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.

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

& 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.
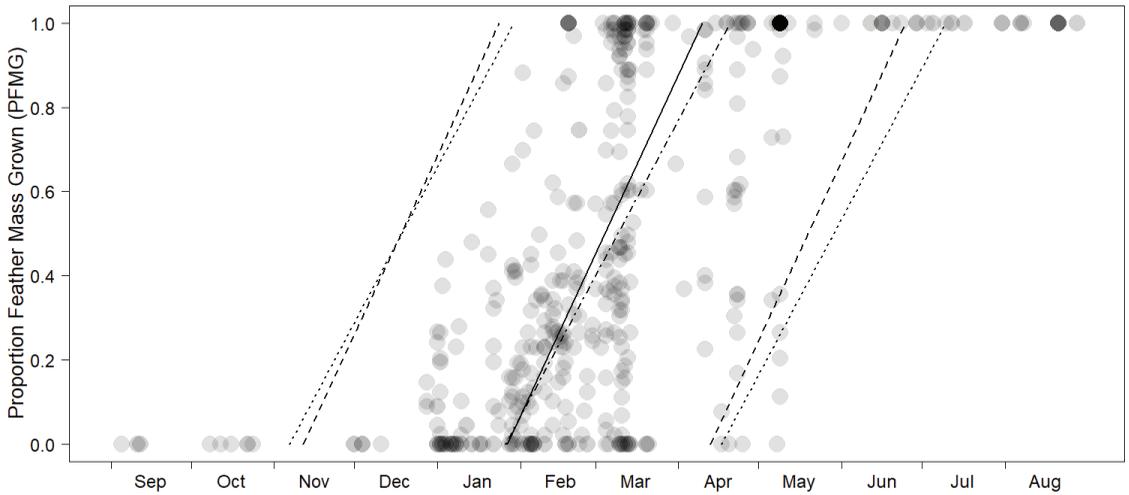
Figure 1. Modified scatter diagram* of the progression of primary moult for adult silvereyes (*Zosterops lateralis*) in New Zealand using PFMG as the moult index. The solid and the dot-dash straight lines represent the progression of moult for the average adult bird in the population using data type 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.
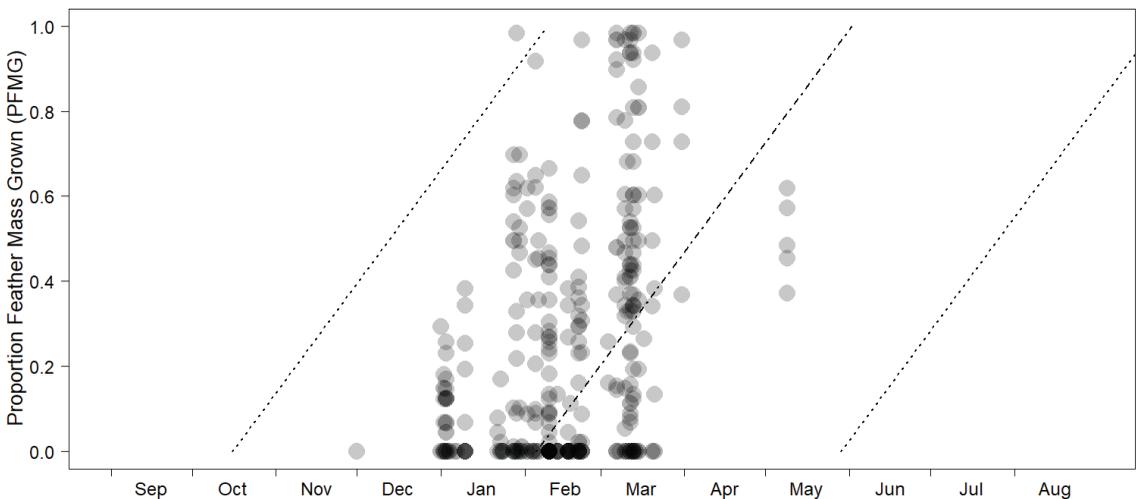
Figure 2. Modified scatter diagram* of the progression of juvenile primary moult in silvereyes (*Zosterops lateralis*) in New Zealand using PFMG as the moult index and data type 5. The dot-dash straight line represents the progression of moult for the average juvenile bird in the population. The dotted 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.
