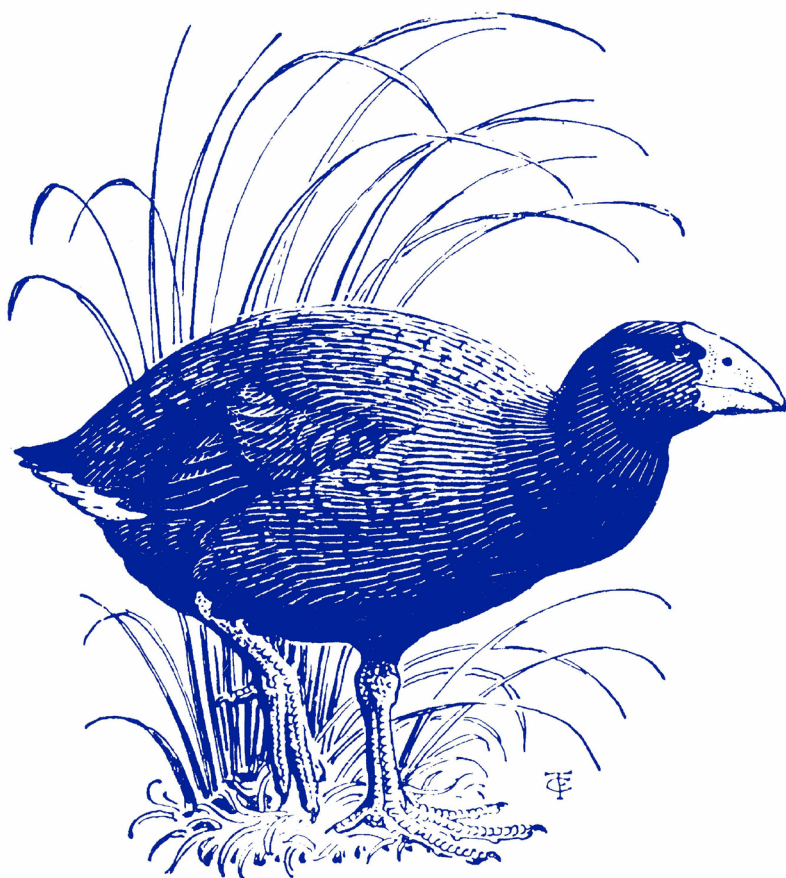


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Using egg floatation to estimate the age and hatching dates of South Island pied oystercatcher (*Haematopus finschi*) eggs

NIKKI J. MCARTHUR*

17A Ida Street, Redwoodtown, Blenheim 7201, New Zealand

SAMANTHA K. KROUSE

Department of Conservation, 161 Cashel Street, Christchurch 8011, New Zealand

DAVID THOMAS

64 Horrell Road, RD 4, Morrinsville 3374, New Zealand

HOLLY THOMPSON

18A Ripon St, Lyttelton 8082, New Zealand

DAVID S. MELVILLE

1261 Dovedale Road, RD 2 Wakefield, Nelson 7096, New Zealand

EMMA M. WILLIAMS

Department of Conservation, 161 Cashel Street, Christchurch 8011, New Zealand

SUSAN WALKER

ANN-KATHRIN V. SCHLESSELMANN

Manaaki Whenua Landcare Research, 764 Cumberland Street, Dunedin 9016, New Zealand

Abstract: Egg floatation is a technique which can be used to estimate egg age and hatching dates of New Zealand shorebird eggs. It can be used to improve the accuracy of nest survival models, help identify nest outcomes, assist with chick survival monitoring and to prioritise the capture of incubating birds. We used egg floatation to estimate the age and hatching dates of South Island pied oystercatcher (*Haematopus finschi*) (SIPO) eggs. We developed regression equations to estimate the age of SIPO eggs by modelling egg angle and egg float height against egg age using a sample of eggs with known hatch dates. For early incubation eggs, we used linear regression to model the relationship between egg age and egg angle only, whereas for late incubation eggs we used multiple regression to model the relationship between egg age and both egg angle and egg float height data. These equations allowed 90% of SIPO eggs to be aged to within five days of their actual age. We recommend that species-specific regression equations describing the relationship between egg float characteristics and egg age be developed for other New Zealand shorebird species, to aid future research, monitoring and conservation management actions on these species.

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*Correspondence: nikki.mcarthur.101@gmail.com

INTRODUCTION

Populations of many of New Zealand's endemic shorebird species are in decline, with the majority of these species assessed as being either Nationally Threatened or At Risk under the New Zealand Threat Classification System (Riegen & Sagar 2020; Walker *et al.* 2020; Robertson *et al.* 2021). In recent decades, significant resources have been invested in research to determine the underlying causes of these population declines, and a number of causal factors have been identified (O'Donnell *et al.* 2016). These include depredation by introduced mammalian and native avian predators (Sanders & Maloney 2002; Steffens *et al.* 2012; Cruz *et al.* 2013; Norbury *et al.* 2021), habitat loss and degradation caused by invasive weeds, water abstraction, flood mitigation activities, land use changes and human-induced climate change (Maloney *et al.* 1999; Robertson & Heather 1999; Norbury & Heyward 2008; McGlone & Walker 2011; O'Donnell & Hoare 2011), and disturbance caused by human activities, such as the recreational use of coastal and riverine habitats (Kearvell 2011). Substantial efforts are now underway throughout New Zealand to reduce these threats to local shorebird populations. For example, mammalian predators are now managed at many coastal and riverine sites throughout the country, with the scale of control varying from sites as small as a few hectares to many tens of thousands of hectares (e.g. Cruz *et al.* 2013; Gale *et al.* 2020; McArthur *et al.* 2021; Schlesselmann 2021).

Many shorebird research and management projects involve monitoring shorebird nest survival and identifying the causes of nest failures, to investigate population dynamics and quantify the efficacy of conservation management actions (e.g. Wills *et al.* 2003; Schlesselmann *et al.* 2018; Norbury *et al.* 2021). Shorebird nests are often found after the full clutch of eggs has been laid and incubation has commenced, so in many cases nest initiation dates are not known, making it difficult to estimate egg age and hatching dates. Shorebird chicks are highly precocial, typically leaving the nest within hours or days of hatching (Marchant & Higgins 1993), making it challenging to intercept chicks in the nest to confirm nest outcomes or monitor subsequent chick survival. Having the ability to predict the hatching dates of eggs is therefore useful, as it improves the accuracy of nest survival estimates by reducing the risk of misassigning the outcome of a nest (Ellis *et al.* 2018) or giving a nest credit for surviving for more exposure days than it actually did (Johnson *et al.* 2007). Accurate estimates of egg age are also critical for assessing temporal variation in nest survival rates, and for modelling nest survival as a function of time-specific covariates (Dinsmore *et al.* 2002). Accurate estimates of egg age can also assist with monitoring chick survival and to prioritise the

capture and banding of incubating parents; e.g. to maximise the number of adults caught for banding during a given breeding season.

