



Genetic identification informs on the distributions of vagrant Royal (*Eudyptes schlegeli*) and Macaroni (*Eudyptes chrysolophus*) Penguins

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Abstract

Understanding the movements of animals that spend much of their life at sea is difficult but important for effective conservation. Determining the at-sea distributions of Macaroni (*Eudyptes chrysolophus*) and Royal (*Eudyptes schlegeli*) Penguins poses particular challenges, including their occurrence in remote locations and difficulties in species identification owing to overlap in morphological characters, particularly in immature birds. Here we use DNA sequencing to examine vagrant Macaroni and Royal Penguins from Antarctica and New Zealand in order to improve understanding of their non-breeding distributions. Our sampling included samples from living birds, museum specimens and scavenged penguin remains recovered from the stomachs of Antarctic toothfish (*Dissostichus mawsoni*) caught north of the Ross Sea. Mitochondrial control region (HVRI) sequences indicated that the two samples from New Zealand were likely Royal Penguins as were the scavenged penguins. Both Macaroni and Royal Penguins were detected at Terre Adélie, Antarctica, despite the nearest breeding colony of Macaroni Penguins being 4000 km away. We provide the first evidence of Royal Penguins reaching the Ross Dependency. All but one of the vagrants were immature birds, supporting suggestions that this age group is the most likely to disperse large distances from the breeding colonies. Our study demonstrates how DNA sequences can assist in identifying taxa with similar or overlapping morphologies, as well as fragmentary bird remains.

Keywords Antarctica · *Eudyptes chrysolophus* · *Eudyptes schlegeli* · Genetic identification · Penguin distribution · Predation

Introduction

Penguins spend most of their time at sea and understanding their movements in this environment is key for their effective conservation. Recent studies of penguin distributions at sea have revolutionised our understanding of how foraging behaviour, life-history and environment are related and are key for predicting how penguins may respond to future environmental pressures, such as climate change (e.g. Bost et al. 2009; Mattern et al. 2018).

The Macaroni Penguin (*Eudyptes chrysolophus*) is the southernmost species of crested penguin and is one of the

most important avian marine predators in the sub-Antarctic and low-Antarctic regions (Brooke 2004; Bost et al. 2009). They breed in colonies in the oceanic islands of the Atlantic and Indian Oceans from South America in the west to Heard Island in the east (Fig. 1).

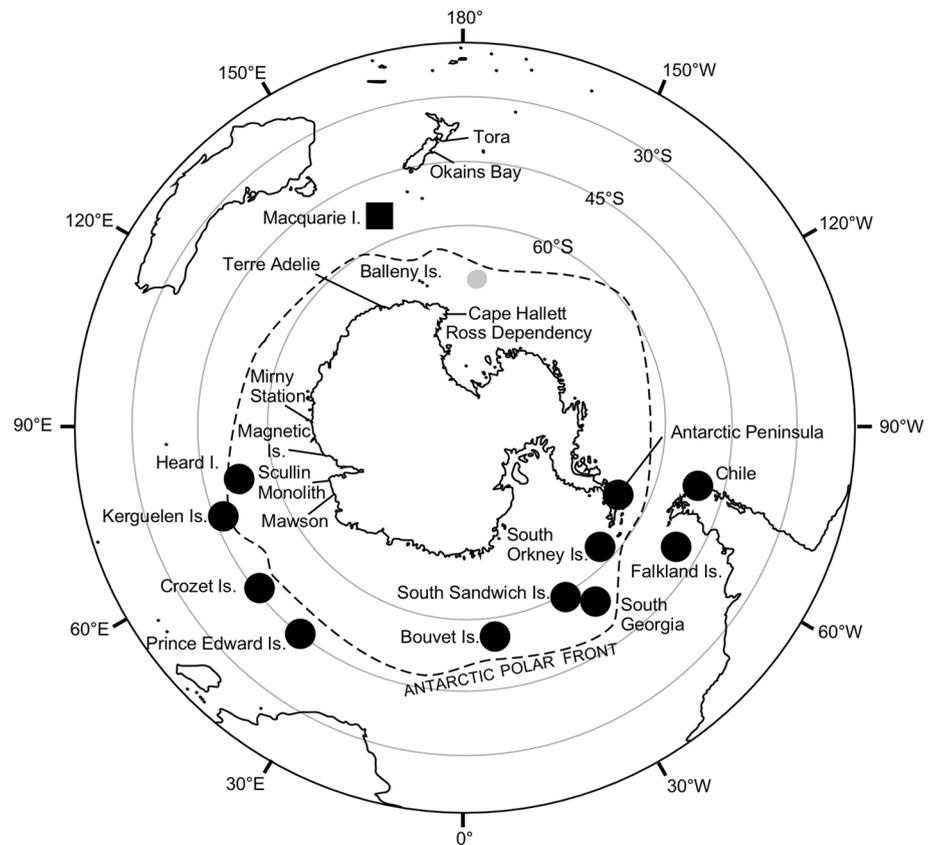
Royal Penguins (*Eudyptes schlegeli*) are closely related to Macaroni Penguins (Cole et al. 2019; Frugone et al. 2019) and they are sometimes considered to be conspecific. The main distinguishing feature between Macaroni and Royal Penguins is face colour, with Royal Penguins having white to grey faces (in contrast to the black faces of Macaroni Penguins). However, this coloration is variable and a continuum from white to black in Royal Penguins has been observed (Shaughnessy 1975). Royal Penguins are slightly larger overall and have longer and deeper beaks than Macaroni Penguins (Hull 1996), although there is overlap between them (Dehnhard et al. 2012). Royal Penguins breed on Macquarie Island and its adjacent islets (Fig. 1), although white-faced birds have also been reported from Marion (one of the Prince Edward Islands), Heard, Crozet

