip durations were influenced by prevailing environmental conditions travelling further during longer duration trips during years dominated by southerly winds (e.g. El Niño conditions) while north-westerly winds appear to create more favourable foraging conditions closer to the coast (https://youtu.be/1c4B9sdL8Y0?t=12m50s).

During three years of research in Milford Sound/Piopiotahi, there has been just one observation of a penguin leaving the fjord. All other data clearly show that while feeding chicks tawaki forage exclusively within the fjord; most of the foraging activity occurring just 1-4 km from their breeding colony. It is noteworthy that the penguins tend to spend most of their time along the northern side of the fjord within one of New Zealand's few marine reserves (http://www.doc.govt.nz/parks-and-recreation/places-to-go/fiordland/places/fiordland-marine-reserves/maps-and-boundaries/piopiotahi-milford-sound/).

Tawaki from Codfish Island/Whenua Hou tracked in the 2016 and 2017 breeding seasons and have shown two types of foraging strategies. Birds either forage very close inshore following the coast line, presumably targeting prey in the kelp forests, or they travelled 20-30 km to the west where the shallow Foveaux Strait seafloor drops away into the deep-water Solander Trough (Mattern & Ellenberg 2017; Mattern et al. unpubl. data).

Overall, it appears that penguins from South Westland show the greatest foraging effort and are most susceptible to environmental perturbations. What this means for tawaki breeding along the open Fiordland coast – especially populations in interface regions where birds can choose to forage inside or outside the fjords (e.g. Breaksea Island, Shelter Islands) needs to be addressed.

Diving behaviour of tawaki is also being studied as part of The Tawaki Project. A maximum dive depth of 99 m has been recorded for a female from Jackson Head. However, most dives are considerably shallower, seldom exceeding 30 m, indicating that tawaki mostly feed close to the surface. Body acceleration has also been recorded which allows a more detailed analysis of the penguins' diving behaviour (e.g. Watanuki et al. 2006). Detailed analysis of all diving data is pending.

Predators

Although Warham (1974) states that seals are unlikely to play an important role in predation of tawaki, recent observations show that tawaki are taken by fur seals (*Arctocephalus forsteri*) in Milford Sound (Daniel Crook, Southern Discoveries, pers. comm.). Moreover, groups of fur seals apparently undertaking coordinated pursuit of tawaki have been observed at the entrance of the fjord (Turgut Ortabas, Southern Discoveries, pers. comm.). Dead tawaki have been found on beaches with obvious signs of shark bites (Mattern, pers. obs.). However, beyond this little is known about predation of tawaki at sea.

On land, stoats have a significant impact on breeding success during some years at some locations. At Jackson Head and Gorge River they have been observed to take eggs and kill tawaki chicks (Wilson & Long 2018, Mattern, pers. obs.). In the 2016 breeding season, an invasion of stoats apparently caused almost complete breeding failure on the western side of

Jackson Head. Yet in 2014, 2015 and 2017 no predation events were recorded at that colony (Wilson & Long 2018). Conversely at Gorge River, 45 km away, where nests were also monitored by motion activated cameras, one egg was taken by a stoat in both 2014 and 2015 but no predation events were recorded in 2016, the year stoats caused breeding failure at Jackson Head (Wilson & Long 2018). The 2016 breeding season followed a mast event in the podocarp forests near Jackson Head and the stoat invasion may have been a result of stoats moving onto the headland as food availability in the neighbouring forests declined. Disappearance of chicks at Jackson Head in 2016 only ceased after traps had been deployed and three stoats killed. A network of self-setting traps has since been established on Jackson Head. The effectiveness of ongoing predator control by the Wilderness Lodge Moeraki and the Department of Conservation at one site north of Haast using brodifacoum bait stations (until 2006) followed by regular 1080 drops is likely to be linked to increasing penguin numbers determined from beach counts during the past 20 years (Gerry McSweeney, pers. comm.).

The endemic weka (*Gallirallus australis*) preys upon tawaki eggs and chicks (McLean, 1990; St. Clair & St. Clair, 1992; Taylor, 2000). Weka have been introduced to some islands where tawaki breed including Open Bay Islands and Solander Island (Taylor 2000). However, Mattern (2013) suggests that if the impact of weka was severe, tawaki populations at those sites would probably have declined in the immediate years following weka introduction; yet both tawaki and weka remain common on both.

Taylor (2000) suggested rats (*Rattus sp.*), and brushtail possums (*Trichosurus vulpecula*) to be potential predators of tawaki eggs and chicks. Rats, mice and brushtail possums are present in the Jackson Head and Gorge River tawaki colonies, they frequently pass by and occasionally investigate tawaki nests but none have been seen preying on tawaki eggs, chicks or harassing adult penguins (Wilson & Long 2018). Rats and possums may scavenge expelled eggs and dead chicks (Mattern, pers. obs.). Dog attacks have been reported at some accessible breeding sites including Jackson Head (Jacinda Amey, DOC Haast, pers. comm.).

Human disturbance through research and unregulated tourism is believed to have a significant impact on tawaki (Taylor, 2000). While people's presence at landing sites do indeed cause delays when penguins want to come ashore, the penguins seem to be more tolerant to research interactions than previously expected (Mattern & Ellenberg, 2015). This is presumably due to the penguins' attachment and investment in their nest rather than a greater tolerance of disturbance (Ellenberg et al., 2015). Unregulated visits to the colony at Munro Beach, South Westland has apparently led to a decline in the numbers of tawaki breeding there although robust data to support this is lacking. Along the Jackson Bay Road, tawaki occasionally get run over by vehicles, particularly during the moult (Geoff Robson, Greenstone Helicopters, pers. comm.)

Threats

Comprehensive summaries of threats have been published in Mattern (2013) and Otley *et al*. (2018), however neither provides a threat level ranking or considers regional differences. In this report, we rank threats into major, medium and minor categories and provide a regional context.

Environmental disasters

Earthquakes

South Westland: Major
Fiordland: Major
Foveaux Strait: Medium

Mattern (2013) notes the high level of geological activity throughout the tawaki breeding range. Geological modelling found that a major earth quake (magnitude 8 or higher) in South Westland is likely to occur in the coming decades and this will have severe effects coastal habitats (Biasi et al. 2015, see also http://projectaf8.co.nz/). When such an earthquake occurs, it will affect most if not all of the tawaki breeding range, although the nesting habits of tawaki on Stewart Island and Codfish island/Whenua Hou where shaking will be less severe makes them less vulnerable to violent earth movements.

A large-scale earthquake would have the greatest impact if it were to strike during the breeding season, particularly nest formation and early incubation (June-July) and during the moult (February) when most adult penguins are in their colonies.

Pollution

Oil spills

South Westland: Medium
Fiordland: Major
Foveaux Strait: Major

Oil spills caused by shipping disasters would likely have a localized impact in the vicinity of the wreckage. The oil spill caused by the wreck of the container vessel *Rena* severely affected some 20-30 km of coast in the Bay of Plenty (Jones et al., 2016), although the impact could have been more widespread if more oil had been spilt (Schiel, Ross & Battershill, 2016). The *Rena* was wrecked close to Tauranga, a major port and city with all the infrastructure required to contain the oil spill and treat oiled wildlife; no such facilities exist close to areas inhabited by tawaki. Foveaux Strait is an important passage for international shipping (https://www.marinetraffic.com/en/ais/home/centerx:170.0/centery:-44.8/zoom:7), so that the region is more likely to experience a disaster than South Westland where there is little inshore boat traffic. In Fiordland, growing tourism numbers is leading to increased ship traffic; spills from large cruise vessels while in the fjords could severely impact local penguin populations. The risk of oil spills has been reduced after the recent termination of new offshore oil exploration leases. With the exception of one petroleum well some 50 km due west of Hokitika, there are currently no active oil exploration permits within the home range of breeding tawaki (http://data.nzpam.govt.nz/permitwebmaps?commodity=petroleum).

Fisheries interactions

Resource competition

South Westland: Minor
Fiordland: Minor
Foveaux Strait: Minor

Otley *et al*. (2018) discuss the potential for resource competition between commercial fisheries and tawaki. The authors conclude that due to the limited dietary information about tawaki, it is difficult to adequately assess competition between fisheries and penguins. That the penguins primarily target larval and juvenile stages of their prey species (van Heezik, 1989, 1990b) reduces the risk for direct competition with commercial fisheries. However, overfishing of prey stocks may reduce spawning biomass which could have an indirect effect on the penguins' diet.

Incidental bycatch

South Westland: Minor
Fiordland: Major (southern Fiordland)
Foveaux Strait: Major

In New Zealand, set net fisheries pose the single most significant cause of incidental mortality in penguins (Crawford et al., 2017). While the species has been assessed as having a low bycatch risk (Richard & Abraham, 2015), this assessment averages the risk across the entire tawaki breeding range. Furthermore, small vessel, inshore fisheries, those most likely to catch penguins, were not the focus of their analysis and these fisheries have very limited observer coverage. Thus, there is no robust estimate of tawaki bycatch. In 2016 two tawaki were killed in set nets in Dusky Sound in southern Fiordland (Crawford et al., 2017). Both birds drowned in nets targeting butterfish, a species that is primarily caught in kelp forests close to the coast, a habitat where tawaki forage. There is no set net ban in place around any of the islands in Foveaux Strait so that the risk of accidental bycatch of tawaki breeding in this region is real.

Marine predators

Otley *et al*. (2018) list inter-specific competition and predation by marine mammals as a threat. They note that recovering populations of Antarctic fur seals (*Arctocephalus gazella*) have top-down effects on Macaroni penguin (*Eudyptes chrysolophus*) populations. New

Zealand fur seal (*Arctocephalus forsteri*) numbers in South Westland may in fact be declining (Otley *et al*. 2018), suggesting that the impact of fur seals locally is likely to be negligible. Population trends for fur seals in Fiordland and Stewart Island are not known but increases are likely. Whether natural predators should (or would) be managed is a moot question, especially since any intervention is limited by the protective status of natural predators in New Zealand.

Terrestrial predators

Stoats

South Westland: Medium
Fiordland: Medium to low
Foveaux Strait: not a threat

Stoats can have a significant effect on the reproductive outcome of tawaki. There is little evidence to suggest that adult penguins are vulnerable to stoat predation (Otley et al., 2018). But the loss of most tawaki eggs or chicks at Jackson Head caused by stoats in August and September 2016 shows the potential severity mustelid invasions (Mattern & Ellenberg 2017, Wilson & Long 2018). The predatory pressure from stoats is highly variable – zero some seasons but almost total breeding failure in other years (Wilson & Long 2018) – and depends both on the availability of alternative prey (e.g. rats) as well as the abundance of stoats (Tompkins, Byrom & Pech, 2013). Mustelids are absent from those Foveaux Strait Islands where Tawaki breed and from some islands in South Westland (Open Bay Islands) and some sites in Fiordland.

Dogs

South Westland: Minor
Fiordland: not a threat
Foveaux Strait: not a threat

Uncontrolled dogs are still common in many of the West Coast's remote communities and occasional kills of tawaki by stray dogs occurs. While this is an unnecessary and avoidable threat, it is unlikely that dog attacks will reach a significance that may have population-wide consequences.

Weka

South Westland: Minor
Fiordland: not a threat
Foveaux Strait: Minor

Weka can only be considered a minor threat where the birds have been introduced by humans, i.e. Open Bay Island and Solander Island. Elsewhere weka are a natural predator of tawaki.

Disease

In the 1970s, an endemic blood parasite *Leucocytozoon tawaki* was isolated from tawaki with sandflies (*Austrosimulium sp*.) identified as the primary vector (Fallis, Bisset & Allison, 1976; Allison, Desser & Whitte, 1978). However, while *Leucocytozoon* appear to cause sporadic chick mortality in yellow-eyed penguins (Argilla, 2015), there is no other published evidence of ill-effects of these parasites in other penguin populations (Jones & Shellam, 1999; Vanstreels, Braga & Catão-Dias, 2016).

Avipox

South Westland: Minor
Fiordland: unknown
Foveaux Strait: unknown

Avipox is the only disease that has been observed to cause mortality in tawaki. So far, the virus has been reported only once in 2017 at a single site in South Westland and only affected a small number of chicks. In Magellanic penguins, fleas have been implicated as the primary vector for the virus (Kane et al., 2012); it seems plausible that in tawaki sandflies, may play this role.

Climate change

Ocean warming

South Westland: unknown
Fiordland: Minor
Foveaux Strait: unknown

Increasing sea surface temperatures have been implicated as a driving factor for population declines in crested penguin populations in New Zealand and elsewhere (Cunningham & Moors, 1994; Taylor, 2000; Hilton et al., 2006; Morrison et al., 2015). The population of Snares penguins has been stable throughout the last century despite significant variations in ocean temperatures (Mattern et al., 2009). With offshore foraging tawaki using similar subtropical water masses, it may be that tawaki are also is less affected by warming oceans than sub-Antarctic breeding crested penguins. However, the true impacts of warming oceans can only be assessed with further studies of their marine ecology and more reliable information about tawaki demography.

Weather extremes (E. Niño/La Niña)

South Westland: Major
Fiordland: Inner fjord birds not a threat, open coast birds unknown
Foveaux Strait: unknown

The strong El Niño in 2015 had a significant impact on the breeding success of offshore foraging tawaki at Jackson Head (Mattern & Ellenberg, 2016). Since the reversal of wind patterns and offshore dispersal of nutrients are believed to be responsible for the longer foraging ranges and lower foraging success in 2015, it must be assumed that similar effects were apparent along the entire open coast of South Westland and Fiordland. Although the 2017 breeding season coincided with a strong La Niña, the substantially higher than normal ocean temperatures were not reflected in the penguins' reproductive success. While still substantially lower when compared to Fiordland and Codfish Island/Whenua Hou penguins, many pairs at Jackson Head raised chicks to fledging. Nevertheless, foraging ranges were longer than during 'normal' years (Mattern, unpubl. data) indicating La Niña did affect the birds, albeit not as severely as El Niño. In Fiordland, the effect of El Niño appeared to be diametrically different with high breeding success and short foraging ranges that were little different to those in 2014 and 2016, indicating that the weather phenomena had no impact on Milford penguins. While no information about foraging behaviour or breeding success is available for Codfish Island/Whenua Hou during the 2015 El Niño, tawaki there performed trips during the 2017 La Niña that were comparable to 2016, when the environmental conditions were average. So, it seems that the penguins may have adequate coping mechanisms reducing the potential impact of weather extremes. However, as with ocean warming, these conclusions are based on few observations and further information is required.