Egg candling is routinely used to estimate egg age and monitor the embryonic development in a number of New Zealand bird species under conservation management, including kiwi (*Apteryx* spp.), kākāpō (*Strigops habroptilus*), takahē (*Porphyrio hochstetteri*) and kakī (*Himantopus novaezelandiae*) (Jamieson & Ryan 2000; van Heezik *et al.* 2005; Bassett 2012; Savage *et al.* 2022). Egg candling involves holding a strong light against the eggshell in a darkened environment so that the internal structures within the egg, including the morphology of the developing embryo, can be viewed through the shell (Bassett 2012). Much of this work tends to be done in the controlled environment of a captive rearing facility or at night (e.g. van Heezik *et al.* 2005; Bassett 2012) and tends to work best for species that have pale eggshells through which it is comparatively easy to see the developing embryo. In contrast, it can be a challenge to create 'darkroom' conditions when monitoring shorebird eggs in the field, and this combined with the dark pigmentation of the eggshells of many of New Zealand's shorebird species can make it difficult to discern details of embryonic development when attempting to candle eggs in the field. As a result, egg candling is seldom used as a field method for aging shorebird eggs in New Zealand, and in the absence of a reliable alternative, some previous New Zealand shorebird nest survival studies have relied on the presence, size and shape of eggshell fragments and other types of 'field sign' in nests to assign nest outcomes and identify nest predators (e.g., Norbury & Heyward 2007). However, this method is prone to error, with the degree of error varying according to the outcome of the nest or the species of predator involved (Ellis *et al.* 2006). The inaccuracy of this method may in part be because parent birds will often remove eggshell fragments from their nests following both hatching and depredation events (Mabee *et al.* 2006; Ellis *et al.* 2018).

In the northern hemisphere, egg floatation is regularly used to age eggs of shorebirds and gamebirds (e.g. Mabee *et al.* 2006; Liebezeit *et al.* 2007; McNew *et al.* 2009). Egg floatation relies on the fact that as an embryo develops, the specific gravity of the egg changes from being greater than, to less than that of water due to the air cell at the blunt end of the egg growing progressively larger as incubation proceeds. A newly laid egg will therefore sink to the bottom of a column of water with the long axis of the egg close to horizontal, but as the embryo develops, an egg will progressively tilt upwards until the long axis of the egg is vertical and will then rise through the water column until

the blunt end of the egg emerges above the water surface (Fig. 1). Estimating egg age using floatation involves measuring both the angle and the height at which known-age eggs are floating in the water column throughout incubation, to describe the relationship between these float characteristics and egg age, which can then be used to estimate the age of eggs with unknown laying dates.

We are not aware of egg floatation having previously been used as a technique to estimate egg age or hatching dates of shorebird eggs in New Zealand. Here, we present a case study describing the development of two regression models that can be used to estimate egg age and hatching dates of South Island pied oystercatcher (*Haematopus finschi*) eggs.

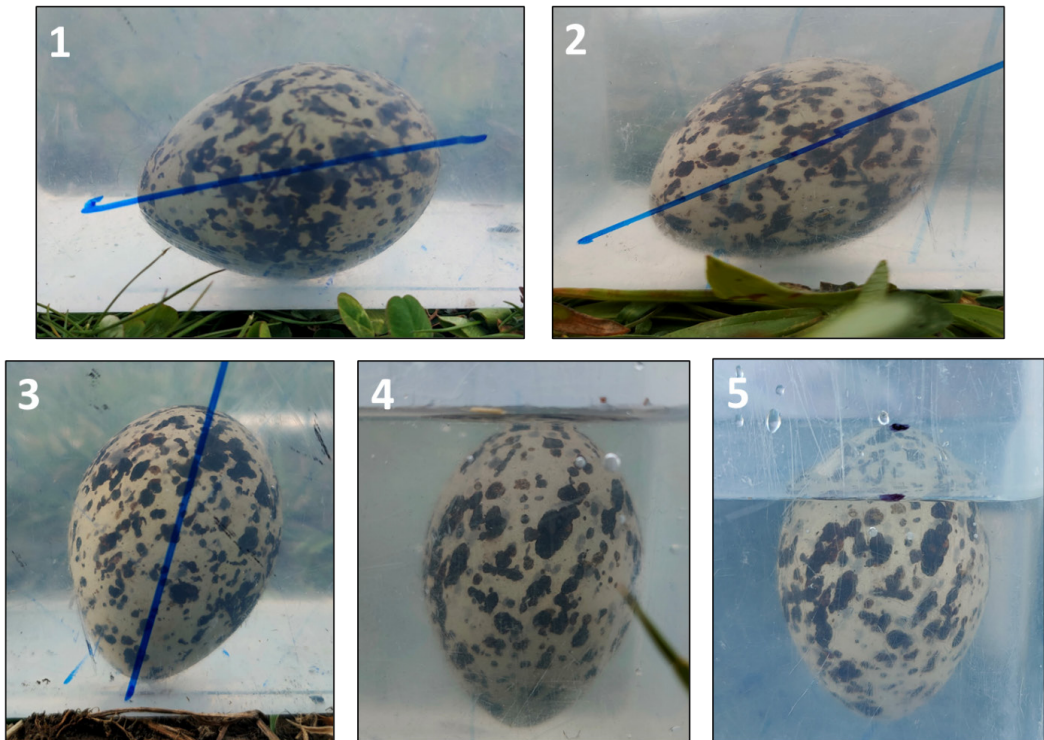


Figure 1: Changes in the floatation characteristics of South Island pied oystercatcher eggs as incubation progresses. 1: (25-28 days until hatching) eggs sink to bottom of the water column and rest at an angle of <30 degrees. 2: (21-25 days until hatching) eggs sink to the bottom of the water column and rest at an angle of 31-45 degrees. 3: (15-21 days until hatching) eggs sink to the bottom of the water column and rest at an angle of 46-90 degrees. 4: (12-15 days until hatching) eggs rise to the surface of the water column and are suspended at an angle of ~90 degrees. 5: (12-0 days until hatching) eggs emerge above the surface of the water and are suspended at an angle of ~90 degrees.

MATERIALS AND METHODS

Study species

The South Island pied oystercatcher (SIPO) is the most numerous and widespread of three oystercatcher species that occur in New Zealand. SIPO breed on rivers, farmland and in subalpine grasslands throughout the South Island and in Hawke's Bay in the North Island. SIPO breed between September and December each year and migrate to coastal sites throughout the North and South Islands during the non-breeding season (Marchant & Higgins 1993). SIPO typically lay clutches of 2-3 eggs (mean = 2.33)

(Marchant & Higgins 1993) and incubate their eggs for 28 days (Baker 1969; Sagar *et al.* 2000).

Field methods

We collected egg float data from SIPO nests situated in the upper Rangitata Valley (43°37'40"S 170°55'21"E) in the South Island of New Zealand during two breeding seasons from September - December in 2021 and 2022. Approximately half of these nests were located on unvegetated or sparsely vegetated gravels in the bed of the Rangitata River and the other half were located on adjacent

farmland in short grass, lucerne (*Medicago sativa*) or on unvegetated bare ground that had recently been used for winter cropping. Nests were located by fieldworkers systematically and repeatedly traversing the study area, using binoculars or spotting scopes to spot adult birds sitting on their nests, or to watch birds that had already flushed from their nests return to resume incubation. The location of each nest was recorded using a handheld GPS device and a motion-activated digital trail camera (Reconyx Hyperfire; Reconyx Inc. Holmen, Wisconsin) was deployed at each nest to record nest outcomes. Trail cameras were placed on the ground 1-2 metres from each nest and fixed in place using either two short wooden stakes (at farmland nests) or by constructing a small stone cairn around the camera (at riverbed nests). Each camera was equipped with either a 16 or 32 GB SD memory card and was programmed to record 10 seconds of video footage whenever triggered by movement at the nest, with a minimum 'stand down' period of 30 seconds between each motion-triggering event. Nests were revisited every 1-4 days to check their status, to float eggs, and to service the camera and retrieve camera footage.