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Fig. 1 Map of the breeding distribution of Macaroni (*Eudyptes chrysolophus*; black circles) and Royal (*Eudyptes schlegeli*; black square) Penguins. The grey circle indicates the area where the penguin remains were found in Antarctic toothfish (*Dissostichus mawsoni*) stomachs. Place names mentioned in the text are indicated



and Kerguelen islands (García and Boersma 2013; authors pers. obs.). Genome-wide nuclear SNP data could not distinguish Royal and Macaroni Penguins but there was evidence of isolation by distance (Cole et al. 2019; Frugone et al. 2019). However, mtDNA control region sequences (HVR1) demonstrated geographic structuring with all Royal Penguin haplotypes forming a cluster in a phylogenetic network, although the two species were not reciprocally monophyletic because some of the white-faced birds from Marion Island and Macaroni Penguins from Kerguelen Island also grouped in this clade (Frugone et al. 2018).

Methods for determining penguin movements include shipboard observations (Reid et al. 1999) and deploying tracking devices, such as satellite tracking and geolocation (Hull et al. 1997; Barlow and Croxall 2002; Bost et al. 2009; Green et al. 2009). During chick rearing both Macaroni and Royal Penguins generally remain within 150 km of their colony but they forage up to 500–600 km during the pre-moult and incubation periods (Hull et al. 1997; Ratcliff and Trathan 2011). Geolocation data have indicated that between breeding seasons Macaroni Penguins travel up to 2500 km from their colony in order to forage in association with the Antarctic Polar Front, a zone of high marine productivity (Bost et al. 2009; Thiebot et al. 2011) (Fig. 1). Immature Macaroni Penguins have been observed at sea to frequent deeper, warmer and less saline

water than adults (Reid et al. 1999). Geolocation data are not available for Royal Penguins between breeding seasons but shipboard observations indicate that adults range up to 1500 km west from Macquarie Island (Reid et al. 1999) and they have been recorded from Tasmania, which is 1500 km to the north, during this time (Woehler 1992a). The movements of immature Royal Penguins are largely unknown.

Vagrant Royal Penguins have been reported from Australia, New Zealand, Falkland Islands and mainland Antarctica (Jouanin and Prévost 1953; Thomas and Bretagnolle 1988; Shirihai 2007; Dehnhard et al. 2012; Miskelly et al. 2019), and Macaroni Penguins have been recorded from as far south as the coast of mainland Antarctica (Merilees 1970; Marchant and Higgins 1990; Woehler 1992b; Bernstein and Tirrell 2008; Miskelly et al. 2013; Golubev 2016). However, the overlap of morphological variation between Royal and Macaroni Penguins makes reliable identification difficult, especially for vagrants (Warham 1972; Williams 1995; Shirihai 2007). Furthermore, it has been noted that vagrant penguins are often immatures (Dehnhard et al. 2012), which, for crested penguins, are more difficult to identify to species than adults.

Here we tested the use of mtDNA sequencing to examine the origins of at least 14 vagrant Macaroni and Royal Penguins from Antarctica and New Zealand. This information

will inform on the at-sea distributions of these species, especially immatures, whose movements are not well known.

Materials and methods

Samples

Three types of vagrant penguin samples were included in our DNA analysis: penguin remains recovered from the stomachs of Antarctic toothfish (*Dissostichus mawsoni*), museum specimens from Antarctica and New Zealand and blood samples from live individuals (Table 1, Fig. 2, Online Resource 1). 5 mm² pieces of muscle tissue were sampled from penguin remains recovered from the stomachs of three Antarctic toothfish that were caught north of the Ross Sea, Antarctica. Three separate penguin body parts were recovered from within one fish: a head from an immature (NMNZ OR.030897; Table 1, Online Resource 1) and two flippers (NMNZ OR.030897 Wing1 and Wing2; Table 1, Online Resource 1). These were genetically tested separately in case they originated from different birds.

