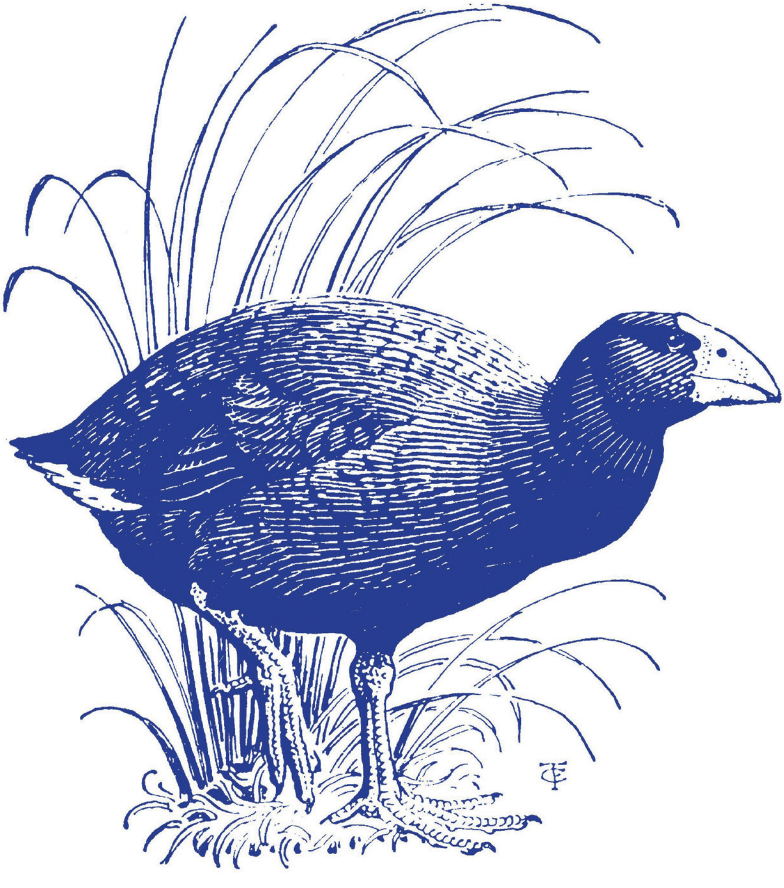
NOTORNIS

Ornithology of the Southern Pacific



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Timing and duration of primary moult in New Zealand's silvereye (tauhou, *Zosterops lateralis*)

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Abstract: Across all bird species, latitude plays an important role in determining patterns in timing, duration, and synchronisation of primary moult but, apart from Africa, moult studies at the southernmost limits of the continents and islands in the southern hemisphere are lacking. The focus of this study is the self-introduced silvereye (tauhou, *Zosterops lateralis*) in New Zealand, one of the most southern countries in the world. Moult data collected by bird banders during the period 1978–2022 were analysed using the Underhill-Zucchini moult model. Silvereyes had an estimated primary moult duration of 74 days, with a mean population start date of 3 February and a mean completion date of 19 April. Post-breeding primary moult in adult silvereyes starts soon after the breeding season and ends shortly before some of the more southern birds embark on their seasonal northward migratory movements. Juvenile primary moult is estimated to start approximately two weeks after the start of post-breeding moult in adults. A literature review suggested that primary moult duration for *Zosterops* species is similar regardless of latitude, but the timing of moult is variable and adjusted to local conditions.

Scott, T.; Scholer, M; Melville, D.S.; Underhill, L.G. 2023. Timing and duration of primary moult in New Zealand's silvereye (tauhou, *Zosterops lateralis*). *Notornis 70(3)*: 97–110.

Keywords: White-eye, Zosteropidae, bird banding, Underhill-Zucchini moult model

INTRODUCTION

The first custom-built statistical model for the study of primary wing feather moult in birds was developed in the late 1980s (Underhill & Zucchini 1988; Underhill *et al.* 1990); however, it was another 25 years before it could be utilised using widely accessible software (Erni *et al.* 2013). Subsequently, there have been many applications of the Underhill-Zucchini model facilitating reviews of primary moult involving multiple species and many sites (e.g. Remisiewicz 2011; Dietz *et al.* 2015; Jackson

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& Underhill 2022; Scott 2023). Although studies of primary moult in New Zealand birds exist (e.g. Gill 1983; Onley 1986; Rasmussen 1988; Sagar 1988; Davies 1997; Beauchamp 1998; Conklin & Battley 2011; Smith *et al.* 2015), no published studies include the application of quantitative techniques, such as the Underhill-Zucchini moult model, to estimate the timing and duration of primary feather replacement.

Latitude is a key variable in determining patterns of moult (see reviews in Remisiewicz 2011; Dietz *et al.* 2015; Jackson & Underhill 2022; Scott 2023). However, latitude serves as a proxy variable, mainly related to seasonality and therefore climate. It is also a measure of how physically challenging climates become for birds during winter, especially at far northern and far southern latitudes, and therefore provides an indication of species migratory habit. In temperate regions, latitude becomes a key driver of climate, through variables such as day length, seasonality, and temperature. These place constraints on food availability and as a result primary moult patterns are increasingly synchronised, taking place at the same stage in the annual cycle of many bird species, namely after the spring breeding season and before the onset of harsh winter conditions (Jenni & Winkler 2020a; Jackson & Underhill 2022). However, our understanding of the relationship between latitude and moult is hampered by the latitudinal range of moult studies available (Scott 2023). The northernmost study to which the moult model has been applied was in Alaska at latitude 71°N (Taylor *et al.* 2018). In contrast, the southernmost published analysis was in Australia, at latitude 39°S (Rogers *et al.* 2014). To extend the latitudinal range of moult studies, researchers need to target species near the southern extremities of Australia (44°S), South America (56°S), and New Zealand (48°S).

This paper extends the latitudinal range of moult studies southwards by quantifying the timing and duration of primary moult of adult silvereyes (tauhou, *Zosterops lateralis*) in New Zealand. We also explore juvenile primary moult. The results are compared to those for other members of the genus *Zosterops* globally. We consider opportunities, suggested by this analysis, for the study of primary moult of birds in New Zealand.

METHODS

Species

The genus *Zosterops* is large and its taxonomy is in a state of flux (Lim *et al.* 2019). BirdLife International (2023) recognised 103 species in the genus *Zosterops*, with 71 classified as Least Concern and the remaining 32 in threat categories: 14 are Near Threatened, nine Vulnerable, two Endangered, four Critically Endangered and three Extinct. Species of the genus *Zosterops* occur widely throughout southern and southeast Asia, Africa south of the Sahara, Australasia, and New Zealand, with many species restricted to islands in the Indian and western Pacific Ocean (van Balen 2008; Gill *et al.* 2022). The silvereye has one of the largest ranges of any *Zosterops* species, occurring in southern and eastern Australia, New Zealand, and islands of the southwestern Pacific Oceans (Higgins *et al.* 2006). It is also one of four species in the genus described as a migrant or partial migrant (van Balen 2008).

The silvereye is a self-introduced species to New Zealand, arriving naturally from Australia and establishing successfully during the 19th century (Neuhäuser & Cuming 2007; Checklist Committee 2022). Silvereyes were first noticed at Milford Sound, South Island, in 1832 (Thomson 1922). By the 1850s they were sighted more frequently and appeared to be expanding northwards from Southland but were not observed north of Cook Strait until 1856. By 1858 silvereyes were considered permanent residents in Wellington, North Island. They continued their northward expansion and reached Hawke's Bay by 1861 and Auckland by 1865. By 1868, silvereyes had reached the northern-most point of the North Island and were established successfully across the mainland (Buller 1888; Thomson 1922). By the 21st century, silvereye was one of the most common and widespread bird species in New Zealand (Heather & Robertson 2005). They are considered valuable insectivores by fruit-growers and gardeners, despite causing some damage to orchards during the fruit season (Buller 1888; Thomson 1922; Wearing & McCarthy 1992; Heather & Robertson 2005).

Data collection

Moult data for silvereyes were collected by bird banders throughout New Zealand during the period 1978–2022. The birds were aged as adult or juvenile based on the amount of wear and fading of the primaries, with juveniles having fresh primaries at the start of their juvenile moult (DSM *pers. obs.*). Additional cues, such as the presence of a gape flange, colouration of the base of the bill (pinkish-orange prior to juvenile moult, blueish-grey in adults), and eye colour (pale greyish-red-brown in younger birds, dark red-brown in adults) were also used to assist in separating age classes. These ageing criteria become less reliable as moult proceeds and it is likely that some juveniles were aged as adults towards the end of moult (DSM *pers. obs.*). Most juveniles would most likely have been aged as adults after the completion of moult. The imperfect ageing criteria of silvereyes thus impact the analyses used to estimate the parameters of moult.

Table 1. Relative masses (%) of the nine primary feathers averaged for two adult silvereyes (*Zosterops lateralis*). The birds were roadkills in Hamilton, North Island, in June and July 2007 (Peter G. Ryan *in litt.*)

Primary	**P1**	**P2**	**P3**	**P4**	**P5**	**P6**	**P7**	**P8**	**P9**
Relative mass (%)	8.73	9.23	9.81	10.31	11.29	12.37	12.66	12.84	12.75

The location and co-ordinates of the banding sites were noted. Banders recorded the primary moult of captured birds using the standard protocol (Ginn & Melville 1983). This involves assigning a moult score to each primary feather (nine in the case of silvereyes), ranging from zero to five (0 = old feather; 1 = missing feather or feather pin; 2 = growing feather, emerging from sheath, up to one third full length; 3 = new feather is one to two thirds full length; 4 = new feather is more than two thirds full length with sheath still present at base; 5 = full length new feather).

Data analysis

Relative masses of silvereye primary feathers were obtained from two silvereyes that were processed as described by Underhill & Joubert (1995) (Table 1). Small sample sizes are appropriate for this purpose because there is minimal variation in the relative masses of the primary feathers for a species (Meissner *et al.* 2018). For both the primary moult in adults and juveniles, the moult scores were converted to Proportion Feather Mass Grown (PFMG) using the relative feather masses. The Underhill & Zucchini (1988) moult model was used to analyse primary moult. The parameters of moult were estimated using the package "moult" (Erni *et al.* 2013) in R (R Core Team 2019). The estimated parameters were the duration of moult, the mean start date of moult and the standard deviation of the start date. Standard errors of each parameter were also estimated by the model. We estimated that 95% of birds start moult in the period given by the estimated mean start date ± 1.96 × estimated standard deviation parameter.

We used two of the five data types of the moult model, data type 2 and data type 5 (Underhill & Zucchini 1988; Underhill *et al.* 1990). Data type 2 assumes that the birds are sampled from a closed population which includes those that have not yet started moult, birds actively moulting and birds that have completed moult. Data type 5 assumes that the closed population consists of birds that have not yet started moult and birds actively moulting. A data type 5 analysis excludes birds which have completed moult. Where adequate data are available, it is preferable to use data type 2, because the moult model is then able to extract information from the birds which have completed moult. When this is done the standard errors of the estimates of the parameters are smaller with data type 2 than with data type 5. Because of the uncertainties with the ageing of silvereyes, a series of moult models was tried using the two different data types and the results were compared and evaluated.

We applied data type 2 to birds aged as adults. However, because of the difficulties of aging juveniles, as explained above, it is likely that a proportion of juveniles near the end of their moult cycle, and all those having completed moult, were aged as adults. To address the issue caused by the erroneous inclusion of the juveniles in the analysis of adult moult, we also applied data type 5 to the silvereye adults to remove the overabundance of birds that had completed moult in the dataset. We applied data type 5 to the juveniles because the juveniles that had completed moult would have been aged as adults. We used data type 2 and data type 5 on the combined sample of silvereyes aged as adults and juveniles. The moult model was first run with one mean start date estimated for both adults and juveniles combined using data type 2. It was then run a second time with two mean start dates estimated (one for adults and one for juveniles) using data type 5. In addition, we used data type 2 on a sample that included adult and juvenile birds as well as birds which were not aged. Our decision on the choice of model which best described the moult of silvereyes in New Zealand was based partly on the biological insights provided by the models, rather than on statistical model selection techniques. We considered whether there were changes in the timing of moult, both latitudinally and temporally.

Two measures that relate to primary moult and provide insight into energetic costs of moult were computed. The first was the average number of simultaneously growing primaries, which is defined as moult intensity. This can serve as a proxy for the direct energetic costs of growing new feathers (Remisiewicz *et al.* 2009; Jenni & Winkler 2020a). For adult silvereyes, the mean number of primary feathers growing simultaneously, along with its 95% confidence interval, was calculated and plotted for each of the nine primaries. The second measure was Proportion Feather Mass Missing (PFMM), as described by Remisiewicz *et al.* (2009). This quantifies the relative size of the wing gap created when primary feathers are being moulted, taking the relative mass of the primaries into account. The larger the wing gap, the greater the

Table 2. Estimated moult parameters of the primary feather tract of silvereyes (*Zosterops lateralis*) in New Zealand using the Underhill-Zucchini moult model and PFMG as the moult index. Samples of birds using adult and juvenile age classes were selected and analysed using either data type 2 or data type 5 (see text). The penultimate analysis in the table is a four-parameter model that gave different start dates to adults and juveniles but kept the duration and standard deviation parameters common to both. Day 1 was 1 September.

Age class	Data type	Moult parameter					Sample sizes		
		Duration (SE)	Start day (SE)	Standard deviation of start day (SE)	Start date (SE)	End date (SE)	Pre-moult	In-moult	Post-moult
Adult	2	72.9 (3.9)	148.9 (2.6)	38.8 (2.0)	27 Jan (2.6)	10 Apr (2.7)	162	301	230
Adult	5	83.8 (9.5)	148.5 (3.0)	41.2 (3.5)	27 Jan (3.0)	20 Apr (8.4)	162	301	–
Juvenile	5	116.4 (17.9)	158.4 (3.8)	57.4 (8.0)	5 Feb (3.8)	2 Jun (16.7)	188	224	–
Adults and juveniles, one start date	2	77.8 (3.4)	155.0 (1.8)	39.6 (1.7)	2 Feb (1.8)	21 Apr (2.6)	350	525	230
Adults and juveniles, two start dates	5	95.2 (8.4)	Ad 145.8 (3.2) Juv 160.2 (2.9)	46.6 (3.4)	Ad 24 Jan (3.2) Juv 7 Feb (2.9)	Ad 29 Apr (7.4) Juv 13 May(8.2)	350	525	–
All data	2	74.3 (2.9)	156.4 (1.6)	37.3 (1.5)	3 Feb (1.6)	19 Apr (2.3)	429	605	261

loss in flight performance (Jenni & Winkler 2020a, 2020b; Hedenström 2023) and therefore PFMM aids in quantifying this important component of the indirect costs of moult. PFMM was estimated for each bird in active moult using the method described by Remisiewicz *et al.* (2009): Primary feather moult scores of 1, 2, 3, 4 are converted to 0.875, 0.625, 0.375, 0.125 respectively and moult scores of 5 and 0 are taken as zero (i.e. no missing feather mass). These proportions are then multiplied by the relative mass of the corresponding primary and summed across all primaries.

RESULTS

We obtained data for 29 of the 44 years of the study period (1978 to 2022). There was a total of 1,295 available moult records for silvereyes in New Zealand: 310 for North Island and 985 for South Island. Latitudinal data were available for 1,289 of the 1,295 records. 84% of these 1,289 moult records were between latitudes 41°S and 42°S. This range covers the northern part of the South Island and the southern part of the North Island. It was therefore not feasible to investigate whether there was a trend over the *c.* 12° latitudinal range of New Zealand (36.4°S to 48.0°S) for which moult data were recorded or whether there was a biologically meaningful difference between birds on the two islands. The mean latitude of the collected moult records was 42°S. Given the 44-year period for which data were available, we also wanted to test whether there was a long-term trend in the parameters of moult. However, 80% of the records were for the period 2002–2012, and 43% for the three years 2010, 2011, and 2012. It was therefore not possible to investigate temporal trends.

There were 693 moult records for adult silvereyes: 162 were pre-moult, 301 were active moult, and 230 were post-moult records (Table 2; Fig. 1). Applying data type 2 to these data, the duration of moult was estimated as 73 days with a mean start date of 27 January and mean end date of 10 April. The start date was unchanged when data type 5 was applied but the duration was estimated to be 84 days, a change consistent with the reality that post-moult juveniles were included in the sample of adults. The standard error of the duration parameter was 3.9 days for data type 2 and 9.5 days for data type 5. The standard deviation parameters were estimated as 39 days and 41 days for data types 2 and 5 respectively (Table 2; Fig. 1). For four adults (0.6% of the data) the moult scores had been recorded in ways suggestive of suspended moult (500000000 on 5 February, 555555500 on 6 February, 555555500 on 3 March, 555555000 on 24 April). All are inliers in relation to the scatter diagram in Fig. 1.

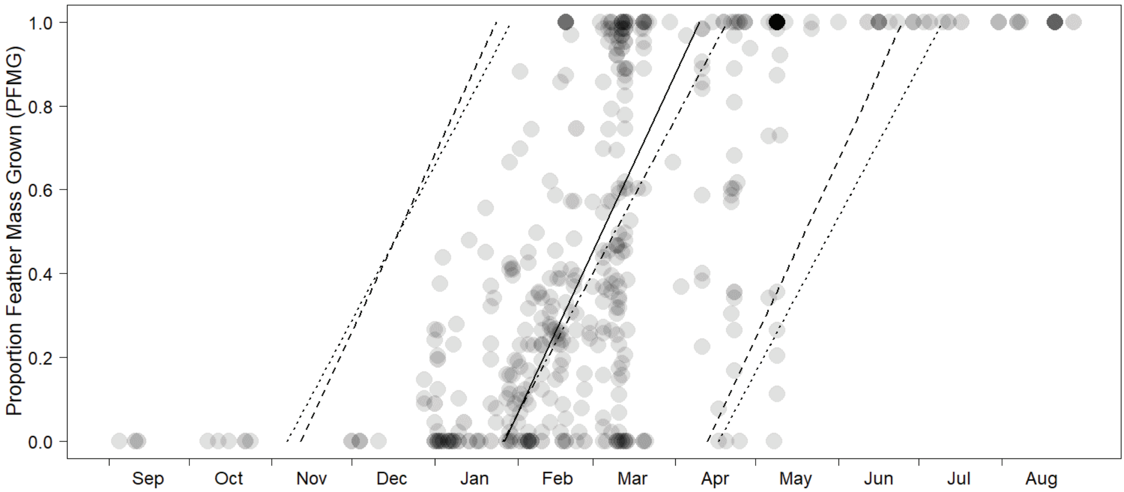

Figure 1. Modified scatter diagram* of the progression of primary moult for adult silvereyes (*Zosterops lateralis*) in New Zealand using PFMG as the moult index. The solid and the dot-dash straight lines represent the progression of moult for the average adult bird in the population using data type 2 and data type 5 respectively. The dashed lines and dotted lines are the 95% intervals calculated from the standard deviation of the mean start date using data type 2 and data type 5 respectively.

* Moult scores are recorded on a discrete scale (each primary is allocated an integer score between 0 and 5). A consequence of this is that conventional scatter plots of moult scores in relation to dates are misleading because there is no representation of the number of records represented by a single symbol in the plot. In this modification of the scatter diagram, the data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade refers to one data point and the darkest shade refers to 69 overlapping data points.