During each nest check the number of eggs present in the nest was recorded and each egg was individually marked by inscribing roman numerals on the blunt end of the egg using either pencil or a fine-tipped permanent marker. Egg float data were collected from each egg present in the nest on the day the nest was found, and during a sample of the subsequent nest checks, however eggs with cracked shells, or those that were pipping were not floated. Eggs were not floated during every subsequent nest check due to either logistical or animal welfare constraints (for example, eggs were not floated on the same day that attempts were made to catch and band either of the incubating birds, to minimise stress and disturbance). Egg float data were collected by immersing each egg in approximately 1 L of lukewarm water (carried into the field using a thermos) in a 1.5 L transparent, square-sided plastic container placed on level ground. Egg angle was measured by tracing the long axis of the egg onto the side of the container using a ruler and marker pen, then measuring the angle (to the nearest whole degree) between the horizontal plane of the water and the ruled line using a protractor. Egg float height was recorded as "NA" for submerged eggs or was measured to the nearest 0.1 mm for eggs floating at, or emerging above, the surface of the water. Float height measurements for floating or emergent eggs were recorded by tracing parallel lines marking both the water surface and the uppermost tip of the floating egg onto the side of the container using a marker pen, then using digital callipers to measure the distance between the two parallel lines. Care

was taken to ensure that the water column was still and undisturbed while these measurements were being taken. Each nest check, including floating the eggs and servicing the trail camera took around 5 minutes to complete.

Egg float data was collected by three different observers (NJM, DT and HT) over a three month period each season. To ensure that these observers were measuring egg float characteristics consistently, all three observers participated in a training exercise at the beginning of each season, and frequently worked together to collect egg float data throughout the season, providing many opportunities to double-check each other's methods and measurements as the season progressed.

For each nest that successfully hatched at least one chick, the hatching date was defined as the earliest date on which a newly hatched chick was observed either in or very close (< 1 metre) to the nest. Most hatching dates were determined by reviewing trail camera footage recorded at the nests, but a minority of hatching dates were determined by direct observation during nest re-checks that happened to be carried out on the day that the first egg in a clutch hatched.

Data analysis

To examine the relationship between our egg float data and egg age we analysed data from eggs with known hatch dates only. We excluded egg float data collected from any nests that failed to hatch any chicks, or from eggs that subsequently disappeared from nests during incubation. Daily nest survival rates and resultant overall nest survival estimates were calculated following Shaffer (2004). We defined egg age as the number of days until hatching and assumed an incubation period of 28 days (Baker 1969; Sagar *et al.* 2000). We defined the first day of incubation as the date on which the last egg in each clutch was laid. This date was not known for the majority of nests we monitored, so we estimated egg age at the time each egg was floated by back-calculating egg age from the date the egg hatched. All eggs in the nest were typically floated during each nest check, so we used the mean egg angle and mean egg float height for the clutch during each nest check as our sample unit.

All analyses were carried out using the R statistical computing environment (v3.6.1; R Core Team, 2019). We fitted regression models to the egg float dataset we collected during the 2021 breeding season to develop equations to estimate egg age and thus predict the day that eggs would hatch, following the approach described in Liebezeit *et al.* (2007). We analysed the data for early incubation (i.e. submerged eggs, 15-28 days from hatching) and late incubation (i.e. floating eggs, 0-15 days from hatching) eggs separately. When some eggs in a

clutch sank and others floated, we categorised the nest as being in late incubation. Because we were interested in predicting hatch dates, we treated egg age as the dependent variable and egg float characteristics as the independent or predictor variables so that the resulting regression parameters had standard errors describing variance in egg age rather than egg float characteristics.

For early incubation eggs, we used linear regression with untransformed egg angles to examine the relationship between egg age and egg angle, after checking that a linear relationship existed between these two variables during the early incubation stage. For late incubation eggs, we used multiple linear regression with untransformed egg float height and egg angle measurements to examine the relationship between egg age and the two predictor variables after checking that a linear relationship existed between egg age and each of the two predictor variables during late incubation. We also used the *corrplot* R package (v0.91; Wei & Simko 2021) to check that there was minimal multicollinearity between the two predictor variables.

For both regression analyses, we identified and removed data points that had a disproportionately large influence on the results, as our aim was to maximise the predictive value of the regression equations rather than use them for exploratory analysis. We used the *olsrr* R package (v0.5.3; Hebbali 2020) to create Cook's distance plots that we used to identify any influential data points which we then removed before re-running the model. We continued re-running each regression until no further influential data points were identified.

To estimate the predictive accuracy of our regression equations we generated the predicted egg age for each of the SIPO nests that we found during the 2022 breeding season by inserting the egg angle and egg float height data into the appropriate (early or late incubation) regression equation. We then subtracted the actual egg age from the predicted egg age for each nest on a given day and used these individual estimates of bias to calculate the mean deviation $\pm$ SE as a descriptive statistic for this bias. This value reflects the amount of uncertainty (i.e. both under- and overestimation) in the predicted egg ages generated using these regression equations. We also calculated the 90th percentiles of this mean deviation to gauge the accuracy of our sample data in estimating egg age. If our sample data are representative of the population, then this method can age 90% of SIPO eggs with error less than or equal to our regression model predictions.

RESULTS

Clutch size, hatching success and causes of nest failure

In 2021 and 2022, of 124 nests monitored, 17% contained one egg, 66% two eggs, and 17% three eggs, with a mean clutch size of 2.0 ± 0.23 (se). The daily nest survival rate was 0.979 (95% CI: 0.972; 0.984), which resulted in overall nest survival across the 28-day incubation period of 0.56 (95% CI: 0.45; 0.64). Of 67 nests that failed to hatch any chicks, 39% failed due to observed depredation or disturbance by introduced mammals or avian predators, 6% were abandoned, 4% were flooded, 4% due to eggs failing to hatch and 3% were destroyed during farming activities (stock trampling or being crushed by machinery). For 43% of monitored nests the reasons for failure were uncertain due to no trail camera operating at the time of nest failure.

Early incubation

We used 48 mean egg float measurements collected from 28 SIPO nests monitored during the 2021 breeding season to model the relationship between egg float characteristics and egg age during early incubation (Fig. 2). Our Cook's distance plots identified six egg float measurements that had a disproportionately large influence on the relationship between egg age and egg float characteristics during early incubation, so we removed these from our analysis leaving us with a final sample of 42 mean egg float measurements from 27 SIPO nests. The coefficient of determination (R^2) of our linear regression model was 0.8429, indicating that this model explained 84% of the variation in days until hatching. According to this model, the number of days until hatching for early incubation nests can be predicted by the following equation:

$$\text{No. of days until hatching} = 30.38 + (-0.12 \times \text{Mean egg angle of clutch})$$

We used 84 mean float measurements collected from 32 SIPO nests monitored during the 2022 breeding season to test the predictive accuracy of our early incubation regression equation. This regression equation had a mean deviation of 2.6 days (± 0.20 se) and a 90th percentile of the predicted error of 4.9 days. Assuming this sample of SIPO egg float characteristics is representative of the population, researchers can expect 90% of their early incubation eggs to be aged within ≤ 4.9 days of true egg age when using this regression equation.

Late incubation

We used 67 mean egg float measurements collected from 36 SIPO nests to model the relationship

between egg float characteristics and egg age during late incubation (Fig. 2). Our Cook’s distance plots identified eight egg float measurements that had a disproportionately large influence on the relationship between egg age and egg float characteristics during late incubation, so we removed these from our analysis leaving us with a final sample of 59 mean egg float measurements from 36 SIPO nests. The coefficient of determination (R^2) of our multiple linear regression model was 0.5383, indicating that this model explained 54% of the variation in days until hatching. According to this model, the number of days until hatching for late incubation nests can be predicted by the following equation:

No.days until hatching
=260.49 + (-2.74 × Mean egg angle of clutch)
+(- 1.13 × Mean egg float height of clutch)

We used 85 mean float measurements collected from 37 SIPO nests monitored during the 2022 breeding season to test the predictive accuracy of our late incubation regression equation. This regression equation had a mean deviation of 2.5 days ($\pm$ 0.22 *se*) and a 90th percentile of predicted error of 5.0 days. Assuming this sample of SIPO egg float characteristics is representative of the population, researchers can expect 90% of their late incubation eggs to be aged within $\leq$ 5.0 days of true egg age when using this regression equation.

