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Primary moult of wrybills | ngutu pare (*Anarhynchus frontalis*)

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Abstract: The wrybill | ngutu pare (*Anarhynchus frontalis)* is a small plover endemic to New Zealand with a unique laterally curved bill. Apart from moult, much of its biology is well understood: adults breed from late August to January on the braided river systems in Canterbury and inland Otago on New Zealand's South Island. From midsummer, late December and January, they migrate north to non-breeding areas in the northern part of the North Island, especially to the large tidal bays, east and west of Auckland, where they undergo primary moult from January to April. The Underhill-Zucchini moult model was used to estimate the mean start and completion dates of primary moult, which were 20 January and 3 April respectively. Adults thus commence primary moult soon after arrival on non-breeding grounds but complete moult around four months before southward migration to their breeding areas in August. They appear to avoid primary moult during winter. Second-year birds start primary moult in December, one month earlier than the adults, but finish at approximately the same time. Primary moult of the wrybill is compared with closely related species, and with other waders that breed on the South Island and migrate to North Island for the non-breeding season.

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INTRODUCTION

The wrybill | ngutu pare (*Anarhynchus frontalis)* is endemic to New Zealand and is unique among birds in having a laterally curved bill (Marchant & Higgins 1993; Conklin *et al.* 2019). Its IUCN threat classification is Vulnerable (BirdLife International 2022). Adult wrybills breed during the austral spring and early summer (between late August and January) on the shingle riverbeds of braided river systems in Canterbury and inland Otago, east of the Southern Alps on the South Island, between 43°S and 45°S (Heather & Robertson 2005; O'Donnell *et al.* 2016). They typically lay two eggs per clutch and often have two clutches in one season (Marchant & Higgins 1993). First clutches are laid from late August and second clutches from late October to late December (Hay 1984). If the first clutch is lost, a replacement clutch is laid (Marchant & Higgins

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1993). During the breeding season the curved bill is an adaptation for probing for insect larvae, mainly the larvae of mayflies *Deleatidium* spp., under stones in riffles (Pierce 1979). By midsummer, the braided rivers cease to flow, food becomes unavailable and predation risk increases (Gray & Harding 2007).

After breeding adult wrybills migrate northwards to non-breeding areas in the northern part of the North Island, especially to the large tidal bays, locally known as "harbours", east and west of Auckland (Davies 1997; Riegen & Dowding 2003). They start arriving from the last week of December and their numbers quickly increase during January (Davies 1997). Juveniles hatched early in the season and non-breeding birds (second-year birds and failed breeders) migrate north earlier than the rest of the breeding population (Davies 1997). The majority of the population spends the non-breeding season in the Firth of Thames and Manukau Harbour north of 38°S, while a small proportion remains on the South Island (Davies 1997, Dowding & Moore 2006, Riegen & Sagar 2020). Primary moult takes place on the non-breeding grounds. In this non-breeding period the bill is used like a scythe, reminiscent of avocets (Turbott 1970; Conklin *et al.* 2019).

Adult wrybills generally depart the North Island and return south to their breeding grounds in August during the late austral winter (Marchant & Higgins 1993). About half of the first-year birds return south to the breeding grounds, but do not breed, leaving about a month after the adult departure, while the rest remain in the North Island (Davies 1997, Heather & Robertson 2005). Numbers of wrybills in the North Island are lowest from mid-November to late December.

The distance between the breeding and non-breeding areas averages c. 800 km. At an average flight speed of 65 km/hour for small plovers (Zwarts *et al.* 1990), the flying time between breeding and non-breeding areas is therefore c. 12 hours. Most wrybills make the northward journey non-stop, but some stop along the way for brief periods (Dowding & Moore 2006). Intermediate staging sites during the northward migration include sites along the east coast of South Island, particularly Lake Ellesmere (43.79°S, 172.50°E), and occasionally Farewell Spit (40.52°S, 172.87°E) in the northern part of South Island (Dowding and Moore 2006). On the return southward migration, it is unclear whether any wrybills fly directly to their breeding grounds. Many migrate south via the estuaries on the east coast of South Island where they have brief stopovers (Dowding & Moore 2006).

Many aspects of wrybill biology are well-documented, including good estimates of population size, trends and survival rates (Riegen & Dowding 2003; Riegen & Sagar 2020). The breeding biology is described (e.g., Hay 1984) and threats are also understood (Dowding & Murphy 2001; Riegen & Dowding 2003). However, one gap is an understanding of the timing of primary moult and how this fits into the annual cycle. Marchant & Higgins (1993) contains anecdotal information about moult, and there is a preliminary quantification in Davies (1997) who found that primary moult within the wrybill population takes place between late December and early May, with second-year birds commencing primary moult before mature adults. Marchant & Higgins (1993) used a subset of the data presented in Davies (1997) and roughly estimated the duration of primary moult of the individual bird to take about 100 days. No further estimates relating to the timing of moult are given.