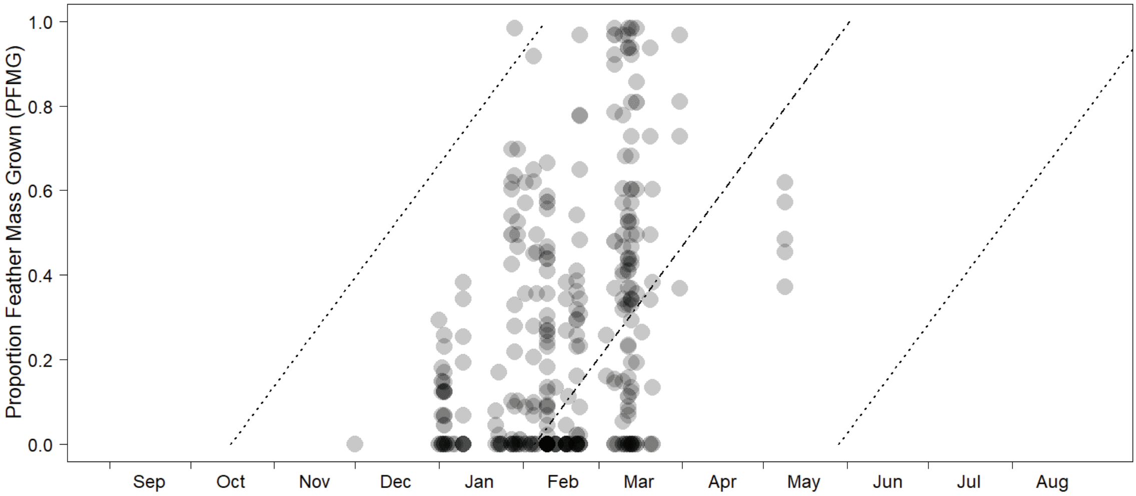

Figure 2. Modified scatter diagram* of the progression of juvenile primary moult in silvereyes (*Zosterops lateralis*) in New Zealand using PFMG as the moult index and data type 5. The dot-dash straight line represents the progression of moult for the average juvenile bird in the population. The dotted lines are the 95% intervals calculated from the standard deviation of the mean start date.

* In this modification of the scatter diagram, the data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade refers to one data point and the darkest shade refers to 22 overlapping data points.

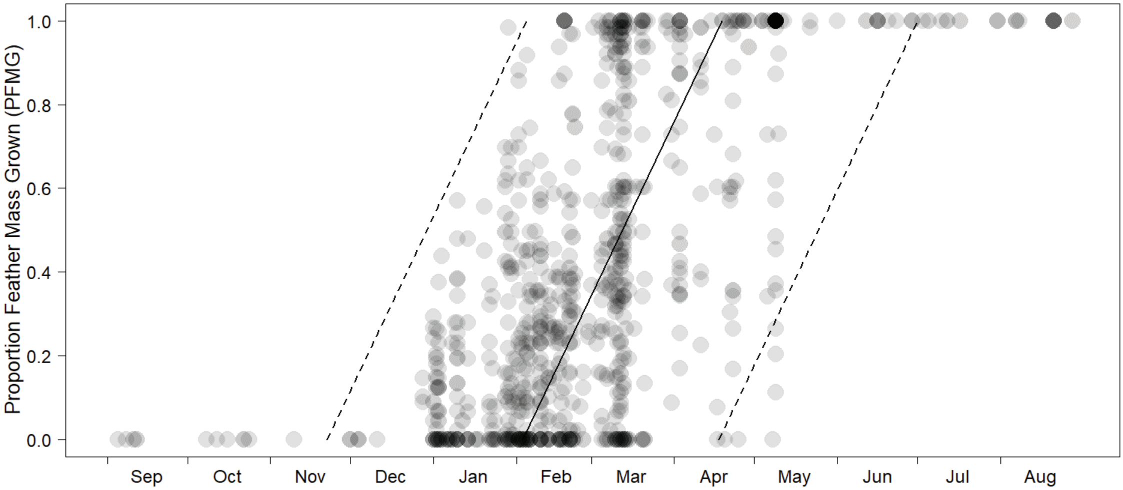

Figure 3. Modified scatter diagram* of the progression of primary moult in silvereyes (*Zosterops lateralis*) in New Zealand using all available data (adults, juveniles and unaged birds), PFMG as the moult index and data type 2. The solid straight line represents the progression of moult for the average juvenile bird in the population. The dashed lines are the 95% intervals calculated from the standard deviation of the mean start date.

* In this modification of the scatter diagram, the data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade refers to one data point and the darkest shade refers to 69 overlapping data points.

It is also possible that, within the natural variation in numbers of feathers actively moulting, a small proportion of birds have moult scores like this and therefore they were included in the analysis. When these four records are excluded, the estimated duration changes by 0.6 days, mean start date by 0.3 days and the standard deviation of start date by 0.1 days. The decision to include or exclude them has no biological impact.

There were 412 moult records for juveniles, of which 188 were pre-moult and 224 were in active juvenile primary moult (Table 2; Fig. 2). The mean start date of juvenile moult was estimated using data type 5 to be 5 February, the standard deviation parameter was 57 days and the estimated duration was 116 days. The duration, however, had a large standard error of 18 days, which points to it being unreliable (Table 2).

When the data for the birds aged as adults and those aged as juveniles were combined, and data type 2 was used, the duration of moult was estimated to be 78 days (standard error 3.4 days). The start date was estimated to be 2 February (standard error 1.8 days), which lies close to the middle of the estimated dates for adults (27 January) and juveniles (5 February) (Table 2). Start dates of 24 January and 7 February were estimated for adults and juveniles respectively when the same combined data were used in a moult model that predicted two mean start dates (one for each age class), one duration, and one standard deviation. Data type 5 was used in this analysis because juveniles which had completed moult would have been classified as adults. It was therefore appropriate to omit the birds which had completed moult from the analysis. This analysis confirmed the delay of approximately two weeks between the start of primary moult in adults and the start in juveniles. The duration was estimated as 95 days (standard error 8.4 days) (Table 2). When the entire dataset (1,295 records, including all unaged birds) was analysed using data type 2, the start date was estimated to be 3 February and the duration to be 74 days (standard error 2.9 days) (Table 2; Fig. 3).

During the replacement of the first eight primaries there were, on average, 2.9 concurrently growing feathers (Fig. 4). During the replacement of the outermost ninth primary this decreased to 2.2. As the proportion of new primary feather mass grown increases, the size of the wing gap in the primary feathers remains fairly constant with a mean of 0.10 (SD = 0.07) (Fig. 5). This means that, on average, adult silvereyes were missing 10% of their primary feather mass during moult (Fig. 5). The largest wing gap was 0.41, which corresponds to 41% of the total feather mass. This was for a bird replacing P4–P9 (moult formula 555443111 on 11 March).

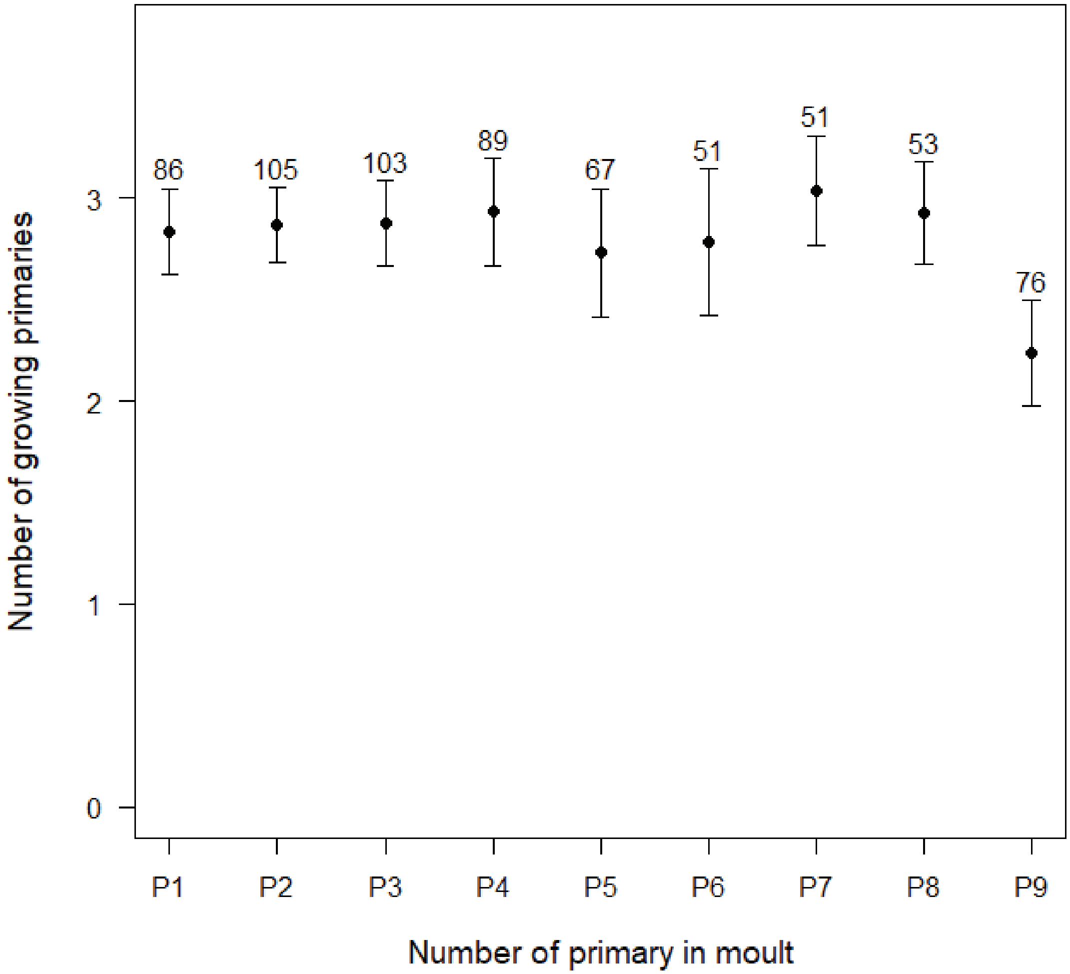

Figure 4. The mean number of primaries growing simultaneously while each of the nine primaries of adult silvereyes (*Zosterops lateralis*) was in moult. The 95% confidence intervals for the mean and the sample sizes are shown.

DISCUSSION

Primary moult of the silvereye

When adults and juveniles were considered separately, the mean dates of the start of primary moult for silvereyes were estimated to be 27 January for adults and 5 February for juveniles (Table 2). However, post-moult juveniles would have been classified as adults and the number of post-moult adults inflated. As a result, the duration of moult in adults and their average end date of moult would have been less reliably estimated. Using data type 2, these misclassified juveniles would have caused the Underhill-Zucchini moult model to bias the adult moult duration to be short. Thus, the estimated 73 days is most likely an underestimation of the duration of primary moult (Table 2). However, when data type 5 was used, and the 230 post-moult adult birds were omitted from the analysis, the standard error of the duration was too large for the result to be reliable.

Because of the concentration of records near the start of moult in juveniles (Fig. 2), the estimated mean starting date for juvenile moult (5 February) can be considered reliable, but the estimates of the duration and end date are not likely to be satisfactory. This is confirmed by the large standard error of the estimate of the duration parameter and the end date (Table 2). Thus, the estimated duration of 116 days is deemed unreliable (Table 2).

When the data for adults and juveniles are

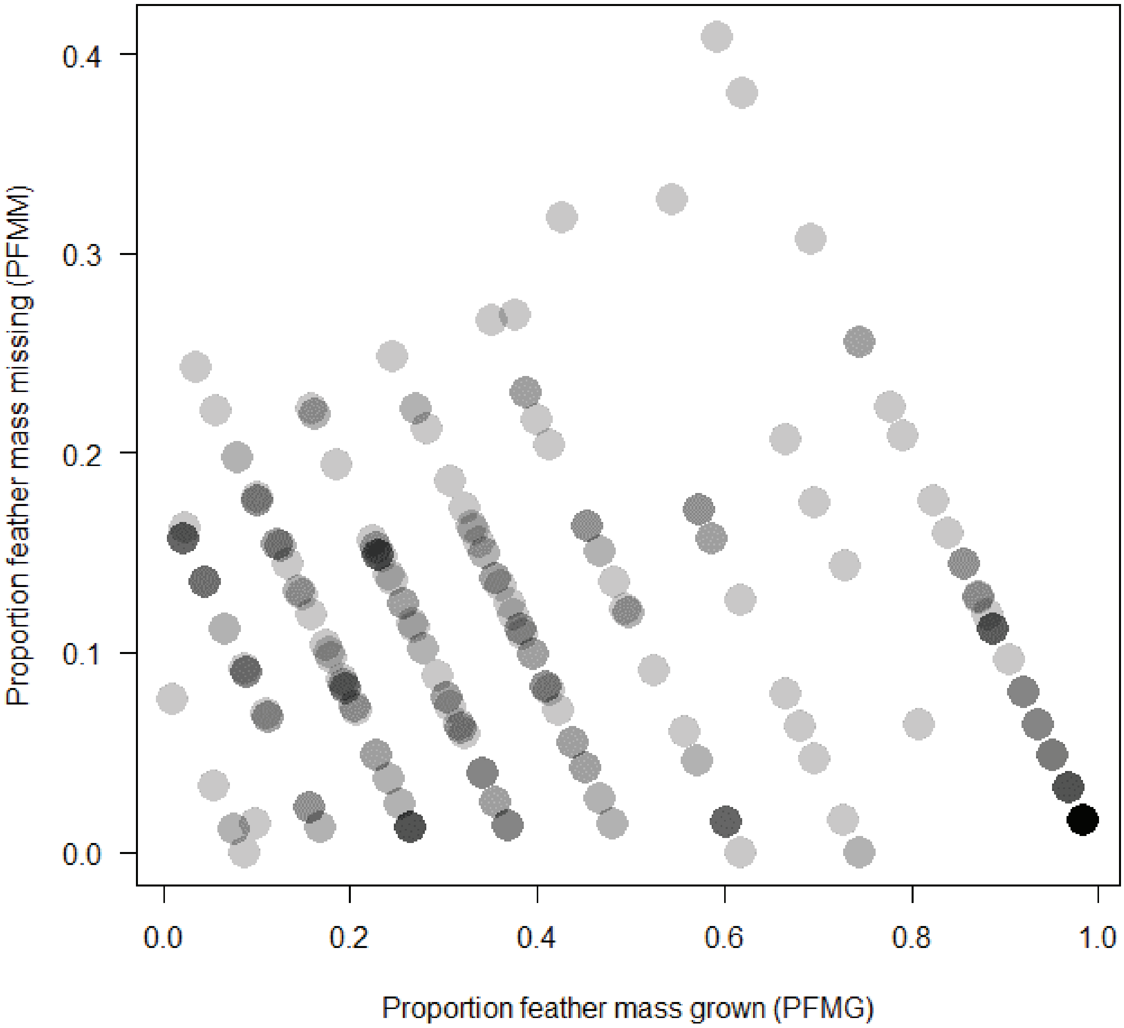

Figure 5. The relationship between Proportion Feather Mass Missing (PFMM) and Proportion Feather Mass Grown (PFMG) is represented by a modified scatter diagram* for adult silvereyes in active moult. The pattern of parallel lines is an artefact of the protocol for the recording of the moult status of each primary as an integer between 0 and 5. Each point in this scatter diagram can represent multiple records.

* In this modification of the scatter diagram, the data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade refers to one data point and the darkest shade refers to 22 overlapping data points.

combined the assumptions of data type 2 are satisfied because all birds are available for sampling throughout the moult period. The differences between the estimates using only the aged birds in a model with a single mean population start date and using all available data were relatively small and biologically meaningless. The estimated durations differed by 3.5 days. This should be seen in the context that the estimated 95% confidence interval for duration, when using all available data, was 74.3 ± 1.96 × 2.9 days or 69 to 80 days. The alternative estimate of 78 days, when using only aged birds, was within this interval.

Therefore, based on the reasoning set out above it is suggested that the most reliable estimates of the parameters of moult for the silvereye in New Zealand are those for the entire silvereye population: a duration of 74 days, a mean population start date of 3 February, and a standard deviation of start date of 37 days (see final row of Table 2; Fig. 3).

Our understanding of juvenile primary moult is incomplete due to the inherent difficulties of ageing silvereyes in the field towards the end and especially after the completion of primary moult (Higgins *et al.* 2006). However, it is evident from the penultimate row of Table 2 that juveniles start moult, on average, about two weeks later than adults.

In Australia, juveniles that hatch by early December from the first clutches of the breeding season, undergo a complete moult, similar to that seen in adults (Swanson 1971). Those that hatch later are often found to be moulting in late April and May (Swanson 1971), while those hatched at the end of the breeding season (February) undergo a partial juvenile moult (Swanson 1971; Higgins *et al.* 2006). This situation probably applies in New Zealand as well but has yet to be demonstrated.

Primary moult in the genus *Zosterops*

In the era of climate change, given that 15 of 100 extant species of this large genus are threatened and another 14 are near threatened, improved knowledge of their biology, including moult, is a priority (BirdLife International 2023; IUCN 2023). Climate change has the potential to alter breeding seasons of species, resulting in shifts in the start of the post-breeding moult and possibly the speed at which it progresses (Morrison *et al.* 2015). However, it is unclear if changes in the timing and/or speed of moult can keep up with changes in breeding seasons (Jenni & Winkler 2020a).

Most *Zosterops* species are residents (van Balen 2008). Primary moult follows closely after the breeding season and it is a complete replacement of the primary feathers (Guest 1973; Greig-Smith 1979; Hulley *et al.* 2004). This is also true for silvereyes (Swanson 1971; Kikkawa & Wilson 1982; Rooke 1984). The silvereye is a multi-brooded species, usually laying two or three clutches in a breeding season (Fleming 1943; Gill 1994; Higgins *et al.* 2006). It undergoes a post-breeding moult annually (Fleming 1943; Mees 1969; Kikkawa & Wilson 1982). Multi-brooded species are expected to delay the start of post-breeding moult and possibly increase the speed of moult if the breeding season extends into autumn as a result of global warming (Jenni & Winkler 2020a). However, autumns and winters may also be milder and therefore there may not be a constraint on moult. Moult speed influences the quality of feathers grown and a rapid moult can produce poorer quality feathers (Serra 2001). Feather quality can affect the vital functions of feathers, such as flight, insulation, and signalling, and thereby impact bird survival (Jenni & Winkler 2020a). Changes in the breeding season and a delayed post-breeding moult may also result in time constraints, causing birds to interrupt a moult which they would otherwise complete (Jenni & Winkler 2020a). It is therefore important to monitor species and the activities in their annual cycle. In the case of silvereye, this includes breeding and moult, with moult being the easiest to monitor and quantify. Monitoring enables researchers to determine what effect climate change is having on the annual cycle and if birds are able to adapt or if conservation measures are appropriate.

Several studies have examined the primary moult of other *Zosterops* species (Table 3). When comparing moult results between studies it is preferable to use those that applied the Underhill & Zucchini (1988) moult model so biological differences and not differences in analysis method are identified (Dietz *et al.* 2015). Of the results presented in Table 3, only Hulley *et al.* (2004) used this model. Despite a latitudinal difference of *c.* 9° between South African and New Zealand populations, the durations of moult for silvereyes in New Zealand (74 days) and two species of white-eyes in South Africa (69–78 days) were similar. Excluding the results obtained by Munro *et al.* (2006), which were based on captive birds with unlimited access to food, other methods of analysis have estimated moult durations between 83 and 90 days for wild white-eyes across a wide range of latitudes (Table 3). We suggest that it is likely that moult durations for *Zosterops* species are similar and independent of latitude (studies cover a latitudinal range of 65°). The timing of primary moult within the annual cycle is variable, adjusted to local conditions and follows breeding, which in turn is related to food availability.

In other genera there is large variability in moult duration, both between and within species, related to latitude, food availability, and migration patterns and distance. This is especially well documented for migrants of the genera *Calidris* and *Charadrius* (Remisiewicz 2011; Jackson & Underhill 2022). The passerine genus with the largest number of analyses using the Underhill-Zucchini moult model is *Ploceus*, with 14 analyses of seven species of weavers from 6°N to 33°S (Scott 2023). Durations range between 67 days for the population of the southern masked weaver (*P. velatus*) at 33°S (Craig *et al.* 2001) to 198 days for the chestnut weaver (*P. rubiginosus*) at 19°S (Oschadleus & Osborne 2005). The relatively short and consistent moult durations at different latitudes in the genus *Zosterops* are an apparent contrast to the varied patterns in other genera. These observations emphasise our incomplete knowledge of moult, especially in the tropics and southern hemisphere, and warrant further investigation.

Table 3. Results of moult studies in *Zosterops*. Species are arranged from north to south. Higgins *et al*. (2006) was a resource for moult studies of silvereyes.