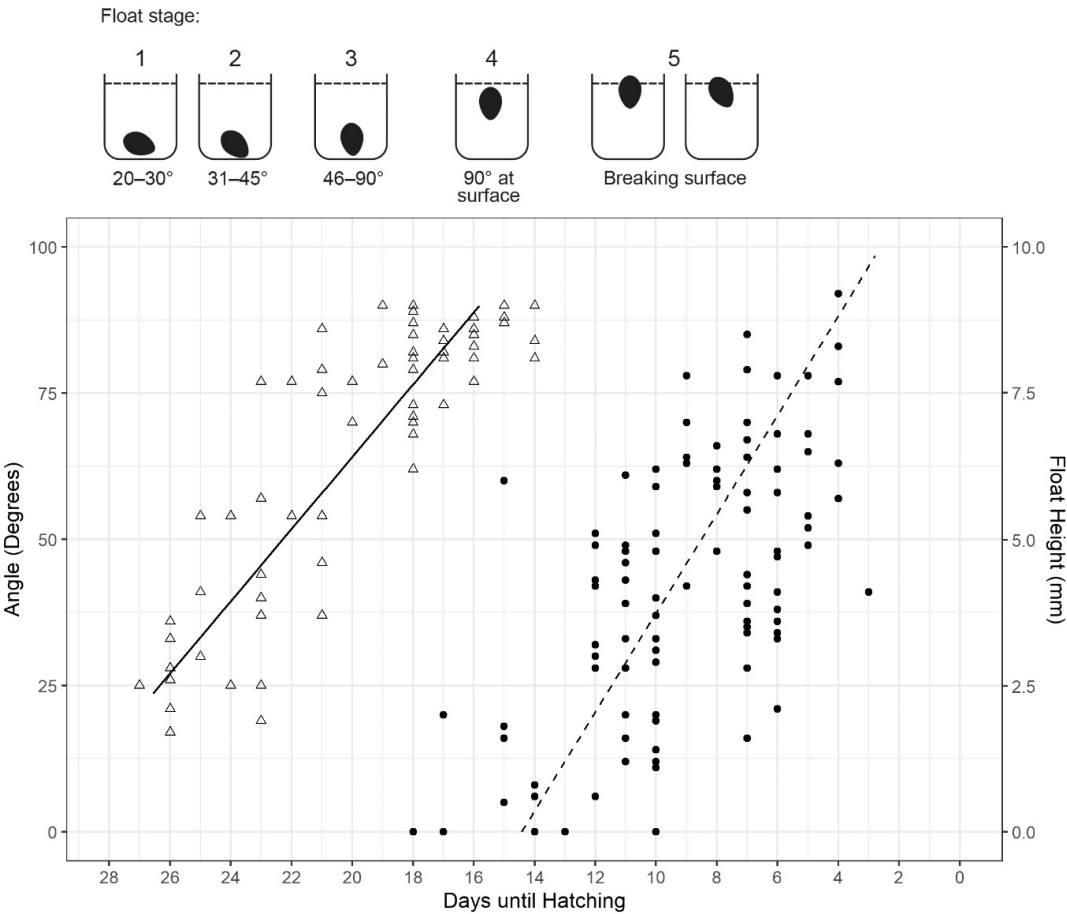


Figure 2. Early incubation (solid line) and late incubation (dashed line) regressions using egg angle data collected from South Island pied oystercatcher (SIPO) nests during early incubation (triangles, n=42) and egg float height data collected from SIPO nests during late incubation (circles, n=59). For late incubation nests we illustrate only the relationship between egg age and egg float height (i.e. egg angle is not plotted), however both parameters were used to generate the regression equation for late incubation nests presented in the results. In this graph we have also placed egg age on the x-axis for ease of display; the regression equations were calculated with egg age as the dependent variable.

DISCUSSION

Using egg angle and egg float height data collected from SIPO nests we have created regression equations that have allowed us to estimate the age of SIPO eggs found at any stage of incubation. Egg floatation has previously been used to estimate the laying and hatching dates for Eurasian oystercatchers (*Haematopus ostralegus*) (Bobeková 2022; Mendez *et al.* 2022), black oystercatchers (*H. bachmani*) (Morse *et al.* 2006; Spiegel 2008) and American oystercatchers (*H. palliatus*) (Vega-Ruiz 2021); however the regression equations presented in this paper appear to represent the first such equations that have been published for any oystercatcher species, or for a New Zealand shorebird species.

These regression equations provide a reasonable level of predictive power: for 90% of eggs the accuracy of egg age estimates was ≤ 4.9 days during early incubation and ≤ 5.0 days during late incubation. Egg angle data collected from early incubation eggs provided slightly more accurate predictions than egg angle and float height data collected from late incubation eggs. The difference in accuracy between early and late incubation eggs may be because egg angles progress rapidly through a relatively wide range of values during early incubation ($\sim 20^\circ$ to 90°), whereas egg float heights progress more gradually through a narrower range of values (0 mm to ~ 10 mm) during late incubation (Mabee *et al.* 2006). Liebezeit *et al.* (2007) suggest that accurate float data may be easier to obtain from early incubation eggs because they are resting on the bottom of the float container, leading to higher predictive accuracy for early incubation nests. We did not notice any appreciable difference in the ease with which we were able to collect egg angle and float height data from early and late incubation SIPO eggs. We found that care had to be taken with early incubation eggs to ensure that they did not pivot in the water column when egg angles were being taken, as the pointed end of the egg sometimes acted as a fulcrum around which the egg would turn if the float container was disturbed. A similar degree of care was also required with late incubation eggs to prevent them from drifting horizontally in the water column when egg float height was being measured.

Egg floatation provides a low-impact and low-risk method for ageing SIPO eggs in the field. The collection of egg float data takes a matter of minutes and can be easily combined with other scheduled nest-check tasks such as checking nest contents, measuring egg dimensions and servicing trail cameras, without greatly increasing the amount of time that incubating birds are kept off their nests. Alberico (1995) found no difference in the hatching success of floated vs non-floated eggs of American avocets (*Recurvirostra americana*) and black-necked stilts (*Himantopus mexicanus*), and Hansen *et al.*

(2011) showed that egg floatation did not impact the hatching success of the eggs of four Arctic shorebird species. Because we floated the majority of SIPO eggs monitored in this study, we were unable to compare the hatching success of floated vs non-floated eggs. However, the overall nest survival rate (survival to hatching) of 0.56 recorded during this study falls within the range of SIPO nest survival rates reported by other researchers who had not used egg floatation to age eggs. For example, Hughey (1985) reported overall SIPO nest survival rates of 0.50 – 0.67 ($n = 13$) and Norbury *et al.* (2021) reported nest survival rates of 0.36 – 0.61 ($n = 36$). This suggests that using egg floatation to age SIPO eggs is unlikely to increase the risk of subsequent nest failure.