Human disturbance

Unregulated visitation

South Westland: Medium
Fiordland: not a threat
Foveaux Strait: not a threat

Tawaki breed in areas that are mostly inaccessible to visitors. Nevertheless, a few tawaki breeding sites, in particular Monro Beach and to a lesser extent Jackson Head, receive frequent, largely unregulated visits from tourists, where people on the beach may deter tawaki from landing and, hence, disrupt provisioning of their chicks. This in turn, could reduce reproductive success and eventually a decline of local penguin numbers. A recent problem is disturbance of moulting tawaki by people wanting to take photographs or 'selfies' with penguins. These incidents usually only affect a few individuals and have little or no population-wide effect. The Wilderness Lodge at Lake Moeraki hold the only concession to take tourists to a nearby beach. Their visits are well regulated and pose no threat to the penguins, however, other less well-behaved people sometimes visit this colony (K-J. Wilson, pers. obs.).

Boat traffic

South Westland: Minor
Fiordland: Medium
Foveaux Strait: not a threat

While there are currently no obvious deleterious effects of boat traffic in Milford Sound/Piopiotahi, projected visitor numbers suggest that a substantial increase in the number of boats cruising the fjord is likely. Many of the boats drive close to the cliff walls on either side of the fjord where the penguins forage. This may pose a risk from prop strikes for diving penguins (e.g. Cannell *et al*. 2016). Although the effects of increasing underwater noise are not understood, it could have detrimental effects on both penguins and the distribution of their prey. There is little information about boat traffic in other fjords. Observations of fishing vessels in the southern fjords in the 1970s showed that many skippers were not considerate of wildlife (K.-J. Wilson, pers. obs.). If this still applies to the newer generation of fishermen and whether it poses a significant threat to local tawaki populations is unknown.

A proposed water pipeline and marine loading facility at Jackson Head could pose a threat to the local penguin population; particularly by stirring up of sediments that then drift towards Jackson Head reducing underwater visibility and compromise the penguins' ability to find food or make landfall.

Research Priorities

While recent research has advanced out knowledge about tawaki, the species remains one of the least known of the world's penguins. The demographic work in particular has raised more questions than answers. It is imperative to develop enhanced monitoring methods to get a better understanding of population trends.

1. Population monitoring

R.1.H1 **Investigate viability of automated monitoring solutions**

Using nest counts to acquire reliable data on demographic parameters has proven to be very difficult. Otley *et al*. (2017) suggest that the use of automated monitoring solutions (e.g. transponder gateways) would be impracticable for the use with tawaki due to the birds unpredictable landing sites. However, most breeding sites have access paths that are used by a large portion of the local penguin population. Therefore, automated identification systems using transponder tagged penguins may be a more reliable – and less resource demanding – method to assess population trends.

Establish transponder marked tawaki subpopulations that can be monitored permanently via an automated transponder reading setup. Viable sites could be Gorge River, Milford Sound, Doubtful Sound and Codfish Island/Whenua Hou; all sites have a more or less permanent human presence which would allow for maintenance of the system.

R.1.H2 **Establish marked populations at sites representative of the species diverse habitat (i.e. West coast, inner & outer Fiordland, Foveaux Strait)**

Using subcutaneous transponders, penguins can be marked with no impact on their hydrodynamics and the necessity for frequent band maintenance. At Jackson Head, Harrison Cove in Milford Sound/Piopiotahi, and on Codfish Island/Whenua Hou many penguins are already marked. In conjunction with automated monitoring gates, these marked populations would probably be a superior way to assess population trends than nest counts. However, each year, fledglings need to be marked. Hence, accessible sites should be chosen.

R.1.H3 **Conduct ground surveys in Fiordland and Stewart Island to establish occupancy densities**

While ground surveys are not suitable to reliably determine true numbers of breeding pairs, it is essential to establish where tawaki colonies are located. Of importance are the inside of the fjords and Stewart Island coast, where there is little information on penguin distribution. Penguin colonies should be mapped in detail to assess future changes.

Survey coastal regions of the major fjords and Stewart Island during the chick rearing period where penguin vocalisations can be used to detect breeding colonies. Ground surveys should be conducted by experienced observers.

R.1.H4 **Monitor breeding success**

Determining the actual breeding success in tawaki is difficult since chicks tend to move around the colony during the crèching stage. As a result, the likelihood of finding older chicks at their nest sites is reduced towards the end of the breeding season.

Develop better ways to monitor breeding success. Marking chicks early in crèching when they tend to return to the nest at night with transponders may be a viable option if used in combination with automated monitoring systems (see above) counting the number that eventually depart seawards. Another option could be to use time-lapse cameras that record penguin traffic on the beach during the fledging period and provide a measure of number of chicks that eventually leave the colony.

R.1.H5 **Examine regional variation in threats to survival (e.g. set net bycatch, predator presence) and breeding failure**.

R.1.M6 **Investigate the potential for range expansion of the species.**

Conduct regular surveys of areas suitable for, but not currently recorded as breeding habitat (e.g. Catlins, Otago Peninsula).

R.1.M7 **Examine the prevalence and distribution of disease pathogens and vectors throughout the species' breeding range.**

Particular emphasis should be on avian pox which caused the death of a chick on the West Coast and avian malaria which affects yellow-eyed penguins.

2. Marine Ecology

R.2.H1 **Examine the effects of environmental perturbations on the species across its diverse range.**

The substantially different effects of El Niño and La Niña on the foraging behaviour and success of penguins from coastal colonies compared to those foraging within a fjord have already been demonstrated. However, the environmental mechanisms underlying these differences are poorly understood. Could it be that fjords provide a safe haven for the species that buffers tawaki from major environmental perturbations? Does this also apply to tawaki from the Foveaux Strait region? Or are there regional differences between the coastal colonies along South Westland and the outer coast of Fiordland?

R.2.H2 **Study differences in foraging behaviour of penguins breeding deep inside fjords with conspecifics from the outer coastlines of Fiordland to assess habitat characteristics, influence on species distribution, and buffer capabilities in the face of environmental change.**

Essentially an extension of R.2.H1. Do tawaki breeding at the interface of fjord and open sea environments benefit from the ability to switch between foraging in one or other environment depending on environmental conditions?

R.2.H3 **Investigate fisheries impact**

The majority of the species breeding range is exempt from the set-net ban that covers most of the South Island's coastline. With their near-shore foraging strategies tawaki are prone to accidental entanglement in set net operations targeting butterfish.

Trial and establish video monitoring of near shore set netters to assess the frequency of tawaki-fisheries interactions and if necessary develop mitigation measures.

R.2.H4 **Monitor pre-moult and non-breeding dispersal**

The pre-moult period is probably the most critical period in any migratory penguin species, especially if the penguins have just completed a resource demanding breeding phase. Hence, foraging success during the pre-moult dispersal is likely to be crucial for annual adult survival. With the apparent enormous distances travelled during this period, the consequences of environmental perturbations at the penguins' travel destinations may have significant effects on survival. A multi-year, multi-site examination of pre-moult dispersal would provide insights into ways habitat variability affects penguin behaviour and survival.

Track tawaki annual pre-moult dispersal using geolocator devices (GLS) that can be deployed for long periods (up to 5 years, minimal maintenance) at key sites (i.e. South Westland, Fiordland, Foveaux Strait). Examine whether this could also be achieved with GPS dive loggers (i.e. similar to Whitehead *et al*. 2016).

We do not know where tawaki go between moult and breeding. Tracking tawaki over their winter dispersal will show whether the penguins are exposed to different threats from those suffered in their breeding range and provide further information about environmental variables dictating their movement patterns and survival.

Track tawaki through their winter dispersal with GLS loggers and satellite transmitters every 3-5 years

R.2.H5 **Establish a marine ecology monitoring programme during the breeding season**

With the limited information about tawaki's marine ecology, there is still a dearth of data to examine how environmental change may affect the species in its different foraging habitats. With advances in tracking technology increasing what aspects of penguins' at-sea behaviour can be recorded, establishing a regular monitoring protocol for comparing changes in foraging behaviour between sites and over time is now viable. Similar programmes have been established for little penguins in Australia which have significantly advanced understanding of environmental impacts and subsequent conservation responses (Pelletier et al. 2014; Saraux et al. 2016).

Deploy GPS dive loggers on 10-15 birds each year at three reference sites throughout the species range and assess annual variations in foraging parameters in response to environmental variables.

R.2.H6 **Examine diet composition**

We know very little about tawaki diet. What the penguins eat inside of fjord ecosystems needs to be investigated. Further information is required on foods from South Westland and the Foveaux Region. While stomach flushing has been found not to adversely affect penguins (Goldsworthy et al., 2016), less intrusive and less laborious methods maybe more suitable for tawaki.

Develop a database (or add to GenBank) of genetic barcodes for all potential prey species (including invertebrates that might not be detected with more traditional approaches). Use DNA faecal samples to determine prey composition at a range of *sites. Examine viability of animal-borne cameras to examine prey encounter rates, pursuit strategies and number of preys taken. Collect feather samples from every handled tawaki to establish a feather database for later analysis of diet composition trends using stable isotope analysis.*

R.2.M7 **Examine effects of Marine Reserves in Fiordland on foraging movements.** In Milford Sound/Piopiotahi, tawaki forage predominantly along the northern fjord boundaries within the Marine Reserve. Do the penguins forage in these regions as a result of environmental benefits due to the Marine Reserve (e.g. no holding pots)?

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Snares penguin
(*Eudyptes robustus*)

Thomas Mattern and Kerry-Jayne Wilson

Summary

The Snares penguin (*Eudyptes robustus*) is endemic to the small Snares archipelago some 200 km south of the New Zealand mainland. Although considered one of New Zealand's sub-Antarctic island groups, The Snares are located north of the Subtropical Front (STF) so that from an oceanographic and ecological perspective the penguins' breeding habitat is part of the same temperate zone as that of the three mainland species; tawaki (*E. pachyrhynchus*), little (*Eudyptula minor*) and yellow-eyed (*Megadyptes antipodes*) penguins. Unlike most other crested penguin species, the Snares penguin population appears to be stable at around 25,000 breeding pairs. However, the species' limited breeding distribution justifies the threat classification 'vulnerable' as listed by the IUCN and 'At Risk – Naturally Uncommon' in New Zealand's current conservation status assessment. Very little is known about the biology of this species. The most comprehensive study of the species was conducted in the late 1960s which focussed predominantly on breeding behaviour. Since then research projects have been few and limited. The diet has been assessed from chick dissection and stomach samples taken from breeding adult penguins indicating that krill is one of the main foods, although hard part remains of fish and squid suggest that these are important prey for the self-sustenance of adults. Limited information is available about the species' foraging behaviour. During incubation, male penguins appear to forage to the east along the STF while females may forage closer to the island. During the chick guard period, GPS logger deployments on 19 female penguins suggested they forage to the north of the island. The winter dispersal has been studied using geolocators which showed that the birds spent the non-breeding period south of Australia.

Previous reviews of Snares penguin biology and priority lists

The first detailed research on Snares penguins was published by John Warham which primarily focussed on terrestrial aspects of their biology (Warham, 1974a). A comprehensive, encyclopaedic review was compiled by Marchant & Higgins (1990a) which cites several sources that cannot be accessed today. Two unpublished reports by the Zoology Department of the University of Canterbury summarize studies of various aspects of the Snares penguin's biology (Johns et al., 1986; Miskelly et al., 1987). A more recent review of the Snares penguin (Mattern, 2013b) was based on the few studies ever conducted on this penguin:

- The ability of Snares penguin chicks to recognise of their parent's voices was studied in the 1980s (Proffitt & McLean, 1990).
- A PhD study examined the foraging ecology in the early 2000s. GPS logger technology was still its infancy and provided limited information about at-sea movements and diving behaviour (Mattern, 2006); a quantitative study of diet was conducted around the same time (Mattern et al., 2009).
- Two further studies investigated incubation positions of eggs (Massaro & Davis, 2004) and the colouration of the penguins' crests (McGraw et al., 2009).
- In 2013, the winter dispersal was studied using geolocation loggers (Thompson, 2016).

Research and conservation priorities for this penguin have been listed in Taylor (2000) and Mattern (2013a). Both are largely based on extrapolation from other species and both stress the need for a better understanding of the species' demography and marine ecology.

Taxonomy

Snares penguins have been recognised as a separate species since the 1950s (Oliver, 1953). Prior to this it was considered a subspecies of the erect-crested penguin (*E. sclateri*) (Falla, 1935). The phylogenetic relationship between Snares penguins and tawaki (*E. pachyrhynchus*) have been debated. In the 1970s, the Checklist of New Zealand Birds considered Snares penguins, tawaki and erect-crested penguins as conspecifics (Kinsky, 1970) despite morphological and ecological differences between each taxa (Stonehouse, 1971; Falla, Warham & Fleming, 1974; Warham, 1974a). Subsequent studies that examined relationships using morphology, protein data, and mitochondrial and nuclear DNA have all supported the recognition of three separate species (Cole *et a*l. in review, Davis & Renner 2003, Baker *et al*. 2006, Ksepka *et al*. 2006). Nevertheless, one recent review of their taxonomic status still considered Snares and Fiordland penguins as conspecific (Christidis & Boles, 2008). Consultations by Birdlife International in 2014 led to the calculation of the Tobias score (Tobias et al., 2010), which demonstrated that Snares penguins should be considered a separate species from tawaki. (https://docs.google.com/spreadsheets/d/1f_19T94NhYfrqZCONBMEoqQ_IMZn8DSGKb6wqQMiiUk/edit?usp=sharing).

There may be a substantial difference in the onset of breeding between the Snares penguins on the main island and those on the nearby Western Chain, with Western Chain penguins breeding 15 to 44 days later than those on the main island (Fleming & Baker, 1973; Sagar, 1977; Miskelly et al., 2001). Considering that the temporal separation of breeding between Fiordland and Snares penguins has been important in the most recent species status, a closer examination of the Western Chain population is urgent (Mattern, 2013b). A phylogenetic comparison using mitochondrial DNA found no evidence to suggest birds from the Snares and Western Chain are different from one another (Cole *et al*. In Review).

Conservation status

Department of Conservation lists Snares penguins as ‘At Risk - Naturally Uncommon’, criteria IE (island endemic) and OL (one location). The IUCN red list classifies the species as ‘Vulnerable’ due to the species being restricted to a single location making them susceptible to stochastic events (BirdLife International, 2017b).

Distribution

Snares penguins only breed on the Snares Islands (S48.024°, E166.603°), a small archipelago (ca. 3 km²) approximately 200 km south of mainland New Zealand. The penguins predominately inhabit the eastern regions of North East Island, Broughton Island and the Western Chain, a chain of rocky islands ca. 5 km to the west of North East Island (Mattern, 2013b). The species has probably always been restricted to these islands, and based on fossil evidence, it is unlikely they ever inhabited the New Zealand South Island (Teresa Cole, unpublished data).

During the breeding season, Snares penguins seem to remain within 200-300 km of the Islands while eggs are incubated, with foraging ranges further restricted to 50-80 km to the north of the Island during the chick guard stage (Mattern, 2006). No information about the at-sea distribution is available for the crèching stage of chick growth or the pre-moult period. When not breeding, Snares penguins forage in sub-Antarctic and sub-tropical seas south of Australia (Thompson, 2016). Moulting Snares penguins are frequently observed on the mainland, the Chatham Islands (Miskelly & Bell, 2004), Tasmania (Woehler, 1992; Cole et al., 2017), and Macquarie Island (Marchant & Higgins, 1990c). There are two reports of Snares penguins reaching the Falkland Islands (Lamey, 1990; Demongin et al., 2010).