Species	Duration (days)	Latitude	Location	Moult period (estimated start date–end date)	Source
Warbling white-eye (*Z. japonicus*)	90	22.50°N	Hong Kong, China	Jun–Sep (23 Jun–21 Sep)	Melville 1989
Warbling white-eye (*Z. japonicus*)	-	21.44°N	Oahu, Hawaii	Jul–Oct	Guest 1973; Van Riper & van Balen 2020
Northern yellow white-eye (*Z. senegalensis*)	85	10–11°S	Nyika Plateau, Malawi/Zambia	Dec–Mar, peak Jan–Feb	Dowsett & Dowsett-Lemaire 1984
Canary white-eye (*Z. luteus*)	-	17.88°S	Broome, Australia	Dec–Apr	Lewis & Macarthur 2011
Silvereye (*Z. lateralis*)	-	18.15°S	Fiji	Jan–May	Langham 1987
Orange River white-eye (*Z. pallidus*)*	78.0	28.39°S	Free State, South Africa	Feb to Apr/May (30 Jan–19 Apr)	Hulley *et al.* 2004
Cape white-eye (*Z. virens*)	-	28.53°S	KwaZulu-Natal, South Africa	Feb–Jun	Craig 1983
Cape white-eye (*Z. virens*)	-	29.83°S	Pietermaritzburg, KwaZulu-Natal, South Africa	Feb–Jun	Earlé 1981; Symes *et al.* 2001
Cape white-eye (*Z. virens*)*	76.7	33.31°S	Grahamstown, Eastern Cape, South Africa	Feb–Apr/May (7 Feb–25 Apr)	Hulley *et al.* 2004
Cape white-eye (*Z. virens*)*	75.5	33.83°S	Durbanville, Western Cape, South Africa	Dec–Mar/Apr (25 Dec–11 Mar)	Hulley *et al.* 2004
Silvereye (*Z. lateralis*)	83	33.87°S	Five Dock, New South Wales, Australia	Jan–Apr	Swanson 1971
Cape white-eye (*Z. virens*)	-	34.02°S	Sedgefield, Western Cape, South Africa	Jan–May	Dowsett 1985
Silvereye (*Z. l. familiaris*)**	52.5	34.07°S	Campbelltown, New South Wales, Australia	Jan/Feb–Apr (7 Feb–31 Apr)	Munro *et al.* 2006
Cape white-eye (*Z. virens*)*	69.7	34.07°S	Rondevlei, Western Cape, South Africa	Jan–Mar/Apr (12 Jan–23 Mar)	Hulley *et al.* 2004
Cape white-eye (*Z. virens*)	-	34.13°S	Sir Lowry's Pass, Western Cape, South Africa	Oct–Apr, peak Feb–Mar	Whitelaw 1985
Cape white-eye (*Z. virens*)*	68.9	34.37°S	Betty's Bay, Western Cape, South Africa	Dec/Jan–Mar (9 Jan–19 Mar)	Hulley *et al.* 2004
Silvereye (*Z. lateralis*)	-	36.88°S	Rumuera, Aukland, New Zealand	Jan–Mar/Apr	Fleming 1943
Silvereye (*Z. lateralis*)	-	36.98°S	Victoria, Australia	Jan–Apr	Rogers *et al.* 1986
Silvereye (*Z. lateralis*)*	74.3	41.70°S	New Zealand	Jan/Feb–Apr (3 Feb–19 Apr)	This study
Silvereye (*Z. lateralis lateralis*)***	49.0	42.53°S	Hobart, Tasmania	Jan–Mar (25 Jan–15 Mar)	Munro *et al.* 2006

* applied the Underhill-Zucchini moult model; ** captive birds, small sample (n = 13); *** captive birds, small sample (n = 19).

Partial migration and moult

The nominate race of silvereye *Z. lateralis lateralis* is the subspecies that colonised New Zealand (Heather & Robertson 2005) and this subspecies is a partial migrant in south-eastern Australia. In particular, a substantial proportion breed in Tasmania then migrate north to south-eastern continental Australia in winter (Griffioen & Clarke 2002; Chan 2005). In New South Wales, Australia, it is an altitudinal migrant (Higgins *et al.* 2006). Mass movements of silvereyes in New Zealand have been recorded from mid-April to June (Dawson 1961; Grant 1970; Dennison *et al.* 1981). The timing of these would coincide with the period shortly after moult but before winter sets in. Flocks of birds have been seen travelling northwards, apparently from the South Island to the North Island (Grant 1970; Buller 1888; Dennison *et al.* 1981). As in Australia, this is a partial migration, because large populations remain on the South Island during winter (Stead 1930 in Fleming 1943; Kikkawa 1962; Grant 1970; Robertson *et al*. 2007). St Paul (1975) noted seasonal altitudinal movements with birds gathering in flocks in low-lying populated areas in winter. In contrast, in southern Africa, the Cape white-eye (*Zosterops virens*) is mainly sedentary; of 135 ring recoveries, only three exceed 100km with the largest distance being 164km (Symes *et al.* 2001; Hulley *et al.* 2004; SAFRING unpubl. data). It is not an altitudinal migrant (Scott 2018; Craig & Hulley 2019), although the possibility was considered by Johnson & Maclean (1994), but there are inferences, based on atlas reporting rates, of seasonal movements in the arid west of South Africa (Nuttall 1997). There are clearly interesting opportunities to study inter-relationships between timing of breeding, moult and movement patterns (partial migrant, altitudinal migrant, and resident) between continents in these southernmost representatives of the genus *Zosterops*. Most comparable studies have been made in northern temperate zones (Jenni & Winkler 2020a, 2020b) and data from the temperate zones of the southern hemisphere are a priority (*cf*. Theuerkauf *et al*. 2022).

Moult intensity

The concept of moult intensity was introduced and developed by Haukioja (1971) and highlighted by Mumme *et al.* (2021). Mumme *et al.* (2021) measured moult intensity by the average number of simultaneously moulting primaries (Fig. 4) and Proportion Feather Mass Missing (PFMM) (Fig. 5). The relevant discussion point here is whether the gaps in the wings are large enough to impair flight to the extent that the birds become near-flightless and are therefore under-represented in mist-netted samples. Impaired flight is recorded at far northern latitudes (Haukioja 1971) and New Zealand is sufficiently far south that this is an issue that needs to be considered in quantitative moult studies. One of the assumptions of the Underhill & Zucchini (1988) moult model is that the probability of being captured is independent of the stage of moult.

Silvereyes consistently moulted an average of *c.* 2.9 primaries during moult (Fig. 4). This contrasts with, for example, the laughing dove (*Spilopelia senegalensis*), which tended to moult one or two primaries simultaneously (Scott *et al.* 2023), but is similar to that of the wood sandpiper (*Tringa glareola*) (Remisiewicz *et al.* 2009). Both the laughing dove and the wood sandpiper are able to fly throughout moult, as are silvereyes. In contrast, Mumme *et al.* (2021) described the moult of 13 warbler species at 40°N in Pennsylvania, USA, which moulted, on average, between four and five primaries simultaneously through the central part of primary moult. These species were then reluctant to fly. The moult durations for these 13 species were between 39 and 53 days.

PFMM is likely to provide a more sensitive approach to assessing flightlessness than the numbers of simultaneously growing primaries. PFMM was first introduced by Ward *et al.* (2007) for the kelp gull (*Larus dominicanus*) and there are analyses for few species. PFMM refines the concept of "raggedness" developed by Haukioja (1971). PFMM takes into account the variation in the sizes of the primaries, which raggedness does not. The difference between PFMM and raggedness will get larger as the relative sizes of primaries change. It will reach an extreme with long-distance migrants, for which the outer primary is up to seven times larger than the innermost primary. An example is the Arctic tern (*Sterna paradisea*) (Underhill & Joubert 1995). In terms of silvereyes, Fig. 5 shows us that PFMM remains fairly constant throughout primary moult and therefore silvereyes do not become flightless.

Opportunities for the study of moult in New Zealand

Latitude plays an important role in determining moult patterns (Jackson & Underhill 2022). With an established community of citizen scientist bird banders, New Zealand has two distinct advantages as a country in which to study moult, both related to latitude. Firstly, it has a sufficient latitudinal range within the mainland, from 34.4°S to 46.7°S, to enable studies of the variation in timing of moult in relation to this variable. Secondly, its location enables the overall latitudinal range of moult studies to be extended further south (48°S) than currently available, while at the same time overlapping latitudinally with Australia (southern limit 44°S) and Africa (southern limit 35°S). Only South America stretches further south (56°S), but it lacks bird banding communities in the far south. Moult studies in New Zealand are therefore vitally important in aiding our understanding of the role latitude plays in moult.

We therefore recommend that the bird banding scheme in New Zealand encourages the routine and ongoing collection of moult data at a latitudinal spread of locations for four reasons: (1) It will help to fill a gap in knowledge because there are few quantitative moult studies in New Zealand; (2) the geographical configuration of New Zealand provides opportunities for studies along a latitudinal range; (3) the southern geographical location of New Zealand provides important opportunities to understand the timing of moult in relation to climate change; (4) the geographical location combined with a well-developed network of bird banders enables a unique contribution to be made to the global understanding of the biogeographical patterns of moult, breeding, and migration.

For the silvereye in particular, a good body of primary moult data is available for the period 2002 to 2012. A dedicated project to collect further data for this species would have the opportunity of using these historical data as a baseline from which to measure future change. This has been done, for example, by Taylor *et al.* (2018) for the dunlin (*Calidris alpina*) in Alaska. They found a 43% increase in the duration of moult over six decades. Jackson & Underhill (2022) pointed out the need for further studies of this nature.

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Seasonal movements, foraging activity, and breeding biology of black-winged petrel (*Pterodroma nigripennis*) from three New Zealand colonies

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Abstract: The black-winged petrel (*Pterodroma nigripennis*) is an abundant procellariiform seabird breeding on islands in the Southwest Pacific and Indian Oceans. The largest populations breed in the New Zealand region where at sea movements and breeding behaviour across the annual cycle remain poorly described. We used geolocators with saltwater immersion sensors to track movements and characterise breeding behaviour of *P. nigripennis* from three New Zealand breeding colonies (Raoul, Burgess, and Rangatira Islands) across a 1,600 km latitudinal gradient. Breeding extended from November to June and in Raoul Island birds pre-laying, incubation, and chick rearing periods lasted 36, 50, and 85 days respectively. During breeding, birds from all colonies foraged within waters of the subtropical convergence zone which for Raoul, required one-way foraging trips of over 1,500 km. During March–June birds migrated east, then north and northwest to core foraging zones predominantly within the North Pacific subtropical front, but a small number of birds also wintered south of Hawaii in equatorial waters. Birds were predominantly nocturnally active during breeding and non-breeding seasons indicating a dependence of nocturnally available prey. These data contribute to a growing understanding of the unprecedented movements and potential partitioning of habitat by Australasian *Pterodroma* petrels within the Pacific Ocean and we summarise and discuss available data.

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Keywords: At-sea behaviour, Pacific migration, subtropical convergence zone, geolocators

INTRODUCTION

The black-winged petrel (*Pterodroma nigripennis*) is one of ten small highly pelagic procellariform seabirds often grouped within the subgenus *Cookilaria* (Onley & Scofield 2007). Black-winged petrels are abundant, with a global population of 8–10 million individuals (Brooke 2004) they are considered Least Concern under IUCN criteria (BirdLife International 2023) and breed widely on tropical, subtropical, and temperate islands within the South Pacific and Indian Oceans (Marchant

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& Higgins 1990). In the New Zealand region, the largest breeding populations occur on Rangitāhua – the Kermadec Islands – with an estimated 2–3 million pairs on Macauley Island (282 ha) being the largest colony of this species (Taylor 2000). Significant colonies are also present on Curtis Island and the Meyer Islands, and the species is rapidly recolonising Raoul Island following pest eradication (Veitch 2004; Gaskin 2011). Over the past 40 years black-winged petrel populations have been expanding in range with prospecting birds observed at a number of sites around the northern North Island and Chatham Islands (Klapste 1981; Jenkins & Cheshire 1982; Tennyson 1991; Ismar *et al.* 2012). Small colonies (<1,000 birds) are now established on islands off the northeast coast of the North Island (Manawatāwhi – Three Kings Islands, Motuopao, Matapia, Simmonds, Motukokako, Poor Knights, Burgess, East, and Portland Islands) and on Rekohu – The Chatham Islands – on Rangatira, Mangere, and Little Mangere Islands (Taylor 2013).

The breeding biology of black-winged petrel was documented by Tennyson (1991) on Mangere Island, and Hutton & Priddel (2002) on Lord Howe Island. However, aspects of the species breeding biology remain poorly described including the duration of the pre-laying period and the degree of synchrony between colonies separated by broad geographic distance. Like many other small petrels the at-sea movements of black-winged petrel remain poorly described. Recent GPS tracking of breeding birds from Phillip Island (Norfolk Island Group) indicates a Tasman Sea distribution during chick rearing (Halpin *et al.* 2022), in accordance with earlier observational studies (Jenkins & Cheshire 1982). Ship-board observations and geolocation tracking suggests migration by this species to the waters of the equatorial and North Pacific Ocean during the austral winter (from July to October) (King 1970; Tanaka *et al.* 1985; Pitman 1986; O'Dwyer *et al.* 2022), although further understanding of the migration routes and population specific differences in migratory distribution are required.

The development of lightweight (<5 grams) combined geolocation and immersion geolocators (here after geolocators) has revolutionised the study of seabird biology and particularly for small petrels (Afanasyev 2004; Bridge *et al.* 2011). Attached to the bird's leg, a geolocator collects light level and saltwater immersion data over long periods (>2 years). Upon retrieval of the device the light data, measured every minute and logged to its maximum intensity every 10 minutes, can be used to calculate twice daily latitude and longitudes for the animal at sea to an accuracy of several hundred kilometres (Phillips *et al.* 2004; Halpin *et al.* 2021). Such data are ideally suited for tracking the seasonal movements of wide-ranging migratory animals such as seabirds. In addition, light data can be used to identify when burrow-nesting species are spending time ashore during the day during breeding, through identification of diurnal dark periods from time-stamped light data. Salt-water immersion data provide insight into the foraging activity of birds allowing description of periods of flight and resting activity, either at sea or on land (when the logger is continuously immersed or dry), and the duration and nature of flight bouts made by birds within and between seasons. With analyses of birds tagged from multiple colonies it is now possible to use geolocator-based data to build a simple population-specific understanding of the intra- and inter-seasonal movements, and breeding and foraging behaviours of birds without extensive field studies that could occupy months, if not years, of researcher time.

In this study we used geolocators to provide an inter-seasonal analysis of the at-sea movements of black-winged petrel from three New Zealand colonies spanning a tropical to temperate latitudinal gradient of approximately 1,600 kilometres. Moreover, using a geolocation-based approach, we provide a description of the at-sea activity of birds using immersion data and the timing of breeding stages for New Zealand's northernmost breeding population, Raoul Island. Comparisons are made between the non-breeding distribution of black-winged petrel and other small *Pterodroma* species tracked within the tropical and subtropical Pacific Ocean.

METHODS

Study sites

Geolocators (MK14 and MK18 tags, British Antarctic Survey) were deployed on adult black-winged petrels captured in breeding burrows at Raoul Island (Rangitāhua; The Kermadecs, 29°16′S, 177°55′W, n = 15) in February and March 2010, at Burgess Island (Mokohinau Islands, 35°50′S, 175°10′E, n = 11) in January and February 2011 and at Rangatira (Chatham Islands, 44°20′S, 176°10′W, n = 6) in February 2009 (Fig. 1). Geolocators were deployed on birds incubating eggs in all cases except for two birds tagged whilst courting in a burrow on Rangatira. Geolocators were retrieved at Raoul Island in January and March 2011, at Burgess Island in January and February 2012 and at Rangatira in February 2010 providing year-long datasets including the chick rearing period in the first year, non-breeding migration and the subsequent pre-laying, and in some cases incubation periods the following season. Geolocators were attached to birds with plastic leg bands, cable tie and superglue using the methods described by Rayner *et al.* (2008) and weighed <1% of the average body mass.

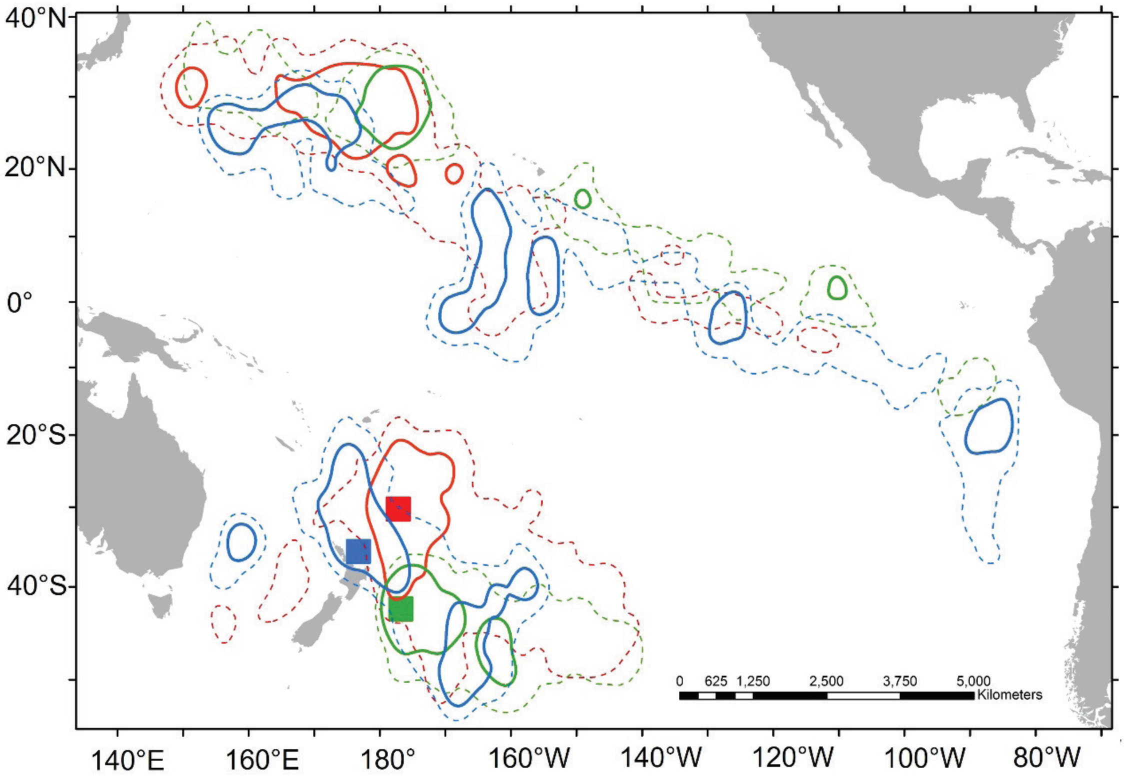

Figure 1. Year-round distribution of black-winged petrels (*Pterodroma nigripennis*) tracked from colonies on Raoul Island (red square), Burgess Island (blue square), and Rangatira (green square) between February 2009 and January 2012. Shown are the 50% (coloured lines) and 75% (hashed coloured lines) kernel contours of all locations for each population including Raoul (red lines; tracked from February 2010–March 2011), Burgess (blue lines, tracked from January 2011–January 2012), and Rangatira (green lines; tracked from February 2009–March 2010).

Tag and track processing

Light data from the geolocators were processed following the methods of Rayner *et al.* (2012). In brief, files downloaded from tags were decompressed using the software Bastrack (supplied by the British Antarctic Survey). The geolocators measured light level every minute and logged its maximum intensity every 10 minutes and the program Transedit was then used to establish sunrise and sunset transition times identified from light-curve thresholds and latitude calculated from length of day and night, and longitude from time of local midday or midnight relative to Greenwich Mean Time. Locations (2 per day) were assumed to have a accuracy of 300 ± 400 km (s.d.) (Phillips *et al.* 2004; Halpin *et al.* 2021); however, those occurring within three weeks of the equinoxes, during global sunlight uniformity, or involving unlikely movements >1,600 km day (Guilford *et al.* 2009) were excluded. Processed tracking datasets were analysed using the R programme ProbGLS (Merkel *et al.* 2016) to create an iterative smoothing function for the tracks providing higher latitudinal accuracy closer to the equinox periods and in positions where birds are near the equator. The analysis followed the methods described by Taylor *et al.* (2020). Geolocators also test for saltwater immersion data every three seconds, with the data binned into 10-minute intervals, resulting in values ranging from 0 (dry) to 200 (immersed for the whole period). As described below, these data were used to calculate at-sea and colony-based activity for tracked birds.