Muscle tissue was also sampled from two dead vagrant penguins from New Zealand and these were later turned into museum specimens (NMNZ OR.029963 and NMNZ OR.030895; Table 1). Both were immature, based on their short crests, one of these was identified from facial colour as a Royal Penguin and the other as a Macaroni Penguin. Two museum skins collected in 1964 from the Ross Dependency in Antarctica and identified morphologically by FC Kinsky as Macaroni Penguins (Hatherton et al. 1965; Kinsky 1969) were sampled (NMNZ OR.010286 and NMNZ OR.010287; Table 1). A 3 mm² piece of toepad was sampled from each specimen with a sterile razor blade.

Blood samples were collected from five individuals (identified morphologically by Y. Cherel as two Macaroni Penguins and three Royal Penguins) from Terre Adélie, Antarctica (Table 1). All but one of the birds were immature, based on their short crests and either darker grey (Macaroni Penguin) or lighter grey (Royal Penguins) chins and throats.

DNA extraction, PCR amplification and sequencing

The DNA extractions and PCR set-ups for the museum specimens were performed in an ancient DNA laboratory that is in a separate building from where modern DNA is analysed. The recent samples (penguin remains and blood samples) were extracted in a modern DNA laboratory. For both blood and tissue DNA was extracted using a DNeasy Blood and Tissue kit (Qiagen), following the manufacturer's instructions but eluting in a final volume of 60 µl of Buffer AE to increase the final DNA concentration.

The mitochondrial control region (Hypervariable Region I; HVRI) was amplified using the *Eudyptes*-specific primers RockCRF and RockCRR and PCR thermocycling conditions of Frugone et al (2018). PCR amplifications were performed in 12 µl reactions with 1 × Mytaq reagent buffer (Bioline, Australia), 5 pmol of each primer and 2 µl of 10 mg ml⁻¹ of bovine serum albumin (BSA). PCR products were purified with digestion at 37 °C for 15 min using 0.5 U shrimp alkaline phosphatase (SAP, USB Corp.) and 2.5 U exonuclease I (ExoI, USB Corp.), followed by inactivation of the enzymes at 80 °C for 15 min. Sequencing was performed in both directions with the ABI Prism BigDye Terminator cycle sequencing kit version 3.1 on an ABI 3730 DNA sequencer (Macrogen, Seoul, Republic of Korea).

Sequence editing and phylogenetic analyses

Sequences were edited in Sequencer 5.2.3 (Gene Codes Corporation). They contained no indels and were aligned by eye to published control region sequences from Royal and Macaroni Penguins that were sampled from breeding grounds (Frugone et al. 2018).

We constructed a median-joining network of haplotype relationships based on a Neighbour-joining tree (Salzburger et al. 2011), following Frugone et al. (2018). MEGA (7.0.14; Kumar et al. 2016) was used to select the best substitution model (K2 + G, G = 0.08) based on the Bayesian information criteria (BIC) and then this model was used to construct a Neighbour-joining tree. This phylogeny was then used to make a network in Haploviewer (available at <http://www.cibiv.at/~greg/haploviewer>).

Results

The morphological examination of the vagrant specimens indicated that all but one were immature birds based on their short crests (Table 2). All the vagrant birds found ashore were moulting, except for the adult Macaroni Penguin (TA2; Table 1) and had reddish-brown bills, consistent with juveniles during their first moult, whilst the two birds extracted from toothfish stomachs had even duller bills (brown-grey), consistent with them being recent fledglings (see Warham 1971). The bill measurements were also consistent with immature birds because most of the measurements were smaller than the minimum sizes recorded for both Royal and Macaroni Penguin adults (Woehler 1995).

The penguin head and two flippers recovered from a single Antarctic toothfish stomach (NMNZ OR.030897) exhibited the same HVRI haplotype. This haplotype was not recovered from any of our other sampled birds nor does it match any published HVR1 sequence on GenBank. We

Table 1 Collection and identification details of the vagrant Macaroni and Royal Penguins sampled in our study