Due to morphological, physiological and behavioural differences between individual shorebird species, the accuracy of egg age estimates can be maximised by developing species-specific regression equations, rather than by using generalised equations generated from egg floatation data pooled from multiple species (Mabee *et al.* 2006; Liebezeit *et al.* 2007). For this reason, the utility of the regression equations presented herein will be restricted to ageing the eggs of SIPO, and we recommend that similar species-specific regression equations be developed using egg angle and egg float height data collected from other New Zealand shorebird species. To maximise the accuracy of other species-specific regression equations and the egg age estimates generated, we recommend that researchers and conservation managers collect egg angle and egg float height measurements from eggs when a nest is initially found, as this increases the chance of floating eggs during early incubation when egg age estimates are usually more accurate. We also recommend that eggs from the same nest be floated on multiple occasions to corroborate measurements taken during initial measurement and to aid the identification of misleading data collected from eggs that are either infertile, have suffered embryonic death partway through incubation or have been abandoned (Ackerman & Eagles-Smith 2010). When using egg floatation data to predict hatching dates, we recommend that fieldworkers calculate the 90th percentile of the predicted error of their regression equation, subtract this value from the predicted hatch date and begin checking nests daily from this calculated date to confirm hatching in nests for which the predicted hatch date has been overestimated.

In summary, we demonstrate that it is feasible to use the egg floatation method to estimate egg age and hatching dates for a New Zealand shorebird species with a level of accuracy similar to those observed in northern hemisphere shorebird species, (e.g., van Paasen *et al.* 1984; Mabee *et al.* 2006; Liebezeit *et al.* 2007). This field method can potentially be used

to improve the accuracy of shorebird nest survival and nest outcome data, aid in the interception of chicks in the nest for chick survival monitoring and allow more efficient prioritisation of the capture and banding of incubating adults. Thus, by acting as a rapid, easy and low-impact field method for estimating egg age and hatching dates, egg floatation has the potential to improve shorebird research and conservation management outcomes in New Zealand.

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

TANYA SCOTT*

Department of Biological Sciences, University of Cape Town, Rondebosch 7701, South Africa

ADRIAN C. RIEGEN

231 Forest Hill Road, Waiatarua, Auckland 8, New Zealand

LES G. UNDERHILL

Biodiversity and Development Institute, 25 Old Farm Road, Rondebosch 7700, South Africa
Department of Biological Sciences, University of Cape Town, Rondebosch 7701, South Africa

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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*Correspondence: tanyascott.za@gmail.com

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. tricolor* (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 $\pm 1.96 \times$ 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

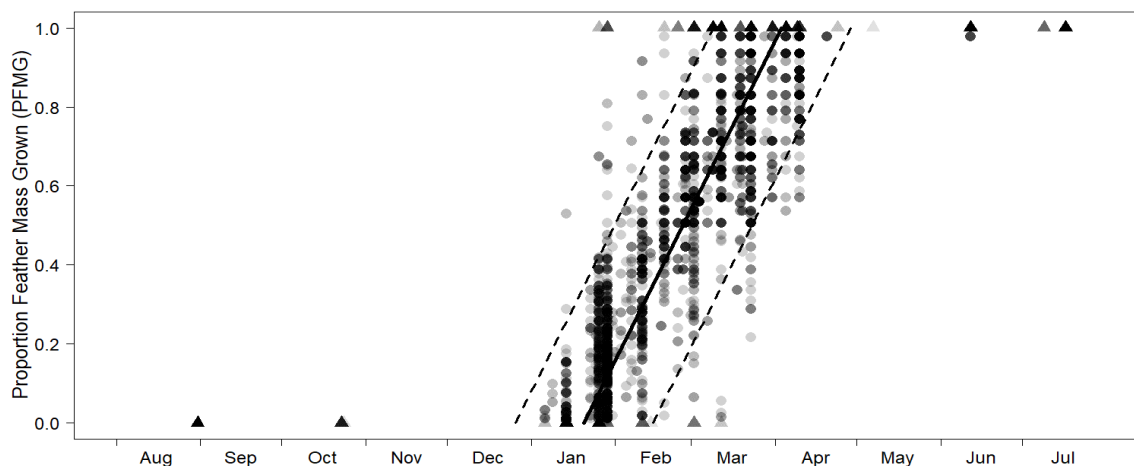


Figure 1. Modified scatter diagram* of PFMG for adult wrybills (*Anarhynchus frontalis*). The solid line links the estimated start date with the estimated end date using PFMG as the moult index and data type 3 of the Underhill-Zucchini moult model. It shows the progression of primary moult for the average 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.

* Molt 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 molt 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 5555550000 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

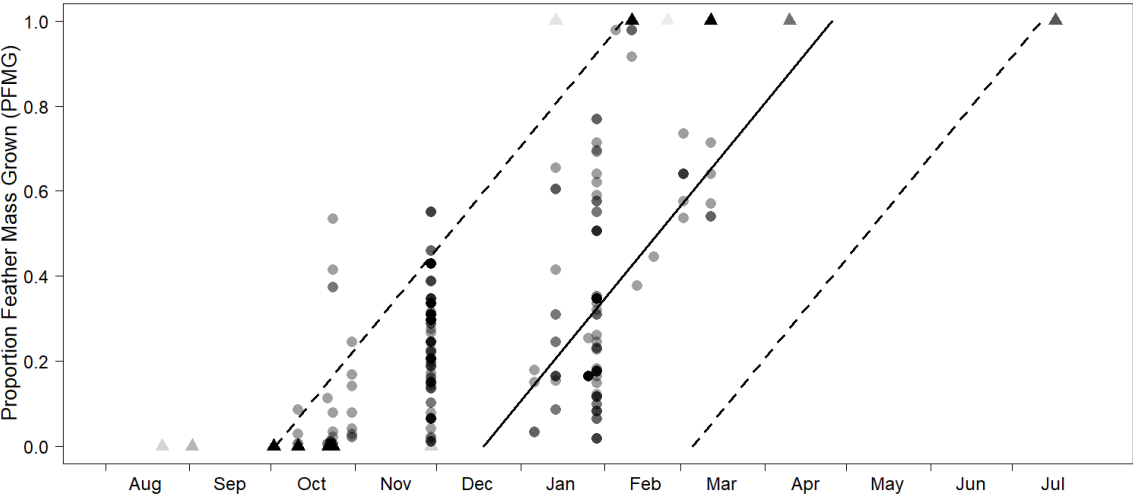


Figure 2. Modified scatter diagram of PFMG for second-year wrybills (*Anarhynchus frontalis*). The straight line links the estimated start date with the estimated end date using PFMG as the moult index and data type 3 of the Underhill-Zucchini moult model. It shows the progression of primary moult for 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

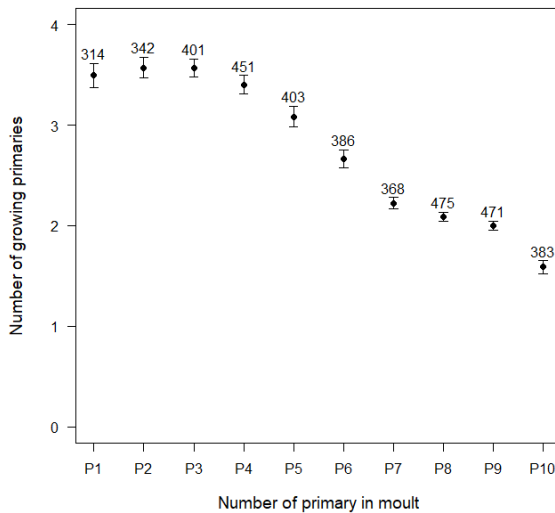


Figure 3. The mean number of primaries growing simultaneously while each of the 10 primaries of adult wrybills (*Anarhynchus frontalis*) was in moult. Sample sizes and the 95% confidence intervals for the mean are shown.