Numbers and population trends

Early estimates of population size ranged from 11,000 to 20,000 breeding pairs (Warham, 1974a; Johns et al., 1986; Warham, Spurr & Clark, 1986; Miskelly et al., 1987). Those estimates were based on chick counts and likely underestimated the true population size (Mattern, 2013b). Nevertheless, these chick counts revealed a general trend of a population increase between 1968 and 1986 although the author was cautious and added that this “general increase” could also be accounted for by variation in reproductive success (Tennyson, 1987). Since 2000, four complete land-based population counts have been conducted by the Department of Conservation; the next census is scheduled for October 2020 (Joseph Roberts, DOC Southland, pers. comm.). These four censuses ranged between 24,666 and 30,000 nests (Table 1) (Hiscock & Chilvers, 2016). Overall, the population can be considered stable today. Based on molecular data of fossil bones, museum skins and contemporary blood samples, the population has probably remained stable over at least the last millennia (Cole *et a*l., in review). Moreover, there is no indication that Snares penguins have experienced major shifts in the prey composition that may have caused population declines (Mattern et al., 2009).

***Table 1**. Population estimates of Snares penguins.*

Year of count	**Method**	**Number of breeding pairs**	**Reference**
1968	chick counts	11,000	Warham (1974)
1982	chick counts	20,000	Warham *et al*. (1986)
1984	chick counts	37,600	Warham *et al*. (1986)
1985	chick counts	23,250	Marchant & Higgins (1990)
2000	nest counts	30,577	Hiscock & Chilvers (2016)
2008	nest counts	24,666	Hiscock & Chilvers (2016)
2010	nest counts	30,672	Hiscock & Chilvers (2016)
2013	nest counts	29,009	Hiscock & Chilvers (2016)

Demography

There is no robust data available on the key demographic parameters. A first attempt at collating a life history table for Snares penguins was based on a banding programme initiated in 1968 and was presented at the 1st International Penguin Conference in 1988. Based on various expedition reports (Johns et al., 1986; Miskelly et al., 1987), the published abstract (McLean, Johns & Miskelly, 1988) states that the oldest bird recorded was 21+ years. From that life table, chick survival varied greatly between years with first year survival ranging from 4.9% in 1982/83 to 39.2% the following year. Fewer than 50% of banded adults found had been sighted as yearlings. Annual survival of birds aged one to five years is given as >50%.

Breeding sites

On North East Island, Snares penguins breed in colonies of ranging from 10 up to 1,400 nests (median: 137 nests, n=112 colonies; Amey *et al*. 2001). Most colonies are located under a forest canopy of the tree daisy (*Olearia lyalli*) or in between *Hebe elliptica* shrubs; larger colonies have killed off all vegetation within the confines of the colony (Mattern, 2013b). On Broughton Island, colonies are situated in the open (Warham, 1974a) while on the Western Chain penguins breed under boulders and in rock crevices (Miskelly, 1984) probably reflecting habitat available rather than penguin preference. Nests are usually scooped-out hollows lined with mud and peat mixed with stones, twigs, or bones (Mattern, 2013b).

Breeding biology

Their breeding biology is the only aspect of the Snares penguins' ecology that has seen comprehensive investigation (Warham, 1974a). The species breeding period is well defined with highly synchronous annual patterns. Adults arrive in early September from their winter dispersal. The two eggs comprising the clutch are laid approximately 4-5 days apart in late September and early October. Both adults stay at their nest until mid-October when male penguins leave the island to forage for about 2 weeks while females incubate the eggs. The male exodus is highly synchronized and appears to happen every year around 13 October, suggesting that day length (photoperiod) may be an important trigger (Mattern et al., 2018a). Once males return, the females leave on a foraging trip which lasts around a week, to return in time for the hatching of the eggs. The smaller first-laid egg (A-egg) usually hatches after the larger, second laid B egg, although in clutches with more pronounced egg-size differences the A-egg may hatch at the same time or even earlier than the B-egg (Massaro & Davis, 2004). Both eggs hatch in about 60% of nests, but chicks from the A-egg usually die within a week after hatching (Warham, 1974a). On rare occasions, both chicks survive until the crèche stage (Mattern, 2013b). The male penguins guard their offspring for their first three weeks after hatching at which time the chicks start to form crèches. During the crèche stage, both parents forage although it is predominantly the females that feed their chicks. It appears that chicks are able to recognize their parents by voice very soon after hatching (Proffitt, 1988; Proffitt & McLean, 1990). Chicks fledge in mid-to late January; by early February, when adults leave on the pre-moult trips, all chicks have left the island (Warham, 1974a).

Moult

Chicks start to shed their down in late December and have completed their moult into juvenile plumage by mid-January (Warham, 1974a). Yearlings return to the island in early November but only start to moult in mid-January; once moulted into their adult plumage the young birds leave the island in early February. Adult Snares penguins return from their pre-moult migration in mid-March. It takes the birds between 24 and 30 days to fully replace their feathers and the island starts to empty of penguins from late April. By late May, all penguins have left the island.

Food and foraging

The limited information on Snares penguin foraging ecology available derives mainly from a three year study that investigated the penguins' at-sea movements using GPS loggers and dive recorders (Mattern, 2006). GPS loggers suitable for use on deep-diving animals were still in their infancy, the study was plagued by technical problems as well as the need to develop best-use practices and programming (Mattern et al., 2005). As a result, the study did not record any data in its first year, partial foraging tracks (the first 2-3 days) of just three male penguins during the incubation period (Mattern et al., 2018a) as well as five data sets from females feeding young chicks in the second year, and, in the third year, 14 GPS data sets on chick rearing females (Mattern, 2006). Better results were achieved with the dive recorders where data representing 18 foraging trips were recorded in the second year, and 14 foraging trips in the third year.

Data suggested that during incubation, male penguins foraged due east of the Snares towards the Subtropical Front (STF) some 200-300 km from the island. Their movement trajectories seemed to coincide with the onset of the spring phytoplankton bloom at the STF (Mattern et al., 2018a). While travelling the penguins were diving no deeper than 30-40 m; however, once at the STF dives of up to 120 m were recorded (Mattern et al., 2018a). No GPS data was obtained for females during the incubation period, but ambient temperatures recorded by the dive loggers on two females indicated that the birds remained in warmer waters north of the STF.

When feeding young chicks, female Snares penguins were foraging within a 100 km radius north and northeast of the island, where they spent on average 32-37 hours at sea traveling up to 160 km. There were marked differences in dive depths between the two years that data was recorded, with penguins diving for longer and to greater depths in 2004 than in 2003 (2003 vs. 2004 - dive time: 56±11 s vs. 80±16 s; dive depth: 18±4 m vs. 29±8 m). A likely depression of the thermocline hence deeper distribution of the penguins' prey probably explains these differences. Most foraging dives were recorded at least 50 km from the Island and it appeared as if the birds sought out warmer waters close to Stewart Island (Mattern, 2006).

In 2014, researchers from NIWA deployed geolocator devices on 45 Snares penguins at the end of the moult. Using light sensors to measure sunrise and sunset times to approximate the penguins' geographic position throughout winter, the study managed to reconstruct the travel paths of a number of birds. The penguins generally headed west, past Tasmania to regions about 1,500 km south of south-central Australia before returning to their breeding colonies in September (Thompson, 2016). It is likely these patterns have remained the same at least over the last several thousand years, as prehistoric Snares (or crested) penguin remains have been often been recorded in Tasmania (Cole et al., 2017).

Predators

The main predators of Snares penguins are assumed to be Hooker's sea lions (*Phocarctos hookeri*), New Zealand fur seals (*Arctocephalus fosteri*) and leopard seals (*Hydrurga leptonyx*) (Mattern, 2013b). Other marine predators probably include sharks and orca (*Orcinus orca*) (Davis & Renner, 2003). Predation at sea is assumed to be infrequent. On land, chicks and injured or sick adult Snares penguins may fall prey to Subantarctic skuas (*Catharacta antarctica lonnbergi*); eggs and small chicks that have fallen out of the nest may sometimes be scavenged by red-billed gulls (*Larus novaehollandiae*) (Mattern, 2013b). Fledglings making their way to the ocean are intercepted and killed by northern giant petrels (*Macronectes halli*) that congregate at the main penguin launching areas in January (Horning & Horning, 1974). The Snares are one of the few regions in New Zealand that has never had introduced terrestrial mammalian predators.

Disease and parasites

A serological study carried out in 1947 on The Snares found that 10.7% of the sampled penguins were carrying the blood parasite *Plasmodium relictum* which is responsible for outbreaks of avian malaria (Vanstreels, Braga & Catão-Dias, 2016). However, we do not know whether such outbreaks have occurred in the past due to a lack of observational data. The authors suggest that the narrow geographic distribution of the penguins combined with the presence of mosquitoes that can act as disease vectors could result in significant disease outbreaks.

Threats

A summary of threats have been published in (Mattern, 2013b). Here, we expand on that list and rank threats into major, medium and minor categories.

Environmental disasters

Oil spills - medium

Oil spills following shipping disasters would likely have a localized impact near and downstream of the wreckage. The oil spill caused by the wreckage of the container vessel *Rena* in 2016 severely affected some 20-30 km of coast line in the Bay of Plenty (Jones et al., 2016), although the impact could have been more widespread if more oil had spilt from the wreck (Schiel, Ross & Battershill, 2016). Compared to the mainland, marine traffic near The Snares is sparse (https://www.marinetraffic.com/en/ais/home/centerx:167.3/centery:-47.9/zoom:8) but as the islands are uninhabited and far removed from oil spill response infrastructure, while an oil spill is unlikely the consequences are dire, particularly so if it occurred during the breeding season when most of the world population is feeding locally. The greatest threat of oil spill, therefore, comes from cruise ships and fishing vessels that visit the islands throughout their summer breeding season.

There are active offshore petroleum exploration permits for seas some 150 km to the northeast of the Snares as well as other petroleum exploratory wells within a 200 km radius spanning from southeast to northeast of The Snares (http://data.nzpam.govt.nz/permitwebmaps?commodity=petroleum). These areas are visited by male penguins during the incubation phase so that any oil leakage could potentially affect the birds. However, with the prevailing eastwards and northwards currents that characterize this section of the ocean, it seems unlikely that oil leaks from these sources would reach The Snares.

Fisheries interactions

Resource competition - minor

There are fisheries that target the Snares penguins' main fish and cephalopod prey species. The commercial fishing zones adjacent to the Snares include a substantial fishery for red cod (*Pseudophycis bachus*) (2017/18fishing season: up to 281,000 kg); arrow squid (*Nototodantarus sloanii*) (up to 2,920,000 kg), and redbait (*Emmelichthys nitidus*) (up to 21,000 kg) (Ministry of Primary Industries, 2018), all of which are believed to be important prey items for adult Snares penguins during the breeding season (Mattern et al., 2009). Hence, there is potential for resource competition.

Incidental bycatch - medium

While the set-net fishery in New Zealand is largely confined to the continental shelf surrounding the mainland, the Snares penguins' tendency to forage close to Stewart Island during the chick-rearing period may expose them to set-nets. Moreover, it appears that some set netters may have been operating near The Snares. If that were the case, it could be devastating considering most of the population are commuting to and from the island throughout the breeding season (Mattern, 2013b).

Marine predators

Hooker's sea lions, New Zealand fur seals and leopard seals occasionally take Snares penguins (Mattern, pers. obs.). Sharks and orca may also kill the occasional penguin (Davis & Renner, 2003). Predation at sea is assumed to be rare, natural thus, may have minimal impact on the penguin population (Warham, 1974a).

Terrestrial predators

The Snares are the only near-pristine island groups in New Zealand. So far none of the introduced mammal predators that prey on mainland penguins have got to The Snares. The accidental introduction of mammals would have catastrophic consequences for the entire island ecosystem. Probably the greatest risk is the introduction of rats as a result of illegal landings from fishing vessels (Dingwall, 1995).

Disease

With the information at hand (or the lack thereof), it is impossible to say to what degree Snares penguins may be affected by diseases. Penguins with what appeared to be a skin disease resulting in bare patches of skin on the face and flippers have occasionally been observed (Mattern, pers. obs.). Currently, The Snares are rarely visited and research deemed by DOC as non-essential and is, thus, discouraged. Hence, a disease outbreak would be unlikely to be detected. Similarly, there is no information on the prevalence of potential disease vectors. As a result, it is impossible to assess the threat level.

Avian malaria - unknown

Avian malaria was detected in Snares penguins in the 1940s (Vanstreels, Braga & Catão-Dias, 2016). Recent outbreaks of the disease in yellow-eyed penguins on the mainland show the growing risk this mosquito-borne parasite poses due to climate change. The Snares, where mosquitoes have been found to be present but not yet recorded breeding there(Vanstreels, Braga & Catão-Dias, 2016), with its many small bodies of standing water probably provide breeding sites for mosquitos (Tompkins & Gleeson, 2006). If a warmer climate translates to an increased prevalence of mosquitoes on The Snares, this may increase the risk of avian malaria outbreaks (Tompkins & Gleeson, 2006). As the Snares are seldom visited, such outbreaks will likely go unnoticed.

Avipox – unknown

In the 2017/18 breeding season, the first death of a New Zealand penguin – a tawaki chick – from infection of the avian poxvirus (*Poxviridae*) has been confirmed (Ralph Vanstreels, pers. comm.). Tawaki are frequent visitors to The Snares, which could facilitate transmission of the disease if suitable vectors were present. While sand flies (the most likely vector for tawaki) are absent on The Snares, mosquitoes are possible vectors. As with outbreaks of avian malaria, it seems unlikely that the current management would allow the detection of an outbreak of this disease.

Climate change

Ocean warming - unknown

Rising sea surface temperatures have been implicated as a factor causing population declines in other crested penguin populations in New Zealand and elsewhere (Cunningham & Moors, 1994; Taylor, 2000; Hilton et al., 2006; Morrison et al., 2015). The population of Snares penguins has apparently been stable throughout the last century despite significant variations in ocean temperatures (Mattern et al., 2009). However, ocean temperatures around New Zealand mainland – the same water mass that also surrounds The Snares – have been rising steadily in the past 20 years and have contributed to the population declines in yellow-eyed penguins (Mattern et al., 2017b). The impact ocean warming may have on Snares penguins is unknown.

Weather extremes (El Niño/La Niña) – unknown

The El Niño weather phenomenon appears to negatively affect tawaki along the open coast of New Zealand; the strong 2015/16 El Niño resulted in extremely poor breeding success (Mattern & Ellenberg, 2016). Snares penguins forage in a similar marine environment; however, whether El Niño conditions also affect their breeding performance is unknown.