Seasonal timing and foraging activity

Estimates of seasonal events during the breeding cycle were calculated based on screening of light, immersion, and location data from the geolocators. Mapping and geospatial processing of locations was conducted using ArcGIS v10.3 Spatial Analyst extension (ESRI). We first calculated kernel density maps for individual birds, with the 50% kernel contour used to define non-breeding ranges and migration timing (Rayner *et al.* 2016). Subsequently population level distribution maps were created by developing kernel density estimates using combined datasets for each population. Both individual and population kernels density maps were calculated in a Lambert Equal-Area Azimuthal (South Pole) projection using a search radius of 200 km and cell size of 80 km (Phillips *et al.* 2005a; Phillips *et al.* 2007; Rayner *et al.* 2011).

Non-breeding migration timing was defined as time spent in the non-breeding core (based on the first and last locations inside or outside the non-breeding 50% kernel contour) and time spent in post- and pre-breeding transit to and from this core and a 1,000 km buffer around the respective breeding colony at the start or end of the breeding season (Rayner *et al.* 2016). During breeding, location data enabled screening of activity to dates when birds were close to their colony and could feasibly visit at night. Subsequently during those dates light data indicated extended periods when birds spent time ashore in dark burrows during the day (i.e. low light data during daylight hours during pre-laying and incubation).

Immersion data supported identification of longer visits to colonies (>12 hours) but also provided a record of when birds possibly made shorter visits to their burrows with immersion records showing as continuously dry for more than one hour. These data were particularly useful for identifying the change in behaviour associated with hatching and the subsequent shift in the behaviour of birds to more frequent short visits to feed their chicks. Quantifying the number of chick feeding visits by adults proved problematic in this species as the visits were typically of short duration (under an hour), occasionally diurnal on Raoul Island, and often with no obvious longitudinal movements back to colonies. These issues meant we could not reliably determine if the longer dry periods observed at night were time spent ashore with chicks or simply longer flight bouts near the colony (Rayner *et al.* 2012). We used the software Actave.net (Mattern *et al.* 2015) to provide temporal data on percent of time immersed, the number of flight bouts and their duration during daylight and darkness (based on the timing of civil twilight) across the year.

Data analysis

Following tests for normality, nonparametric ANOVA (Kruskal Wallis tests) were used to test for differences between range and activity parameters of the three populations during the non-breeding season and between breeding stages (non-breeding, pre-laying, incubation, and chick rearing) for Raoul birds for which tracking data where available. Pairwise comparisons were conducted using Steel-Dwass-Critchlow-Fligner tests to protect error rate against multiple comparisons. Pairwise differences in time spent on the water between night and day across breeding stages were conducted using Wilcoxon rank-sum tests. Analyses were conducted with a threshold of significance at $\alpha = 0.05$ using JMP 11.2.0 (SAS Institute).

RESULTS

Geolocators were retrieved from black-winged petrels at Raoul Island in January and March 2011 (n = 11/15, 73%), at Burgess Island in January and February 2012 (n = 6/11, 55%) and at Rangatira in February 2010 (n = 5/6, 83%). Downloaded geolocators provided 6,432, 2,367, and 2,473 locations with activity data for Raoul, Burgess, and Rangatira respectively. Data for one logger on a Raoul Island bird was corrupted and could not be used.

Of birds tagged on Raoul Island during incubation, 82% (9/11 birds) indicated behaviour consistent with successfully rearing a chick in the 2010 breeding season (a schedule of short 1–3 hour mainly night-time visits to the burrow every 1–3 days from February to June) and all these birds were recaptured whilst incubating in January and March 2011.

On Burgess all six geolocators retrieved showed that birds tagged during incubation in January 2011 had abandoned breeding during February–April, and then left on migration. Activity data for three birds showed sporadic 1-day long visits to the burrow in February indicating nest failure during incubation. One of these birds was incubating an infertile egg at the time of logger attachment. For the other three individuals, data showed short (1–3 hours) visits to the burrow, indicative of chick rearing behaviour, until the early departure of these birds in March or April, suggesting the chick had died or was abandoned by its parents. All birds were recaptured in their burrows in late January 2012; however, only one was incubating an egg. One bird was found on the surface after being depredated by an Australasian Harrier (*Circus approximans*), fortunately with the geolocator attached to the remaining leg.

On Rangatira, the three birds tagged whilst incubating (two others were tagged courting in a burrow) in February had abandoned breeding attempts and left on migration during March–April. Activity data for two showed sporadic and longer 1-day visits to the burrow from early March indicating nest failure in late incubation. The other bird made frequent and short (1–3 hour) visits to the burrow, indicative of chick rearing, until the early departure of the bird on migration in late March suggesting the chick had died or been abandoned. All three birds were recaptured incubating eggs in February 2010. The two birds tagged in one burrow without an egg made sporadic visits before migration departure in April. They were recaptured the following season with an infertile egg.

Seasonal distribution and timing

The three populations showed extensive overlap in their foraging habitats during the breeding season, predominantly east of New Zealand to waters approximately 45 degrees south in the Subtropical Convergence Zone (Fig. 1). Birds from Raoul and Burgess made a smaller number of trips into the Tasman Sea to 35–45 degrees south. During the season birds were active on their colonies the average maximum ranges from the colony of failed breeders from Burgess (4,373 ± 1,221 km), Rangatira (5,006 ± 555 km), and breeding birds from Raoul (4,226 ± 608 km) were not significantly different from each other (Kruskal Wallis chi squared X^2 [DF = 2, N = 21] = 3.74, P = 0.15).

Breeding black-winged petrel from Raoul showed significant changes in foraging distribution across the season in 2010 and 2011 (Table 1; Fig. 2). There was a significant difference in the maximum range of birds between pre-laying, incubation, and chick rearing (Kruskal Wallis chi squared X^2 [DF = 2, N = 21] = 6.20, P < 0.05). Following pre-breeding migration and mating, birds conducted a pre-laying exodus of 36 ± 3 days, foraging south in subtropical convergence waters of the Tasman Sea and South Pacific Ocean up to 3,591 ± 1,127 km from the colony. Egg laying occurred late-December to early-January. During incubation foraging range contracted significantly compared to pre-laying (2,424 ± 1,063 km; Steel-Dwass Z = -2.14, P < 0.05) with birds ranging south and southwest to the subtropical convergence over 14 ± 5-day trips (based upon average incubation shift lengths). The total incubation period was 50 ± 8 days. Hatching occurred in mid-February to mid-March with no significant change in chick rearing maximum foraging range in comparison with incubation (2,764 ± 1,014 km, Steel-Dwass Z = 0.37, P = 0.93),

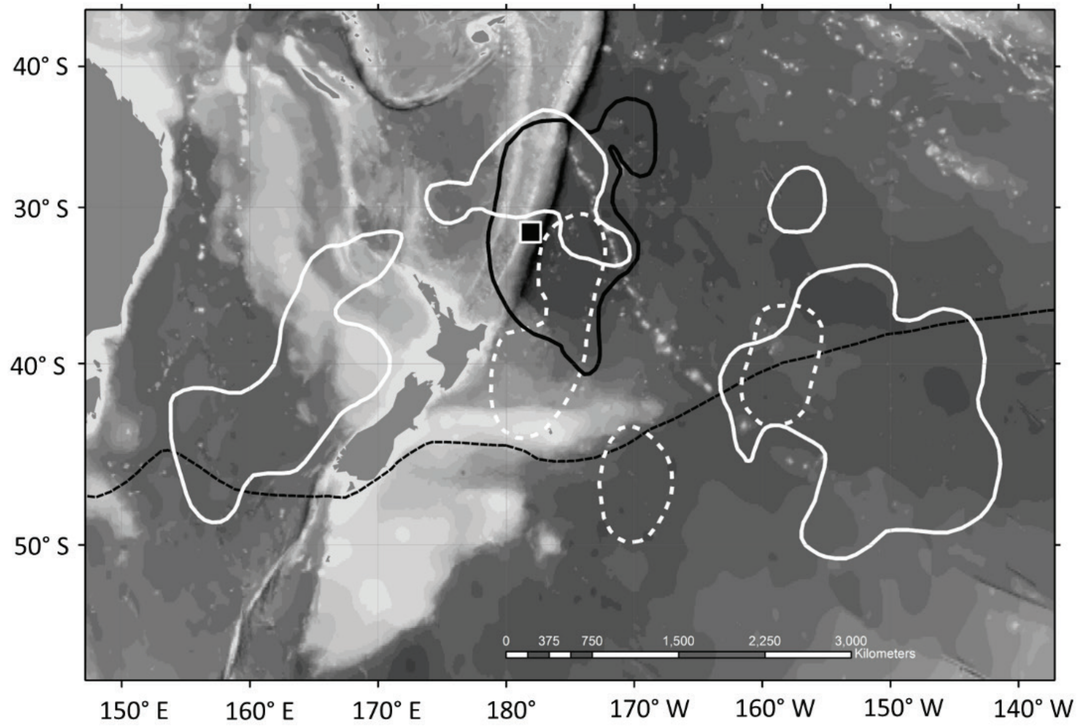

Figure 2. Distribution of breeding black-winged petrel (*Pterodroma nigripennis*) from Raoul Island (black square) as shown by 50% kernel contours during pre-laying exodus (n = 10; solid white lines), incubation (n = 6; hashed white lines) and chick rearing (n = 6; solid black line). Approximate location of Southern Ocean subtropical convergence shown by black hashed line adapted from Harris & Orsi (2001).

Table 1. Summary of annual cycle stages and maximum distance (mean ± SD; range in parentheses) from the colony for breeding black-winged petrel (*Pterodroma nigripennis*) on Raoul Island and non-breeding birds on Mokohinau and Rangatira. *Calculated from hatch and laying dates for birds in successive years (2009 and 2010) see methods. Superscript numbers in each sample stage represent sample size of individuals.

Seasonal Stage		Max distance from colony (km)
Raoul pre-laying^{10}	First arrival: 7 Nov–5 Dec Pre-laying exodus duration: 36 ± 3 days (range 31–39 days)	3,956 ± 541 (3,425–4,816)
Raoul incubation ^{6}	Laying dates: 31 Dec–15 Jan Incubation period: 50 ± 8 days (range 43–61 days) * Shift length: 14 ± 5 days (range 6–19 days)	3,067 ± 643 (2,059–3,900)
Raoul chick rearing ^{6}	Hatch date: 15 Feb – 16 Mar Chick rearing period: 85 ± 6 (range 79–94 days)	2,798 ± 929 (1,745–3,503)
Raoul migration ^{9}	Departure: 4 May–15 Jun Post-breeding transit: 50 ± 11 days (range 32–62 days) Non-breeding core: 1 Jun–11 Aug until 3 Sept–15 Nov Pre-breeding transit: 42 ± 31 days (range 10–92 days)	8,869 ± 770 (7,475–9,688)
Burgess ^{5} & Rangatira^{5} migration	Departure: 3 Mar–17 Apr Post-breeding transit: 57 ± 19 days (range 37–89 days) Non-breeding core: 21 Apr–25 Jun till 9 Sept–9 Nov Pre-breeding transit: 30 ± 21 days (range 17–77 days)	9,869 ± 716 (8,490–10,861)

although with apparent clustering of foraging locations closer to Raoul as based on the kernel 50% contour. The chick rearing period was 85 ± 6 (range 79–94 days).

Breeding birds from Raoul commenced migration during May and June. Failed breeders from Burgess and Rangatira departed earlier in March and April (Table 1). All birds followed a similar post-breeding migration pathway moving eastwards across the South Pacific Ocean, then northeast to the equatorial waters of the eastern tropical Pacific Ocean. From here the birds tracked west and northwest to reach core non-breeding habitats between 0 and 30 degrees north after approximately 50 days (range 32–89 days; Table 1; Fig. 1 & 3). There was no significant difference in post-breeding migration duration between populations. However, failed breeding birds from Burgess and Rangatira arrived earlier (April–June) than birds from Raoul (June – August) reflecting their earlier departure times. Birds from all three colonies departed southward on pre-breeding migration between early September and mid-November. Most birds flew eastwards before heading south and southwest towards New Zealand. The return migration took approximately 50 days (range 10–92 days) for birds to reach their breeding colonies, which was not significantly different between these populations (Table 1).

Activity

Flight activity of black-winged petrel changed consistently across the annual cycle with birds from all three populations spending less time in flight and conducting fewer flight bouts during the non-breeding season than the breeding season (Table 2; Fig. 4 & 5). Within the non-breeding season there were no significant differences in daylight and night-time flight activity, foraging trip number and foraging trip duration between the three populations (Kruskal Wallis tests $P > 0.05$).

Birds from all populations spent significantly more time on the water during the day (combined population average 51 ± 8% (range 34–64) than at night (combined population average 24 ± 6% (range 13–37) (combined all population Kruskal Wallis chi squared X^2 [DF = 2, N = 18] = 14.28, $P < 0.001$; Fig. 4). There were significant differences in flight activity between breeding stages for birds tracked from Raoul. Time on the water during the day was significantly different between seasons (Kruskal Wallis chi squared X^2 [DF = 2, N = 24] = 29.14, $P < 0.0001$) with birds spending more time on the water during pre-laying than during incubation and chick rearing (Steel-Dwass tests $P < 0.01$) which were not significantly different from each other. Time on the water at night was significantly different between seasons (Kruskal Wallis chi squared X^2 [DF = 2, N = 24] = 13.70, $P < 0.001$) with birds spending more time on the water during pre-laying than during incubation and chick rearing (Steel-Dwass tests $P < 0.05$ and $P < 0.01$ respectively) which were not significantly different from each other. The number of flight bouts differed between seasons (Kruskal Wallis chi squared X^2 [DF = 2, N = 24] = 10.67, $P < 0.01$) with bouts being significantly longer during

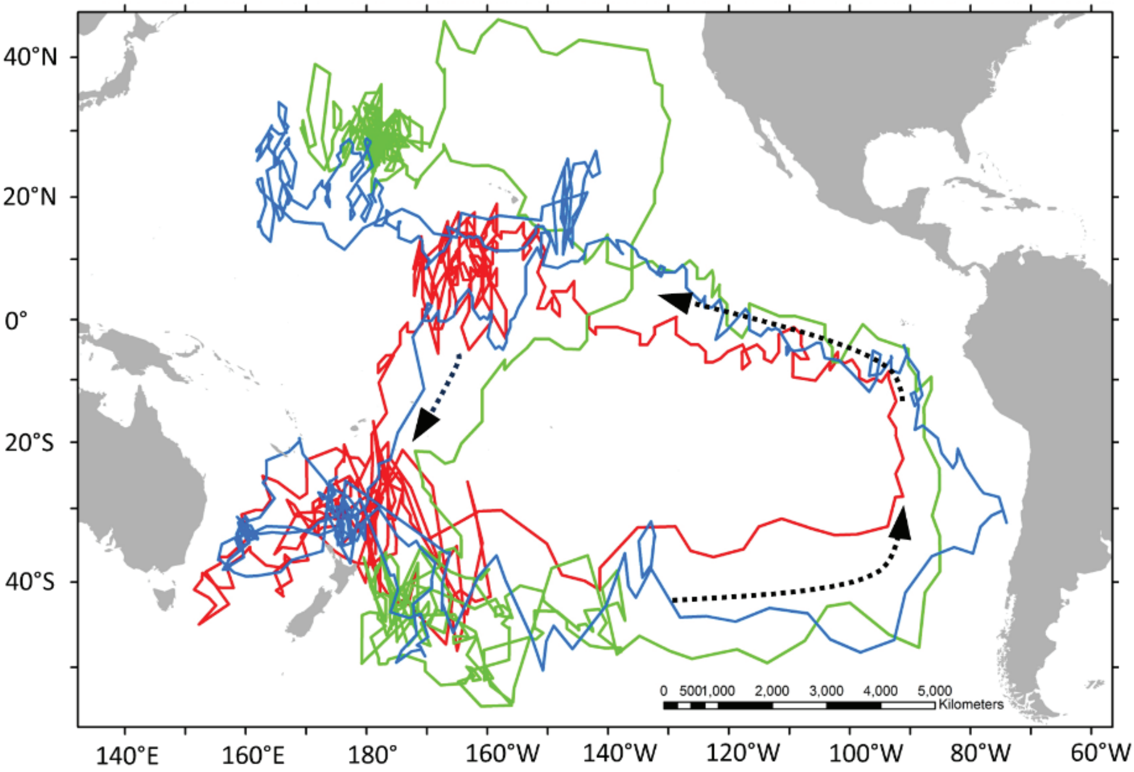

Figure 3. Representative annual tracks of three black-winged petrels (*Pterodroma nigripennis*) from Raoul (red line), Burgess (blue line), and Rangatira (green line) showing migration routes taken between breeding habitat around the New Zealand archipelago and non-breeding habitat in the equatorial and North Pacific Ocean. General patterns of movement shown by black arrows.

incubation and chick rearing in comparison with pre-laying (Steel-Dwass tests P < 0.01 and P < 0.01 respectively; Table 2) but not significantly different from each other. There was no significant difference in flight bout duration between breeding stages.

Birds spent significantly more time sitting on the water during the day than night across all stages: pre-laying (day 24%, night 9%, Wilcoxon test Z = 3.74, P < 0.001), incubation (day 10%, night 5%, Wilcoxon test Z = -2.51, P < 0.05), and chick rearing (day 11%, night 3%, Wilcoxon test Z = -3.53, P < 0.001) (Table 2; Fig. 5).

Table 2. Seasonal activity for breeding black-winged petrel (*Pterodroma nigripennis*) from Raoul Island. Superscript numbers in each sample stage represent sample size of individuals.

Seasonal Stage	Time spent wet (%)		Number of flight bouts	Duration of flight bouts (min)
	Day	Night		
Non-breeding^{10}	55.0 ± 5.1	22.5 ± 4.5	15.2 ± 1.1	37.2 ± 2.9
Pre-laying^{10}	23.7 ± 8.2	8.2 ± 3.1	20.5 ± 6.9	32.2 ± 5.0
Incubation^{6}	9.8 ± 1.7	4.7 ± 1.4	26.8 ± 2.2	33.7 ± 6.1
Chick rearing^{9}	11.1 ± 2.0	3.7 ± 0.9	25.8 ± 1.4	37.1 ± 3.1

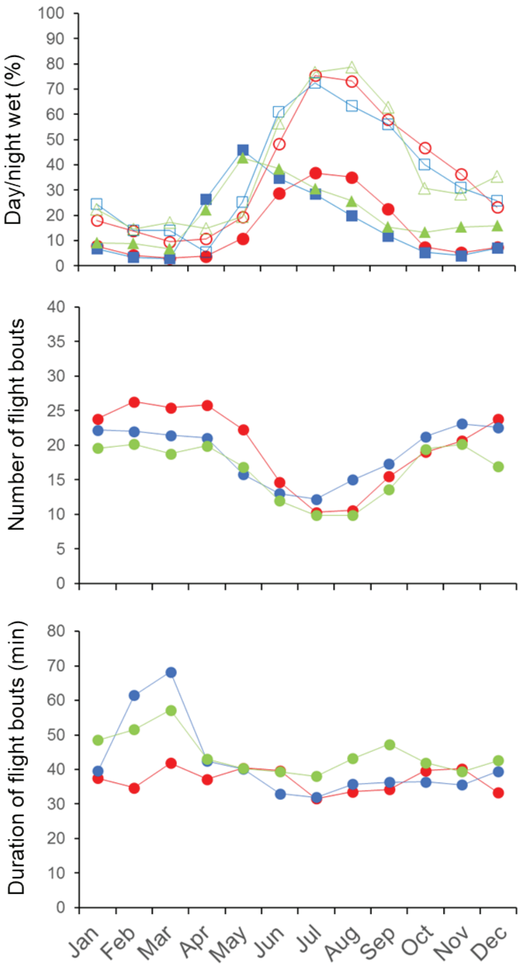

Figure 4. Mean monthly activity metrics for black-winged petrels (*Pterodroma nigripennis*) tracked from Raoul (red symbols), Burgess (blue symbols), and Rangatira (green symbols) including A) percent of time spent on the water during day (unfilled circles) and night (filled circles); B) number of flight bouts and C) duration of flight bouts.