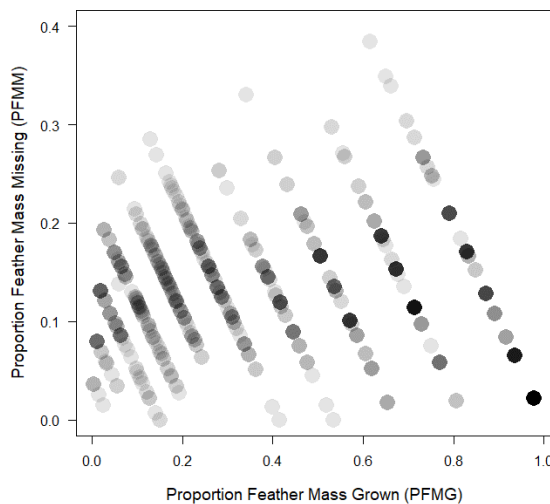


Figure 4. The relationship between Proportion Feather Mass Missing (PFMM) and Proportion Feather Mass Grown (PFMG) for adult wrybills (*Anarhynchus frontalis*) in active moult. The pattern of parallel lines is an artefact of the way in which primary moult scores for each feather are recorded as integers 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).

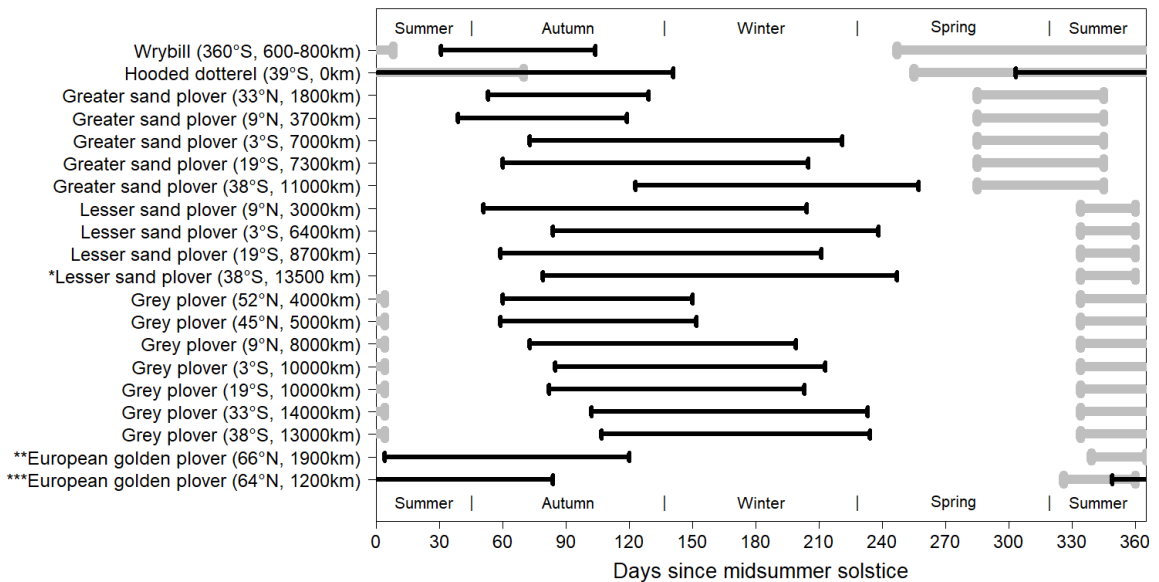


Figure 5. Representation of the relationship between the timing of breeding (grey bars) and the timing of moult (black bars) for 20 studies of six species in the subfamily Charadriinae. The common name is followed by (a) the latitude at which moult took place and (b) the distance between the breeding 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). Moulting 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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SHORT NOTE

When one pair is enough: determining the incubation period for tākoketai | black petrels (*Procellaria parkinsoni*)

ELIZABETH BELL
PO Box 607, Blenheim 7240

The incubation period for black petrels | tākoketai (*Procellaria parkinsoni*) has long been accepted as c. 57 days following research by Dr Mike Imber on Te Hauturu-o-Toi | Little Barrier Island and Great Barrier Island | Aotea, Hauraki Gulf | Tīkapa Moana between 1971 and 1983 (Imber 1987, Heather & Robertson 2005, Marchant & Higgins 1990). This incubation period was determined from only a single breeding pair on Te Hauturu-o-Toi – “the only incubation period I timed was 56.5 days” (Imber 1987, p27) – and may not be representative of the species as a whole.

The population of black petrels on Great Barrier Island has been monitored since 1995 (Bell et al. 2023) and over this period, data have been collected on the incubation period. Egg-laying and hatching dates from 110 breeding pairs recorded between 2001 and 2017 were used to determine the incubation period for black petrels: 42 to 71 days (mean ± SEM = 56.5 ± 0.4 days) (Table 1, Figure 1).

Table 1. Incubation period for tākoketai | black petrels (*Procellaria parkinsoni*) on Great Barrier Island | Aotea, 2001-2017.

Breeding season	Number of breeding pairs	Range (days for egg incubation)	Mean (± SEM)
2001/02	15	52-71	57.7 ± 1.2
2002/03	10	42-59	51.1 ± 1.6
2003/04	5	45-61	52.8 ± 3.1
2007/08	5	66-71	67.8 ± 1.1
2008/09	8	53-58	55.9 ± 0.7
2009/10	10	52-59	55.5 ± 0.6
2010/11	2	49-55	52.0 ± 3.0
2012/13	30	49-64	56.8 ± 0.6
2013/14	9	54-58	56.6 ± 0.5
2014/15	5	54-63	57.4 ± 1.6
2015/16	6	53-59	56.3 ± 0.9
2016/17	5	56-67	58.2 ± 2.2
Total	110	42-71	56.5 ± 0.4

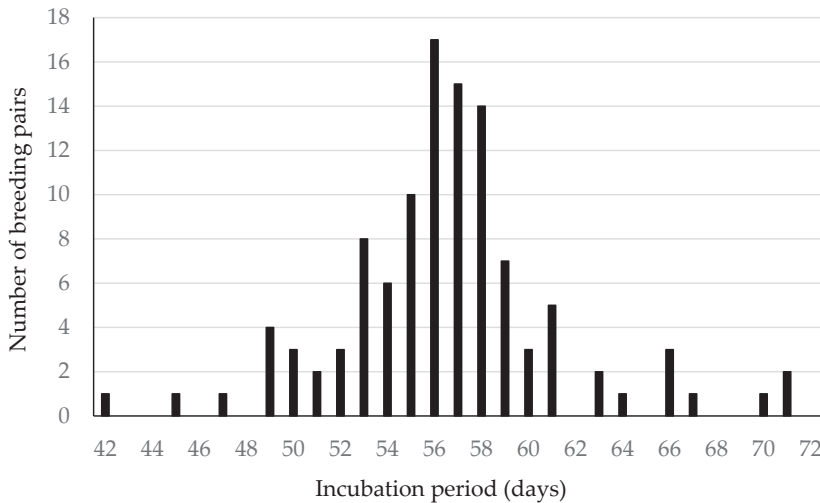


Figure 1. Incubation period for tākoketai/black petrels (*Procellaria parkinsoni*) on Great Barrier Island | Aotea, 2001-2017.

There are three incubation periods within the data set that are less than 49 days (42 days from one breeding pair in 2002/03, 45 days and 47 days from two breeding pairs in 2003/04) (Figure 1, Table 1) which is highly unusual for a large petrel such as black petrels (Warham 1990). These could be due to transcription errors in the dataset, an egg being missed during an earlier check, or a possible second egg in the chamber (i.e., one laid earlier than the other by a different female) which was missed on an earlier check. There are also three incubation periods within the dataset that are over 69 days (70 days from one breeding pair in 2001/02 and 71 days for two breeding pairs in 2007/08) (Figure 1, Table 1). However, petrels are known to leave eggs chilled for periods of time (in some cases up to ten days for black petrels) and these eggs can remain viable when cold (pers. obs., Warham 1990). If these six outlier instances are excluded, the mean incubation rate and standard error does not change (mean $\pm$ SEM = 56.5 ± 0.4 days) whereas if only the three shortest incubation periods are excluded, then the mean incubation rate ($\pm$ SEM) is marginally higher at 56.9 ± 0.4 days.