The objective of this paper is to estimate the timing of primary moult of wrybills, using a larger sample than was available to Davies (1997) and using the three-parameter moult model of Underhill & Zucchini (1988). The parameters estimated by the model are the duration of moult, the average starting date, and a measure of how synchronised moult is in the population. A full description of the model and best practice strategies for fitting it are provided by Scott *et al.* (2023). We consider how estimates of the parameters fit the annual cycle.

Taxonomically, the wrybill is placed in the monotypic genus *Anarhynchus*, but it is closely related to the genus *Charadrius* (Burton 1972; Conklin *et al.* 2019). We therefore compare the timing of moult of the wrybill with that of species in the genus *Charadrius* for which estimates of timing and duration of moult obtained using the Underhill-Zucchini moult model are available. We also compare it with the timing of moult for other members of the suborder Charadrii that breed in the South Island in the austral spring and early summer and migrate to the North Island for the non-breeding season.

METHODS

Data collection

From the mid-1980s to early 2000s, more than 500 wrybill were caught at Jordan's Farm on the shores of the Kaipara Harbour, northwest of Auckland (36.57°S 174. 42°E). From 1991 to 2021, almost 7000 were caught on the western shores of the Firth of Thames (37.15°S 175.31°E). Both these locations were non-breeding sites. Small numbers were mist-netted at night, usually when targeting other species, and the rest were caught using cannon nets at high tide roosts particularly on shelly beaches. When large catches were made during cannon netting, processing was speeded up by ringing and releasing birds not in moult. Mensural data and primary moult details were obtained only for the birds that were actively moulting.

Table 1. Relative masses of the 10 primary feathers used in this study, averaged for seven *Charadrius* species: *C. dubius* (Meissner *et al.* 2018), *C. hiaticula* (Meissner *et al.* 2018, PG Ryan *in litt.*), *C. leschenaultii* (Jackson 2017, Meissner *et al.* 2018), *C. marginatus* (P Kuun *in litt.*), *C. pallidus* (Underhill & Joubert 1995, M. Remisiewicz *in litt.*), *C. pecuarius* (Meissner *et al.* 2018, M. Remisiewicz *in litt.*, PG Ryan *in litt.*), *C. tricollaris* (Meissner *et al.* 2018, PG Ryan *in litt.*).

Primary	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
Relative mass (%)	4.07	4.99	5.92	7.09	8.69	10.61	12.06	13.76	15.48	17.33

Birds were aged as juveniles, second-year birds and adults. Juveniles are birds in their first year of life and show uniformly even fresh plumage on the non-breeding grounds, have more hints of pale brown and lack the black breast band (Davies 1997). Second-years are birds that are more than one year old but less than two years, and can be differentiated from adults between late December and early March because their primaries are more worn and they are in a later stage of moult. However, once they lose their outer primaries, second-year birds are no longer distinguishable from adults (Davies 1997). Adults are either undertaking primary moult between early January and late April, or are showing signs of breeding plumage including black breast bands and (in males) the thin black forehead. Primary moult was scored from the innermost primary to the outermost according to the standard method (Ginn & Melville 1983): old feathers scored 0, growing feathers scored 1–4 depending on their length and a fully grown new feather scored 5.

Data analysis

The conversion of moult score to Proportion Feather Mass Grown (PFMG) requires primary feather mass data (Underhill & Joubert 1995). Since feather mass data were unavailable for wrybill, the averages of the relative masses of each of the 10 primaries of seven species in the closely related genus *Charadrius* were calculated (Table 1). Within the genus *Charadrius* there was little variation in the relative feather masses. Primary moult of adult and second-year wrybills was modelled separately for the two age classes according to the Underhill & Zucchini (1988) moult model with PFMG as the moult index. The parameters of moult (duration, mean start date and standard deviation of mean start date) and their standard errors were estimated using the package "moult" (Erni *et al.* 2013) in R (R Core Team 2019). Because moult score was mainly recorded for birds in active moult, we used data type 3 of the Underhill & Zucchini (1988) moult model, which is the appropriate data type when records are restricted to birds actively moulting. It was estimated that 95% of birds start moult in the period given by the estimated mean start date ± 1.96 × estimated standard deviation parameter.

Two measures were computed to provide insight into the direct and indirect energetic costs of primary moult. Firstly, moult intensity is the average number of simultaneously growing primaries and is a proxy for the energetic costs of feather production (Remisiewicz *et al.* 2009; Jenni & Winkler 2020a). For adult wrybills, the mean number of simultaneously growing primaries and its 95% confidence interval were estimated for each of the 10 primary feathers. Secondly, Proportion Feather Mass Missing (PFMM), provides a measure of the relative size of the wing gap created when primary feathers are being moulted, taking into account the relative mass of the primaries. PFMM helps to quantify the costs associated with a reduction in wing area, as larger wing gaps result in increased flight costs due to decreased flight performance (Jenni & Winkler 2020a, 2020b; Hedenström 2023). PFMM was calculated for each adult bird in active moult using the method described in Remisiewicz *et al.* (2009) and Barshep *et al.* (2013).