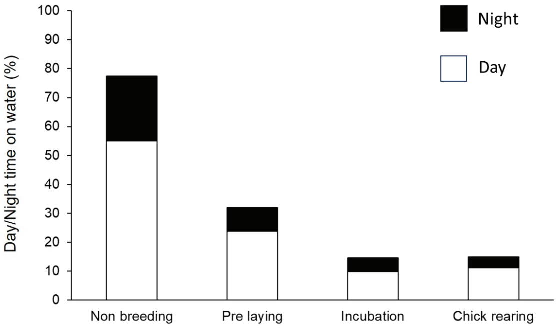

Figure 5. Proportion (%) of time at sea spent on the water during day and night for black-winged petrels (*Pterodroma nigripennis*) from Raoul during the non-breeding, pre-laying, incubation, and chick rearing seasons.

DISCUSSION

The results of this study add to historic and contemporary data demonstrating the extreme, "ocean scale" habitat use of small *Pterodroma* petrels within the Pacific Ocean (King 1970; Bartle *et al.* 1990; Spear *et al.* 2007; Rayner *et al.* 2011, 2016). Black-winged petrels breeding on Raoul, Burgess, and Rangatira made extensive use of the waters of the Tasman Sea and South Pacific Ocean during the breeding season, consistent with previous ship-board observations and tracking studies in the Tasman Sea (Halpin *et al.* 2022). There was extensive overlap in the range of birds from the three colonies, particularly in the waters of the subtropical convergence zone east of New Zealand (Fig. 6). Birds made regular long trips to, and within, this productive frontal region. The New Zealand section of the subtropical convergence is an important foraging habitat for many breeding seabirds including Chatham petrel (*P. axillaris*) (Rayner *et al.* 2012), Cook's petrel (*P. cookii*) (Rayner *et al.* 2008), Buller's albatross (*Thalassarche bulleri*) (Stahl & Sagar 2000), northern royal albatross (*Diomedea sanfordi*), and Antipodean albatross (*D. antipodensis*) (Nicholls *et al.* 2002).

The breeding behaviour of black-winged petrel from Raoul Island observed in this study is consistent with our understanding of the breeding biology of small (160–200 g) *Pterodroma* petrels in general. Features of the breeding cycle in this genus include an extended pre-laying exodus from the colony following mating, long incubation shifts, and a long chick rearing period (Marchant & Higgins 1990; Tennyson 1991; Hutton & Priddel 2002; Brooke 2004; Rayner *et al.* 2012). The pre-laying exodus in black-winged petrels in our study (36 days) was similar to the Chatham petrel (34 days) (Rayner *et al.* 2012) and the incubation and chick rearing periods (50 and 85 days) were similar to black-winged petrels from Lord Howe Island (45 and 85 days; Hutton and Priddell (2002), Cook's petrel (47 and 87 days; Imber *et al.* (2003), Bonin petrel (*P. hypoleuca*) (49 and 82 days; Pettit *et al.* (1982), and Pycroft's petrel (*P. pycrofti*) (45 and 80 days; Marchant and Higgins (1990). Incubation shift length in this study (14.5 days) was similar to the species discussed above.

Changes in the at-sea distribution of seabirds across the breeding season reflects the energetic demands of breeding duties as well as seasonal shifts

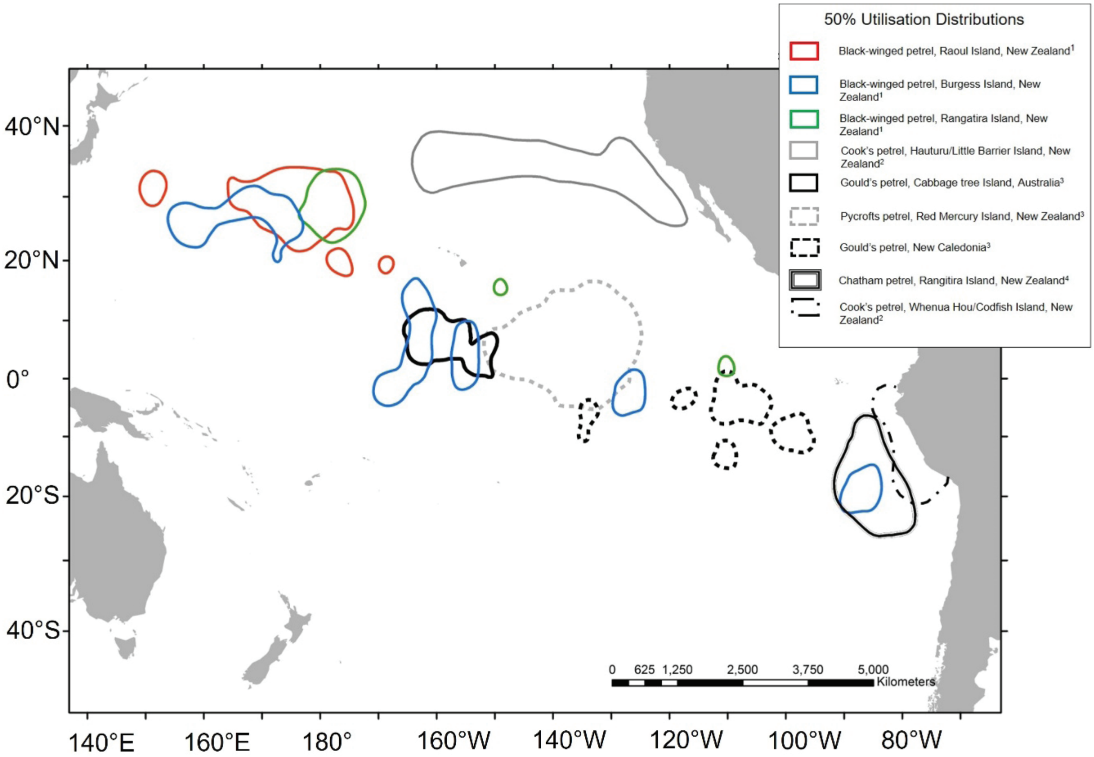

Figure 6. Core kernel utilisation distributions (50%) for non-breeding small *Pterodroma* petrels tracked from Australasian colonies between 2007 and 2011. Data sourced from current the study, Rayner *et al.* (2011), Rayner *et al.* (2012), and Rayner *et al.* (2016).

in oceanographic productivity with time (Phillips *et al.* 2005b; Gonzalez-Solis *et al.* 2007; Weimerskirch 2007; Peron *et al.* 2010). In breeding black-winged petrels from Raoul Island, reduced foraging range sizes between pre-laying, incubation, and chick rearing likely reflects the reduced time available between colony visits as a necessity of incubation shifts, and then chick provisioning duties. Though there was no difference between maximum ranges of birds during incubation and chick rearing, the concentration of the 50% kernel around Raoul during chick provisioning suggests birds can meet the needs of chicks by foraging, in part, in subtropical waters nearer to their colony. Similarly, Halpin *et al.* (2022) found that during chick rearing, GPS tracked black-winged petrels from Phillip Island alternated between short trips, closer to the colony, and longer trips southwards of several thousand kilometres presumably for maintenance of parental body condition. Future GPS-based studies of breeding birds from Raoul and other sites would help clarify the effects of breeding stages on the energetic budgets of these populations.

Breeding failure of black-winged petrel on Burgess and Rangitara during our study was concerning, but unlikely attributed to tag attachment methods as these same methods were applied successfully on the Raoul birds. Moreover, our work on *Pterodroma* petrels that breed in New Zealand has shown little impact of geolocator deployments on breeding success and or migration return rates including Cook's petrel (Rayner *et al.* 2007, 2008, 2011), Chatham petrel (Rayner *et al.* 2012), and white-headed petrel (*P. lessonii*) (Taylor *et al.* 2020). These observations are also consistent with international studies examining the impact of lightweight geolocators on procellariiform and charadriiform seabirds (Kürten *et al.* 2019; Nicoll *et al.* 2022). Other colony-specific factors including competitor and predator disturbance are likely more influential. On Burgess Island, black-winged petrels have recently established a small population (Ismar *et al.* 2012) but, with little shrub or tree cover, appear susceptible to predation by Australasian harrier when arriving at breeding sites before dark. During our field work on this island predated birds of multiple species, including one black-winged petrel tagged with a geolocator, were found. Some of the black-winged petrel nests were on the surface under dense grasses and downy chicks may have been visible to harriers flying low over the colony. Harriers are also present on Rangatira; however, a more likely factor in poor breeding success at this site is nest disturbance by large numbers of broad-billed prion (*Pachyptila vitatta*), a major cause of nest failure in the endangered Chatham petrel on this island at unmanaged sites (Gummer *et al.* 2015).

The migratory movements of black-winged petrel from New Zealand populations were similar in terms of timing, pathway and non-breeding distribution to birds tracked from Lord Howe and Phillip Island in 2017 and 2021 (O'Dwyer *et al.* 2022) allowing for general conclusions on the migratory behaviour of the species. Overall, black-winged petrels breeding in Australasia migrate first eastwards across the South Pacific Ocean, then northeast towards the equator, and then west and northwest into the subtropical North Pacific Ocean during April–November. Post-breeding movements in this species are protracted (up to 90 days) with most birds reaching core non-breeding grounds between 22 and 33 degrees north on the southern side of the North Pacific Current, a warm water current flowing west-to-east between 30 and 50 degrees north forming the northern boundary of the North Pacific Subtropical Convergence (Howell *et al.* 2012). Interestingly, in the case of the New Zealand tracked populations, a small number of individuals occupied non-breeding core ranges south of Hawaii in the central North Pacific between 0 and 15 degrees north (Howell *et al.* 2012) (Burgess (2/6 birds, 33%), Rangatira (1/5 birds, 20%), (Raoul (1/11 birds, 9%)). Observed differences in non-breeding core distributions may reflect habitat flexibility in this species or be mediated by breeding failures and or life history characteristics. For example, failed breeding birds from Burgess and Rangatira initiated their migrations earlier than Raoul birds thus encountering differing seasonal productivity which could have influenced habitat selection. Possibly these birds also represent a younger, less experienced cohort, still establishing migratory core choices as observed in other species (Clay *et al.* 2018; Powers *et al.* 2022).

Broad-scale segregation is an important component of resource partitioning by procellariform seabirds at high latitudes (Navarro *et al.* 2015; Quillfeldt *et al.* 2015) and our study supports growing geolocator-based data indicating such segregation of non-breeding habitats is also prevalent in small *Pterodroma* petrels in the tropical and subtropical Pacific Ocean (Fig. 6). In the North Pacific black-winged petrels from Australasia (O'Dwyer *et al.* 2022; this study) occupy a different region of the subtropical gyre than northern Cook's petrel (*Pterodroma cookii cookii*) tracked to the eastern section of this frontal system during 2007–2009 (Rayner *et al.* 2011). Southwards in the eastern equatorial Pacific Ocean Rayner *et al.* (2016) demonstrated spatial and habitat segregation between three taxa tracked between 2010 and 2011: Gould's or white-winged petrel (*P. leucoptera leucoptera*) occupying the North Equatorial Counter Current south of Hawaii (10°N–5°S, 150–165°W), *P. leucoptera caledonica* 3,000−6,000 km southeast over the East Pacific Rise in the South Equatorial Current (0−15°S, 135−100°W), and Pycroft's petrel occupying a region between *P. l. leucoptera* and *P. l. caledonica* also in the North Equatorial Counter Current (0−10°N, 140−135°W). In the South Pacific Ocean, Chatham petrels tracked during 2009 and 2010 occupied waters centred at 20°S, 84°W within the Humboldt Current (Rayner *et al.* 2012) whereas southern Cook's petrel *P. cookii orientalis*, tracked during 2007–2009 were distributed further east towards the coast of South America (Rayner *et al.* 2011). Clearly seasonal differences in productivity could explain different habitats selected by these species as not all were tracked across in the same years. However, several lines of enquiry suggest that species-specific non-breeding distributions may be an interannual feature across this massive oceanic region: first, work combining tracking and isotope data from contemporary and historic specimens of Cook's petrel suggest long-term, population specific, stability in core migratory destination over century-long time-spans (Rayner *et al.* 2011), and second, modelling of species distributions within the same year (i.e. Rayner *et al.* 2016) indicates population-specific habitat niches based on responses to environmental parameters such as thermocline depth, sea surface temperature and bathymetry. Future research combining new high-resolution lightweight tracking technologies across multiple species within the same season will provide fascinating insights within this new frontier of avian habitat selection.

Our analysis of geolocator immersion data from black-winged petrel across the annual cycle showed an activity pattern similar to previous migratory seabirds with decreased time resting on the surface, and more frequent and longer flight bouts during the breeding season than during the non-breeding period (Rayner *et al.* 2012; Ramirez *et al.* 2013). This reduced flying activity outside of breeding is expected during a time when birds moult most of their main body and flight feathers (Warham 1996). For breeding birds from Raoul Island more time was spent on the water during pre-laying than during incubation and chick rearing reflecting the well-known energetic demands of these latter stages. Comparisons of night and day activity data supports previous work showing that black-winged petrel is predominantly a nocturnal forager during the non-breeding season with less time sitting on the water and more time in flight, during which they surface seize and make short plunge dives to capture prey (Bonnet-Lebrun *et al.* 2021). However, our data also indicate that, during breeding, birds are more active at night across all breeding stages and although they almost certainly forage opportunistically during the day, targeting nocturnal prey appears their primary foraging strategy. In the tropical Pacific the diet of black-winged petrel is dominated by small mesopelagic fishes which migrate vertically at night to surface waters and make up over 85% of the diet (Spear *et al.* 2007). It is likely that such taxa form at least part of the diet of breeding birds, but further studies are required.

In conclusion, the results of our geolocator-based study of three populations of black-winged petrel in New Zealand show that during breeding birds regularly forage south of their colonies within waters of the Subtropical Convergence Zone which for some colonies, i.e. Raoul, require long foraging trips over 1,000 km one way. During the non-breeding season birds occupied wintering core foraging zones predominantly within the North Pacific subtropical front, as observed in other Australasian populations. However, a small number of birds also wintered south of Hawaii in equatorial waters. The timing of migration and breeding was consistent between breeding populations with the species showing similar breeding traits to other small *Pterodroma* petrels studied to date. Geolocator immersion data indicate that throughout the year black-winged petrel forage extensively by night, most likely on vertically migrating prey.

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Why did they die? Analysing the cause of death of grounded seabirds lodged at an avian rescue centre in Auckland, New Zealand

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Abstract: Procellariiform seabirds are vulnerable to numerous threats, including the growing issue of urban light pollution. Seabirds that are found grounded are often treated by avian/wildlife rehabilitation centres, but approximately 30% do not survive. Here, we necropsied 19 grounded Cook's petrels (tītī, *Pterodroma cookii*) that did not survive and report the cause of death and injuries. We also investigate potential risk factors, including association with light pollution, seabird sex, age, and sensory features. We found that a 70% of Cook's petrels had head trauma, internal bleeding, and/or wounds as the main causes of death ($p > 0.05$). These injuries are consistent with collisions, likely due to disorientation from light pollution. Most Cook's petrels were not stressed or in poor body condition, suggesting Cook's petrels are typically healthy before being affected by lights. In the sample of Cook's petrels studied, mortality was significantly biased towards young and male seabirds. Despite this apparent sex difference in collision risk, there was no detectable sex difference in measured sensory features, e.g. males did not have significantly larger eyes than females. The potential sex bias in death suggests male seabirds could be more vulnerable to light pollution, which warrants further research. Further research is also required to determine whether individual differences in sensory features relate to grounding risk, as our study only included a subset of dead seabirds. We also recommend that all grounded seabirds are taken to rehabilitation centres rather than released immediately.

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INTRODUCTION

Artificial light at night (ALAN) or light pollution, a by-product of human urban development, is a growing concern for many animal species as it affects different aspects of behaviour and migration patterns (Lorne & Salmon 2007; Eisenbeis *et al.* 2009; Bocetti 2011; Rodríguez *et al.* 2017b; Van Langevelde *et al.* 2017; Hudecki & Finegan 2018). In particular, natural and anthropogenic factors threaten seabirds, including light pollution (Croxall *et al.* 2012; Dias *et al.* 2019).

Sensory ecology is the study of how an animal interacts with its environment using its sensory features, such as vision and olfaction and can be used to mitigate threats to seabirds (Madliger 2012; Friesen *et al.* 2017). Sensory ecology could also be used to understand light attraction in seabirds. ALAN interacts with the seabird's sensory ecology, and as a result, seabirds may become disorientated and attracted to lights causing them to land and become grounded (Rodríguez *et al.* 2015; Rodríguez *et al.* 2017a; Heswall *et al.* 2022). Fledgling seabirds are especially at risk, potentially due to underdeveloped vision from a lack of exposure to visual information while underground (Mitkus *et al.* 2018; Atchoi *et al.* 2020).

Records of seabird groundings are widespread, spanning locations such as Hawai'i (Telfer *et al.* 1987; Rodríguez *et al.* 2015), Canary Islands (Rodriguez & Rodriguez 2009), Maltese Islands (Laguna *et al.* 2014), Canada (Wilhelm *et al.* 2021), the United Kingdom (Syposz *et al.* 2018), and New Zealand (Deppe *et al*. 2017; Whitehead *et al.* 2019; Fischer *et al*. 2021). Once a seabird is grounded, the likelihood of mortality may increase, with susceptibility to predators, starvation, dehydration, and mammalian predator control traps (Imber 1975; Blight & Burger 1997; Darby & Dawson 2000; Troy, Holmes & Green 2011; Merkel & Johansen 2011; Rodriguez *et al.* 2012; Rodriguez *et al.* 2014). Furthermore, recent seabird studies have reported bleeding and brain damage from colliding with anthropogenic structures (Travers *et al.* 2021; Coleman *et al.* 2022).

Auckland (Tāmaki Makaurau) (36.8509°S, 174.7645°E) is a large New Zealand (Aotearoa) city (1.4 million people), geographically located next to one of the world's most important seabird hotspots (Barbera 2012; Gaskin & Rayner 2013; Whitehead *et al.* 2019). The Hauraki Gulf (1.2 million hectares) is in the north of the New Zealand North Island (Te Ika-a-Māui) and is home to approximately 27 native and endemic seabird species (Barbera 2012; Gaskin & Rayner 2013; Whitehead *et al.* 2019). In Auckland, the associated light pollution from the city likely threatens marine and terrestrial native ecosystems (McNaughton *et al.* 2021). Seabird groundings correlate significantly with Auckland city's lighting, with more seabirds grounded near brighter locations (Heswall *et al*. 2022).

Many seabirds that breed on the islands of the Hauraki Gulf, including Cook's petrels (tītī, *Pterodroma cookii*), must fly over Auckland to reach foraging grounds in the Tasman Sea (Gaskin & Rayner 2013). The risk to seabirds is further intensified because the region is rich in breeding sites and colonies and is especially rich in burrow-nesting procellariiforms (Gaskin & Rayner 2013; Whitehead *et al.* 2019). Due to the differences in visual development, burrow-nesting procellariiforms are highly sensitive to ALAN (Atchoi *et al.* 2020), and especially at risk of disorientation and collision with infrastructure (Rodríguez *et al*. 2019). For example, in 2018 a major ALAN incident occurred when 64 Buller's shearwaters (*Puffinus bulleri*) and four flesh-footed shearwaters (*Ardenna carneipes*), were attracted by vessel lights and grounded on a cruise ship near Little Barrier Island/Te-Hauturu-O-Toi in the Hauraki Gulf (Morton 2018).

Cook's petrel, a burrow-nesting procellariiform, is especially affected by light pollution (Heswall *et al.* 2022). This species breeds on the east side of the Auckland Isthmus, on Te-Hauturu-O-Toi and Great Barrier Island/Aotea, but must cross the city to reach their foraging grounds in the Tasman Sea (Gaskin & Rayner 2013; Heswall *et al.* 2022). During their flight over Auckland city, they are exposed to light pollution and are sometimes found grounded (Heswall *et al.* 2022).