Sample identifier	Species ID from morphology	Putative species ID from HVR1 sequences	Sample type	Sampling location	Other specimen collection information	Collection date	GenBank accession number
Penguin remains from Antarctic toothfish stomachs							
NMNZ OR.030897 Wing1	Unknown	Royal	Muscle tissue from flipper	66° S 177° W	San Aotea II, trip 1595B, set 153 sample 46	28/4/2002	MZ488325
NMNZ OR.030897	Immature Macaroni or Royal	Royal	Muscle tissue from head	66° S 177° W	San Aotea II, trip 1595B, set 153 sample 46	28/4/2002	MZ488325
NMNZ OR.030897 Wing2	Unknown	Royal	Muscle tissue from flipper	66° S 177° W	San Aotea II, trip 1595B, set 153 sample 46	28/4/2002	MZ488325
NMNZ OR.30896	Immature, unknown	Royal	Muscle tissue from head	66.45° S 177.01° W	San Aotea II, trip 1595, set 123. Caught at a depth of 1190 m	23/3/2002	MZ488326
NMNZ OR.030898	Unknown	Royal	Muscle tissue from flipper	Not recorded	Janas/ZMTW trip 1593B, set 225, sample 224	24/5/2002	MZ488328
Museum specimens							
NMNZ OR.010286	Immature Macaroni	Royal	Toepad	Sabrina Island, Balleny Islands, Antarctica	Collected by FC Kinsky	9/3/1964	MZ488334
NMNZ OR.010287	Immature Macaroni	n/a	Toepad	Cape Hallett Station, Antarctica	Collected by T. Riggert	12/2/1964	–
Live and recently dead birds							
NMNZ OR.029963	Immature Royal	Royal	Toepad	Tora, New Zealand	Collected by J. Boyne	21/2/2013	MZ4883345
NMNZ OR.030895	Immature Macaroni	Royal	Muscle tissue from head	Okains Bay, Banks Peninsula, New Zealand	Collected by M. Thacker	17/2/1997	MZ488327
TA1	Immature Macaroni	Royal	Blood	Terre Adélie	Collected by Y. Cherel	22/1/2007	MZ488330
TA2	Adult Macaroni	Macaroni	Blood	Terre Adélie	Collected by Y. Cherel	6/2/2007	MZ488329
TA1	Immature Royal	Royal	Blood	Terre Adélie	Collected by Y. Cherel	8/3/2007	MZ488331
TA2	Immature Royal	Royal	Blood	Terre Adélie	Collected by Y. Cherel	28/1/2007	MZ488332
TA3	Immature Royal	Royal	Blood	Terre Adélie	Collected by Y. Cherel	10/2/2007	MZ488333

Museum specimens are from the Museum of New Zealand Te Papa Tongarewa

n/a no amplification, ID identification

therefore conclude that these remains are likely to be from a single penguin.

NMNZ OR.030898 shared a haplotype with a Royal Penguin. The adult Macaroni Penguin sampled from Terre Adélie exhibited an identical haplotype to the most common haplotype detected in Macaroni Penguins. The remaining samples all exhibited unique haplotypes.

The network of relationships between HVR1 haplotypes (Fig. 3) was similar to that obtained by Frugone et al. (2018) with most of the Macaroni Penguin haplotypes forming a star-like topology. The Royal Penguin samples formed a cluster together with some of the Macaroni Penguins from Kerguelen and two white-faced penguins from Marion Island (the Royal Penguin cluster). The Balleny Islands and



Fig. 2 Photos of the heads of immature penguins (*Eudyptes* spp.) recovered from the stomachs of Antarctic toothfish (*Dissostichus mawsoni*). Left: NMNZ OR.030896, Right: NMNZ OR.030897

Banks Peninsula penguins, which had been identified as Macaroni Penguins, fell within the Royal Penguin cluster, as did the three immature Royal Penguins from Terre Adélie and the Royal Penguin from Tora. All of the sequences we obtained from the scavenged penguin remains also fell in the Royal Penguin cluster, although NMNZ OR.030896 was in an intermediate position between the Royal and Macaroni Penguin haplogroups.

The bird from Terre Adélie that was identified as an immature Macaroni Penguin also grouped within the Royal Penguin cluster. The adult Macaroni Penguin from Terre Adélie was the only specimen that did not group in the

Royal Penguin cluster, instead it was identical to the central and most common haplotype in the Macaroni Penguin cluster.

Discussion

Identification of Royal and Macaroni Penguins

Most of the vagrant birds examined in this study grouped in the cluster of haplotypes that were largely found in

Table 2 Bill measurements and other features of the Royal Penguin museum specimens sampled in this study

Sample identifier	Culmen length (mm)	Culminicorn width (mm)	Bill depth (mm)	Moulting	Chin feather colour	Crest length	Beak colour
NMNZ OR.030897	57.9	8.7	20.2	No	Mottled grey and white	Short*	Brown-grey with slight reddening at maxillary fungus and mandible tip
NMNZ OR.030896	47.7	7.7	16.8	No	Mottled grey and white	Short*	Brown-grey with clear reddening at maxillary fungus and mandible tip
NMNZ OR.010286	49.4	8.8	21.4	Yes	Mottled grey and white	Short*	Reddish-brown, darker at base
NMNZ OR.010287	64.3	9.2	22.3	Yes	Mottled grey and white	Short*	Reddish-brown, darker at base
NMNZ OR.029963	65.0	10.2	24.8	Yes	Mottled grey and white	Short*	Reddish-brown, darker at base
NMNZ OR.030895	54.6	9.2	20.5	Probably moulting	n/a (no chin feathers)	Short*	Reddish-brown, darker at base

Only the specimens with heads were included. Measurements follow Warham (1975)