The date the bird was netted was recorded as the number of days since 1 August. Terminology around seasons is austral unless otherwise stated. When we compare the timing of breeding and primary moult between species in the southern and northern hemispheres, we make the comparison in terms of days since the midsummer solstice to bring the hemispheres into alignment.

RESULTS

During the sampling period, moult data was recorded for 2410 adult and second-year wrybills captured during ringing operations on the shores of Kaipara Harbour and Firth of Thames. There were 1999 moult records for adult wrybills: 2% (37) had all old primaries, 87% (1737) were actively growing new primaries and 11% (225) had all new primaries (Table 2, Fig. 1). Using data type 3 of the moult model, the primary moult of the average adult bird in the population was estimated to start on 20 January (standard error 1.0 days) and end on 3 April (standard error 1.0 days). The duration was estimated to be 73 days (standard error 1.9

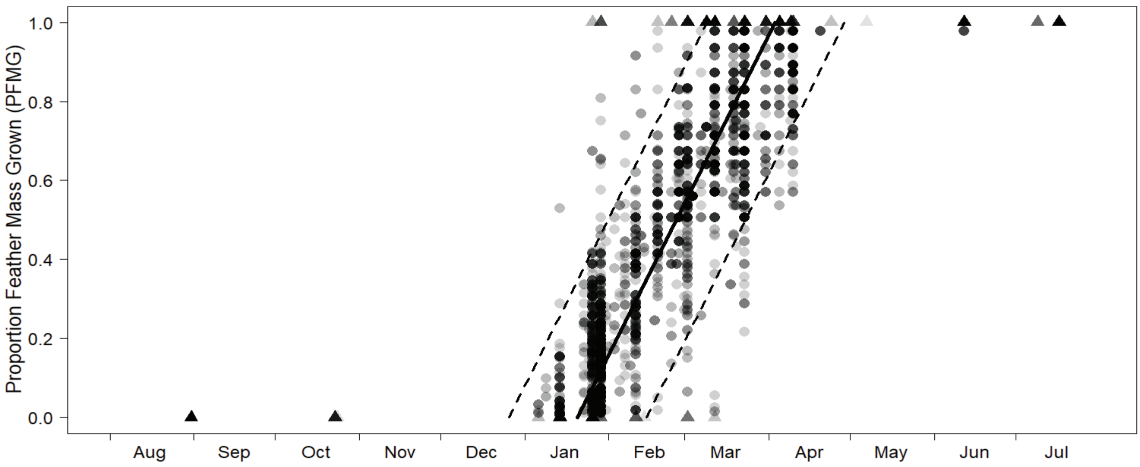

Figure 1. Modified scatter diagram* of PFMG for adult wrybills (*Anarhynchus frontalis*). The solid line links the estimated start date with the estimated end date using PFMG as the moult index and data type 3 of the Underhill-Zucchini moult model. It shows the progression of primary moult for the average adult bird in the population. The dashed lines are the 95% intervals derived from the standard deviation of the mean start date and the parallelogram enclosed by them should contain 95% of adult birds in active moult. The circle data points are the birds in active primary moult which were used to estimate the parameters of the moult model. The triangle data points are pre- and post-moult birds that were not used in the model.

* Moult scores are recorded on a discrete scale (each primary is given an integer score between 0 and 5). A consequence of this is that conventional scatter plots of moult scores in relation to dates can be misleading when points overlap 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 triangles and the intensity of the shading represents the number of records at each point. The lightest shade of the circles and the triangles refers to one data point, the darkest shade of the circles refers to 31 overlapping data points and the darkest shade of the triangles refers to 73 overlapping data points.

days). The standard deviation of the start date was 13 days (Table 2, Fig. 1). Consequently, the period during which 95% of the adult wrybill population started moult was estimated to be 51 days, between 26 December and 15 February (Fig. 1). Likewise, the interval during which 95% of wrybills were expected to complete moult was 9 March to 29 April.

Four adult wrybills (0.2% of adults in active moult) had moult scores that suggested possible suspended moult (scored from the innermost primary to the outermost: 5550000000 on 14 and 26 January, 5555550000 on 29 January and 5555555000 on 2 March). These moult scores all lie within the 95% confidence intervals of the mean moult line in the scatter diagram in Fig. 1. It is also possible that within the natural variation of the number of actively moulting primaries a small proportion of the population could have moult scores such as these and therefore they were included in the analysis. When the four moult records are excluded from the analysis, the estimated duration decreases by 0.1 days, the mean start date increases by 0.1 days and the standard deviation of the start date remains the same. Therefore, including or excluding these four points has no biological impact.