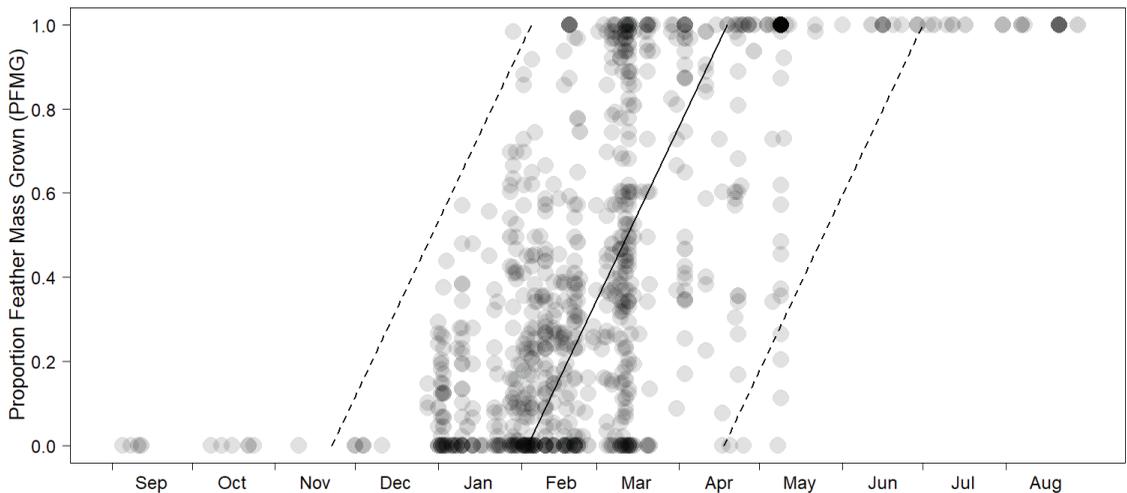
Figure 3. Modified scatter diagram* of the progression of primary moult in silvereyes (*Zosterops lateralis*) in New Zealand using all available data (adults, juveniles and unaged birds), PFMG as the moult index and data type 2. The solid straight line represents the progression of moult for the average 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).
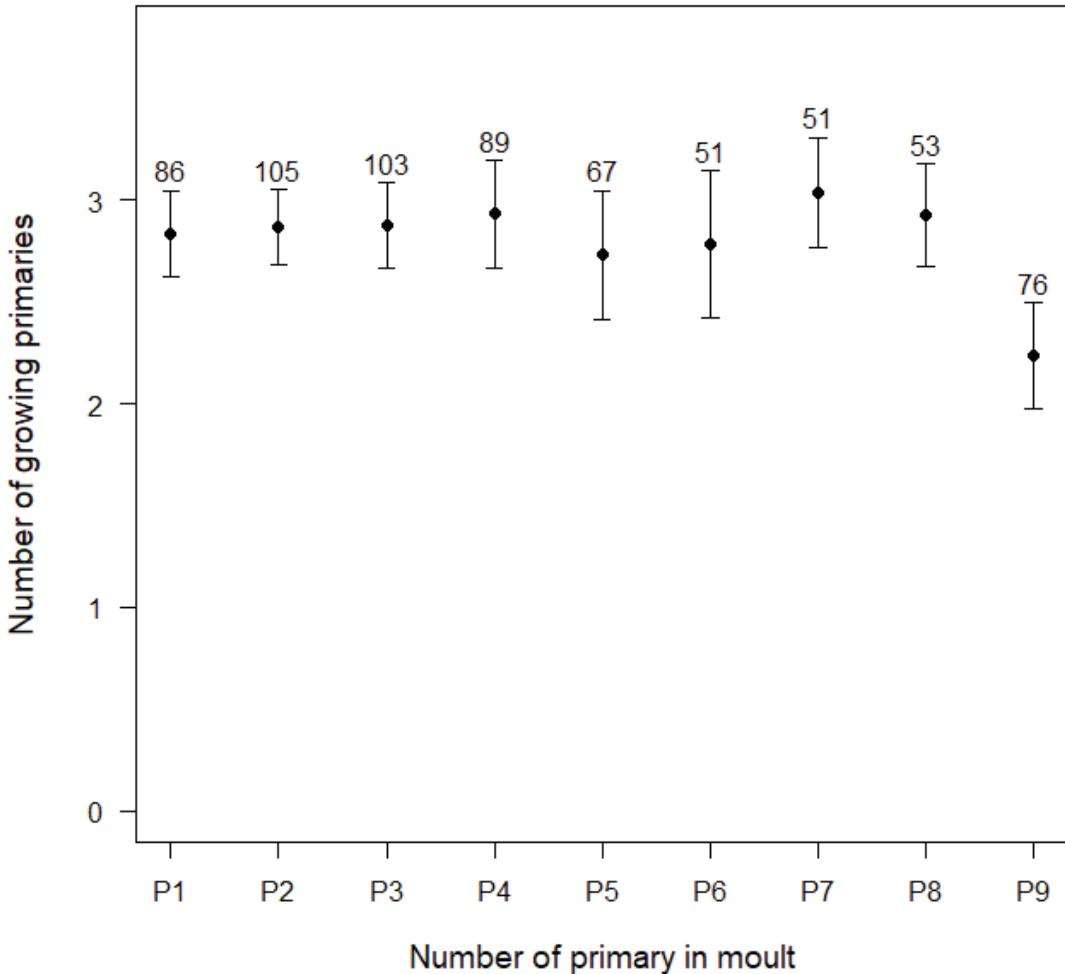
Figure 4. The mean number of primaries growing simultaneously while each of the nine primaries of adult silvereyes (*Zosterops lateralis*) was in moult. The 95% confidence intervals for the mean and the sample sizes are shown.