Human disturbance

Cruise vessels – minor

The Snares are visited by various cruise vessels that operate in the New Zealand sub-Antarctic region. While landings are not permitted passengers are usually transported close to the shore in inflatable boats. While Snares penguins appear to have a greater tolerance to human presence than other penguin species, constant exposure to human disturbance may still affect the birds (Ellenberg et al., 2012). People in boats may be perceived differently by the penguins than people on land, which makes it difficult to assess to what degree penguins may be affected by cruise boat visitors.

Visitors to the island – minor

The Department of Conservation restricts visitors to The Snares to essential conservation and research and this has limited research on the penguins (Mattern, 2013b).. , Compared to penguin species on the mainland, Snares penguins are remarkably tolerant to the presence of humans. Only intensive interactions like daily handling of eggs over extended periods have been found to be a significant cause of stress for the penguins, while infrequent close-quarter interactions have no apparent effect on the birds (Ellenberg et al., 2012). As such, researcher impact if managed properly does not negatively impact on the birds.

Research Priorities

Together with the endangered erect-crested penguin, Snares penguins are the least known and studied of the world's penguin species. Considering the relative proximity of The Snares to the New Zealand mainland research on the species should be logistically more feasible than species inhabiting the other sub-Antarctic islands. However, because their population is stable, research on the species is deemed non-essential by the Department of Conservation. If the population starts declining it will be difficult to assess the driving causes, and develop effective management strategies, a scenario that has emerged in the recent decades for erect-crested and to a lesser extent for eastern rockhopper penguins. We suggest that research that provides baseline information on Snares penguins is important.

1. Population monitoring

R.1.H1 **Continue comprehensive ground surveys at 3-6-year intervals**

The ground surveys conducted by the Department of Conservation in the past 20 years have provided the only robust and reliable population assessments available for any of the New Zealand penguin species. It is vital that this research continues using similar methodologies. The interval of these surveys ideally should be shorter. In the past surveys were conducted every 7 or 8 years (with the exception of a re-survey two years after a decline in penguin numbers was detected). If the population was affected by a disease outbreak or environmental catastrophes, these may not be detected for some years.

Conduct complete ground counts of penguins on the entire Snares archipelago, on two consecutive years at 3-6 year intervals

R.1.H2 **Investigate viability of automated monitoring solutions**

While ground surveys allow reliable and robust censuses of the Snares penguin breeding population, the infrequent nature of these surveys makes it difficult to detect population trends in a timely manner. As with the other sub-Antarctic crested penguin species, the use of automated time-lapse camera monitoring systems may offer a viable solution to this dilemma (Black, Rey & Hart, 2017; Black et al., 2018; Jones et al., 2018). Investigations into best practices and reliability of such systems should be of a high priority.

Deploy a network of cameras to establish deployments and maintenance protocols and examine accuracy of penguin counts from time-lapse imagery under different conditions (i.e. forest vs open, small vs. large colonies).

R.1.H3 **Initiate studies to gather information on key demographic parameters, including survival rates, breeding success and recruitment.**

Breeding success is one of the key demographic parameters and is vital for population modelling. Time-lapse photography may be suitable to monitor breeding success as well as return rates of juveniles. Survival rates can only be determined using a marked population; the penguin landing at Station Cove would be ideal for an automated ID gateway.

Establish a network of time-lapse cameras to determine annual breeding success. Larger colonies may be most suitable. The best set-up for the monitoring systems need to be determined so that eggs, chicks and later crèches can be counted from the footage.

R.1.M4 **Investigate the causes of breeding failure and whether colony properties such as exposed vs. forest colonies and colony size influence breeding success.**

R.1.M5 **Examine prevalence of diseases and abundance of disease vectors**
Particularly, with regards to avian pox which has recently caused mortality in tawaki chicks and avian malaria which has become an issue in mainland Yellow-eyed penguin populations.

R.1.L6 **Determine the degree of asynchrony in timing of breeding between the main island and Western Chain.**

R.1.L7 **Study the impact skuas, pinnipeds and giant petrels have on mortality of eggs, chicks and adults.**

2. Marine Ecology

R.2.H1 **Record baseline information on foraging ecology during breeding**
Our current knowledge of the Snares penguin's marine ecology is based on a few deployments of GPS dive loggers in the early 2000s. The data does not provide enough information to assess how the penguins may be affected by a changing climate and increasing ocean temperatures. A five-year research programme (similar to the one currently conducted on tawaki) will provide a solid baseline that can be used in the future. Ideally, this research would be conducted in tandem on the main island and the Western Chain to establish whether the apparent differences in the timing of breeding are reflected in the foraging behaviour of the penguins.

i. *Deployment of GPS dive loggers during all stages of breeding; 10 males & females during incubation; 10-20 females during chick guard, 10-20 males & females during crèching.*
ii. *Diet composition to be examined using stable isotope analysis of feathers and blood, prey DNA analysis of penguin faeces and the deployment of camera loggers (in combination with GPS dive loggers, see above).*

R.2.H2 **Examine pre-moult and winter dispersal**
The pre-moult period is probably the most crucial period for any migratory penguin species, especially if the penguins have just completed their resource demanding breeding. Hence, foraging success during the pre-moult dispersal is likely to be crucial for adult survival.

Track Snares penguins' annual pre-moult dispersal using geolocator devices (GLS) that can be deployed for long periods (up to 5 years, minimal maintenance). Examine whether this could also be achieved with GPS dive loggers (i.e. similar to Whitehead *et al*. 2016).

Tracking Snares penguins during their winter dispersal will show whether the penguins are exposed to different threats to those close to their breeding colonies and provide further information about environmental variables dictating their movement patterns and survival.

Track Snares penguins through their winter dispersal with GLS loggers and satellite transmitters every 3-5 years

R.2.H3 **Comprehensive study of diet composition using faecal DNA analysis and deployment of animal-borne cameras.**

R.2.H4 **Stable isotope analysis of blood, ideally in conjunction with tawaki, during incubation period to examine which water masses are visited during longer foraging trips.**

R.2.M5 **If timing differences between the main island and Western Chain are verified, conduct comparative study of at-sea movements of birds from both areas.**

3. Disease monitoring

R.3.M1 **Screen the population for avian malaria**
Repeat the study from the 1940s to determine the prevalence of *Plasmodium* in the penguins and other resident seabird species (e.g. sooty shearwaters) and introduced songbirds (blackbirds, thrush).

R.3.M2 **Investigate prevalence of disease vectors**
The Snares may provide ideal breeding ground for disease vectors like mosquitoes. Particularly problematic areas (e.g. ponds, depressions prone to flooding) on the island need to be located and mapped to facilitate their future management.

R.3.M3 **Investigate potential gateways for disease vectors**
Assess the presence of potential disease vectors and investigate how these could arrive on The Snares. This is essential to develop effective quarantine protocols.

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Eastern Rockhopper Penguin

(*Eudyptes filholi*)

Kerry-Jayne Wilson and Thomas Mattern

Summary

The rockhopper penguins are the smallest of the crested penguins and although outnumbered by erect-crested penguins (*Eudyptes sclateri*) within New Zealand, are nevertheless globally the most widespread and most numerous of the New Zealand breeding *Eudyptes* penguins. Rockhopper penguins have a circumpolar range, breeding on many islands in the sub-Antarctic Zone. Currently three taxa are recognised with just one of these, the eastern rockhopper penguin (*Eudyptes filholi*) breeding in the New Zealand Region; on Campbell, Antipodes and Auckland Islands as well as nearby Macquarie Island. In the early to mid-20th century Campbell Island was the stronghold for the eastern rockhopper penguin, but numbers there have declined by about 94 % since the 1940s. Eastern rockhopper populations have also declined in numbers at both Antipodes and Auckland Islands, although the extent of decline is not adequately quantified for those islands. Rockhopper penguin populations have also declined at most other breeding islands elsewhere in the Southern Ocean.

A reduction in food availability due to ocean warming associated with climate change is implicated in the declines on Campbell Island and presumably elsewhere, although at some colonies on Campbell Island other threats including predation and harassment by New Zealand sea lions (*Phocarctos hookeri*) have contributed to the declines observed.

The breeding biology, foods and marine ecology of rockhopper penguins has been studied to varying extents at Campbell Island, but there is little information on these birds from the Antipodes Islands. For the Auckland Islands even the distribution of colonies is inadequately mapped and estimations of their numbers there are rough at best.

Taxonomy

All rockhopper penguins were once considered to be a single species (*E. chrysocome*) (Marchant & Higgins 1990). Birdlife International (2017) and the Global Penguin Society recognise two species, the northern rockhopper penguin (*E. moseleyi*) (Cuthbert 2013) and the southern rockhopper penguin (*E. chrysocome*), the latter with two sub-species (Pütz *et al*. 2013, del Hoyo & Collar 2014). Although many recent papers treat the resident eastern rockhoppers as a subspecies (*E. chrysocome filholi*) (e.g. Morrison et al 2015) the New

Zealand checklist elevates these to full species status, the resident eastern rockhoppers as *E. filholi* and the western rockhoppers as *E. chrysocome* (Gill *et al*. 2010). Both northern and western rockhopper penguins have been recorded in New Zealand as very rare vagrants. In this report we follow Gill *et al*. (2010) and Banks *et al*. (2006) in treating the eastern rockhopper penguin as a full species. A guide to distinguishing between the three rockhopper taxa is given by Heather & Robertson (2015).

The northern rockhopper penguin breeds only on the Tristan da Cunha Islands and Gough Island in the South Atlantic Ocean and Ile Amsterdam and St Paul Islands in the Indian Ocean (Cuthbert 2013). The western rockhopper penguin breeds in southern South America and the Falkland Islands and the more widespread eastern rockhopper on sub-Antarctic Islands in the Indian and Pacific Oceans (Pütz *et al*. 2013). In the wider New Zealand Region, they breed on the Campbell, Auckland, Antipodes and Macquarie Islands (Pütz *et al*. 2013).

All rockhopper taxa have declined in numbers with the global populations of the southern taxon (including both eastern and western rockhoppers) by 34% and northern rockhopper penguins by 57% in the last 37 years (BirdLife International 2018).

Previous reviews of eastern rockhopper penguin biology and priority lists

The chapter by Pütz *et al*. (2013) presents a good review of what is known about the southern rockhopper penguin, presenting information on both eastern and western taxa. Marchant & Higgins (1990) is more encyclopaedic drawing together snippets of information often overlooked in other reviews but as they treat all three rockhopper taxa as a single species, information presented there needs to be used with care. The comparative review of the crested penguin species by John Warham (1975) is still a useful detailed overview particularly of those populations breeding in the New Zealand Region. Other descriptions of the rockhopper penguin (e.g. Morrison 2013, De Roy *et al*. 2013) were written primarily for a general audience and provide rather brief introductions to the species.

Two recent workshops, one for seabirds in general (Wilson & Waugh 2013) the other for New Zealand penguins (Wilson & Otley 2014) identified research required for the conservation of New Zealand penguins. Neither went through peer review and both are less detailed than required for our purposes. Research and conservation priorities for Rockhopper Penguins have been listed by Birdlife (2010), Taylor (2000) and with less detail by Pütz *et al*. (2013) and Baird (2016).

Our review and the research and conservation priorities listed herein relate specifically to the New Zealand populations of the eastern rockhopper penguin.

Conservation status

The Department of Conservation lists the eastern rockhopper penguin as 'nationally vulnerable' (Robertson et al. 2017) and IUCN as 'vulnerable' (Birdlife 2018).

Distribution

Within the New Zealand Region eastern rockhopper penguins breed on Campbell, Auckland and Antipodes Islands and on nearby Macquarie Island (Pütz *et al*. 2013, Marchant & Higgins 1990). The distribution of rockhopper penguin colonies on Campbell Island has been mapped three times, the early 1940's, in 1984 (Moors 1986, Cunningham & Moors 1994) and 2012 (Morrison *et al*. 2015). Morrison *et al*. (2015) includes a table showing the history of occupation of each Campbell Island colony in 1958, 1975, 1984, 1985-87 and 2010-12. Most colonies are either on the western most peninsula or on the exposed west coast of the Island.

On the Antipodes Islands rockhopper penguins breed in amongst the much more numerous erect-crested penguins. The maps of crested penguin colonies in Hiscock and Chilvers (2014) and Hiscock (2013) show 103 colonies fairly evenly distributed around the main island and on Bollons, Archway and the eastern most of the Windward Islands. There is an implied assumption that eastern rockhopper penguins are present in most if not all of these colonies.

The distribution on the Auckland Islands is poorly documented. Known colonies have been mapped by Bell (1975) and by Cooper (1992), but both surveys were primarily boat-based with observations made as the vessel cruised slowly along the cliff-bound north, west and south coasts where most rockhopper penguins breed. As most colonies are small and surveying these rugged, cliff-bound, exposed coasts is challenging, it would be easy to miss entire colonies. The 14 known breeding colonies are mostly on the southern half of the west coast and the western sector of the north coast of the main Auckland Island, with just one colony on the south coast of Adams Island, one on Disappointment Island, and four colonies between Chambres Inlet and Falla Peninsula on the east coast (Bell 1975, Cooper 1992).

Rockhopper penguins occur as vagrants or beach-cast individuals on the New Zealand mainland and at The Snares (Marchant & Higgins 1990, Powlesland 1982) but few sightings are identified to species level and as all three rockhopper taxa have been positively identified in the New Zealand Region (Heather & Robertson 2015) these records do not provide reliable insights into the non-breeding distributions of eastern rockhopper penguins. Cole *et al.* (in review) genetically identified >40 prehistoric or archaeological midden crested penguin bones collected from North and South Islands, none were from rockhopper penguins. Given the abundance of eastern rockhopper penguins on the New Zealand sub-Antarctic Islands and Macquarie Island, the paucity of records from the New Zealand mainland may be indicative of a more southerly non-breeding foraging range than for the other New Zealand crested penguins.

Numbers and population trends

Campbell Island, once the stronghold of the eastern rockhopper penguin, indeed one of the largest populations of any of the rockhopper taxa, has suffered massive declines since the first population estimate was made by J.H. Sorensen who was a coast watcher there during the Second World War. Since then his initial estimate of five million birds has been reassessed, considering counts, observations, nesting densities and photographs (mostly unpublished) made by more recent observers. Sorensen's estimate was initially revised downward to about 1.6 million breeding rockhopper penguins (814,550 pairs) (Moors 1986, Cunningham & Moors 1994), then Morrison *et al*. (2015) again adjusted the estimate using knowledge not available to the earlier researchers, suggesting there were 619,925 breeding pairs on Campbell Island in the early 1940's. Based on colony photos taken in 1942 and re-photographed in 1987, Cunningham and Moors (1994) estimated that by 1984-87 numbers had declined by 94% to about 103,100 individuals which would translate to a maximum of 51,550 pairs. The 1984 estimate further adjusted to 42,528 pairs (Morrison *et al*. 2015) (Table 1). Cunningham and Moors (1994) calculated the area occupied by penguin colonies in the 1940's was 406,600 m^2 but just 25,500 m^2 in the 1980s. They thought that the decline had begun by 1945 (with a major reduction in numbers until 1956) and attributed the decline to warming ocean temperatures, with a temporary increase in penguin numbers in the 1960's during a cooling period (Cunningham & Moors 1994).