There were 434 moult records for second-year wrybills, of which 57% (247) had all old primaries, 37% (159) were actively moulting their primaries and 6% (28) had all new primaries (Table 2, Fig. 2). Using only the records of active moult in the moult model (data type 3), the duration of primary moult in second-year wrybills was 128 days (standard error 33.6 days) with a mean start date of 18 December (standard error 15.3 days) and an end date of 26 April (standard error 21.3 days). The standard deviation of the start date for second-year wrybills was 39 days (Fig. 2). There were no records of moult in first-year wrybills.

Wrybills underwent a complete, continuous moult starting with the innermost primary (P1) and ending with the outermost (P10). Adult wrybills initially moulted several inner primaries concurrently and then fewer as the longer, heavier outer primaries are grown. During the replacement of the first four primaries (P1 to P4), there was an average of 3.5 feathers growing simultaneously

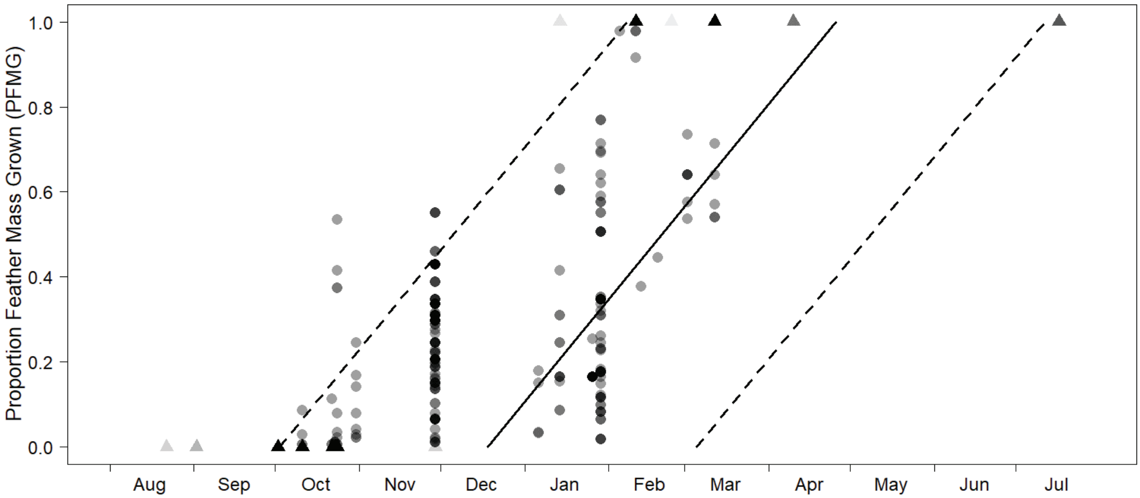

Figure 2. Modified scatter diagram of PFMG for second-year wrybills (*Anarhynchus frontalis*). The straight line links the estimated start date with the estimated end date using PFMG as the moult index and data type 3 of the Underhill-Zucchini moult model. It shows the progression of primary moult for the average second-year bird in the population. The dashed lines are the 95% intervals derived from the standard deviation of the mean start date and the parallelogram enclosed by them should contain 95% of second-year birds in active moult. The circle data points are the birds in active primary moult which were used to estimate the parameters of the moult model. The triangle data points are pre- and post-moult birds that were not used in the model. Intensity of shading from light to dark represents the number of overlapping records at each point: for both circles and triangles the lightest shade represents one data point; the darkest circles represent 7 overlapping data points, while the darkest triangles represent 181 overlapping data points.

(Fig. 3). This decreased to 3.1 and 2.7 for the P5 and P6 respectively and further decreased to an average of 2.1 for P7 to P9 (Fig. 3). There were the fewest concurrently growing primaries, 1.6, during the moult of P10 (Fig. 3). The mean size of the gap in primary feathers during primary moult in adults was 0.126 (SD = 0.056) (Fig. 4). This means that on average birds in active moult were missing 13% of their primary feather mass. The largest wing gap recorded was 0.384 for a bird moulting five of its 10 primary feathers simultaneously (moult formula 5555543122 on 27 February) (Fig. 4). The correlation between PFMG and PFMM in adults was –0.123, so that PFMM explained 1.5% of the variability of PFMG. In other words, the size of the wing gap, measured as PFMM, was independent of the stage of primary moult (Fig. 4). Second-year birds had a mean wing gap size of 0.094 (SD = 0.048).

DISCUSSION

Primary moult of wrybills

Adult wrybills undergo a complete pre-basic post-breeding moult and start moulting their primaries soon after arriving on the North Island. Primary moult occurs on average between 20 January and 3 April. Second-year birds also undergo a complete moult starting in December, one month earlier than the adults, but finishing at approximately the same time. Both adults and second years appear to avoid moulting during the winter months, although these are relatively mild along the coastline of northern North Island.