Rehabilitation is very important for the conservation of seabirds; many are injured from bycatch, pollutants, and light pollution (Montesdeoca *et al*. 2017; Costa *et al.* 2021). A study in Portugal showed that over 2000 seabirds were admitted into a rehabilitation centre over a seven-year period (Costa *et al.* 2021). Another study in Spain showed that ~1,900 seabirds were admitted into a rehabilitation centre in a ten-year period (Montesdeoca *et al*. 2017). In Auckland, when birds are found grounded or injured, they are often taken to BirdCare Aotearoa, a Department of Conservation permitted avian rehabilitation centre. The centre received 184 grounded Cook's petrels from 2020 to 2022 (The Wild Neighbours Database Project 2021). Almost 70% of these Cook's petrels survived and were released, but approximately 30% died due to injuries (Table 1). Understanding the cause of death will help us determine whether light pollution-related collisions and injuries are important sources of mortality and improve our understanding of the impact of ALAN on seabirds.

Here we document and analyse the types of injuries and the likely cause of death of the Cook's petrels taken to BirdCare Aotearoa that did not survive. We determine whether their injuries are likely associated with light pollution events, i.e. collisions with anthropogenic structures. We did not include seabirds which died from other causes such as animal or fisheries interaction. We also determine whether some individual characteristics may increase the risk of death, such as sex, age, and size of sensory features.

MATERIALS AND METHODS

This research was conducted at BirdCare Aotearoa. Established in 2009 and located in Green Bay, Auckland, New Zealand, this rehabilitation centre receives ~6,500 native and non-native avian patients each year (The Wild Neighbours Database Project 2021). From January 2020–December 2021, of those Cook's petrels that died (N = 56), 19 individuals were kept frozen for study (The Wild Neighbours Database Project 2021).

Study species

For this study, we focussed on Cook's petrels, the procellariiform most commonly admitted to BirdCare Aotearoa (184 Cook's petrels were found during 2020–2021 compared to 29 grey-faced petrels; Table. 1). Procellariiformes are the seabird group most often associated with groundings due to light pollution (Telfer *et al.* 1987; Rodríguez *et al.* 2015; Heswall *et al*. 2022). Grounded Cook's petrels were found along urban areas near streetlights, roads, and buildings (The Wild Neighbours Database Project 2021). We did not include individuals that had been found injured during an animal or a fisheries interaction, i.e. hook in bill, so we just focused on those found grounded.

Table 1. Seabird species, including their population sizes and the numbers admitted to BirdCare Aotearoa (2020–2021) and those which survived and were released. [1] Taylor & Gaskin 2013**,** [2] Miskelly 2013, [3] Taylor 2013a, [4] Taylor 2013b, [5] Bell 2013, [6] Sagar 2013, [7] Southey 2013, [8] The Wild Neighbours Database Project 2021.

Common Name	Latin	Te Reo Māori	Population size in New Zealand	Numbers admitted to rehab centre [8]	% survived [2]	Number of birds used in this study
White-faced storm petrel	*Pelagodroma marina maoriana*	Takahikare	>1,000,000 [7]	5	50	-
Grey-faced petrel	*Pterodroma gouldi*	Ōi	~300,000 [4]	29	54.6	-
Cook's petrel	*Pterodroma cookii*	Tītī	>300,000 [1]	184	69.9	19
Fairy prion	*Pachyptila turtur*	Tītī wainui	>8,000,000 [2]	3	0	-
Grey petrel	*Procellaria cinerea*	Kuia	~100,000 [5]	1	0	-
Sooty shearwater	*Ardenna grisea*	Tītī	>20,000,000 [6]	4	0	-
Flesh-footed shearwater	*Ardenna carniepes*	Toanui	<24,000 [3]	2	0	-

Preparation

Necropsies on 19 individual Cook's petrels (Table 1) were performed from January to May 2022. Specimens were stored in freezers at approximately -20°C and defrosted before dissections. First, we conducted an external examination of the body, assessing the overall body score from 1 to 5 based on pectoral muscle mass (Fig. 1). For this study, we used the body score conditions (Fig. 1) used by the veterinarians at BirdCare Aotearoa as a proxy of bird health (Kaytee n.d.). Age recorded was based on plumage condition and categorised as either juvenile – fresh feathers and no evidence of moult, or adult – frayed feathers at various moult stages (Spear *et al.* 1995). Any external injuries, whether deep or superficial, including bruises and broken or dislocated limbs were recorded as wounds (Table 2). We conducted necropsies starting from the head and working toward the distal end of the body.

On completion of external examinations, the head was examined for trauma. We classified head trauma as any bruising or bleeding to the head and/or brain (Table 2). Morphometric measurements including the skull length - from the Supraoccipital to the end of the nasal, the skull width – from the left extended part of the Squamosal to the right extended part of the Squamosal, and the depth – from the top of the Frontal to the base of the Basioccipital, were taken using digital callipers (mm). Eyeball volume was calculated according to the equation:

$$\text{Eyeball volume (cm}^3\text{)} = 2 * 1.33\pi a^2 b$$

Used to calculate the volume of an oblate spheroid (Garamszegi *et al.* 2002; Martínez-Ortega *et al.* 2014), where a represents the equatorial (largest) radius, and b represents the polar (smallest) radius.

Specimens were then dissected by means of a transverse incision below the rib cage and opened through lateral incision to access the internal

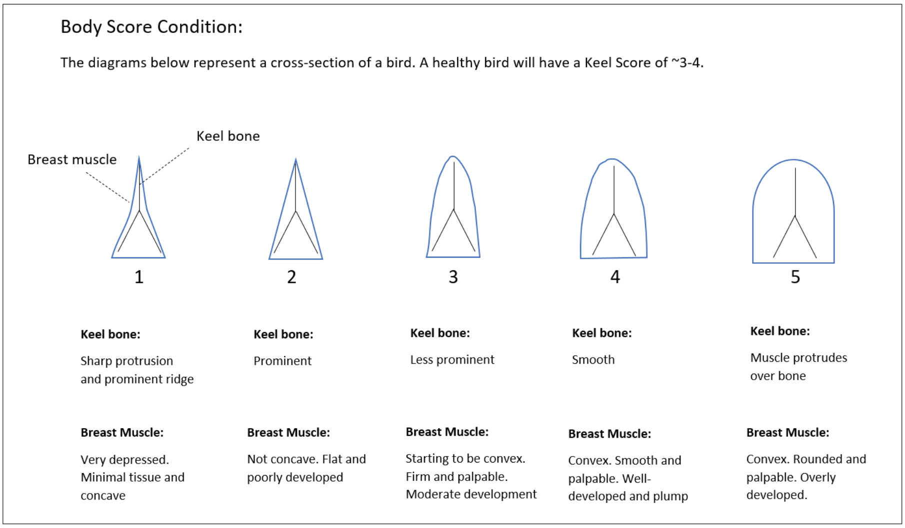

Figure 1. Description of the different body score conditions used to assess overall Cook's petrel (*Pterodroma cookii*) health. Ventral view of the keel (inner, black straight lines) and pectoral/breast muscle (blue outer perimeter lines), greater muscle mass indicates better condition.

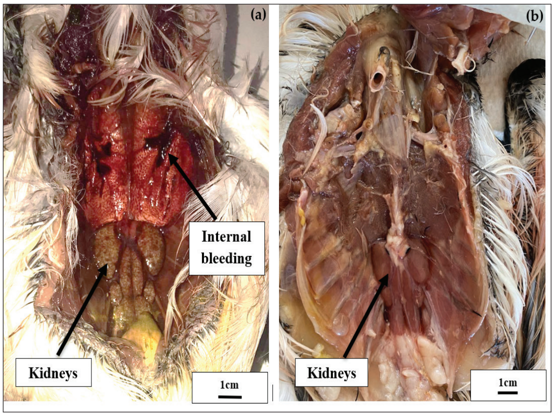

Figure 2. Image of (a) kidney failure and internal bleeding compared with (b) functional kidney and no internal bleeding from Cook's petrel (*Pterodroma cookii*) necropsies. Arrows indicate the location of kidneys and internal bleeding. Image credits: Agustina Dominguez.

organs. Lifting the skin (epidermis and dermis) allowed assessment of any bruises on the pectoral muscles. Lateral cuts on the ribcage were used to enter the cavity and evaluate the internal organs. Any punctures or internal bleeding were recorded (Fig. 2).

We inspected each organ internally and then removed it to assess it for abnormalities in shape and colour. We first examined the liver and the gastrointestinal (GI) system. The GI system was then removed by means of cutting the mesenteries, and each part was cut open to reveal the contents. We also recorded gut contents, identifying any unusual items such as plastics and parasites. The heart was examined for external abnormalities. We removed the heart from the connecting arteries and veins and dissected it to check for internal parasites. We then examined and removed the lungs and kidneys. If the kidneys, heart, or liver were discoloured and/or calcified, we classified that as stress (L. Miller *pers. comm.* 17 February 2022) (Table 2; Fig. 2). Birds were sexed by inspecting the gonads.

Statistical Analysis

Statistical analysis was carried out using R Studio version 4.2.1 (RStudio Team 2020). We used both the Chi-squared test as well as general linear models with Poisson distribution. We used both these tests to determine which type of injury was more prevalent, if body score condition was related to death, and if there was a sex and age bias in mortality numbers.

To test for any correlations between sensory ecology (absolute and relative eyeball volume) and the age and sex group, we used general linear models with Poisson distribution. The packages we used included 'ggplot2' (Wickham 2011) and 'tidyverse' (Wickham *et al.* 2019).

Table 2. Description of each category of injury for Cook's petrel (*Pterodroma cookii*).

Injury	Description
Head Trauma	bruising or bleeding to the head and brain
Internal bleeding	bleeding found inside the internal cavity
Wounds	fractures, cuts, punctures, open wounds, dislocations
Long term stress	emaciation and abnormal discolouration and/or calcifications of the liver, kidney or heart, and parasites

RESULTS

Cause of death

Grounded seabirds generally had four types of injuries (Table 2), and some seabirds displayed more than one category of injury (Fig. 3a,b). 7% of Cook's petrels showed signs of a combination of head trauma, internal bleeding, and wounds, while 17% displayed only internal bleeding with no other injuries (Fig. 3a). All four categories of injuries were equally common ($p > 0.05$; Appendix 1). 70% of seabirds had collision-related injuries such as head trauma, wounds, internal bleeding, or a combination of all three (Fig. 3a,b). However, 17% of seabirds in this study had signs of stress, with 3% having a combination and stress and internal bleeding (Fig. 3a,b).

Body score

Body score condition was not significantly related to death as roughly half of the seabirds that died were in good condition (3–5 body score) at death (body score condition of 3, $p = 1$; body score condition of 4, $p = 0.219$). This suggests that pre-existing poor health before being grounded was not the main driver of mortality (Fig. 4a; Appendix 2).

Sex and Age

There was a significant difference between sexes, with more males identified in the necropsies ($n = 12$) compared to females ($n = 3$) (GLM; $p < 0.057$; Appendix 3; Fig. 4b). This result was replicated using Chi-squared test ($\chi 2 = 6.107$, df = 1, $p = 0.013$).

All 19 Cook's petrels necropsied were juveniles (GLM; $p < 0.048$; Appendix 4; Fig. 4b). As above, this result was replicated using a Chi-squared test ($\chi 2 = 19$, df = 1, $p < 0.0001$).

Visual sensory features

There was no significant difference between absolute and relative eyeball volume between sexes and age groups ($p > 0.05$; Appendix 5). The average absolute eyeball volume was 29.27 cm^3 (±0.9 cm^3), and the average relative eyeball volume was 0.95 cm^3 (±0.159) (Appendix 6).

DISCUSSION

The majority of Cook's petrels found grounded in Auckland city, and that later died in rehabilitation had head trauma and internal bleeding.

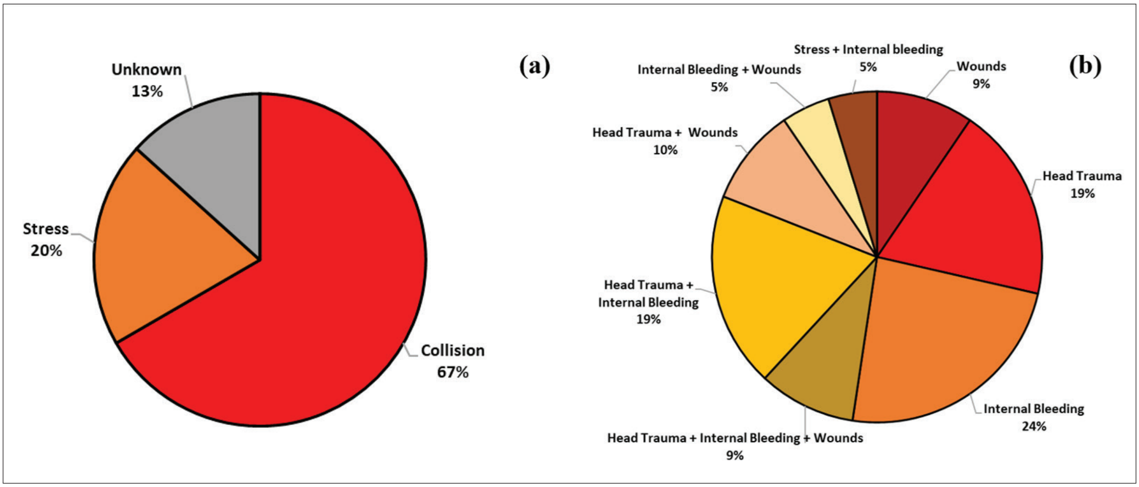

Figure 3. Cause of death and injuries which are collision-related, stress-related and unknown for each Cook's petrel (*Pterodroma cookii*) (a), and the percentage of the categories of collisional-related injuries (b).

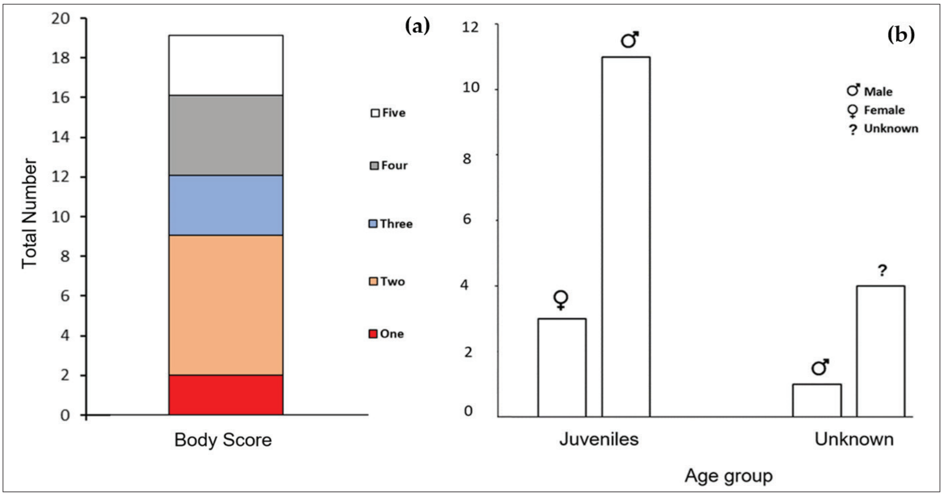

Figure 4. (a) The body score, and (b) the sex and age group of the 19 Cook's petrels (*Pterodroma cookii*) used in this study.

These are injuries consistent with collisions rather than other threats such as fisheries bycatch. Our results support previous research, which found that grounded seabirds in other parts of the world typically have injuries associated with collisions from anthropogenic structures due to disorientation by lights (Travers *et al.* 2021; Coleman *et al.* 2022).

Body Score and stress

We did not find any associations between mortality and body condition scores, indicating that seabirds are not necessarily stressed or in poor condition prior to being affected by ALAN. Indeed, a study on short-tailed shearwaters (*Ardenna tenuirostris*) showed that the fledglings grounded by light pollution often had a better body condition than those that were beach wrecked (Rodriguez *et al.* 2017a). Another study researching a variety of other seabird species also noticed this trend (Cuesta-García *et al*. 2022). We do not have any data on the body score condition for seabirds which survived and were released by BirdCare Aotearoa or for seabirds that were never grounded, limiting our ability to contrast recovered and dead bird body condition. Collecting such data in the future would facilitate comparisons of those that died and those that were released.

Only 17% of the seabirds in this study had signs of long-term stress. A potential cause of this could be a lack of food, which can affect seabird survival and breeding cycles. This has been studied in seabirds, including the little blue penguin (*Eudyptula minor*), and yellow-eyed penguin (*Megadyptes antipodes*) where both studies showed that prey availability influenced survival (Perriman *et al*. 2000; Muller *et al.* 2022). Although the vast majority of seabirds had collision-related injuries rather than signs of long-term stress, stress was evident in some of the seabirds. Therefore, it may be beneficial in the long term to study why seabirds experience stress and ways to potentially mitigate this.

Sex and age

We found that juvenile males were the most likely to be fatally injured. This illustrates that sex and age are contributing factors to collision death. There have been sex and age differences recorded in seabird foraging patterns, migratory patterns, and bycatch numbers (Taylor *et al.* 2002; Deakin *et al.* 2019; Beck *et al.* 2021; Schultz *et al.* 2021). For example, in northern gannets (*Morus bassanus*), breeding females tended to forage further offshore compared to breeding males (Stauss *et al.* 2012; Lewis *et al.* 2022), and a difference in timing of departure between male and female northern gannets has also been described (L. Miller *pers. comm.* 23 March 2023). However, to our knowledge, there has been no record in the literature of a seabird sex bias for light attraction. The only other study that examined sex in relation to ALAN found no sex bias in Cory's shearwater (*Calonectris borealis*) (Rodríguez *et al*. 2012). Our results may be the first record of a potential sex bias for seabird mortality in New Zealand from light pollution. This sex bias could be a result of differences in behaviour and migratory patterns between males and females. However, there is little research on Cook's petrel life history, indicating that more research is required.

Regarding age differences, it is relatively well-established that fledglings are more susceptible to light attraction, especially during their first flights (Telfer *et al.* 1987; Rodriguez *et al.* 2014; Deppe *et al.* 2017; Travers *et al.* 2021). Fledglings are inexperienced but potentially curious (Telfer *et al.* 1987; Isangedighi *et al.* 2020), which could result in their attraction to, and disorientation by lights, leading to a higher chance of collision and injuries. Our findings corroborate this as many juvenile fledglings, especially Cook's petrel fledglings, were admitted to the rehabilitation centre. Recent studies in Gran Canaria Island, Spain, recorded that the majority of seabirds admitted were because of light pollution and that many were juveniles (Montesdeoca *et al.* 2017). We report for the first time in New Zealand that there was a greater proportion of juvenile Cook's petrel with fatal injuries compared to adults since no adults were found from our necropsies of the Cook's petrels.

Sensory features

Although we found age and sex differences in mortality, there was no difference in the size of the visual organs according to age and sex. Thus, any differences in the attraction rates or risk of mortality are unlikely to be due to age or sex differences in the size or sensitivity of the seabirds' visual or sensory organs. Further research is required to compare the visual capacity of seabirds grounded by light pollution and those which were not grounded by light pollution.

Across species, the number of groundings from light pollution could be related to species differences in sensory features (Heswall *et al*. 2022). This could be because those with larger eyeball volumes relative to their body size have a greater visual capacity to be attracted to the lights (Kiltie 2000). Therefore, seabird species with larger eyeballs could be more likely to be disorientated and collide with buildings and/or land on the ground. Similarly, a study on bycatch numbers has shown that seabird species with larger sensory features, such as a larger eye socket volume relative to their body size, were more likely to be attracted to fishing vessels and become bycatch (Heswall *et al.* 2021).