The Campbell population was assessed again in 2012 using a combination of ground counts and photographs, this time estimating the population to be 33,239 breeding pairs, a decline of 21.8% from an adjusted population of 42,528 pairs in 1984 and a 94.6% decline from an adjusted estimate of 619,925 breeding pairs in 1942 (Morrison *et al*. 2015) (Table 1). The recent declines were greatest between 1984 and 1996 after which time the overall population increased concurrent with lower sea surface temperatures (SST) (Morrison *et al*. 2015). They calculated the decline between 1984 and 2012 to be slower (k = 0.991) than that between 1942 and 1984 (k = 0.940). The population trends were not identical across all colonies, the differences linked to predation by New Zealand sea lions (*Phocarctos hookeri*) at those colonies most accessible to the sea lions (Morrison *et al*. 2017).

In November 1950 R.A. Falla (in Warham & Bell 1979) suggested that rockhopper penguins outnumbered erect-crested penguins on the Antipodes Island, the reverse to that recorded by all later surveys. In 1978 a total of 50,000 pairs spread between 86 colonies were estimated to breed on the Antipodes Islands (R.H. Taylor in Marchant & Higgins 1990). No information for the basis for this estimate is given. A survey in 1995 found a maximum of 3,400 pairs on Antipodes and Bollons Islands (Taylor 2000) with a total of 4,000 when the

Archway Islands were also included (Tennyson *et al*. 2002). Photos of the Ringdove Bay colony showed a huge decline from tens of thousands in 1950 to just a few individuals in 1995 (Taylor 2000).

A further estimate of rockhopper numbers was made for the Antipodes Island in 2011; of the 39,701 penguins counted in ground counts, 2475 (7%) were rockhoppers, the rest being erect-crested penguins (Hiscock & Chilvers 2014). In total 42,689 nests were counted, the remainder from observation points or from a boat, suggesting there were about 2,988 pairs of rockhopper penguins (7% of 42,689) on the Antipodes in 2011 (Table 1).

A partial survey of penguin colonies at the Antipodes Island in 2014 found that the breeding population in those colonies resurveyed had declined on average by 19% since 2011 (Chilvers & Hiscock, in review). In January 2014, a major storm caused extensive landslides on the Antipodes Islands with 44% of the penguin colonies losing area due to landslides or were partially buried by landslide debris (Chilvers & Hiscock, in review). The magnitude of the decline was roughly proportional to the area of colony affected, with an 11.7% decline in colonies not impacted by landslides, but 39.9% in colonies that had lost at least 75% of their area to landslides (Chilvers & Hiscock, in review). With global climate change major storms such as the one in January 2014 are predicted to become more frequent.

There are no accurate estimates of the numbers of Rockhopper Penguins at the Auckland Islands. Based on a single day, boat-based survey of the west coast of the main island, plus surveys of parts of the east coast from a dingy during the 1972-73 summer, Bell (1975) estimated there to be between 5,000 and 10,000 pairs at the Auckland Islands. The only other estimate is that by Cooper (1992) based on a two-day visit to the islands in January 1990. They surveyed the northern and western coasts of the main island and the southern coast of Adams Island from a boat and visited the four known colonies on the east coast. They located nine breeding colonies and based on an apparent reduction in area occupied estimated the total population to be 2,700 – 3,600 pairs (Cooper 1992). R. Russ was present during both surveys and thought the colonies were much smaller than he remembered from 1972-73.

While undertaking actual counts is logistically challenging, molecular based monitoring using population genetics and genomics may provide an alternative way to estimate population trends, perhaps even allowing effective population sizes to be estimated (T. Cole pers. comm.).

***Table 1**. Population estimates of eastern rockhopper penguins in the New Zealand region.*

Year of count	**Campbell Island**	**Antipodes Islands**	**Auckland Islands**	**Reference**

1942	619,925 pairs**			Morrison *et al*. 2015
1972/73			5,000-10,000 pairs*	Bell 1975
1978		50,000 pairs*		R.H. Taylor in Marchant & Higgins 1990
1984-87	42,528 pairs**			Morrison *et al*. 2015
1990			2,700 – 3,600 pairs	Cooper 1992
1995		4,000 pairs		Tennyson et al. 2002
2011		2,988 pairs		Hiscock & Chilvers 2014
2012	33,239 pairs			Morrison *et al*. 2015

**estimate of questionable accuracy.*

***adjusted population estimates, the original estimates are included in the text above.*

Numbers have also declined at Macquarie Island where in 2007 the estimate of 32,000–43,000 pairs was significantly less than past estimates (BirdLife International 2018).

Rockhopper Penguins and sea surface temperatures

Cunningham and Moors (1994) were the first to link population trends in Campbell Island rockhopper penguins to changes in sea surface temperature (SST), but then the best SST data available were weekly measurements taken near the entrance of Perseverance Harbour, not necessarily indicative of SST where the penguins fed. Average SST were already increasing in the 1940's and the 5-year running means peaked at 9.7°C in 1948-49 and 9.6°C in 1953-54. Temperatures cooled after 1957 to a low of 8.9°C in 1965, then rose to 10.2°C by 1970 (Cunningham & Moors 1994). The 1946-56 warm period was when they believed penguin populations declined most rapidly. There was a temporary resurgence in penguin numbers in the one colony where the best data is available following that cool period, the population increase lagging behind the temperature decline, the lag equating to the years it takes fledglings produced to recruit into the breeding population (Cunningham & Moors 1994).

Recent advances in satellite technology, the online availability of oceanographic data and computing power has allowed much more robust analyses of the relationship between SST and changes in penguin populations. Morrison *et al*. (2015) were able to compare a 100-year time series (1913-2012) of extended reconstructed sea surface temperatures (ERSST) with changes in penguin populations. The ERSST data were based on ship and buoy SST measurements prior to 1985 and since then also included satellite measurements. Monthly ERSST data were downloaded for a rectangular area centred on Campbell Island, encompassing the expected foraging radius of the penguins during chick-rearing (Morrison *et al*. 2015). While they also used a 5-year moving average for ERSST in their analysis, they could do this for winter as well as summer ERSSTs. In addition to the average ERSST, they were able to compare population changes against temperature anomalies (Morrison *et al*. 2015).

Morrison *et al*. (2015) showed that on Campbell Island rockhopper penguin numbers declined during warm periods and recovered during cool periods, although the initial decline began before the regional ERSST began to increase. Since 1996 penguin numbers have rebounded a little, coincident to the current global warming hiatus, lower ERSST and increased abundance of a key prey species (Morrison *et al*. 2015). The timing of population fluctuations and changes in ERSST are not exact, one changing a few years before the other, partly due to the lag before fledglings join the breeding population but complicated by other marine factors (Morrison *et al*. 2015). They predict the long-term population decline will begin again once global climate warming resumes.

ERSST for both summer and winter from 1913 to 2012 reveal three periods of contrasting trends: a cool period 1913–1950, a warm middle era 1951–1989 with cooler years in the late 1960s, and a return to cooler temperatures 1990–2012, with a few warmer years in the early 2000s (Morrison *et al*. 2015). The average difference in monthly ERSST values was just 0.30^{o}C between the 1913–1944 era when rockhopper populations were large and the 1945–1995 period of decline, and this was driven more by temperature increases over winter than summer. The increase in penguin numbers between 1996 and 2012 corresponds to a decline of just 0.06°C relative to the preceding warm period, driven primarily by lower temperatures over spring and summer (Morrison *et al*. 2015).

The frequency of seasonal temperature anomalies is probably more significant than the ERSST means. During the 1913-1944 cool period just 3.1 % of years had ERSST temperature anomalies, whereas during the 1945–1995 warm period 17.6 % of years were unusually warm, but none were as warm as those anomalous years in the 1996–2012 cool period (Morrison *et al*. 2015).

The penguins are not responding to SST directly but to changes in food availability within foraging range from their breeding colonies, with better foraging conditions during years with low SST than warmer SST. It appears that rockhoppers experienced greater food availability, consequently higher reproductive success and survival during the cooler period after 1990. The average year class strength of Southern blue whiting (*Micromesistius australis*), the main prey of the Campbell Island rockhopper penguins was c.3.8 times greater during the recent cool era (1990–2009) than the warmer years of 1977–1989 (Dunn & Hanchet 2014 from Morrison *et al*. 2015).

Stable isotope ratio analysis (SIA) of carbon and nitrogen can provide information on the trophic level targeted. SIA is based on the predictable and quantifiable ways that the ratio of carbon isotopes ^{13}C and ^{12}C, expressed as δ13C and nitrogen isotopes ^{15}N/^{14}N expressed as δ15N change at different trophic levels (Hilton *et al*. 2006). Hilton *et al*. (2006) compared δ15N and δ13C from the feathers from living penguins with those from museum specimens, some collected during the 19th century, to see how diet may have changed over time.

Hilton *et al*. (2006) treated all rockhopper penguins as a single taxon, thus including in their analysis the northern rockhoppers from Tristan du Cuna and Amsterdam Islands, western rockhoppers from the Atlantic and eastern rockhoppers from the Indian, and Pacific Oceans. They include data from rockhopper penguins from Campbell and Antipodes Islands and it is the results from these two sites discussed here. δ13C decreased significantly over time at seven breeding sites, including the Antipodes, but not at Campbell Island where no significant isotopic trends were evident (Hilton *et al*. 2006). The decrease in δ13C values at Antipodes Islands, and those other sites where δ13C declined, is indicative of decreases in primary productivity in the seas exploited by penguins from those sites, correlated with the observed declines in those penguin populations (Hilton *et al*. 2006). There was some evidence of a long-term decline in δ15N at some sites, indicative of a shift in diet to prey of lower trophic status, although this was not significant for Antipodes Island (Hilton *et al*. 2006).

Breeding biology

Rockhopper penguins breed in colonies that range in size from a few tens to thousands, in some colonies nest density may exceed two nests per square metre. On the Antipodes Islands, rockhopper penguins nest in mixed colonies alongside erect-crested penguins, the rockhoppers often with some form of overhead shelter, tending to be above, inland from and in rougher terrain than the larger erect-crested penguins (Warham 1975, Warham & Bell 1979). Rockhoppers may nest in small caves, under boulders and among tussocks up to 200 m inland and up to 100 m above sea level (Morrison 2013).

As with other crested penguins rockhoppers lay a single clutch of two eggs each year. The smaller first laid A egg followed 4-5 days later by the larger B egg (Pütz *et al*. 2013, Warham 1963). The breeding biology has been studied intensively at Macquarie Island (Hull *et al*. 2004 and references cited therein). Incubation begins once the B egg is laid and normally the A egg, or the chick from the A egg is lost during incubation or soon after hatching. Proportionality more rockhopper penguin A eggs hatch than in most other crested penguins, but only under exceptional circumstances do both chicks fledge. The incubation period is 32-

34 days with the female taking the first incubation spell while the male is at sea, his opportunity to replenish body reserves after a month ashore. At Macquarie Island the male's foraging trip lasts on average 12 days (range 9-17 days) (Warham 1963), at Campbell Island 13-16 days (Morrison *et al*. 2017) during which time the female must remain ashore incubating the eggs. After hatching the male remains at the nest guarding his chick for about three weeks, during which time the female alone provisions the chick, usually returning with food daily. On first leaving his chick the male usually makes a multi-day foraging trip, typically of 7-11 days, replenishing his own body reserves after a fast of over three weeks when he was confined to the nest (Pütz *et al*. 2013, Morrison *et al*. 2016).

The cause and function of egg-size dimorphism in crested penguins has been debated by many researchers over the last 50 years but has yet to be satisfactorily resolved. The debate continues, and the current theories are discussed by Morrison (2016).

Once the guard stage is over, chicks form creches while waiting for their parents to return with food. Once the male ends his post guard foraging trip, both parents return to feed their chick at or close to the nest every few days, until the chick fledges about 70 days after hatching (Morrison *et al*. 2016, Pütz *et al*. 2013). Well-fed rockhopper penguin chicks can reach a peak weight greater than that of their parents, slimming down before fledging (Warham 1975). As with other crested penguins there is delayed maturity and few breed before they are five years of age, but contrary to Warham's (1975) assertion that they breed annually thereafter, more recent research at Macquarie Island showed just 8% of males and 3% of females bred in all three study years (Hull *et al*. 2004). Their breeding biology is similar at Campbell Island (Morrison *et al*. 2017).

At Macquarie Island the first males arrived at their breeding colonies between 14 and 17 October in 1960, 1961, 1993, 1994 and 1995 (Warham 1963, Hull *et al*. 2004), with the timing of the breeding cycle constant between years (Hull *et al*. 2004). The females joined their mates at the nest on average 6.5 days later. Laying was well synchronised as in other crested penguins (Warham 1975). At Macquarie Island eggs were laid between 7 and 18 November (Warham 1963); the median date of laying the A egg was 13 or 14 November (1993-1995) and the B egg 17-19 November (Hull *et al*. 2004). The interval between arrival and laying of the second egg was 17 to 21 days (Warham 1963).

At Macquarie Island the median hatching date was 18-21 December (1993-1995) (Hull *et al*. 2004) with both parents present at the time of hatching. At Antipodes Island the guard stage lasted until at least 27 December 2002, the median end of the guard stage being 30 December (Sagar *et al*. 2005). During the guard stage females usually returned from mid-afternoon each day to feed chicks, while during post-guard stage males returned most evenings with female parents returning less often; the chicks being fed most days in both guard and post-guard stages (Sagar *et al*. 2005). At Macquarie Island chicks fledged between 24 February and 10 March (Warham 1963), the median date over three years ranging from

21 to 24 February (Hull *et al*. 2004). The timing of the breeding season is similar at Campbell island (Morrison 2016, Morrison *et al*. 2014, 2016) with the dates for each stage of the cycle in Table 1 of Morrison *et al*. (2014).

At the Antipodes Islands rockhopper penguins breed about 12 days earlier than at Macquarie Island, probably arriving about 7 October, a month after the erect-crested penguins with whom they share colonies. Antipodes rockhoppers laid about 1 November with eggs hatching about 4 December (Warham 1972, Warham & Bell 1979). By late January chicks were well grown, some were fully feathered by 5 February; the first chicks left the island on 9 February 1969 and most had fledged by 20 February (Warham 1972, Warham & Bell 1979). Breeding at Campbell Island is earlier than Macquarie but later than at Antipodes Island, with the peak of egg-laying about 9 November (Warham 1972). At Campbell Island chicks fledge mid-February (Morrison et al 2017).