The estimated mean start and end dates of primary moult in second-year wrybills were 18 December and 26 April respectively, and the estimated duration was 128 days, all with relatively large standard errors (Table 2). The large standard

Table 2. Estimated moult parameters of the primary feather tract of wrybills (*Anarhynchus frontalis*) using data type 3 and PFMG as the moult index. Day 1 was 1 August.

Age class	Duration (SE)	Start day (SE)	Standard deviation of start day (SE)	Start date (SE)	End date (SE)	Sample size of birds in active moult
Adult	72.9 (1.9)	173.4 (1.0)	13.0 (0.3)	20 Jan (1.0)	3 Apr (1.0)	1737
Second-year	128.2 (33.6)	140.4 (15.3)	39.3 (5.8)	18 Dec (15.3)	26 Apr (21.3)	159

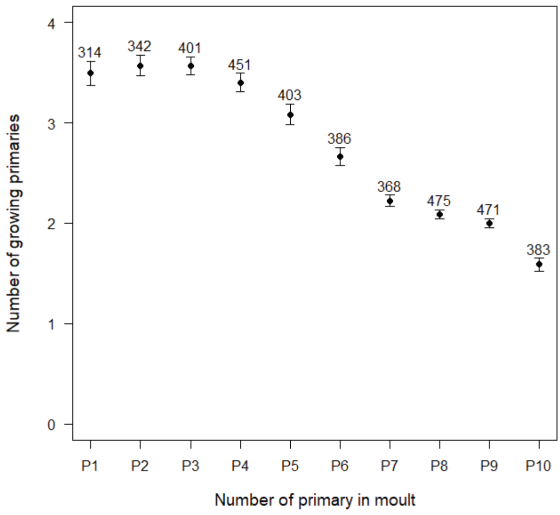

Figure 3. The mean number of primaries growing simultaneously while each of the 10 primaries of adult wrybills (*Anarhynchus frontalis*) was in moult. Sample sizes and the 95% confidence intervals for the mean are shown.

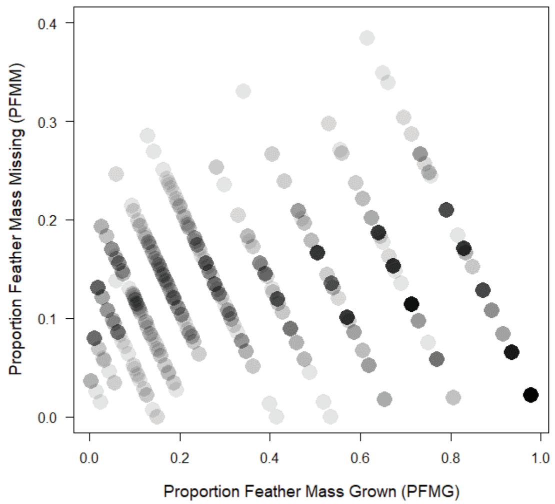

Figure 4. The relationship between Proportion Feather Mass Missing (PFMM) and Proportion Feather Mass Grown (PFMG) for adult wrybills (*Anarhynchus frontalis*) in active moult. The pattern of parallel lines is an artefact of the way in which primary moult scores for each feather are recorded as integers between 0 and 5. The intensity of the shading represents the number of records at each point: the lightest shade represents one data point, and the darkest shade represents 90 overlapping data points.

errors can be attributed to small sample size and the lack of moult records late in the moult period (Fig. 2). This in turn is related to the fact that second-year birds are not easily distinguished from adults once they are moulting their outer primaries (Davies 1997). Because most of the data are focused on the first half of the moult period, the estimated mean starting date of moult in second-year wrybills is likely to be reliable. It is also likely that adults and second-years complete moult around the same time. However, the timing of primary moult of second-year wrybills needs further investigation.

The mean size of the wing gap (0.12), as described by PFMM, during primary moult in adults (Fig. 4) was similar to that recorded for Wood Sandpipers (*Tringa glareola*) (0.10) (Remisiewicz *et al.* 2009). Near the start of moult, adult wrybills moult up to six primaries simultaneously which is similar to wood sandpipers, which moult up to five primaries (Remisiewicz *et al.* 2009). This is followed, in both species, by a reduction in the number of simultaneously growing primaries as moult progresses. Although the number of simultaneously growing primaries in wrybills was larger near the beginning of moult than near the end (Fig. 3), the size of the wing gap decreased only marginally towards the end of moult, as indicated by the small negative correlation between PFMG and PFMM.