*Shorter than those of adults

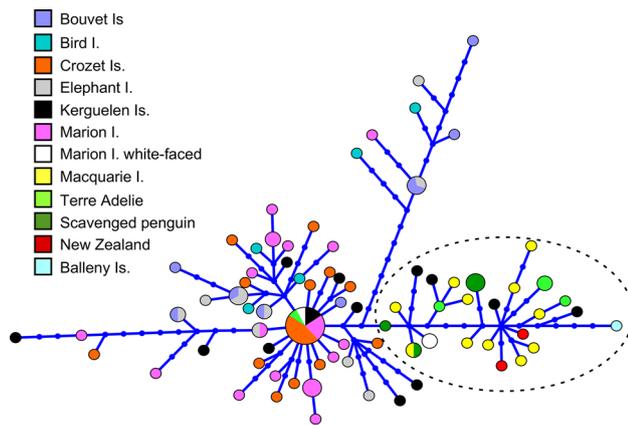


Fig. 3 Haplotype network for mitochondrial DNA HVR1 sequences of Macaroni (*Eudyptes chrysolophus*) and Royal (*Eudyptes schlegeli*) Penguins. The Royal Penguin cluster of haplotypes is indicated by a dotted line

Royal Penguins suggesting that they are likely to be Royal Penguins. However, it cannot be ruled out that they are from Kerguelen Island, Marion Island or an unsampled location. Macquarie Island (the breeding ground of Royal Penguins) seems the likely source of these penguins, given its proximity to New Zealand and the regions of Antarctica where the vagrant birds were found (Fig. 1).

We found that several of the birds identified morphologically as Macaroni Penguins were more likely to be Royal Penguins, based on their position in the haplotype network. This finding confirms the difficulty in distinguishing between Royal and Macaroni Penguins by morphology, which is especially true for immature birds. Our results suggest that the previous records of Macaroni Penguins in the Ross Dependency may have been misidentified Royal Penguins.

Extended distributions of immature Royal Penguins

The collection locations of the samples we examined are well south of the Antarctic Polar Front, which is thought to be the main foraging area of Macaroni (Bost et al. 2009) and Royal Penguins (Hindell et al. 2012) in the non-breeding season. The time of year that our vagrant birds were observed (January–May) is consistent with the majority of observations of Royal Penguin vagrants in Tasmania (Woehler 1992a), Terre Adélie (Thomas and Bretagnolle 1988) and New Zealand (Gill et al. 2010). Most of our sampled Royal Penguins were immature (or their age could not be determined). This is consistent with previous observations of vagrant Royal Penguins where it is this age class, rather than adults, that disperse large distances from Macquarie Island (Jouanin and Prévost 1953; Woehler 1992a; Dehnhard et al. 2012). Similar observations have been made for Macaroni

Penguins (Merilees 1970). The records of probable fledgling Royal Penguins in the Ross Dependency in March–April suggest that some juveniles may swim to this region straight after fledging, because chicks leave Macquarie Island in January–February (Warham 1971).

The distribution of vagrant Macaroni Penguins

Our genetic results confirmed the morphological identification of a Macaroni Penguin from Terre Adélie. This bird was observed in early February, which contrasts with Reid et al. (1999) who found that the most distantly recorded adult Macaroni Penguins in their study were recorded in late September/early October (they found that distant immature birds were observed in late March). Other records of Macaroni Penguins from mainland Antarctica are located much closer to breeding colonies and at a similar time of year to our record (Fig. 1): Mawson Station on 17 February 1964 (Merilees 1970), Scullin Monolith on 5 February 1985 and Magnetic Island on 27 January 1987 (Woehler 1992b) and Mirny Station on February 2000 and February 2012 (Golubev 2016).

There are no confirmed records of Macaroni Penguins in the Ross Dependency. Our genetic results indicate that the Balleny Island specimen is likely to be a Royal Penguin. The Cape Hallett specimen, from which we could not obtain DNA, has similar morphology and measurements to the Royal Penguins sampled (Table 2) and nothing in its morphology indicates that it is a Macaroni Penguin. The Terre Adélie Macaroni Penguin is the mainland Antarctica record most distant from a breeding colony.

Scavenging of penguin remains by toothfish

The Antarctic toothfish is a large predatory fish endemic to the seas surrounding Antarctica (Hanchet et al. 2015). It is a commercially important fish and supports a longline fishery in the vicinity of the Ross Sea, with the highest catches taken from 1000 to 1600 m depth (Hanchet et al. 2015). Although Antarctic toothfish primarily eat fish and cephalopods, they are thought to be opportunistic feeders and obtain a substantial part of their diet from scavenged prey, such as penguins, seals, flying seabirds and fishing discards (Fenaughty et al. 2003; Roberts et al. 2011; Stevens et al. 2014; Seong et al. 2021). Previous records of penguin remains found in the stomach contents of Antarctic toothfish include an Emperor Penguin chick (*Aptenodytes forsteri*), six putative Chinstrap Penguins (*Pygoscelis antarcticus*) (Roberts et al. 2011; Seong et al. 2021), one King Penguin (*Aptenodytes patagonicus*; NMNZ OR.027644) and seven Adélie Penguins (*Pygoscelis adeliae*; NMNZ OR.027759, NMNZ OR.029729–30, NMNZ OR.029283–4, NMNZ OR.030900–1).