Morrison *et al*. (2016) compared breeding success and foraging trip durations, the frequency at which chicks were fed and chick growth in rockhopper penguins at Campbell Island in 2011 when food was abundant, with 2012 when food was scarce. In 2012, both hatching success (0.69 in 2011, 0.58 in 2012) and reproductive success (0.60 in 2011, 0.35in 2012) were lower, and mean foraging trips during guard and creche stages longer than in 2011 when feeding conditions were more favourable. Chicks were fed about half as often in 2012 and mean chick mass at 30-31 days of age in 2011 was 1466 +/-201 g compared to 1025 +/-233 g in 2012 (Morrison *et al*. 2016).

It has been suggested that the breeding regime of crested penguins, where the male has an unbroken three- to five-week period fasting ashore during late incubation and the guard stage, followed by a multi-day foraging trip before he can begin to provision the chick, limits these penguins ability to respond when food is in short supply (Morrison *et al*. 2016). This they postulate, renders crested penguins more vulnerable to climate change than other penguin species where both sexes alternate brooding and feeding during the guard stage.

At Macquarie Island year to year nest site and mate fidelity has been reported to be about 50%. (Pütz et al 2013), a statement at odds with Hull *et al*.'s (2004) finding that few individuals breed in consecutive years. At Campbell Island nest site and mate fidelity was high (Morrison unpubl. data).

At Macquarie Island a few non-breeding birds were ashore from the start of the breeding season until the end of the guard stage. They had limited success at finding partners until incubation and chick rearing was underway when fewer aggressive breeding penguins were present, and non-breeders had greater freedom to wander through the colony seeking partners (Warham 1963). Some non-breeding birds managed to acquire nest sites vacated by failed breeders and form partnerships (Warham 1963).

At Campbell Island first year non-breeding penguins began coming ashore in early December and were common from mid-December through January. The last count was made just before observers left the islands in late January in both 2011 and 2012 was the highest suggesting numbers ashore may have continued to increase later in the summer (Morrison *et al*. 2016). At Macquarie Island yearlings were first seen ashore about 10 December, they were quieter than and dominated by older penguins, some formed short-lived liaisons with other immatures, non-breeding adults or even chicks.

Moult

At Campbell Island sub-adults moult in January (Morrison *et al*. 2017) while at Antipodes Island most yearlings had moulted by about 15 February and all adults appeared to be at sea on their pre-moult excursion on 12 March (Warham & Bell 1979). On Macquarie Island the pre-moult absence lasts 28-35 days suggesting that adults would return to the Antipodes to moult about 5-10 April (Warham & Bell 1979). At Macquarie Island yearlings began moult around 16 January, non-breeding adults in late February and breeding birds from late March (Warham 1963).

Food and foraging

Rockhopper Penguins are opportunistic foragers, with variation in their diet and foraging ecology between the different breeding populations, presumably reflecting availability more so than preference (Pütz *et al*. 2013).

The most common prey taken by eastern rockhopper penguins at Campbell Island in 1985 and 1986 were dwarf cod (*Austrophycis marginata*), and juveniles of southern blue whiting and hake (*Merluccius australis*), in contrast to a euphausiid dominated diet elsewhere (Cunningham & Moors 1994, Cooper *et al*. 1990, Sagar *et al*. 2005). At Macquarie Island, euphausiids principally *Euphausia vallentini* comprised 62% and 70% of food by weight in two different studies (Horne 1985, Hindell 1988, Hindell *et al*. 1995) in which the euphausiid *Thysanoessa gregaria* (Horne 1985) and the fish *Krefftichthys anderssoni* (Hindell *et al*. 1995) were other important prey. At Macquarie Island one *Zanclorhynchus spinifer* was 60 mm long and five *Nothothenia* sp were <100 mm in length (Horne 1985).

Cooper *et al*. (1990) reviewed what was then known about crested penguin diet and compare the foods of southern rockhopper penguins across their range. The prey species taken by Campbell Island rockhopper penguins are listed in Table 2. Xavier *et al*. (2018) recorded eight species of juvenile and sub-adult cephalopods taken by rockhopper penguins at Campbell Island, with *Onykia ingens*, *Martialia hyadesi* and *Octopus campbelli* being the most important species by frequency of occurrence, number and mass. At the time of writing only an abstract of the paper by Xavier *et al*. (2018) was available. There is little other information on the diet of rockhopper penguins from the New Zealand Region.

Table 2. *Foods known to be taken by Eastern Rockhopper Penguins at Campbell Island. From Cooper et al. (1990) with additional cephalopods from Xavier et al. (2018)*

Crustaceans	**Fish**	**Cephalopods**
Euphausia sp	*Electrona subaspera*	*Kondakovia longimana*
Thysanoessa sp	*Paranotothenia magellanica*	*Alluroteuthis antarcticus*
T. gregaria	*Austrophycis marginata*	*Moroteuthis injens*
Hyperiid amphipods	*Micromesistius australis*	*Octopus dofleini*
Cyllopus sp	*Halargyreus johnsoni*	*Onykia ingens*
C. magellanicus	*Merluccius australis*	*Martialia hyadesi*
Gammarid amphipods,	Congiopodidae	*Octopus campbelli*
Calanoid copepods		
Heterosquilla tricarinata		
Nectocarcinus sp		
Majidae		

The mean fledgling weights of Campbell Island chicks in 1987 and 1988 was 1992 g (1560-2400 g), significantly lighter than western rockhopper penguins at the Falkland Islands, the difference attributed to their fish diet (Cunningham & Moors 1994).

A fish-based, high tropic level diet is often assumed to be better for penguins than a diet based on lower trophic level cephalopod and crustacean prey. However, contrary to predictions a study using stable isotopes found that during incubation male Campbell Island rockhopper penguins were heavier in 2011 when lower trophic level, offshore, pelagic, zoo-plankton dominated their diet than in 2012 when their diet was primarily benthic, inshore, fish and cephalopods (Morrison *et al*. 2014). Similarly, in 2011 average chick mass was higher than in 2012. They attributed this unexpected result to the low energy density of the southern blue whiting that was thought to dominate their diet in 2012 (Morrison *et al*. 2014).

Information of foods consumed as well as parasites, bacteria and the sex and genotype of the bird can now be obtained by molecular analysis of scats. This is non-invasive and samples can be obtained even during very brief visits. Any study wishing to utilise this method will need to ensure a genetic database (such as GenBank's BLAST; https://blast.ncbi.nlm.nih.gov/Blast.cgi) of all potential prey items is available to compare sequence data to, as a reduced database will limit the power of the analysis and miss potential food species.

Within the New Zealand Region there has been just one study tracking rockhopper penguins at sea. This was conducted on the Antipodes Island from 18 December 2002 to 3 January

2003 (Sagar *et al*. 2005). During the guard stage eight tracked females foraged 22-54 km (mean 36.4 km) from their colony. The mean distance travelled on a feeding trip was 81.6 km (range 50-114 km), going NNE to feed where the sea was 500-1500 m deep, or east to waters >1500 m in depth (Sagar *et al.* 2005). During the guard stage the mean duration of feeding trips for tracked birds was 1.37 days, significantly longer than that of birds unimpeded by tracking devices. Two female penguins were tracked on post-guard trips, for one the trip duration was 5.67 days, the maximum distance from the colony 104 km, in total traveling an estimated 243 km. The other was at sea for 6.92 days, at furthest was 119 km from the colony and travelled about 325 km (Sagar *et al.* 2005). Both foraged along the subantarctic slope in waters >1500 m deep.

Rockhopper Penguins spend the five to six months between breeding seasons at sea, seldom if ever touching land. Campbell Island adult Rockhopper penguins spent the winter south-east or east of the island some birds travelling about 15,000 km during that period (Thompson, 2016). On average the maximum distance from the Island was about 2,000 km, with one bird 4,000 km from the island.

Predators

Of the three islands in the New Zealand Region where rockhopper penguins breed, Antipodes Island had only mice (*Mus musculus*) (eradicated in 2016). At Campbell Island sheep (*Ovis aries*), cattle (*Bos taurus*), Norway rats (*Rattus norvegicus*) and cats (*Felis catus*), all since eradicated were present. At the Auckland Islands feral cats, pigs (*Sus scrofa*) and mice are present on the main island but there are no introduced mammals on Disappointment and Adams Islands, the only other islands in the Auckland archipelago where rockhopper penguins breed. On Campbell Island disturbance by sheep or people did not contribute to population declines as population trends were similar in colonies accessible and inaccessible to these mammals (Moors 1986, Cunningham & Moors 1994). Rats did eat penguin eggs and small chicks, but only cracked or broken eggs could be taken by rats and it was not determined if the chicks eaten were preyed upon or scavenged by the rats (Moors 1986, Cunningham & Moors 1994). There was no evidence to suggest cats preyed on the penguins. Today, within the New Zealand Region, introduced predators co-occur with breeding rockhopper penguins only on the main Auckland Island, but as most penguin colonies are at the base of cliffs, introduced predators appear to have little if any impact.

Genetic means can now be used to detect prey items in the scats of predatory mammals (http://www.ecogene.co.nz). This method may provide clues as to the scale of impact invasive mammals have on the Auckland Island rockhopper penguin populations.

Native predators do however kill rockhopper penguin eggs, chicks and adults. Subantarctic skuas (*Catharacta antarctica lonnbergi*) are present on all islands where these penguins breed and they take both eggs and chicks. Skuas were the main cause of egg and chick loss at Campbell Island in 2011 and 2012 when skua predation was studied at the Penguin Bay rockhopper colonies (Morrison *et al*. 2017). In the smallest of the four colonies (mean 26 pairs/year) 44% of eggs were taken by skuas, compared with just 7% in the largest of the colonies (mean 1476 pairs/year) where there were proportionality fewer peripheral nests. Many of the A eggs were scavenged rather than predated and whether they were taken by skuas, they would not have resulted in a fledged chick. Proportionality fewer B eggs were taken by skuas in larger than the smaller colonies (Morrison *et al*. 2017). Skuas were better able to steal eggs when the smaller females were incubating than the larger more aggressive male penguins (Morrison *et al*. 2017).

At the Antipodes Islands northern giant petrels (*Macronectes halli*) gathered on the shoreline when penguins fledged, they ate dead chicks but were not seen to actually kill penguin chicks (Warham & Bell 1979). On Campbell Island northern giant petrels were observed or implicated in killing a small number (<10 per breeding season) of sub-adult and adult rockhopper penguins (Morrison et al. 2017).

At Macquarie Island rockhopper penguins were seen bearing injuries from attacks by New Zealand fur seals (*Arctocephalus forsteri*) (Warham 1963). Fur seals were seen preying on rockhopper penguins at Campbell Island in the 1940’s (Bailey & Sorensen 1962) but not between 2010 and 2012; conversely New Zealand sea lions regularly preyed on sub-adult and adult penguins in the latter but not in the former period (Morrison *et al*. 2015, 2017). Sea lions were uncommon at Campbell Island in the 1940’s (<20 pups born/year) but more common in the 21st century (>681 pups born in 2009) (Morrison *et al*. 2015). The sea lions could only access some of the Campbell Island rockhopper penguin colonies but at those colonies they can contribute to a decline in penguin numbers. At the Penguin Bay colonies sea lions were estimated to kill 6% of the adult penguins present in 2011 and 3.6% in 2012 (Morrison *et al*. 2017), and their calculations of adult survival suggest that sea lions accounted for most if not all the adult mortality during chick rearing. Most of the sea lion predation was probably by just one or two male sea lions, although at least six individuals were seen to kill penguins. Predation occurred only in the water or during chases where the penguin managed to jump ashore and was then caught by the pursuing sea lion. Sea lions also contributed to egg, chick and adult deaths by trampling when the mammals blundered their way through penguin colonies (Morrison *et al*. 2017). While sea lions are contributing to the ongoing decline of the Penguin Bay colonies, these colonies represent just 9% of the Campbell Island rockhopper penguin population. Thus, control of the sea lions is not recommended (Morrison *et al*. 2017).

Disease and parasites

In 1985-87 rockhopper penguin chicks and adults at Campbell Island died of avian cholera caused by the bacterium *Pasteurella multocida* (Cunningham & Moors 1994). Deaths from avian cholera seemed more prevalent where Norway rats had hoarded scavenged chicks, suggesting that rats may have played a role in transmitting the disease (Duignun 2001, Cunningham and Moors 1994). Avian malaria antibodies were present in yellow-eyed penguins (*Megadyptes antipodes*) sampled at Campbell Island but were not found in rockhoppers from that Island (Duignun 2001, Taylor 2000).

Ticks are present on most penguin species. An RNA virus, similar to the infectious bronchitis virus of chickens, was isolated from the tick *Ixodes uriae* from Campbell Island rockhopper penguins (Duignun 2001).

Both ecto and endo parasites probably occur on all penguin species; they are unlikely to affect penguins at the population level but can accentuate the effects of other factors affecting health such as starvation. Cestodes of the genus *Tetrabothrius* occur in the intestines of rockhopper penguins (Duignun 2001).

A serological survey on rockhopper and yellow-eyed penguins on Campbell Island in the 1980’s reported no antibodies for various poultry viruses including the agents of infectious bronchitis, reticuloendotheliosis, Newcastle disease, infectious laryngotracheitis, avian encephalomyelitis, infectious bursal disease, Marek’s disease, and fowlpox (Duignun 2001). Antibodies against *Chlamydiophila psittaci*, the cause of avian psittacosis and a Flavivirus have been found in rockhopper penguins from Macquarie Island (Duignun 2001).

There was no evidence to suggest that disease had been implicated in the decline of rockhopper penguins at Campbell Island (Duignun 2001).

Threats

Land-based threats

The reason/s for the population decline that has occurred since the 1940’s at Campbell Island and since at least 1978 at the Antipodes Islands were probably due to marine based threats. Ashore, introduced mammals are unlikely to have had a significant role in declines of rockhopper penguins. Norway rats, feral cats, feral sheep and feral cattle were present on Campbell Island but all have now been eradicated. There is no known link between these mammals and the declines in penguin numbers, although prior to their eradication rats may have helped spread avian diseases. The house mouse was the only species of introduced mammal on the Antipodes Islands (eradicated in 2016). There is no information on the impact introduced pigs, cats and mice have on rockhopper penguins on the main Auckland Island but, as most penguin colonies are at the base of cliffs, the penguins are probably protected from depredations by these mammals. Pigs may restrict those main island locations where penguins can breed.

Sub-Antarctic skuas take penguin eggs and chicks, and giant petrels, fur seals and sea lions occasionally prey on fledglings and even adult penguins. Predation by sea lions is an issue at some Campbell Island colonies. Predation by these native predators does not appear to have population level effects on penguin numbers but have contributed to localised declines at some colonies accessible to sea lions. Predation by skuas at colonies already in decline for other reasons can accentuate the fragmentation of colonies and by creating a greater proportion of edge nesters result in increased losses of eggs or chicks (Morrison *et al*. 2017).

The major storm in 2014 clearly impacted Antipodes Islands penguin populations (Chilvers & Hiscock in review). With global warming storms are predicted to become more frequent and more intense and could further reduce breeding habitat or kill penguins. Storm impact is perhaps more likely on the Antipodes Islands; the Campbell and Auckland Island colonies are perhaps in locations where landslides are less likely.