Moult of the wrybill in relation to other species

The wrybill belongs in the taxonomic subfamily Charadriinae, which includes most plovers and dotterels, within the family Charadriidae. There are about 67 extant species in this family (Gill *et al.* 2022). A total of 18 studies of primary moult using the Underhill-Zucchini moult analyses have been undertaken on four migratory species in the Charadriidae at a wide array of latitudes: Greater sand plover (*Charadrius leschenaultia*) (five studies), lesser sand plover (*Charadrius mongolus*[1]) (four), grey plover (*Pluvialis squatarola*) (seven) and European golden plover (*Pluvialis apricaria*) (two) (Jackson & Underhill 2022). Greater sand plover, lesser sand plover and grey plover are long-distance migrants, but grey plover is taxonomically distinct from the two *Charadrius* plovers. European golden plover is a short-distance migrant. There is a single study on a resident member of the family, the hooded dotterel (*Thinornis cucullatus*), which inhabits ocean beaches in south-eastern Australia (Rogers *et al.* 2014).

Primary moult is the only activity in the annual cycle for which quantitative estimates are available for these waders (Rogers *et al.* 2014; Yang *et al.* 2020; Jackson & Underhill 2022; Table 2); the timing of breeding is more descriptive in nature, summarised

1 Wei *et al.* (2022) proposed splitting lesser sand plover (*Charadrius mongolus*) into two species: Siberian sand plover (*C. mongolus*) and Tibetan sand plover (*C. atrifrons*). This proposal is currently under discussion (Gill *et al.* 2022).

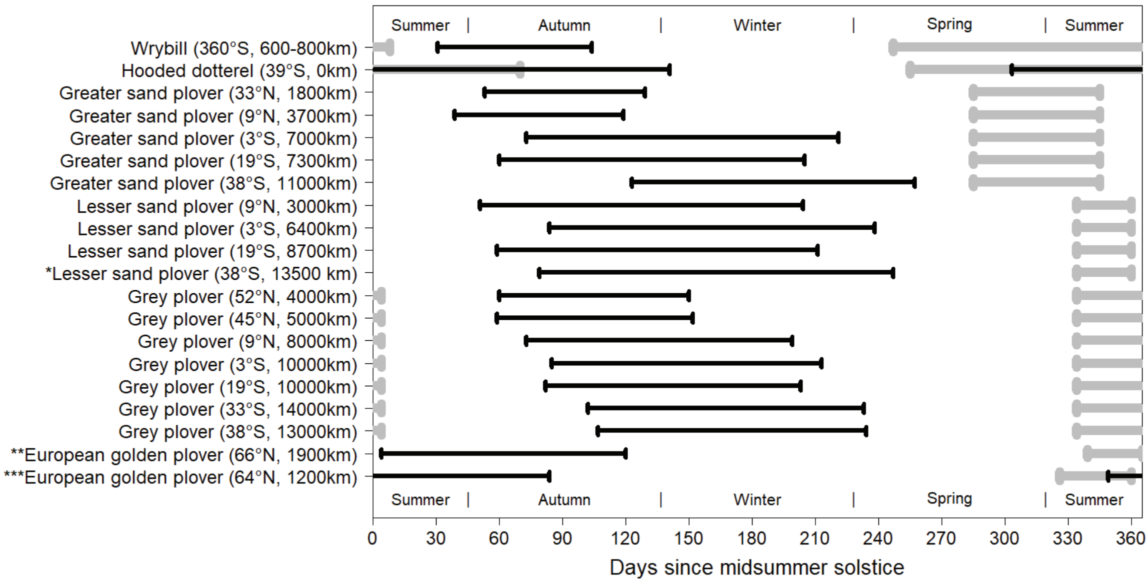

Figure 5. Representation of the relationship between the timing of breeding (grey bars) and the timing of moult (black bars) for 20 studies of six species in the subfamily Charadriinae. The common name is followed by (a) the latitude at which moult took place and (b) the distance between the breeding grounds and the non-breeding grounds. The seasons relate to seasons on the breeding grounds. The timing of breeding is estimated to months using handbooks (Marchant & Higgins 1993, Del Hoyo *et al.* 1996), but the timing of moult was estimated to days using the Underhill-Zucchini moult model (see text). The timing is measured in days since the midsummer solstice of the hemisphere in which the species breeds. None of the species considered breeds in the tropics, so the appropriate midsummer solstice was clearcut.

*Lesser sand plover (38N) estimated primary moult duration was considered unreliable by Jackson (2017).

**Starts primary moult on breeding grounds, then migrates to non-breeding grounds to complete moult.

***Starts and completes primary moult on breeding grounds, then migrates to non-breeding grounds.

by months (Marchant & Higgins 1993; Del Hoyo *et al.* 1996) (Fig. 5). Based on the periods of moult estimated using the Underhill-Zucchini analyses and the described egg-laying periods for each species, four patterns are evident in Fig. 5.