The Royal Penguin remains obtained from Antarctic toothfish stomachs were likely to be scavenged. Royal Penguins have a maximum dive depth of 226 m (Hull 2000), which is much shallower than the depths that Antarctic toothfish typically frequent (Hanchet et al. 2015). It is likely that the penguins were killed and partially consumed by another predator and their remains sunk to where they were eaten by Antarctic toothfish. We consider that there are two potential predators: killer whales (*Orcinus orca*) or leopard seals (*Hydrurga leptonyx*). ‘Type B’ killer whales, which mainly eat seals, have been observed chasing and feeding on penguins (Andrews et al. 2008 and references therein; Pitman and Durban 2010; Ainley and Ballard 2012). ‘Type B’ killer whales occur in the Ross Sea, where the penguin remains we studied were obtained, but are less common than the fish-eating ‘Type C’ killer whales (Ainley and Ballard 2012). Leopard seals are also well-known predators of penguins and are common in the Ross Sea (Ainley et al. 2005). Both ‘Type B’ killer whales and leopard seals leave bird remains similar to our samples of flippers and heads. Pitman and Durban (2010) observed ‘Type B’ killer whales eating the breast muscles of penguins and discarding the rest of the carcass. Leopard seals also often leave behind a relatively clean skeleton, including the feet and head, when eating birds, such as penguins (Penney and Lowry 1967; McKinlay et al. 2014).

In conclusion, our identification of vagrant penguins reveals that immature Royal Penguins, an age class whose movements were largely unknown, can travel large distances to Antarctica. We provide the first evidence of Royal Penguins reaching the Ross Dependency and propose that juveniles may be more regular in this area than previously realised. Our study also demonstrates the usefulness of DNA sequences for identifying taxa with similar or overlapping morphologies, as well as fragmentary and degraded bird remains (Galbraith et al. 2013; Dalén et al. 2017).

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00300-021-02961-x>.

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Author contributions AT, CM and LS conceived and designed the research. LS and AT conducted the experiments. YC contributed samples. LS analysed the data and drafted the manuscript. All authors edited, read and approved the manuscript.

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Data availability DNA sequences have been submitted to GenBank.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest to disclose.

Ethical approval Penguins were cared for in accordance with the guidelines of the ethics committee of IPEV, who approved our fieldwork.

References

- Ainley DG, Ballard G (2012) Trophic interactions and population trends of killer whales (*Orcinus orca*) in the Southern Ross sea. *Aquat Mamm* 38:153–160. <https://doi.org/10.1578/AM.38.2.2012.153>
- Ainley DG, Ballard G, Karl BJ, Dugger KT (2005) Leopard seal predation rates at penguin colonies of different size. *Antarct Sci* 17:335–340. <https://doi.org/10.1017/S0954102005002750>
- Andrews RD, Pitman RL, Ballance LT (2008) Satellite tracking reveals distinct movement patterns for type B and type C killer whales in the southern Ross sea, Antarctica. *Polar Biol* 31:1461–1468. <https://doi.org/10.1007/s00300-008-0487-z>
- Barlow KE, Croxall JP (2002) Provisioning behavior of macaroni penguins *Eudyptes chrysolophus*. *Ibis* 144:248–258. <https://doi.org/10.1046/j.1474-919X.2002.00046.x>
- Bernstein N, Tirrell P (2008) New southerly record for the macaroni penguin (*Eudyptes chrysolophus*) on the Antarctic peninsula. *Auk* 98:398–399. <https://doi.org/10.1093/auk/98.2.398>
- Bost C-A, Thiebot JB, Pinaud D, Cherel Y, Trathan PN (2009) Where do penguins go during the inter-breeding period? Using geolocation to track the winter dispersion of the macaroni penguin. *Biol Lett* 5:473–476. <https://doi.org/10.1098/rsbl.2009.0265>
- Brooke ML (2004) The food consumption of the world’s seabirds. *Proc R Soc Lond B* 271:S246–S248. <https://doi.org/10.1098/rsbl.2003.0153>
- Cole TL, Dutoit L, Dussex N, Hart T, Alexander A, Younger JL, Clucas GV, Frugone MJ, Cherel Y, Cuthbert R, Ellenberg U, Fiddaman SR, Hiscock J, Houston D, Jouventin P, Mattern T, Miller G, Miskelly C, Nolan P, Polito MJ, Quillfeldt P, Ryan PG, Smith A, Tennyson AJD, Thompson D, Wienecke B, Vianna JA, Waters JM (2019) Receding ice drove parallel expansions in Southern Ocean penguins. *PNAS* 116:26690–26696. <https://doi.org/10.1073/pnas.1904048116>
- Dalén L, Lagerholm VK, Nylander JA, Barton N, Bochenski ZM, Tomek T, Rudling D, Ericson PGP, Irestedt M, Stewart JR (2017) Identifying bird remains using ancient DNA barcoding. *Genes* 8:169. <https://doi.org/10.3390/genes8060169>
- Dehnhard N, Ludynia K, Almeida A (2012) A royal penguin *Eudyptes schlegeli* in the Falkland islands. *Mar Ornithol* 40:95–98
- Fenaughty JM, Stevens DW, Hanchet SM (2003) Diet of the Antarctic toothfish (*Dissostichus mawsoni*) from the Ross Sea, Antarctica (subarea 88.1). *CCAMLR Sci* 10:113–123
- Frugone MJ, Lowther A, Noll D, Ramos B, Pistorius P, Dantas GPM, Petry MV, Bonadonna F, Steinfurth A, Polanowski A, Raya Rey A, Lois NA, Pütz K, Trathan P, Wienecke B, Poulin E, Vianna JA (2018) Contrasting phylogeographic pattern among *Eudyptes* penguins around the Southern Ocean. *Sci Rep* 8:17481. <https://doi.org/10.1038/s41598-018-35975-3>