Given the remoteness of these islands pollution and human disturbance appear unlikely (Taylor 2000). The islands are uninhabited with only occasional visits from small parties of scientists or conservation workers.

A few ship-based ecotourist groups visit the Islands each year. At Campbell and Auckland Islands sites where tourist landings are permitted are well away from rockhopper penguin colonies. No tourist landings are allowed at the Antipodes Islands.

The flipper bands previously used on crested penguins increase drag when the birds are swimming, they can cause excessive feather wear and can spring slightly open and catch on vegetation or other obstructions (Taylor 2000). These bands are no longer used on crested penguins.

Marine-based threats

Changes in the marine environment associated with global climate change pose much greater threats to rockhopper penguins than any land-based threats. Fluctuations in the populations of rockhopper penguins at Campbell Island are correlated with changes in sea surface temperatures (Cunningham & Moors 1994, Morrison *et al*. 2014) and it seems likely that rockhopper penguins on the Antipodes and Auckland Islands could be similarly affected. Stable isotope ratios from Antipodes Island rockhopper penguins showed a decreasing trend in δ13C since specimens were first collected in 1861, indicating that rockhopper penguin declines may be related to a decrease in either ocean productivity or prey availability (Hilton *et al*. 2006).

Rockhopper penguins are considered to be at low risk from fishery bycatch (Crawford *et al*. 2017). Whether competition with fisheries for favoured food species occurs in the New Zealand Region remains unclear.

An oil spill close to islands where rockhopper penguins breed, perhaps unlikely, could be disastrous.

Their remote locations mean that pollution is unlikely to affect New Zealand rockhopper penguins. Ingestion of plastic and entanglement in plastic debris and abandoned fishing gear is possible, and likely to become more frequent, but is probably less likely for New Zealand breeding sub-Antarctic penguins than many other seabird species.

Research priorities

1. Population monitoring & demography

R.1.H1 Establish consistent survey protocols for each of the three island groups. Networked autonomous operating time-lapse cameras can be used to monitor penguin colonies (e.g. Black *et al*. 2017, 2018) to cover periods between ground surveys.

R.1.H2 Campbell Island. A combination of Island-wide censuses during November in two consecutive years at random 3-6-year intervals, combined with annual counts at the accessible Penguin Bay colonies (Morrison *et al*. 2015, Block *et al*. 2001), perhaps using time-lapse camera networks.

R.1.H3 Antipodes Island. A combination of Island-wide censuses randomly conducted every 3-6 years (Block *et al*. 2001), combined with annual counts at selected colonies perhaps using aforementioned time-lapse cameras. The last Island wide census was done in 2011 although some colonies were recounted in 2014. Establish photo points to document changes in areas utilised.

R.1.H4 Map and census Auckland Island colonies. Most are on the almost inaccessible west coast. The use of camera drones may be an option *(e.g. Brisson-Curadeau et al*. 2017, Weimerskirch *et al*. 2018, Hodgson *et al*. 2018).

R.1.H5 In assessing priorities, the best population trend data is for Campbell Island, however at Antipodes Island data can be collected simultaneously for the endangered, endemic erect-crested penguins that breed in the same colonies.

R.1.H6 Demographic research; priorities are age at first breeding, mortality at all life stages, recruitment into the breeding population, colony and mate fidelity. This requires annual visits and long-term observation of marked animals. This is highly desirable but logistically challenging, perhaps feasible at the Antipodes or Campbell Islands. Automated mark-recapture monitoring may be an option using implanted transponders and reader gates (e.g. Gendner *et al*. 2005).

R.1.M7 Repeat photo-points on Campbell Island in November on two consecutive years at3-6 year intervals using high resolution overlapping photos to count penguins (Morrison *et al*. 2017.)

R.1.M8 There is no reliable trend data for the Auckland Islands. The small colonies on the east coast are the easiest to access but trends there may not be representative of the larger inaccessible west coast colonies.

R.1.M9 Taylor (2000a) recommended analysis of the demographic data collected at Campbell Island on flipper banded birds, plus an assessment of the survival of penguins marked with flipper bands and those with transponders.

2. Marine ecology

R.2.H1 Foraging range using GPS devices during the breeding season at Antipodes and Campbell Islands. Ideally during all stages of the breeding cycle but most crucial is the chick rearing period. Female rockhopper penguins were tracked at Antipodes Island during guard and post guard stages December 2002- January 2003 (Sagar *et al.* 2005).

R.2.H2 Satellite/GLS tracking of Campbell and/or Antipodes breeding penguins during the pre-moult period. Repeating such a study every 3-5 years will provide information about potential shifts in the ocean environment.

R.2.H3 Satellite/GLS tracking of Campbell and/or Antipodes breeding penguins and, if feasible fledglings, to find out where they go between moult and breeding. Ideally, such a study would be conducted every 3-5 years.

R.2.H4 Collect faecal samples for DNA analysis to determine prey composition (e.g. Deagle *et al*. 2010) at Campbell, Antipodes and Auckland Island colonies as opportunity allows. Animal-borne camera deployments may become an option in the near future (e.g. Mattern *et al*. 2017).

R.2.M5 Investigate spatial and temporal links between population trends, prey abundance and oceanographic parameters including SST and primary productivity (Putz *et al*. 2013).

R.2.M6 Relate foraging ecology to Campbell Plateau oceanography in an attempt to understand why the species has declined so dramatically.

R.2.M7 Collect feathers and blood for stable isotope analysis as an adjunct to other research at Campbell, Antipodes and Auckland Island colonies when opportunity allows (e.g. Hilton *et al*. 2006).

R.2.L8 Similar studies as above at the Auckland Islands are desirable but due to logistic constraints lower priority.

3. Breeding biology

R.3.H1 Breeding success, cause of breeding failure and timing of the breeding cycle at Campbell and/or Antipodes Islands.

R.3.M2 Data on chick growth, meal sizes and fledgling weights at Campbell and/or Antipodes Islands.

R.3.M3 The use of time-lapse cameras in obtaining data on the timing of the breeding season and other aspects of breeding biology should be explored. This feasibility study need not be done on rockhopper penguins.

R.3.L4 Data on site and mate tenacity for rockhoppers at Campbell and/or Antipodes Islands.

R.3.L5 Similar studies at the Auckland Islands are desirable but due to logistic constraints lower priority.

4. Predators and diseases

R.5.H1 More data on the impact sea lions may have on those Campbell Island rockhopper colonies also inhabited by sea lions is desirable.

R.5.M2 Repeat the disease screening that was conducted at Campbell Island in 1988.

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Erect-crested penguin

(*Eudyptes sclateri*)

Kerry-Jayne Wilson and Thomas Mattern

Summary

The erect-crested penguin (*Eudyptes sclateri*) is probably the least researched of all the world's penguins. Historically recorded on Campbell Island, it now breeds only on the Bounty and Antipodes Islands. Their numbers declined throughout the 20th century, although that decline may have slowed in the last two decades. The reasons for the decline are unknown, but for this species introduced predators and fishery bycatch are not implicated. Erect-crested penguins are related to, larger than and distinct from, the two other crested penguins endemic to New Zealand, Fiordland penguin (*E. pachyrhynchus*) and Snares penguin (*E. robustus*). Another now extinct crested penguin, , was probably also endemic to the New Zealand region, and based on mitochondrial DNA, was sister to the erect-crested. This taxon (currently referred to as *Eudyptes* Clade X) was probably hunted to extinction following human arrival.

Erect-crested penguins are assumed to feed well offshore and migrate to parts unknown between breeding seasons. They arrive at the Antipodes and Bounty Islands in September, chicks are fledged in late January, there is a pre-moult exodus of about one month, many moulting at their breeding colonies. Once moult is finished the penguins remain at sea until they return to breed about six months later.

As with other *Eudyptes* penguins, Erect-crested penguins are sexually dimorphic, with males being heavier and with larger bills than females. Weights and measurements of sexed adults are given by Warham (1972) who found yearlings and even fledglings showed dimorphism in bill measurements (Warham 1972, 1975).

Previous reviews of Erect-crested penguin biology and priority lists

The chapter by Davis (2013) presents a good review of what little is known about this enigmatic penguin. Marchant & Higgins (1990) is more encyclopaedic drawing together snippets of information often overlooked in other reviews. The comparative review of the crested penguin species by John Warham (1975) is still a useful overview particularly of those species that breed in the New Zealand Region.

Other descriptions of the erect-crested penguin (e.g. Miskelly 2013, De Roy *et al*. 2013) were written primarily for the lay person and provide brief introductions to the species.

Two recent workshops, one for seabirds in general (Wilson & Waugh 2013) the other for New Zealand penguins (Wilson & Otley 2014) identified research required for the conservation of New Zealand penguins. Neither went through peer review and both are less detailed than required for our purposes. Research and conservation priorities for erect-crested penguins have been listed by Taylor (2000), Davis (2013) and Baird (2016); all are brief, all identify on-going declines being of concern, and serve to emphasise how little is known about the species, its threats or the conservation actions required.

Conservation status

The Department of Conservation lists the erect-crested penguin as 'declining' (Robertson *et al*. 2017) and IUCN as 'endangered' (Birdlife 2017), due to its restricted breeding range and recent population declines.

Distribution

Erect-crested penguins breed on the Bounty Islands (Proclamation, Tunnel, Depot, Ruatara, Penguin, Lion, Spider, Funnel, Molly Cap and North Rock) and Antipodes Islands (Antipodes, Bollons, Archway and Windward Islands (Robertson & van Tets 1982, Davis 2013, Taylor 2000, Hiscock & Chilvers 2014, Clark *et al*. 1998). A few have bred on Disappointment Island in the Auckland group but none has been seen during annual visits since 2015 (P. Sagar pers. comm.) In the 1940s and in 1958 small numbers bred in amongst rockhopper penguins on Campbell Island (Bailey & Sorensen 1962), but perhaps not the several hundred suggested by Davis (2013). In 1938 and 1939 a pair nested on Otago Peninsula (Richdale 1941) but there are no recent records of them breeding on Campbell Island or the New Zealand mainland. A female erect-crested penguin bred with a male Snares penguin at The Snares in 2013; an egg was laid but the breeding attempt failed (Morrison & Sagar 2014).

Erect-crested penguins are seldom seen at sea, during the breeding season sightings have been made 160 km ESE, and 255 km E of the Bounty Islands and on approach to those islands (Marchant & Higgins 1990). They are assumed to be pelagic when not breeding or moulting, but where they go is unknown. Most sightings and beach-stranded birds found along the south-eastern coasts of the South Island have been found between March and July suggesting that at least some of the penguins move north during winter (Powlesland 1984, Marchant & Higgins 1990).

Between breeding seasons, they are regularly seen on The Snares, the other sub-Antarctic Islands and Chatham Islands, less often on south-east coast of the South Island and Stewart Island, as vagrants in Wellington, Wairarapa, Hawke's Bay and very rarely elsewhere around the North Island (Taylor 2000, Powlesland 1984). Dates of observation and the location of vagrant erect-crested penguin sightings are listed by Marchant & Higgins (1990). Beyond New Zealand, vagrants have been seen at Macquarie Island (e.g. Keith & Hinds 1958) and southern Australia (Norman *et al*. 1996), and very rarely at the Falkland Islands, Marion Island and Heard Island, where they have been observed attempting to breed with the crested penguin species resident on those Islands (Morrison & Sagar 2014) with one at sea record in the southern Indian Ocean (Speedie 1982).

Numbers and population trends

On the Antipodes Islands, erect-crested penguins breed in mixed colonies along with eastern rockhopper penguins (*E. filholi*); the two species readily identified from one another during ground counts but not when counted from clifftop observation points or from boats, as is necessary for some colonies.

There are few attempts to estimate population numbers of erect-crested penguins but substantial differences in methodology limit direct comparisons (Taylor 2000, Davis 2013). Robertson & van Tets (1982) estimated 115,000 breeding pairs to be present on the Bounty Islands in 1978 using nest densities on one island to extrapolate to the entire Bounty Island land area deemed suitable for breeding. A similar approach was used in 1997, that estimate being just 27,956 pairs, but as the two studies used different estimates of the area suitable for nesting the two counts are not strictly comparable (Taylor 2000). A total of 2,774 Erect-crested penguin nests were counted on Proclamation Island, Bounty Islands 12-16 November 1997 (Amey 1998).

Equally unreliable seems to be a population estimate for on the Antipodes Islands also of 115,000 pairs in 1978, with no details presented describing the methodology that was used to derive this “very rough” (Taylor 2006, p278) population estimate.

Therefore, estimates provided by Robertson & van Tets (1982) and Taylor (2006) – and by extension numbers provided in Marchant & Higgins (1990) which are based on these sources – are of unknown reliability and we have chosen to use them with great caution.

What can be said with certainty, based on photographic evidence, is that the erect-crested penguin population on Antipodes Island declined substantially between 1949 and 1989 (Taylor 2006, p275). Between 1995 and 1998, numbers declined by a further 26% (Table 1) when comparable census methods were employed in both years (Davis 2013).

A full ground census on the Antipodes Islands in 2011 recorded about 39,700 breeding pairs which appears to be comparable with the 1998 estimates (Hiscock & Chilvers 2014). Hiscock (2013) includes the location of and the counts made at each individual colony in 2011 and for each sector of the Island in 1995, 1998 and 2011. Twenty-four colonies mapped in 1978 had been abandoned by 2011 (Hiscock & Chilvers 2014).

The most recent partial survey in November 2014 found the breeding population in those colonies resurveyed had declined, on average, by a further 19% since 2011 (Chilvers & Hiscock, in review). In January 2014, a major storm caused extensive landslides on the

Antipodes Islands with 44% of the erect-crested penguin colonies losing area due to landslides or were partially buried by landslide debris (Chilvers & Hiscock, in review).

About 20 birds nest on Inner Windward Island, Antipodes Islands (Tennyson *et al*. 2002).

Table 1. *Estimates of the number of active Erect-crested penguin nests on Antipodes Islands.*

Year of count	Estimated number of active nests	Decline since previous estimate	Source
1995	52,081	n/a	Davis (2013)
1998	38,540*	26%	Davis (2013)
2011	39700**	no change	Hiscock & Chilvers (2014)
2014	***	19%**	Chilvers & Hiscock (in review)

* 1998 figure derived from a partial count only.

**34,226 (93%) of the 36701 penguin nests counted in ground counts were erect-crested penguins, the remaining 2475 were rockhopper penguins, in all 42,689 nests were counted, the remainder from observation points or from a boat, 39,700 is 93% of that total.

**Calculated using ground counts in colonies censused on both occasions.

***Partial count only.

From the information at hand it is certain that the erect-crested penguin populations on both Antipodes and Bounty Islands have undergone significant declines in the 20th Century. However, more robust data are required to assess the extent of those declines and current population trajectories.