Rehabilitation

Our study highlights the importance of rehabilitation centres in mitigating the effects of these threats and risks to wildlife such as seabirds (Lalas *et al*. 2023). These organisations offer the possibility of helping individuals in distress, in this case, grounded seabirds attracted by anthropogenic light pollution (Rodriguez *et al.* 2017b; Heswall *et al.* 2022). It also highlights the importance of admitting seabirds to rehabilitation centres for health assessments and care. This is because if some seabirds are not assessed, they could be released with injuries which could reduce their chances of survival. Furthermore, these centres provide resources and data for future studies to explore the impact of threats to seabirds and other species.

Conclusion

In conclusion, our results show that a large majority of grounded seabird deaths were due to injuries associated with collisions. Many of these seabirds were healthy outside of collision injuries, suggesting that collisions with anthropogenic structures due to disorientation from light pollution are an important source of mortality. This research is one of the first studies in Auckland and Aotearoa to describe the injuries of seabirds from light pollution, and the effects of age and sex. Since all of these Cook's petrels in this study were fledglings, once a year during the fledging season (March-May), turning off non-essential lights could potentially minimise risks to seabirds. Furthermore, it confirms the necessity of bringing all grounded seabirds to rehabilitation centres rather than releasing them immediately as they could have underlying trauma, which upon immediate release, could be fatal.

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Appendix 1. Output of the general linear model where the predictor variable are 'Injuries' and the base category is the 'wounds' group. The response variable is the number of each 'Injury' group. Bold and * indicates significance.

Injuries	Estimate	Std. Error	Z value	P value
Head Trauma	0.47	0.570	0.824	0.409
Internal Bleeding	0.47	0.570	0.824	0.409
Long term stressor	0.00	0.632	0.000	1.000

Appendix 2. Output of the general linear model where the predictor variable is the 'body score' and the base category is the 'five' group. The response variable is the number of each 'body score' group.

Variable	Estimate	Std. Error	Z Value	P value
One	2.88E-01	7.64E-01	0.377	0.706
Two	-4.06E-01	9.13E-01	-0.44	0.656
Three	-1.46E-16	8.17E-01	0	1
Four	8.47E-01	6.90E-01	1.228	0.219

Appendix 3. Output of the general linear model where the predictor variable is sex and the base category is 'unknown' sex group. The response variable is the number of each sex group. Bold and * indicates significance.

Variable	Estimate	Std. Error	Z Value	P value
Sex – Male	1.098	0.577	-0.377	**0.057 ***
Sex – Female	-0.287	0.763	-0.377	0.706

Appendix 4. Output of the general linear model where the predictor variable is the 'Age' and the base category is the 'unknown' age group. The response variable is the number of each 'Age' group. Bold and * indicates significance.

Variable	Estimate	Std. Error	Z Value	P value
Age – Adult	-19.368	4356.881	-0.004	0.996
Age – Juvenile	1.029	0.521	1.976	**0.048 ***

Appendix 5. Output of the general linear model where the predictor variable is both 'sex' and 'age' and the base category is 'unknown' group. The response variable is the absolute and relative eyeball volume.

	Absolute eyeball volume				Relative eyeball volume			
Variable	Estimate	Std. Error	T value	P value	Estimate	Std. Error	T value	P value
Sex – Female	-6.278	5.7836	-1.085	0.296	-0.194	0.206	-0.948	0.359
Sex – Male	-0.944	4.983	-0.018	0.852	-0.076	0.177	-0.428	0.675
Age – Juvenile	2.691	4.675	0.576	0.574	0.153	0.166	0.919	0.374

Appendix 6. Morphological and sensory measurements of the 19 juvenile Cook's petrels used in the necropsies.

Variable	Mean	Standard Deviation	Standard Error
Skull length (mm)	68.83	7.59	0.91
Skull width (mm)	36.68	53.68	8.86
Skull depth (mm)	21.09	1.86	0.40
Bill length (mm)	28.38	1.27	0.24
Bill depth (mm)	6.67	0.45	0.17
Bill width (mm)	8.98	0.95	0.32
Wing length (mm)	231.07	8.11	0.53
Eyeball volume (cm^3)	29.27	4.57	0.85
Relative eyeball volume (cm^3)	0.95	0.16	0.16

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SHORT NOTE

Long-distance dispersal by a *Coenocorypha* snipe

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Members of the family Scolopacidae (sandpipers and snipes) include some of the most extreme long-distance migrants known among birds (Conklin *et al*. 2017; Zhao *et al*. 2017). More than 60% of scolopacids breed in the Arctic and migrate to the Southern Hemisphere in the non-breeding season (Hayman *et al.* 1986; Higgins & Davies 1996). Among the record holders are eastern bar-tailed godwits (*Limosa lapponica baueri*) that migrate non-stop from Alaska to New Zealand, a distance of up to 11,690 km (Gill *et al.* 2005; Battley *et al.* 2012). Even this distance has recently been eclipsed by a godwit that flew 13,560 km non-stop from Alaska to Tasmania (Alaska Science Centre 2022).

At the other end of the dispersal spectrum, New Zealand's *Coenocorypha* snipes are among the most sedentary members of the family. Following a 5-year study of a colour-banded population of Snares Island snipe (*C. huegeli*), Miskelly (1999) reported a maximum dispersal distance of 350 metres for females, and only 260 metres for males. Longer dispersal distances have been reported for *Coenocorypha* snipe of four taxa moving between islands within an archipelago (Table 1). These records were based on unmarked birds found at sites where they were previously considered to be absent. However, until recently, these dispersal records involved minimum water crossings of no more than 2.5 km (Table 1).

We here report the first known record of a Chatham Island snipe (*C. pusilla*) on the main Chatham Island (Rēkohu / Wharekauri), other than the presence of subfossil bones there (Higgins & Davies 1996; Millener 1999). This recent record likely resulted from a bird flying across Pitt Strait, with a minimum water-crossing distance of 23.5 km (Fig. 1).

By about 1900, Chatham Island snipe were understood to be confined to Rangatira / South East

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Island, following introduction of predatory mammals to the three other large islands in the Chatham Islands (Fleming 1939; Roberts & Miskelly 2003). Snipe were successfully reintroduced to Mangere Island from Rangatira in 1970 (Bell 1974). The birds on these two nature reserves are considered genetically indistinguishable (Baker *et al.* 2010), and both islands are likely sources for Chatham Island snipe that are occasionally seen on nearby Pitt Island (Higgins & Davies 1996; Roberts & Miskelly 2003; Table 1 & Fig. 1).

The 'main island' snipe was found freshly dead on the deck of the house at Durham farm (owners Gary & Eileen Cameron), about 0.7 km east of Stony Hill, south-west Chatham Island, on the morning of 7 May 2022. The bird had fresh soil on its bill, indicating that it had been probing for food shortly before it died. Necropsy revealed puncture wounds consistent with the bird having been killed by a domestic cat (*Felis catus*) (Noel Hyde *pers. comm.* to CMM). Preserved as a study skin and spread wing (Te Papa OR.031240), it was DNA-sexed as a male using the method of Griffith *et al.* (1998). Its adult plumage, dull yellow legs, and the small size of the only testis found (1.5 x 0.5 mm) indicated that it was a subadult. All primary and secondary flight feathers were fully grown and in fresh condition.

As this bird was found at an unexpectedly large distance from known snipe populations, we compared its mitochondrial (mtDNA) haplotype and nine variable microsatellite loci with reference

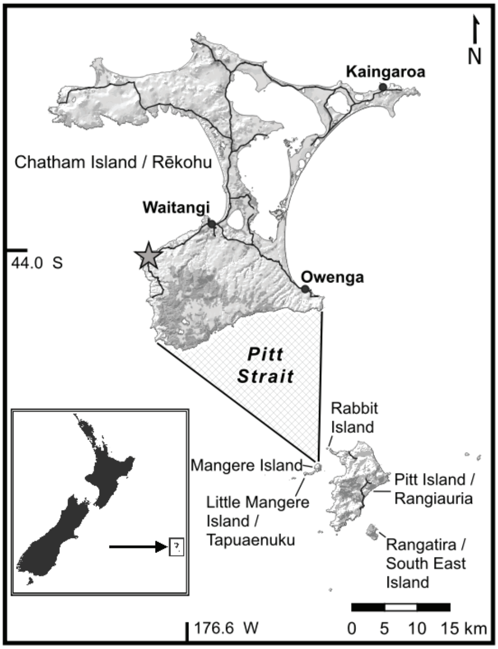

Figure 1. Map of the Chatham Islands, showing localities mentioned in the text. The location of Durham farm is shown by the star. The male snipe found dead there most likely came from Mangere Island (possibly via Rabbit Island), after a minimum water-crossing of 23.5 km and a minimum land-crossing of 12 km, with a minimum total distance travelled of 40 km.

Table 1. Dispersal records for four taxa of *Coenocorypha* snipe, based on detection of one or more birds at sites where they were previously considered to be absent. 'Max' = the direct line distance (km) from the shoreline of the nearest known potential source population to the site where the bird(s) was or were found. 'Min' = the longest water gap (km) that the bird(s) would have had to cross if the path with the shortest water crossing was followed. Data referring to the bird found on Chatham Island in May 2022 are in bold.

Taxon	Scientific name	Nearest population	Where detected	Max	Min	Source
Chatham Island snipe	***Coenocorypha pusilla***	Mangere Island	Little Mangere Island	0.5	0.3	Miskelly 1990
		Mangere Island	Rabbit Island	2.6	2.3	Miskelly, Bester *et al.* 2006
		Mangere Island	Northern Pitt Island	5.6	2.3	Te Papa OR.031242 (this paper)
		Mangere Island	**Chatham Island**	**40.3**	**23.5**	**Te Papa OR.031240 (this paper)**
		Rangatira	South-east Pitt Island	2.9	2.2	Higgins & Davies 1996
Snares Island snipe	*C. huegeli*	Putauhinu	Rerewhakaupoko	2.4	1.4	Tony Heaslip *pers. comm.* to CMM
		Kundy Island	Big Island	2.2	1.2	Russel Trow *pers. comm.* to CMM
Auckland Island snipe	*C. aucklandica aucklandica*	Ewing Island	Dundas Island	4.9	2.5	Miskelly *et al.* 2020
Campbell Island snipe	*C. a. perseverance*	Jacquemart Island	Campbell Island	2.6	0.9	Barker *et al.* 2005; Miskelly & Fraser 2006

data from other *Coenocorypha* snipe populations, to determine whether it had likely come from Rangatira or Mangere Island. The alternative hypothesis was that it was from an unknown population that had survived *in situ* in the presence of introduced mammals, as has recently been inferred for snipe on Rose and/or Enderby Islands in the Auckland Islands archipelago (Shepherd *et al.* 2020). We also included a subadult female snipe from northern Pitt Island in the genetic analyses (Te Papa OR.031242, found cat-killed at Rauceby homestead on 20 July 2022; Table 1). MtDNA sequencing and analysis followed Baker *et al.* (2010), and microsatellite genotyping and analysis followed Baker *et al.* (2010) and Shepherd *et al.* (2020). DNA sequences have been deposited in the GenBank repository (accession numbers OQ807039–OQ807040, OQ815888–OQ815891).

Both birds were genetically indistinguishable from Rangatira and Mangere birds. They both exhibited the most common mtDNA haplotype sequenced from these two populations (Fig. 2). Their microsatellite alleles all occurred in the Chatham Islands reference samples, and the same seven microsatellite loci were fixed as in previous samples (Baker *et al*. 2010). A STRUCTURE analysis (Pritchard *et al*. 2000) assigned both birds with high assignment probability (q = 0.99) to a cluster comprised of the Rangatira and Mangere Island reference samples. These genetic data support the hypothesis that the two birds had dispersed from either or both of the two known populations.

Assuming that the snipe had flown across Pitt Strait (Fig. 1), its arrival could not be explained by the immediately previous weather conditions, as there had been winds from a northerly quarter since the start of May 2022, with southerly winds on two days in late April (Timeanddate 2022).

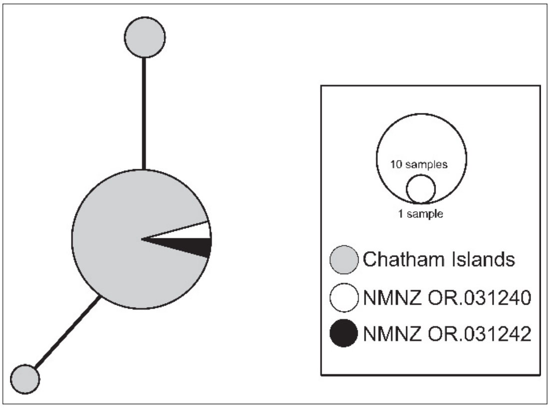

Figure 2. Median-joining network between mtDNA haplotypes of Chatham Island snipe. Each haplotype is separated by a single mutation and circle size is proportional to haplotype frequency. Chatham Islands = combined samples from Rangatira and Mangere Islands (see Baker *et al.* 2010); NMNZ OR.031240 = Chatham Island vagrant male; OR.031242 = Pitt Island vagrant female.

Given previous understanding of the dispersal ability of *Coenocorypha* snipes (Table 1), a bird crossing Pitt Strait was an extraordinary event. Furthermore, the bird likely crossed at least 12 km of main Chatham Island before coming to grief at the second occupied house that it could potentially have encountered when heading north or north-west from the south coast (Fig. 1). While we do not know whether it spent much time on the ground on Chatham Island, it may have (briefly) benefited from extensive feral cat control undertaken to protect Chatham Island taiko (*Pterodroma magentae*) and parea (*Hemiphaga chathamensis*) in south-west Chatham Island (Imber *et al.* 1994; Aikman *et al.* 2001; Mike Bell & Dave Boyle *pers. comms* to CMM).

Chatham Island snipe have the lowest wing-loading of the five living *Coenocorypha* snipe taxa (Miskelly 1990; Miskelly, Bell *et al.* 2006), and male Chatham Island snipe have lower wing-loadings than females (P = 0.07; Miskelly, Bell *et al.* 2006). These data point to Chatham Island snipe having greater dispersal potential than other *Coenocorypha* snipe, and males as being the sex with the potential to fly furthest.

While this record may prove to be exceptional, it demonstrates that *Coenocorypha* snipe are more capable dispersers than is generally understood (Oliver 1955; Heather & Robertson 1996; Higgins & Davies 1996). Ancestral *Coenocorypha* snipe were even more capable dispersers, based on their presence on oceanic islands that required crossing water gaps of at least 730 km (i.e. the distance between Campbell Island and Antipodes Island, both of which are inhabited by populations of subantarctic snipe *C. aucklandica*).

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SHORT NOTE

Riflemen (tītitipounamu, *Acanthisitta chloris*: Acanthisittidae) eating seeds of silver beech (tawhai, *Lophozonia menziesii*: Nothofagaceae)

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Rifleman (tītitipounamu, *Acanthisitta chloris*) is one of two surviving species in the family Acanthisittidae (New Zealand wrens), and is considered to be almost entirely insectivorous (Oliver 1955; O'Donnell & Dilks 1994; Higgins *et al.* 2001). The few observations of food items other than invertebrates consumed by riflemen include birds in South Westland feeding on fruit of *Raukaua edgerleyi* (raukawa) and *R. simplex* (haumakoroa: both Araliaceae) between April and July, with fruit comprising 2–4% of their diet in these months, but less than 1% when averaged throughout the year (O'Donnell & Dilks 1989, 1994). Riflemen have also been observed taking fruit of tutu (*Coriaria arborea*: Coriariaceae) (Greg Sherley *pers. comm.* to CMM, April 2023). We here report the first known observations of riflemen consuming seeds.

All observations were by GAP on 28 March 2023, between 1030 & 1240 h, along river flats east of Routeburn Flats hut (*c.* 700 m above sea level, 44.72°S 168.29°E), on the Routeburn Track, Mt Aspiring National Park. The forest along this section of the Routeburn Track is mixed southern beech (Nothofagaceae), dominated by red beech (tawhairaunui, *Fuscospora fusca*). GAP observed numerous small flocks of riflemen foraging on the forest floor, and took many photographs of them. Identification of food items was based on high-resolution digital images, taken with a high shooting speed (20 frames per second) Canon R5 camera with a Canon RF 100–500 mm lens (f/4.5–7.1L IS USM) set at 500 mm focal length, allowing rapid autofocusing with image stabilisation. As this was his first encounter with the species, Glenn did not realise the significance of the foraging behaviour observed until he was able to share his observations and images with others.

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The weather was cold, with occasional light rain and sleet. A cold front with strong winds the previous day had caused much fresh leaf fall (GAP, *pers. obs*). Groups of 2–6 riflemen were foraging along the track, focussing their effort on areas with less leaf litter, including the track itself, and footbridges (Fig. 1). At least 15 birds were seen on the track, with a further 8 or so on the ground to the side of the track. The birds were very focussed on foraging, and could be approached within a few metres before they moved away. When they did move, they generally hopped a little further along the track, rather than flying into the surrounding vegetation. The birds foraging on the ground included juveniles, and adults of both sexes.

The images revealed the birds to be foraging among fallen leaves of silver beech (tawhai, *Lophozonia menziesii*), rather than the locally more abundant red beech (Fig. 1). Several images revealed that the birds were holding silver beech seeds cross-wise in the distal half of their bills, and they appeared to be squeezing the amorphous seed contents out (Fig. 2). We suspect that it was this whitish paste that the birds were consuming, rather than swallowing the entire nut. Several images showed riflemen with small quantities of this paste adhering to their bills, and none of the 800+ images showed an entire nut in a bird's gape.

Figure 1. Adult female rifleman among silver beech leaves on a footbridge on the Routeburn Track, 28 March 2023. Image: Glenn Pure.

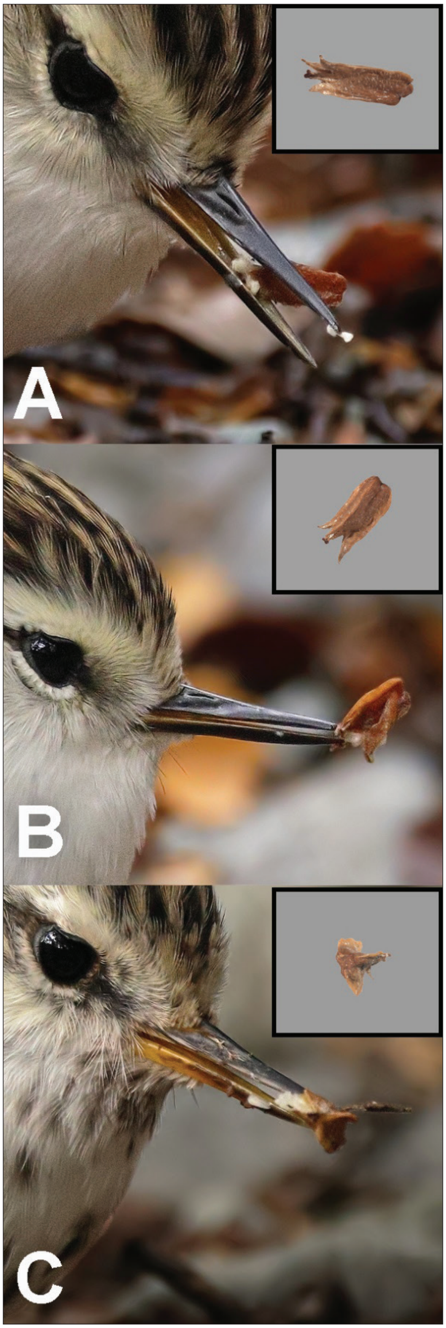

Figure 2. Riflemen extracting the contents of silver beech seeds from the hard nut, Routeburn Track, 28 March 2023. A & B: Adult females; C: Juvenile. Main images: Glenn Pure; insets of silver beech seeds at similar orientations: Jean-Claude Stahl, Te Papa. The birds were eating seeds that had likely fallen the previous day; the reference seeds (picked out of roadside gravel and leaf-litter collected by CMM at Kawatiri, Nelson, on 18 April 2023) were older and drier.

The caterpillars of at least 20 species of moths (Lepidoptera: Oecophoridae, Hepialidae, Psychidae, and Noctuidae) have been identified from beech forest litter (from under hard beech (*Fuscospora truncata*) near Wellington; Dugdale 1996). However, none of the Routeburn images revealed anything suggestive of insect larvae being held by riflemen.