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
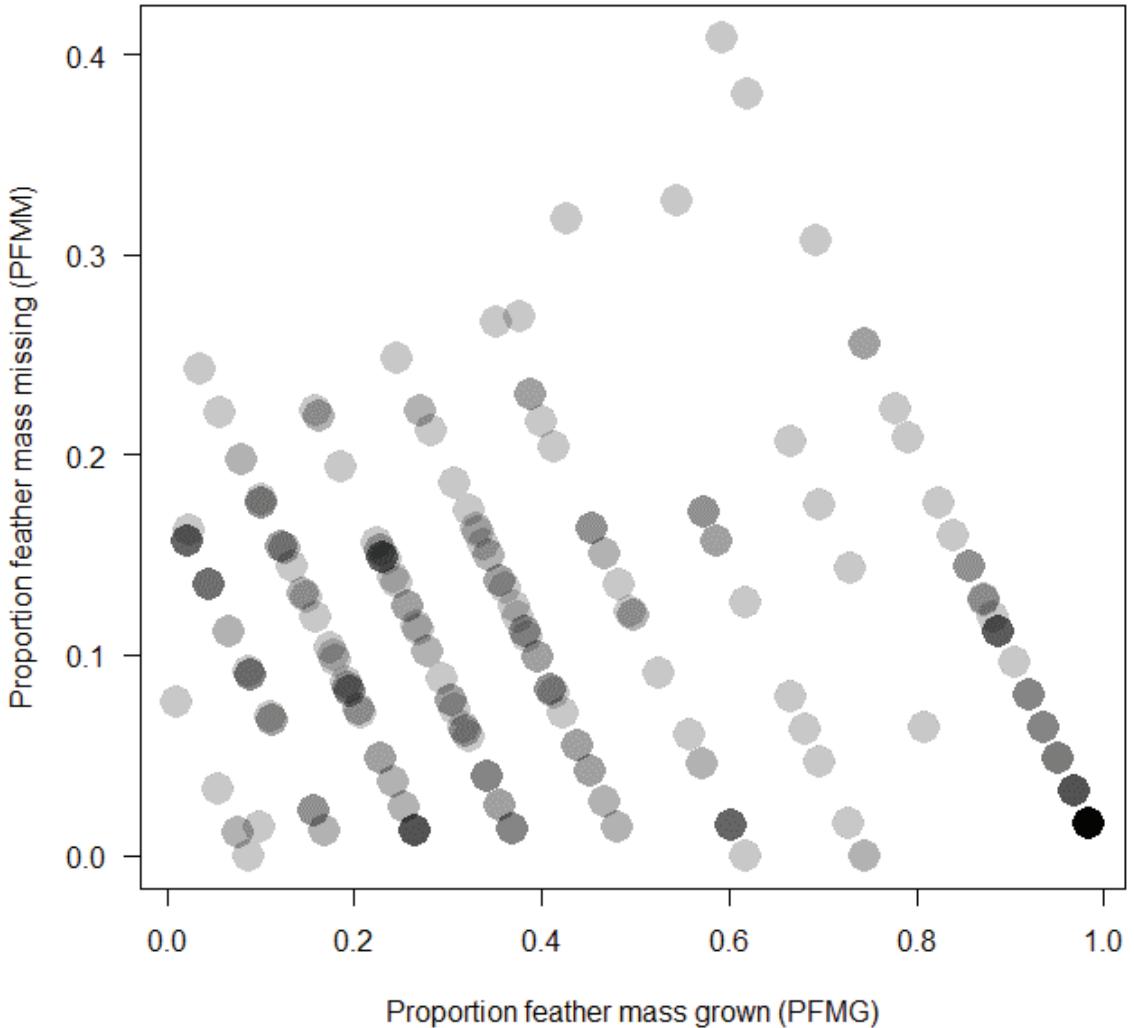
Figure 5. The relationship between Proportion Feather Mass Missing (PFMM) and Proportion Feather Mass Grown (PFMG) is represented by a modified scatter diagram* for adult silvereyes in active moult. The pattern of parallel lines is an artefact of the protocol for the recording of the moult status of 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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