The incubation period of black petrels is consistent with other *Procellaria* species (Marchant & Higgins 1990); kareta/kauae mā/white-chinned petrel (*P. aequinoctialis*) ranges from 57 to 62 days (Mougin 1971, Hall 1987), tāiko | Westland petrel (*P. westlandica*) 51 to 68 days (Baker & Coleman 1977) and kuia | grey petrel (*P. cinerea*) 52 to 61 days (Barrat 1974).

Despite the data from Imber (1987) being derived from only one breeding pair, the analysis of this larger dataset confirms that the 57-day incubation period is accurate for black petrels.

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Keywords: tākoketai, black petrel, incubation, egg, *Procellaria*

SHORT NOTE

Colony size and dispersal of white-fronted terns (*Sterna striata*) banded at Kaikōura Peninsula, New Zealand, 1959–1971 and 1999–2016

LINDSAY K ROWE

T198 24 Charles Upham Drive, Rangiora 7400

White-fronted terns (*Sterna striata*) are widely found around the coasts of New Zealand (Higgins & Davies 1996; Heather & Robertson 2005; Mills 2013) including the Kaikōura Peninsula (42.428°S, 173.710°E) (Mills & Shaw 1980). They are considered “Near-threatened” by BirdLife International (2023) and are listed as “At risk: declining” under the New Zealand Threat Classification System (Robertson *et al.* 2021). White-fronted terns have been banded in New Zealand from at least 1945 (Cunningham 1951). Summaries of banding activities in New Zealand from 1951 onwards show that Brian Bell probably banded the first white-fronted terns in the north-east South Island, 359 at the Kaikōura Peninsula in 1958–1959 (Kinsky 1959). Banding continued from 1959–1960 when birds were banded by Brian Bell (111 birds), L.K. Clark (100 birds) and Ken Rowe (369 birds) (Kinsky 1960).

This note reports observations on white-fronted terns banded under permits held by Ken Rowe in 1959–1971 and son Lindsay Rowe in 1999–2016.

The main study area was a 1 km stretch of coastline between First Point and Whalers Bay at the Kaikōura Peninsula, centred on 42.428°S, 173.710°E. From 1959 to 1971, parties led by Ken Rowe made visits to Kaikōura Peninsula to band red-billed gull (*Chroicocephalus novaehollandiae scopulinus*) chicks over one weekend from 23 November to 16 December with extra visits in January 1959 and 1962 (Rowe submitted 2024). Banding white-fronted tern (*Sterna striata*) chicks was ancillary to banding the gulls. In 1999, when the author became a resident of Kaikōura, visits to the colonies were generally two to 10 days apart from October to February, but with some longer intervals.

Chicks were banded once they were big enough to retain the bands. Aluminium butt closure bands (4.5 mm internal diameter) were used until 1962, harder wearing monel bands through to 1963, and stainless steel bands thereafter.

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Correspondence: lindsay.jan.rowe@xtra.co.nz

Table 1. Number of white-fronted terns chicks banded at Kaikōura Peninsula from 1959 to 1971. nv denotes no visit.

Season	November or December visit	January visit	Total
1959–60	360	9	369
1960–61	101		101
1961–62	300		300
1962–63	259	154	413
1963–64	31		31
1964–65	15		15
1965–66	0		0
1966–67	8		8
1967–68	nv		nv
1968–69	0		0
1969–70	nv		nv
1970–71	0		0
1971–72	100		100
Total	1174	163	1337
Seasons	11		11
Average	107		122
SD	135		160
95% CL	±80		±94

Dispersal/resighting data used are from slips sent by the precursors to, and the Department of Conservation (DOC) Banding Office to Ken Rowe or the author that have not been lost through many household shifts, or from files sent to the author from DOC. Resightings include both live and dead birds.

From 1959-1971, 1,337 white-fronted tern chicks were banded at Kaikōura (Table 1). During this period there was a wide range in the number of chicks banded per year, from zero to 360 per visit in November/December, with an average of 121 chicks/year. While these figures will be less than the total numbers of chicks that fledged each year, the 1-day snapshot gives an indication of the variability of breeding at this site. A more definitive set of annual totals was gained during 1999–2016 when visits were made almost weekly throughout the season and an effort was made to band all chicks. During this period, 3,927 chicks were banded (0–952 chicks/season, averaging 218; Table 2, Fig. 1). There were four seasons (2010, 2012, 2013 and 2015) when no colony established despite birds roosting at the site pre-season; in 2014 none of the 10 eggs seen hatched.

This variation in numbers from year to year is not unusual as white-fronted terns have been noted as being intermittent or capricious in their breeding at a site, often breeding at a site for a few years and then breeding elsewhere before returning (Higgins & Davies 1996; Heather & Robertson 2005; Mills & Shaw 1980; Mills 2013). Adult Kaikōura-bred white-fronted terns were preyed on at a colony at the Clarence River mouth (33 km N of Kaikōura) in 2015 (LKR *unpubl. data*). At that time there was no active colony at Kaikōura Peninsula and it is likely that the Clarence River colony consisted of birds that would otherwise have bred at Kaikōura Peninsula. Another example of intermittent site selection was a bird banded as a nestling at Kaikōura Peninsula in 1961 that bred at the Clarence River colony four years later and was back at Kaikōura at ages 10 and

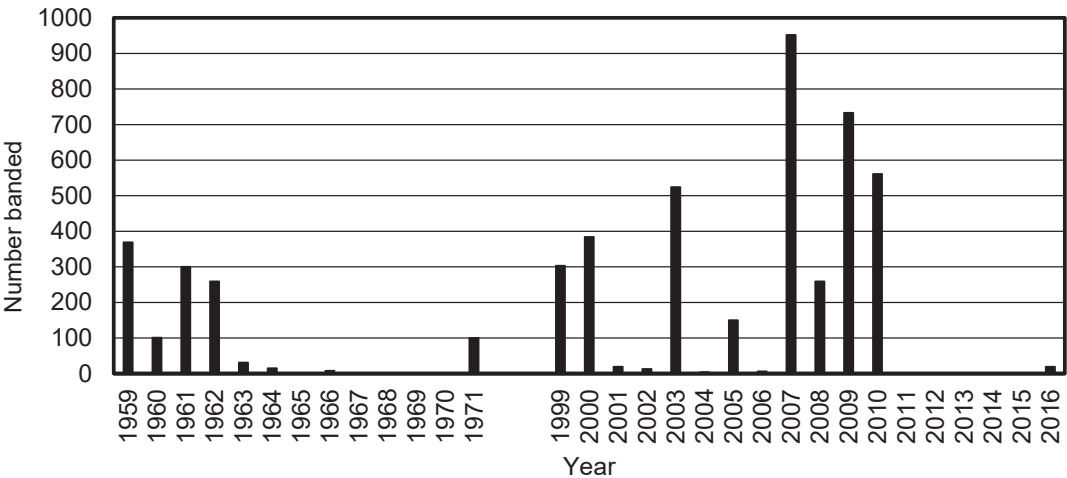


Figure 1. Annual numbers of white-fronted tern chicks banded at Kaikōura Peninsula. 1959-1971 were numbers banded over one weekend in November or December; 1999-2016 were season totals. There were no visits in 1967 and 1969, no colonies were present in 2010, 2012, 2013 and 2015, and no chicks hatched in 2014.

Table 2. Number of white-fronted terns chicks banded at Kaikōura Peninsula from 1999 to 2017.