Firstly, wrybill breed in spring/early summer, migrate a short distance north and then undergo a fast primary moult (73 days) in late summer/early autumn. Due to the fast moult, wrybills are able to separate breeding and moult and avoid moulting in winter.

Secondly, the hooded dotterel undergoes a slow primary moult (203 days), so that it is energetically less expensive (Rogers *et al.* 2014). This enables the birds to breed and moult at the same time from spring to autumn and still avoid the winter period (Rogers *et al.* 2014).

Thirdly, greater sand plover, lesser sand plover and grey plover breed over a short period on their northern hemisphere Palearctic breeding grounds in late spring/early-to-midsummer, and then migrate southwards to their wintering grounds, mostly on coastlines of the Indian and Atlantic Oceans, where they moult at variable rates (76–155 days) (Serra & Rusticali 1998; Serra *et al.* 1999; Balachandran *et al.* 2000; Minton & Serra 2001; Pearson *et al.* 2002; Serra *et al.* 2006; Jackson 2017; Yang *et al.* 2020; Jackson & Underhill 2022). Those that migrate a short distance and have northerly non-breeding grounds with harsh winters undertake a rapid primary moult, mainly in autumn, to avoid winter. Those that migrate further south to warmer wintering grounds with more benign climates in the southern hemisphere prolong moult through their non-breeding wintering period which occurs during the austral summer. Following moult, they migrate north back to the breeding grounds. Greater sand plover experiences warmer conditions on their breeding grounds than lesser sand plovers and grey plovers and subsequently have an earlier breeding season. They also arrive in and depart from their breeding and wintering grounds earlier (Jackson 2017; Jackson & Underhill 2022).

Lastly, European golden plover breeds early summer and overlaps primary moult with incubation and the rearing of chicks (Machín *et al.* 2018). Moult and breeding are thought to overlap in this species because food, in the form of arthropods, is abundant through the Arctic summer. There are two populations of European golden plovers, the continental population (66°N) and the Icelandic population (64°N) (Machín *et al.* 2018). The continental population has a shorter breeding season because the weather conditions are more severe. They are only able to moult the first five to seven primaries at the breeding grounds and then they migrate a short distance to stopover and wintering areas, where they complete primary moult in autumn (Machín *et al.* 2015, 2018). The Icelandic population starts primary moult earlier in the season, overlapping incubation and moult to a greater degree. These plovers remain on the breeding grounds until the completion of primary moult (Machín *et al.* 2018).

Wrybills breed in spring through to early summer, whereas plovers breeding in the northern hemisphere (e.g. greater sand plover, lesser sand plover, grey plover) have shorter, more compact breeding seasons in early summer. Wrybill moult in late summer-early autumn, after its short-distance migration, as opposed to autumn through to winter in the northern-breeding plovers, which schedule moult differently in relation to their migration distance (Fig. 5).

There are four other waders in New Zealand that, similar to wrybill, have populations breeding in South Island that migrate to North Island where they spend the non-breeding season. These are the South Island pied oystercatcher | tōrea (*Haematopus finschi*), banded dotterel | pohowera, (*Charadrius bicinctus*), pied stilt | poaka, *Himantopus leucocephalus*) and black stilt | kakī, (*Himantopus novaezelandiae*). However, not all individuals of each species breed on South Island and not all migrate north.

The South Island pied oystercatcher is New Zealand's most abundant resident wader (Riegen & Sagar 2020). It typically breeds inland on the braided rivers and farmland on the South Island, east of the Southern Alps (Sagar 2013). Breeding attempts have occurred in Hawke's Bay and southern Wairarapa in the southern part of North Island since the 1980s (Sagar 2013). Egg-laying starts in early August, peaking in September and October, and comes to an end in December (Marchant & Higgins 1993; Sagar 2013). From late December, the oystercatchers start moving to their non-breeding coastal areas with the majority migrating northwards where they remain until mid-July (Sagar & Geddes 1999; Sagar 2013). While three-quarters of the population occurs on North Island during this time, mainly in the Auckland region, some birds remain on the South Island, but at coastal sites, where they undergo moult (Riegen & Sagar 2020). Complete post-breeding moult in adult oystercatchers takes place from January to May and was estimated to have a duration of 126 days (Marchant & Higgins 1993; T Bate in prep.). Post-breeding moult starts soon after arrival on non-breeding grounds from northward migration. Adult South Island pied oystercatchers begin to return south to their breeding grounds in early June, with peak migration in late July and continuing into early August (Marchant & Higgins 1993). Therefore, they use most of the period on the non-breeding grounds for primary moult. In contrast, wrybills have a relatively short primary moult duration of 73 days (Table 2), finishing in early April, and migrating south to the breeding grounds in August, avoiding moulting in winter.