- Frugone MK, López ME, Segovia NI, Cole TL, Lowther A, Pistorius P, Dantas GPM, Petry MV, Bonadonna F, Trathan P, Polanowski A, Wienecke B, Bi K, Wang-Claypool CY, Waters JM, Bowie RCK, Poulin E, Vianna JA (2019) More than the eye can see: genomic insights into the drivers of genetic differentiation in royal/macaroni penguins across the Southern Ocean. *Mol Phylogenet Evol* 139:106563. <https://doi.org/10.1016/j.ympev.2019.106563>
- Galbraith M, Tennyson A, Shepherd LD, Robinson P (2013) High altitude New Zealand record for a long-tailed skua (*Stercorarius longicaudus*). *Notornis* 60:245–248
- García BP, Boersma PD (2013) Penguins: natural history and conservation. University of Washington Press, Seattle
- Gill BJ, Bell BD, Chambers GK, Medway DG, Palma RL, Scofield RP, Tennyson AJD, Worthy TH (2010) Checklist of the birds of New Zealand, Norfolk and Macquarie Islands, and the Ross Dependency, Antarctica, 4th edn. Ornithological Society of New Zealand & Te Papa Press, Wellington
- Golubev SV (2016) Records of macaroni penguins (*Eudyptes chrysolophus*) from Mirny Station, East Antarctica. *Notornis* 63:176–178
- Green JA, Wilson RP, Boyd IL, Woakes AJ, Green CJ, Butler PJ (2009) Tracking macaroni penguin during long foraging trips using ‘behavioural geolocation.’ *Polar Biol* 32:645–653. <https://doi.org/10.1007/s00300-008-0568-z>
- Hanchet S, Dunn A, Parker S, Horn P, Stevens D, Mormede S (2015) The Antarctic toothfish (*Dissostichus mawsoni*): biology, ecology, and life history in the Ross sea region. *Hydrobiologia* 761:397–414. <https://doi.org/10.1007/s10750-015-2435-6>
- Hatherton T, Dawson EW, Kinsky FC (1965) Balleny Islands reconnaissance expedition, 1964. *N Z J Geol Geophys* 8:164–179. <https://doi.org/10.1080/00288306.1965.10428105>
- Hindell MA, Bradshaw CJA, Brook BW, Fordham DA, Kerry K, Hull C, McMahon CR (2012) Long-term breeding phenology shift in royal penguins. *Ecol Evol* 2:1563–1571. <https://doi.org/10.1002/ece3.281>
- Hull CL (1996) Morphometric indices for sexing adult royal *Eudyptes schlegeli* and rockhopper *E. chrysocome* penguins at Macquarie Island. *Mar Ornithol* 24:23–27
- Hull CL (2000) Comparative diving behaviour and segregation of the marine habitat by breeding royal penguins, *Eudyptes schlegeli*, and eastern Rockhopper Penguins, *Eudyptes chrysocome filholi*, at Macquarie Island. *Can J Zool* 78:333–345. <https://doi.org/10.1139/z99-192>
- Hull C, Hindell M, Michael K (1997) Foraging zones of royal penguins during the breeding season, and their association with oceanographic features. *Mar Ecol Prog Ser* 153:217–228. <https://doi.org/10.3354/meps153217>
- Jouanin C, Prévost J (1953) Captures de manchots inattendus en Terre Adélie et considérations systématiques sur *Eudyptes chysolophus schlegeli* Finsch. *L’oiseau Et La Revue Francaise D’ornithologie* 23:281–287
- Kinsky FC (1969) New and rare birds on Campbell Island. *Notornis* 16:225–236
- Kumar S, Stecher G, Tamura K (2016) MEGA7: molecular evolutionary analysis version 7.0 for bigger datasets. *Mol Biol Evol* 35:1547–1549. <https://doi.org/10.1093/molbev/msw054>
- Marchant S, Higgins PJ (1990) Handbook of Australian, New Zealand and Antarctic birds, vol 1. Oxford University Press, Melbourne
- Mattern T, Pütz K, Garcia-Borboroglu P, Ellenberg U, Houston DM, Long R, Lüthi B, Seddon PJ (2018) Marathon penguins—reasons and consequences of long-range dispersal in Fiordland penguins/Tawaki during the pre-moult period. *PLoS ONE* 13:e0198688. <https://doi.org/10.1371/journal.pone.0198688>
- McKinlay B, Heseltine S, Loh G (2014) Seabird predation by vagrant leopard seals (*Hydrurga leptonyx*) at Otago, New Zealand. *Notornis* 61:48–50