Silver beech seeds are highly variable in size and shape. They average 5.4 x 3.5 mm (though can be as long as 7 mm and as slender as 2 mm), and have three (occasionally two) narrow wings along the length of the seed (Fig. 3; Wardle 1967; Webb & Simpson 2001; Ford *et al.* 2016). Seeds of Nothofagaceae lack endosperm; however, their cotyledons contain fat reserves (Webb & Simpson 2002; Ford *et al.* 2016), and this is likely to be the whitish paste that the birds were extracting.

Figure 3. Silver beech seeds (2 x life size). The scale bar is 15 mm, with tick marks at 5 mm. Riflemen have bills that are 11–15 mm long, and silver beech seeds average 5.4 mm long (Higgins *et al.* 2001 and Webb & Simpson 2001 respectively). Image: Jean-Claude Stahl, Te Papa.

With an average weight of 2.9 mg, each silver beech seed is about 35% the size of a red beech seed (mean weight 8.2 mg; Beggs 1999). Seeds of both species contain similar energy by weight (21.4–21.8 kJ/g; Beggs 1999), although red beech seeds contain proportionately more nitrogen, phosphorus, and potassium (Beggs 1999). The larger and more nutritious red beech seeds are favoured by introduced rodents, and endemic kākā (*Nestor meridionalis*) and yellow-crowned parakeets (*Cyanoramphus auriceps*) (Beggs 1999). We suggest that riflemen are limited to eating the much smaller silver beech seeds due to the birds' small body size and weak jaw muscles. The images of riflemen holding silver beech seeds suggest that they may have been selecting seeds that were more slender than average (Fig. 2 cf. Fig. 3), although no attempt was made to assess sizes and shapes of seeds available on the forest floor at the time.

Silver beech seeds are mainly shed from mid-March to early April, with highly variable quantities of seed produced and shed between years (Wardle 1967; Kelly *et al*. 2012). Autumn 2023 was observed and predicted to have moderate levels of beech seed fall in northern Fiordland and western Otago (Colin O'Donnell & Graeme Elliott, *pers. comms* to CMM, May 2023). We do not know if riflemen are able to eat silver beech seed before it is shed, and this would be difficult to observe in the forest canopy. However, foraging on the ground is unusual behaviour for riflemen (O'Donnell & Dilks 1994; Higgins *et al.* 2001). The number of birds observed feeding on the ground on 28 March 2023 suggests that they were seeking a resource that they couldn't get at their usual foraging heights. It is possible that silver beech nuts became softer and more pliable after prolonged contact with damp ground (suggestion by Colin O'Donnell, *pers. comm.* to CMM, April 2023). We suggest that foraging along the track and footbridges, which were kept relatively clear of leaves by human foot-traffic, facilitated searching for the tiny seeds, compared to nearby areas of deep leaf litter.

This first record of seed-eating by riflemen was facilitated by high-resolution, low light photography and high frame rates, allowing small food items to be photographed and identified before they were consumed. We do not know if this is rare foraging behaviour, or whether it has been overlooked previously. Riflemen occur widely in beech forests, and we note that black beech (*Fuscospora solandri*) and mountain beech (*F. cliffortioides*) have seeds which are similar in size to those of silver beech (Webb & Simpson 2001; Ford *et al.* 2016). Although beech seed fall is seasonal and is variable between years (Kelly *et al*. 2012; Ford *et al.* 2016), it can be abundant, and may provide an energy-rich food at a time of year (autumn) when beech-forest invertebrates become less available (Fitzgerald *et al.* 1996).

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Keywords: *Acanthisitta chloris*, Acanthisittidae, diet, Nothofagaceae, rifleman, seed consumption, seed-eating, southern beech

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SHORT NOTE

Plumage colour aberrations in erect-crested penguins (*Eudyptes sclateri*) on Antipodes Island

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Plumage colour aberrations occur due to mutations that alter the production and deposition of pigment cells in the feathers (van Grow 2006). These mutations are often due to genetic factors, but environmental stressors (e.g. poor nutrition or contaminants) and ontogenetic processes (e.g. senescence) have also been identified as contributing factors (Guay *et al*. 2012; van Grouw 2012; Camacho *et al*. 2022).

The most frequently reported colour mutations in seabirds are melanism, albinism, leucism, and isabellinism (Carpenter-Kling *et al*. 2017). Aberrant plumage colouration has been reported in some form for most species of penguins (Woehler 2023). Melanism results from excess melanin production or deposition and produces black plumage (Sage 1962). On the other hand, albinism stems from a lack of melanin production resulting in white plumage and skin, with red or pink eyes (Sage 1962).

Leucism occurs when the deposition of pigment cells is interrupted resulting in fully or partially white feathers (Forrest & Naveen 2000; van Grouw 2006). Unlike albinism, leucistic individuals do not exhibit the changes in skin and eye colouration (Sage 1962; Nogueria & Alves 2011). Interestingly, "albino" as well as leucistic individuals were highly valued by taxidermists in New Zealand and elsewhere for their unique plumage (Crane & Gill 2018). In crested penguins, full or partial leucism has been reported in macaroni penguins (*Eudyptes chrysolophus*) (Carpenter-Kling *et al*. 2017) and royal penguins (*Eudyptes schlegeli*) (Falla 1937).

Isabellinism is a form of partial albinism resulting in a lightening of black feathers to a light brown colouration (Everitt & Miskelly 2003). The mutation arises from a single autosomal recessive gene with incomplete dominance and has been observed in king (*Aptenodytes patagonicus*), yellow-eyed (*Megadyptes antipodes*), Adélie (*Pygoscelis adeliae*), gentoo (*Pygoscelis papua*), chinstrap (*Pygoscelis antarcticus*), Magellanic (*Spheniscus magellanicus*), Humboldt (*Spheniscus humboldti*), and African penguins (*Spheniscus demersus*) as reviewed in Everitt & Miskelly (2003). In crested penguins, isabelline plumage has been reported in macaroni, royal, Snares (*Eudyptes robustus*), and Southern rockhopper penguins (*Eudyptes chrysocome*) (Everitt & Miskelly 2003).

However, the term isabelline has recently come into question as the most appropriate description for this colour mutation (Traisnel *et al*. 2018). True isabellinism results from a lack of pheomelanin, which is a pigment that these penguins do not produce (Traisnel *et al*. 2018). A similar brown colouration in other birds results from incomplete oxidation of eumelanin causing rapid bleaching due to sunlight (van Grouw 2012, 2013). This mutation is sex-linked and is most commonly seen in females (Traisnel *et al*. 2018). The authors suggest the use of the term "brown" to refer to "isabelline" penguins.

Plumage colour aberrations have not yet been formally reported in the erect-crested penguin, with the exception of a melanistic individual photographed on St. Kilda Beach, Dunedin in 1934 (Fall 1935). Interestingly, a melanistic crested penguin illustrated by Buller (1888: plate p. 294) is now thought to represent a melanistic erect-crested penguin (Oliver 1953; Stonehouse 1971). On Antipodes Island, in December 2022, we observed

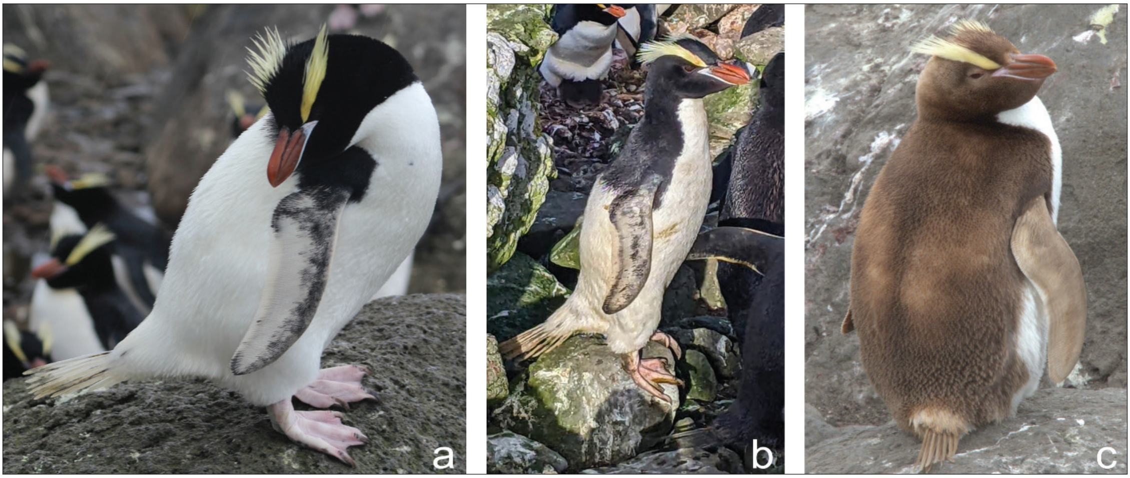

Figure 1. Plumage colour aberrations observed in erect-crested penguins (*Eudyptes sclateri*) on Antipodes Island, December 2022. Three adults were observed including (a) partially leucistic adult male, (b) partially leucistic adult female, and (c) isabelline or "brown" adult female.

three individual erect-crested penguins presenting two different colour aberrations. We encountered a male erect-crested penguin exhibiting partial leucism on the south coast of Antipodes Island on 5 December 2022 in colony SCW-001 (49.7062°S, 178.7482°E; Mattern 2023). The back plumage was uniformly white except a black saddle extending between the base of the wings (Fig. 1a). The wings themselves were mottled with black on the leading edge fading to white on the trailing edge. This individual was seen multiple times in different locations within the colony associating with females of normal plumage colour.

A partially leucistic female was identified in the same colony on 7 December 2022 (Fig. 1b). The overall pattern was very similar to the partially leucistic male, but both individuals were observed in different parts of the colony at the same time. Additionally, the back saddle extended lower on the female and the wings had a heavily mottled appearance encircled by an outline of black feathers. Unlike the male, this female was seen only once walking through the colony and was not observed associating with any males.

On 8 December 2022, an isabelline or "brown" female was spotted preening on the rocks at colony SCW-004 (49.7028°S, 178.7399°E). The plumage pattern mimicked the standard erect-crested pattern, but all black areas were replaced with chocolate brown feathers (Fig. 1c). The coloration appeared to be lighter in areas around the mid-back, top of the head, tail, and on the wings. This colony was only visited once during the expedition.

To our knowledge, these colour aberrations have not been formally reported in erect-crested penguins (Everitt & Miskelly 2003; Woehler 2023). However, an image reproduced on the back-cover of Taylor (2006) appears to depict another isabelline or "brown" female erect-crested penguin. The apparent lack of such observations is likely due to the inaccessibility of their breeding islands and the low frequency of large-scale surveys (Mattern & Wilson 2019; Davis *et al*. 2022).

The underlying cause for these colour aberrations in erect-crested penguins have not been analysed. Poor nutrition seems unlikely given their overall good body condition (Davis *et al*. 2022; Mattern 2023). Progressive greying could not be evaluated with the current observations but has been reported in Adélie (Golubev 2020) and African penguins (Traisnel *et al*. 2018), as well as in yellow-eyed penguins over the age 20 (UE *pers. obs*.). Therefore, a genetic mechanism appears to be the most likely cause, but further genetic studies and long-term monitoring is needed.

In forthcoming expeditions, we will continue to survey breeding colonies and will record the presence of any other plumage aberrations such as full leucism or melanism, both of which are reported in other crested penguin species. We will also record any resighting of the reported individuals.

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SHORT NOTE

Female North Island brown kiwi (*Apteryx mantelli*) involved in incubation and chick care

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Parental care in many bird species varies across their range but for many there is a large gap in understanding the drivers of sex differentiation in providing parental care (Cockburn 2006). Male-only care is suggested as relatively uncommon in birds and is found predominantly in Gondwanan taxa that lack female only care (Cockburn 2006). Some kiwi have male only incubation, but biparental incubation becomes more prevalent in populations from colder, southern sites and the extremely southerly populations are cooperative breeders where the dominant male may not incubate at all (Colbourne 2002).

New Zealand bird guides (e.g. Scofield & Stephenson 2013; Robertson & Heather 2015) indicate that incubation by North Island brown kiwi (*Apteryx mantelli*) is male only. This is considered similar in the little spotted kiwi (*A. owenii*), whereas all other kiwi have both male and female incubating (Oliver 1955; Robertson 2013; Scofield & Stephenson 2013; Heather & Robertson 2015; Jahn *et al*. 2022). Colbourne (2002) records that rarely a female North Island brown kiwi may incubate egg(s) for up to a week before being replaced by the male. Oliver (1955) records that the male makes the nest although the female may assist where this involves digging a burrow. The female is seen as a major contributor through the production of a large egg or eggs which is assumed to partly preclude her from other nesting assistance.

The outcome of this understanding is that researchers focus on males, since more immediate management information can be gained by having transmitters on males than on females. Modern transmitters record a range of information including whether the bird is alive, incubating, or dead, how long it has been incubating, and how long it was active over each of the past two

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nights and averaged over the last four days (NIB Chick Timer V3.4; wildtech.co.nz/kiwi). The logical outcome of only putting transmitters on males is that information on the role of females is inferred. Assuming behaviours are the same in all habitats, all populations, all climates and all seasons assumes a rigidity of behaviour that would be unusual for birds (Cockburn 2006).

Pataua North Landcare (35°42'S, 174°29'E), Whangarei, received a permit in 2017 to reintroduce 40 kiwi over three years to approximately 1,000 ha of regenerating native broadleaf/kauri/podocarp forest (McKelvey & Nicholls 1959) under intensive pest control. Wildtech V3.4 "chick timers" transmitters were fitted to one leg and broadcast information at ten-minute intervals. Transmitters were attached to 31 of the 38 birds eventually released, to confirm the establishment of a breeding population. Transmitters were removed from most birds after six months. To reduce further workload and focus on breeding, transmitters were retained on the male and female of four pairs. All nesting attempts and chick care was then followed by monitoring their transmitters, augmented by the use of five trail cameras (Bushnell Trophy Cam and Multrie S-Series Game Camera) at some nests and some roost sites. The greatest focus was on two pairs that were most easily accessible.

Taking the historical average rainfall over the past ten years (2011–2020) for the kiwi breeding season of June to February; www.metservice.com/whangarei), most pairs attempted only one or two nests. In contrast during a recent higher rainfall breeding season (2022–2023), up to three nesting attempts per pair were made (Table 1). Clutch size was one or two although one nest of three eggs was found. Most eggs were fertile and a few (3) nests produced two chicks. Annual production per pair varied from one to five. As a consequence of more nesting attempts in the seasons with higher rainfall, more chicks were produced.

Males incubated for the majority of the time at all nests, and time away from the nest was lowest immediately before and at hatching. Chicks could hatch up to a week apart (nests were not checked other than by cameras in order to minimise disturbance). On three occasions, the male moved to incubate at a newly prepared nest containing eggs the day of leaving the previous nest. This was recorded in both the pairs for which we have detailed information, and are presented as detailed examples.

Example 1: Alick was sitting on one egg in an earth burrow but the following day he was on an egg in a wooden nest box. The following day he returned to his first nest but subsequently abandoned that nest and incubated the egg in the nest box. His chick hatched in the nest box 58 days later suggesting that his partner, Renai, had incubated the egg for up to 12 days before Alick started incubation.

Example 2: Jo was on a nest with two eggs and as hatching approached, his partner Kiri became site attached under a puriri (*Vitex lucens*) tree which had been used for nesting in previous years. She reduced her night foraging time away from the nest site from 8–9 hours to 6 hours for 13 days (incubating birds markedly reduced their time foraging at night and remain incubating instead). When the chicks hatched at the first nest, Kiri moved to that area of the first nest and Jo moved to the new nest under the puriri tree 200 m away. His transmitter continued to broadcast at incubation frequency. Kiri remained in the area of the previous nest where the chicks were last seen for three days.

Example 3: Six weeks later, Kiri focussed her activity 300 m up the same valley and became site attached in a shallow burrow. Within days her transmitter changed to incubation mode and her nightly time away from the nest dropped to four hours. The camera on Jo's nest had previously pictured Kiri visiting and the pair copulated outside the nest. Twenty days after Kiri had switched to

Table 1. Breeding statistics for North Island brown kiwi (*Apteryx mantelli*) at Pataua North, Whangarei, New Zealand, in five seasons of average rainfall compared with a season of high rainfall (2021–2022). Average rainfall is taken from mean for the last ten years (2011–2020). *these only include multiple nests of two pairs followed in detail. Values are means.

	Average rainfall	**Higher rainfall**
Mean rainfall (mm, June–February)	999	2,278
Number of kiwi pairs	4	4
Mean number of nesting attempts	1.3 (n = 9)	2.0
Mean clutch size	1.5 (n = 13)	1.4 (n = 5)
Number of chicks produced per pair per season	1.2 (n = 11)	2.3 (n = 8)
Proportion of male incubation time*	95% (n = 4)	84% (n = 4)
Number of pairs with evidence of female incubation	2 of 2	2 of 2
Number of pairs with evidence of female chick care	Unknown and not followed	Unknown but suggestive at two nests

incubation mode, Jo hatched a chick at their second nest. He remained with the chick for three days and then moved to the burrow where Kiri was incubating. He then began incubating their third nest and his transmitter remained in incubation mode. Kiri moved back to the area of the previous nest as expected if looking after the chick

In total Jo incubated for 173 continuous days for the three nests. He eventually abandoned incubation at the third nest after 36 days. His total time on nest two was only 62 days so Kiri had incubated that nest for at least 13 days but possibly as high as 20 days. Assuming the minimum incubation plus chick care time of 75 days, she appeared to have incubated on the third nest for up to 22 days.

On both occasions when the male, Jo, took over incubation from Kiri, she moved to the previous nest presumably to be with their chicks. Trail camera footage at four nests, showed Kiri visiting the nest after the first chick had hatched and walking away from the nest area with the chick. In contrast, Alick had abandoned an unhatched egg and Renai did not have a chick to care for. Camera footage at nests where a follow-on nest was not prepared, showed chicks departing the nest with either of their parents. After nests were no longer used for roosting, we had no information on how long the female or male stayed in the same vicinity as their chicks as none of the chicks' carried transmitters.

We challenge the current widespread assumption that male North Island brown kiwi construct the nest (Oliver 1955). This would seem unlikely for the two pairs we observed where the females began using a new nest while the males (Alick and Jo) were incubating and had few active hours away from the nest. Furthermore, the females produced an egg and began incubating so it was ready for the male as soon as he finished the current nest. More information on the scale and prevalence of this type of female investment is required for North Island brown kiwi.

Despite the widely recorded observation that only the male incubates, our observations suggest that while this is usual, in areas and seasons when multiple nests are possible, the female can initiate the nest and incubate for up to the first three weeks. Moreover, she can incubate simultaneously with her mate but on a different nest. Other cases of female investment in nesting have also been observed; the most extreme example known was a female-female pair in Motatau (35°30′58S, 174°02′11E) who took turns at incubating eggs which were infertile (Paul Cornille *pers. comm.*). Further research is needed over multiple seasons to determine how common and for what duration female incubation occurs.

Regarding parental care, our numerous observations of the female visiting a nest with newly hatched young, and leaving with one of them, in addition to the observation that the female changed her range to where chicks were last seen are all strongly suggestive of female parental care. Where the male does not move immediately to a new nest, he participates in chick care. How long parental care continues is unknown but we have found pairs roosting together with a third, smaller bird when we have been catching birds for transmitter change. This is suggestive that some parental care may continue for at least six months.

Our observation of considerable involvement of females in incubation and possibly chick care were in a season of high rainfall, soft ground, and multiple nests. This meant the male was less available to assist. We have no data to show this also occurs in seasons when pairs only have one nest. Closing this information gap relies on females with transmitters rather than the current standard practice of only tracking males.

The practice of removing eggs or newly hatched chicks, as occurs under Operation Nest Egg (ONE), would deprive those birds of parental care. It is interesting that Jahn *et al*. (2022) records a significantly shorter life span of ONE birds compared with wild reared birds. They record that ONE birds lived about half as long as wild or captive reared birds (Jahn *et al*. 2022). This should not be seen as a reason to condemn ONE since the program has led to the establishment of many new populations including that at Pataua North. It does, however, further demonstrate a large gap in understanding parental care in kiwi.

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