Based on the timing of breeding cycles, it has been suggested that erect-crested penguins breeding on the Bounty and Antipodes Islands may represent separate ‘cryptic’ taxa. However, a brief examination of mitochondrial DNA by Cole *et al*. (in review) did not show any genetic structure in samples obtained, refuting the separate taxa hypothesis.

Cole *et al*. (in review) used ancient DNA to genetically identify penguin bones collected from natural fossil deposits and archaeological middens throughout New Zealand. For those few erect-crested penguin bones (probably vagrants) found, comparison of the mitochondrial Control Region (a commonly used ‘population’ proxy for assessing genetic diversity) from the bone samples (*n*=2), with historical museum skins (*n*=10) and contemporary blood (*n*=18). did not indicate any decline in genetic diversity over time, however, as so few bone samples were available, the results should be interpreted with caution. Future assessment of population demographics using genomic information derived from Single Nucleotide Polymorphisms or whole Genomes, techniques currently in development, may provide clues on the extent of decline in numbers and genetic diversity of erect-crested penguins.

Monitoring

Regular monitoring of erect-crested penguins – at least of the Antipodes population – is of high priority. The last full Island survey was conducted between 22 October and 6 November 2011 (Hiscock & Chilvers 2014). They used ground counts in GPS mapped colonies and present methodology appropriate to and repeatable for Antipodes Island. Hiscock (2013) describes the survey methodology in greater detail and identifies each of the then extant colonies. They arbitrarily recommend their survey be repeated at five yearly intervals, we suggest two consecutive years at random 3-6 year intervals. Some colonies were recounted in 2014 (Chilvers & Hiscock (in review) (Table 1).

There is no monitoring of the Bounty Island population.

Breeding biology

On the Antipodes Islands erect-crested penguins breed on rocky coastal slopes and ledges along with rockhopper penguins, the smaller, later arriving rockhoppers tending to use higher and more broken ground than the erect-crested penguins (Warham 1972). Erect-crested penguins put little effort into nest building, at best nests consist of a few stones or bits of vegetation, some pairs laying directly onto bare rock (Davis 2001, 2013). On the Bounty Islands, the penguins nest around the margins of open spaces and in crevices, avoiding the open flatter ground occupied by the more aggressive Salvin's albatross (*Thalassarche salvini*) (Robertson & van Tets 1982, figures 5 & 6, P. Sagar pers. comm).

There has been no full season study of the breeding cycle of the erect-crested penguin. The classic paper by John Warham (1972) was based on observations made at the Antipodes Islands between 28 January and 12 March 1969. Further observations were made during a short visit in October 1990 (Miskelly & Carey 1990) and from September to November 1998 (Davis 2001).

At the Antipodes Islands erect-crested penguins lay three to four weeks earlier than the rockhopper penguins that share the island with them (Warham 1975). Erect-crested penguins return to the Antipodes Islands in September, males a week or so before the females, and are ashore for about 23 days before eggs are laid. The first returning bird was seen by shipwrecked mariners on 5 September 1893 who recorded the first egg being laid on 2 October (Warham 1972). As with other *Eudyptes* penguins they lay two eggs, the first being much smaller than the second. The larger B eggs were laid between 9 and 16 October 1990, peak B egg laying being 12 October, with the A eggs about 5 days earlier (Miskelly & Carey 1990). Chicks hatch in the second half of November after an incubation period of about 35 days. Peak fledging was about 30 January in 1969, with just a few chicks remaining by 12 February (Warham 1972). There are no data on breeding success from the Antipodes Islands, and only very limited data on breeding success at the Bounty Islands (Clark *et al*. 1998).

The breeding season is said to be two to three weeks later on the Bounty Islands than at the Antipodes (Robertson & van Tets 1982), although in 1997 at the Bounty Islands the first eggs were laid on 5 October (Clark *et al*. 1998) and the first egg had pipped on 17 November (Amey 1998).

Both parents share incubation duties, there is no data on the length of incubation spells. As with other crested penguins, chicks are guarded by the male for the first three weeks after hatching, during which time the females return to feed the chick most days (Warham 1972, 1975). After about 10 December the chicks are left alone, often forming crèches. When parents return, the chick chases after its parent with 6-10 deliveries of food during a feeding chase (Warham 1972); food transfer parent to chick taking place up to 10 m from the nest (Warham 1975). Parents appear to leave for the sea soon after feeding their chick.

Egg-size dimorphism is more extreme than in con-generic species with the second laid (B) egg being 85% heavier than the first laid (A) egg (Davis 2013, Miskelly & Carey 1990). Measurements of A and B eggs for Antipodes Island penguins are given by Davis (2013) and Miskelly & Carey (1990) and for Bounty Island birds by Amey (1998). The mean interval between laying A and B eggs was 5.4 days, the longest between egg interval for any bird (Davis 2013). The erect-crested penguin is an obligate brood reducer; 80% of A eggs were lost before or on the day the B egg was laid, and the remainder lost within six days of laying the B egg (Davis 2001, 3013, Miskelly & Carey 1990). Little if any attempt was made to incubate the A egg before the B egg was laid. Davis (2001) suggested that the eggs are so dissimilar in size that it is essentially impossible to incubate both successfully. Penguins laying later tended to produce larger eggs than early laying birds, and early layers tended to lose the A egg sooner than those that laid late. Davis (2001) suggested that the A egg serves as a primer stimulating the birds into full breeding mode. Why then do other *Eudyptes* penguins, where egg dimorphism is less extreme, often incubate both A and B eggs, and hatch both chicks, the Fiordland penguin sometimes even fledging two chicks?

The cause and function of egg dimorphism in crested penguins has been debated by many researchers over the last 50 years but has yet to be satisfactorily resolved. The debate continues, and the current theories are discussed by Morrison (2016).

There is no data on pair and site fidelity or age at first breeding for erect-crested penguins.

Moult

Most of those erect-crested penguins that had bred had departed on their 30-35-day pre-moult sojourn at sea by 4 February 1969 (Warham 1972). By 27 February 1969 about 75% of the breeding birds appeared to be ashore in pre-moult fat and by 11 March half the birds had begun to shed feathers (Warham 1972). Males tended to arrive before females and many pairs appeared to moult together at their nest site. Most non-breeders had finished their moult by about 6 March. In 1908 shipwrecked sailors recorded the penguins leaving Antipodes Islands having finished moult about 17 April (Warham 1972).

Yearling erect-crested penguins returned to the Antipodes Islands, presumably most to their natal colonies, in late January to early February, most had finished moult by 21 February 1969, but a few remained ashore in early March (Warham 1972). They attained adult plumage at the end of this moult.

Warham (1972) gives weights of a small sample of sexed erect-crested penguins at the start and finish of their moult, both sexes lost about 50% of their pre-moult weight during 26-30 days ashore. They left before the tail feathers were fully grown.

Food and foraging

Cooper *et al*. (1990) reviewed what was then known about crested penguin diet, but that paper contains no information of the diet of erect-crested penguins. Feathers have been collected at the Bounty Islands for stable isotope analysis, but results are not yet available (D. Thompson pers. comm.). Information of foods consumed as well as parasites, bacteria and the sex and genotype of the bird can now be obtained by molecular analysis of scats. This is non-invasive and samples can be obtained even during very brief visits. Any study wishing to utilise this method will need to ensure a genetic database (such as GenBank's BLAST; https://blast.ncbi.nlm.nih.gov/Blast.cgi) of all potential prey items is available to compare sequence data to, as a reduced database will limit the power of the analysis and miss potential food species.

Erect-crested penguins are assumed to be off-shore foragers making long feeding trips (Davis 2013). To date there has been no at-sea tracking of erect-crested penguins. Dr David Thompson, NIWA, plans to deploy geolocation tags on penguins at the Bounty Islands hopefully in 2019 with retrieval one year later.

Predators

Subantarctic skuas (*Catharacta antarctica lonnbergi*) prey on penguin eggs and chicks. Fur seals (*Arctocephalus forsteri)* are known to occasionally kill erect-crested penguins and leopard seals (*Hydrurga leptonyx*) may kill the occasional one (Davis 2001, 2013). Northern giant petrels (*Macronectes halli*) gathered on the shoreline when penguins fledged; they ate dead chicks but were not seen to kill erect-crested penguin chicks (Warham & Bell 1979).

Disease and parasites

There has been no research conducted into diseases or mortality factors of erect-crested penguins (Duignan 2001).

Threats

The reason/s for the population decline that has occurred, at least since 1978 and probably earlier is unknown. The usual suspects, introduced mammals can be eliminated for erect-crested penguins; mice *(Mus musculus)* which were unlikely to pose a threat to penguins, were the only species of introduced mammal on the Antipodes Islands and were eradicated there in 2016. The Bounty Islands have always been free of introduced mammals. Erect-crested penguins are considered to be at low risk from fishery bycatch (Crawford *et al*. 2017). There is only one record of an erect-crested penguin accidentally caught during fishing operations; a bird foul hooked in the flipper by a ling (Molva spp.) longliner; it was released alive (Crawford *et al*. 2017). Given the remoteness of both island groups pollution and human disturbance appear unlikely (Davis 2013, Taylor 2000). Both island groups are uninhabited with only occasional visits from small parties of scientists or conservation workers.

Changes in the marine environment associated with climate change are more likely to have caused population declines. Fluctuations in the populations of rockhopper penguins at Campbell Island are correlated with changes in sea temperature (Cunningham & Moors 1994, Morrison *et al*. 2014) and it seems likely that erect-crested penguins on the Antipodes and Bounty Islands could be similarly affected. Stable isotope ratios from Antipodes Island rockhopper penguins showed a decreasing trend in δ13C since specimens were first collected in 1861, indicating that rockhopper penguin declines may be related to a decrease in either ocean productivity or prey availability (Hilton *et al*. 2006). This is likely to have also affected erect-crested penguins though evidence to support this is circumstantial.

In January 2014 a major storm caused extensive landslides on the Antipodes Islands, with 44% of the erect-crested colonies losing area due to landslides or were partially buried by landslide debris, with an average 19% decline since those same colonies were surveyed in 2011 (Chilvers & Hiscock in review). The magnitude of the decline was roughly proportional to the area of colony affected, 11.7% decline in colonies not impacted by landslides, 39.9% in colonies that had lost at least 75% of their area to landslides (Chilvers & Hiscock, in review). With global climate change major storms such as the one in January 2014 are predicted to become more frequent and could further reduce available breeding habitat or kill penguins. The Bounty Islands are essentially bare rock, so landslides are unlikely to impact erect-crested penguins there.

On the Bounty Islands the growing population of fur seals occupy an ever-increasing area on those islands in the group accessible to seals thus displacing penguins, with the movements of rampaging bull seals further disturbing penguins (P. Sagar pers. comm.).

Given their restricted breeding range a nearby oil spill, perhaps unlikely, could be disastrous.

Feral sheep (*Ovis aries*), cattle (*Bos taurus*), Norway rats (*Rattus norvegicus*) and cats (*Felis catus*), were present on Campbell Island but all have now been eradicated. There is no known link between these mammals and the apparent local extinction of erect-crested penguins on Campbell Island.

Research Priorities

Given that this is probably the least known and least accessible of all penguin species, research and conservation management recommendations presented here are of necessity somewhat subjective. As an endangered species with a restricted range whose numbers have declined markedly for unknown reasons, evidence-based management is urgent. Some of the research identified below for the Antipodes Islands could be undertaken in conjunction with the annual Antipodean albatross monitoring.

1. Population monitoring & demography

R.1.H1 At Antipodes Islands, island-wide censuses randomly conducted every 3-6 years (Block *et al*. 2001). Census methodology for the Antipodes has been described in detail by Hiscock (2013) who includes nomenclature used to identify each colony. Ideally combine this with annual counts at selected colonies (perhaps using time-lapse camera networks, e.g. Black *et al*. (2017, 2018)). The last Island wide census was done in 2011 although some colonies were recounted in 2014.

R.1.H2 Population counts at the Bounty Islands pose even greater logistic challenges but are equally important. The only two archipelago wide population estimates are not strictly comparable but do indicate that major declines have occurred. At the Bounty Islands, drones may make spot counts possible (e.g. Hodgson *et al*. 2015). Barry Baker will look at aerial photos taken at the Bounty Islands for albatross census to see if they can also be used to count penguins.

R.1.H3 Repeat the Proclamation Island (Bounty Islands) counts (Amey 1998) at random 3-6-year intervals in October or November. Ground-truthing may make it possible to determine trends using aerial photography, perhaps using drones.

R.1.H4 Nothing is known about erect-crested penguin demography, priorities are age at first breeding, mortality at all life stages, recruitment into the breeding population. Automated mark-recapture monitoring may be an option using implanted transponders and reader gates (e.g. Gendner *et al*. 2005). Highly desirable but logistically challenging, perhaps feasible at the Antipodes Islands.

R.1.M5 Photo points from previous Antipodes Islands expeditions to be re-photographed at frequent intervals.

R.1.M6 Document the impact the growing fur seal population has on erect-crested penguins on the Bounty Islands.

R.1.M7 Undertake analyses using genomic data of both Antipodes and Bounty Island populations to test for gene flow and model population demography.

R.1.M8 In conjunction with research on rockhopper penguins at Campbell Island, scan colonies to see if any erect-crested penguins still nest there.

2. Marine ecology

R.2.H1 Determine the foraging range using GPS devices during the breeding season at Antipodes Islands. Ideally during all stages of the breeding cycle but most crucial are those during the chick rearing period.

R.2.H2 Satellite/GLS tracking of Antipodes breeding penguins during the pre-moult period.

R.2.H3 Research on Bounty Island penguins is equally important but logistically expensive. Satellite tracking may be feasible but units deployed are expensive and would not be recovered. Dr David Thompson, NIWA, plans to deploy geolocation tags on penguins there hopefully in 2019 with retrieval of these one year later.

R.2.M4 Satellite/GLS tracking of Antipodes breeding penguins to find out where they go between moult and breeding and if feasible track fledglings to document post fledgling dispersal. This study should be repeated every 3-5 years.

R.2.M5 Collect feathers and blood for stable isotope analysis as an adjunct to other research (e.g. Hilton *et al*. 2006). Feathers were collected at the Bounty Islands by D. Thompson, (NIWA) but results are not yet available.

R.2.M6 Collect faecal samples for DNA analysis to determine prey composition (e.g. Deagle *et al*. 2010) at Antipodes and Bounty Island colonies as opportunity allows.

R.2.M7 Animal-borne camera deployments may become an option in the near future (e.g. Mattern *et al*. 2017).

3. Breeding biology

R.3.H1 Breeding success and cause of breeding failure at Antipodes Island initially, Bounty Islands if possible.

R.3.L2 More accurate data on timing of the breeding cycle at Antipodes and Bounty Islands.

R.3.L3 Data on chick growth, meal sizes and fledgling weights.

R.3.L4 Again, the use of time-lapse cameras should be explored to work towards a better understanding of the breeding biology.

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