The banded dotterel is a breeding endemic and common small plover of New Zealand. It breeds mainly on gravel riverbeds in braided rivers on the eastern side of the North and South Islands (Heather & Robertson 2005). Eggs are laid between August and December (Pierce 2013a). Adults undergo a complete post-breeding moult. In contrast to wrybill and South Island pied oystercatcher, adult primary moult occurs in November to February on or near the breeding grounds and is completed before the birds move to wintering grounds (Thomas 1972; Minton 1987; Marchant & Higgins 1993). Body moult is usually completed by February/March (Thomas 1972; Marchant & Higgins 1993). Birds breeding inland on the southern half of South Island migrate to south-eastern mainland Australia and Tasmania in March (Minton 1987; Pierce 1999; Heather & Robertson 2005; Riegen & Sagar 2020). Birds breeding inland north of Canterbury migrate north within New Zealand in February and those breeding inland on the North Island move to the coast in January to February (Pierce 1999; Heather & Robertson 2005). Most coastal breeding birds are sedentary (Pierce 1999; Heather & Robertson 2005). Banded dotterels start returning to breeding grounds on the North Island in July but those that breed in inland South Island and southern South Island only start returning in August to September (Barter & Minton 1987; Heather & Robertson 2005; Pierce 2013a).

The pied stilt is a common wader in New Zealand and usually breeds in colonies on riverbeds, lake shores and damp ground near water (Heather & Robertson 2005; Adams 2013). The breeding season extends from July to January (Heather & Robertson 2005) with egg-laying peaking August to October in lowland areas and October to November inland (Heather & Robertson 2005). After breeding, the stilts which breed on the riverbeds and ephemeral wetlands in southern North Island and South Island move to coastal locations between December and February and those in inland southern South Island migrate northwards to harbours in northern North

Island (Heather & Robertson 2005). Birds breeding in coastal areas on both islands and those breeding in northern North Island do not usually migrate. Adults undergo a complete post-breeding moult which takes place between mid-December and early April. Most individuals are moulting their wing feathers by mid-January with primary feathers being the last feathers to be replaced (Pierce 1982). Pied stilts return to lowland breeding grounds in June to July and inland breeding grounds August to October (Heather & Robertson 2005).

The black stilt was once widespread throughout New Zealand but is now critically endangered. Breeding is confined to the braided rivers and wetlands of the Mackenzie Basin of South Canterbury and North Otago, South Island (Pierce 2013b). Black stilts arrive on the breeding grounds from July to August and eggs are laid from September to December, with a peak in October (Marchant & Higgins 1993; Heather & Robertson 2005; Dowding & Moore 2006; Pierce 2013b). In late January and February, after breeding, most black stilts move locally within the Mackenzie Basin but small numbers move to the Canterbury coast, eastern South Island and some migrate north to Kawhia and Kaipara Harbours, western North Island (Marchant & Higgins 1993; Pierce 1982; Pierce 2013b). As in pied stilts, post-breeding moult in adult Black Stilts is complete and occurs from mid-December to early April. Most birds in the population are undergoing wing moult by mid-January, moulting their primaries last (Pierce 1982).

The moult strategy of second-year wrybills, starting primary moult before the main arrival of adults, is also observed in two Palearctic wader species which migrate to New Zealand, namely second-year red knots (huahou, *Calidris canutus*) and bar-tailed godwits (kuaka, *Limosa lapponica*) (Davies 1997). Similar findings of an earlier moult in second-year birds are reported for shore plovers (tuturuatu, *Thinornis novaeseelandiae*) (Dowding & Kennedy 1993) which are endemic to New Zealand. In red knots and bar-tailed godwits first-year birds do not undertake a return migration to their breeding grounds with the adults but remain on the non-breeding grounds (Heather & Robertson 2005). At this time, they are then approximately nine months of age and become second-year birds during this period. They then commence moult before the adults return on migration (Heather & Robertson 2005). Shore plovers are slightly different in that they are sedentary, but also do not breed until they are two years old (Dowding & Kennedy 1993). This means that birds in their second year of life are able to start moult earlier than the adults. Second-year birds of all these species moult more slowly than the adults, so that they finish at the same time as the adults. In this way, the moult strategy of young birds merges into that of adults.

Suggestions for further research

This is the first quantitative moult study of a migratory wader which breeds in the southern hemisphere and migrates northwards within the same hemisphere after breeding. Notable features are that wrybill breeding habitat becomes uninhabitable after the breeding season, and that wrybill migrate a relatively short distance, spending the non-breeding season in winter conditions. There is potential for several comparisons: (1) with the other waders breeding in the braided rivers of New Zealand; (2) with waders in southern South America, which migrate northwards after breeding (such as the Magellanic Oystercatcher); and (3) with populations of some short-distance migratory waders in the northern hemisphere, such as the population of purple sandpipers *Calidris maritima* that migrates from Norway to Scotland (Summers *et al.* 2004).

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