- Merilees WJ (1970) A record of the macaroni penguin for Australian Antarctic. *Emu* 70:88. <https://doi.org/10.1071/MU970088a>
- Miskelly CM, Crossland AC, Sagar PM, Saville I, Tennyson AJD, Bell EA (2013) Vagrant and extra-limital bird records accepted by the OSNZ records appraisal committee 2011–2012. *Notornis* 60:296–306
- Miskelly CM, Crossland AC, Saville I, Southey I, Tennyson AJD, Bell EA (2019) Vagrant and extra-limital bird records accepted by the Birds New Zealand records appraisal committee 2017–2018. *Notornis* 66:150–163
- Penney RL, Lowry G (1967) Leopard seal predation on Adélie penguins. *Ecology* 48:878–882. <https://doi.org/10.2307/1933751>
- Pitman RL, Durban JW (2010) Killer whale predation on penguins in Antarctica. *Polar Biol* 33:1589–1594. <https://doi.org/10.1007/s00300-010-0853-5>
- Ratcliffe N, Trathan P (2011) A review of the diet and at-sea distribution of penguins breeding within the CAMLR convention area. *CCAMLR Sci* 18:75–114
- Reid TA, Hull CL, Eades DW, Scofield RP, Woehler EJ (1999) Shipboard observations of penguins at sea in the Australian sector of the Southern Ocean, 1991–1995. *Mar Ornithol* 27:101–110
- Roberts J, Xavier JC, Agnew DJ (2011) The diet of toothfish species *Dissostichus eleginoides* and *Dissostichus mawsoni* with overlapping distributions. *J Fish Biol* 79:138–154. <https://doi.org/10.1111/j.1095-8649.2011.03005.x>
- Salzburger W, Ewing G, Haeseler AV (2011) The performance of phylogenetic algorithms in estimating haplotype genealogies with migration. *Mol Ecol* 20:1952–1963. <https://doi.org/10.1111/j.1365-294X.2011.05066.x>
- Seong GC, Choi S-G, Chung S, An DH, Kim HW, Baek GW (2021) Morphological dietary composition of Antarctic toothfish (*Dissostichus mawsoni*) along the East Antarctic continental slope. *Polar Biol* 44:499–508. <https://doi.org/10.1007/s00300-021-02820-9>
- Shaughnessy PD (1975) Variation in facial colour of the royal penguin. *Emu* 75:147–152. <https://doi.org/10.1071/MU9750147>
- Shirihai H (2007) A complete guide to Antarctic wildlife: birds and marine mammals of the Antarctic continent and the Southern Ocean. Princeton University Press, Princeton
- Stevens DW, Dunn MR, Pinkerton MH, Forman JS (2014) Diet of Antarctic toothfish (*Dissostichus mawsoni*) from the continental slope and oceanic features of the Ross sea region, Antarctica. *Antarct Sci* 26:5012–5512. <https://doi.org/10.1017/S095410201300093X>
- Thiebot JB, Chérel Y, Trathan PN, Bost CA (2011) Population segregation in the wintering areas of Macaroni penguins. *Mar Ecol Prog Ser* 421:279–290. <https://doi.org/10.3354/meps08907>
- Thomas T, Bretagnolle V (1988) Non-breeding birds of Pointe Géologie Archipelago, Adélie land, Antarctica. *Emu* 88:104–106. <https://doi.org/10.1071/MU9880104>
- Warham J (1971) Aspects of breeding behaviour in the Royal Penguin *Eudyptes chrysolophus schlegeli*. *Notornis* 18:91–115
- Warham J (1972) Black-faced penguins on The Snares. *Notornis* 19:92–93
- Williams TD (1995) The penguins: Spheniscidae bird families of the world, vol 2. Oxford University Press, Oxford
- Woehler EJ (1992a) Records of vagrant penguins from Tasmania. *Mar Ornithol* 20:61–73
- Woehler EJ (1992b) Records on nonbreeding seabirds from the Australian Antarctic territory, 1954–1988. *Mar Ornithol* 20:84–90
- Woehler EJ (1995) Morphology of royal and macaroni penguins, and geographic variation within eudyptid penguins. The penguins. Surrey Beatty & Sons Pty Ltd., Chipping Norton, pp 319–330

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