Season	First egg seen	First chick seen	Last chick	Chicks banded
1999-2000	29 November	19 December	20 January	303
2000-2001	16 November	2 December	22 January	384
2001-2002	10 November	10 December	15 December	19
2002-2003	3 November	26 November	29 January	13
2003-2004	26 October	16 November	14 February	524
2004-2005	Missed	26 December	16 January	4
2005-2006	24 October	26 November	8 January	150
2006-2007	5 November	6 December	13 December	6
2007-2008	23 October	8 November	11 January	952
2008-2009	13 October	23 November	31 December	229
2009-2010	3 November	19 November	9 January	733
2010-2011	–	–	–	0
2011-2012	13 November	13 December	17 January	561
2012-2013	–	–	–	0
2013-2014	–	–	–	0
2014-2015	25 November	–	–	0
2015-2016	–	–	–	0
2016-2017	22 November	9 January	16 January	19
Total	–	–	–	3927
Seasons	13	13	13	18
Minimum	13 October	8 November	13 December	0
Average	6 November	4 December	12 January	218
Maximum	29 November	9 January	14 February	962
SD (days)	14	17	17	298
95% CL (days)	8	9	9	±138

16 years (Mills & Shaw 1980). Mills & Shaw also reported birds from colonies at the Clarence River, Ure River (65 km north), Lake Grassmere (86 km north) and Wairau River mouth (104 km north) bred at Kaikōura Peninsula.

Dates of colony establishment also varied on an annual basis. Over the period 1999–2016, eggs were first seen from 13 October to 29 November (range 47 days), chicks were first banded from 8 November to 9 January (range 62 days), and the last chicks were banded on 13 December to 14 February (range 63 days) (Table 2). The variability in breeding between seasons is shown by curves of accumulated banding throughout the seasons (Fig. 2) and reveal that laying by white-fronted terns is not always as highly synchronised as suggested by Mills & Shaw (1980) as it can take 18 to 30 days to band the majority of chicks.

Three Kaikōura Peninsula banded juvenile white-fronted terns were found dead in Australia: D-192398 at Somerton Park, South Australia, 2,302

km, 9 months 25 days after banding; D-115371 at Pittwater Beach, New South Wales, 2,187 km, 10 months 27 days; and D-9756 at Montague Island, New South Wales, 2,137 km 12 months 16 days. Hindwood (1946) speculated that a small proportion of New Zealand white-fronted terns (mainly juveniles) migrated to south-east Australia. This was subsequently confirmed by New Zealand banding studies (e.g. Clark & Dawson 1957; Kinsky 1963; Robertson 1964), and the records reported here.

In the DOC banding database, location coordinates were rounded down to 10' (e.g. 42°25' S, 173°42'E was coded as 422S 1734E) which leads to an inherent distance error up to ± 23 km. Of the 430 resightings (live or dead), 304 were less than 10 km NNW of the banding site, and so most were likely found on the colony; only two could be confirmed as off the colony and these were less than 5 km away.

There were 128 sightings over 50 days after banding and for 75 of them the calculated distances suggest that they were resighted on the

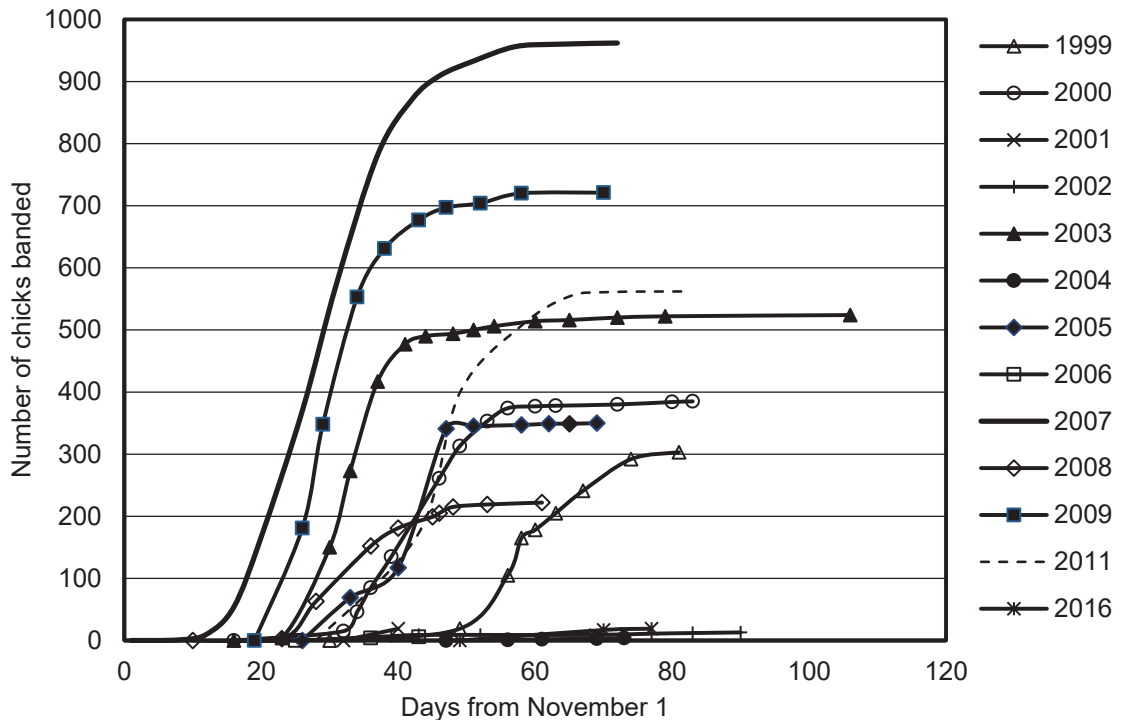


Figure 2. Timing of colony growth of white-fronted terns at Kaikōura Peninsula as shown by the accumulated number of birds banded. No colonies were present in 2010, 2012, 2013 and 2015, and no chicks hatched in 2014.

colony. Another 35 were noted 30–35 km NNE of the banding site, likely all at the Clarence River, where 24 had eggs or chicks on 12 December 1965. A bird banded at the Pinnacle Rock (13 km WSW of Kaikōura Peninsula; 46 km SSW of Clarence River) was also seen there on eggs on that date. As no chicks were banded at Kaikōura Peninsula or Pinnacle Rock that season, the colony may have moved to the Clarence River.

Excluding the three band recoveries in Australia, 15 birds (including one from Pinnacle Rock) were found >40 km from Kaikōura Peninsula: three to the south, and 12 to the north of which seven were in the North Island. The furthest north was at Waihi, 593 km from Kaikōura Peninsula and the only bird sighted on the North Island east coast. In the South Island, birds were sighted between Picton (130 km N of Kaikōura Peninsula) and Moeraki Beach (400 km S). The Waihi recovery greatly exceeds the previous within-New Zealand recovery distance for a banded white-fronted tern (305 km; Robertson 1964).

The oldest recovery was a dead bird, D-12952, picked on a beach at the Kaikōura Peninsula 25.1 years after banding. The next oldest was D-12906 killed by a stoat at 24.0 years-old, followed by eight at 17.0 years and four at 16.0 years. Mills & Shaw (1980) reported recoveries at Kaikōura Peninsula

aged 18 years. Only Heather & Robertson (2005) have reported a longer-lived bird, a banded bird that lived over 26 years. Two other long-lived recoveries were reported by Robertson (1972 & 1974) at 17.1 and 21.1 years respectively.

Juvenile birds from Kaikōura Peninsula were recovered at Wairau River 105 km N at 53 days after banding, Manawatu estuary 250 km N at 86 days, and Oamaru 370 km S after 59 days, indicating dispersal at a young age.

Data reported in this paper supports previous findings referring to: the intermittent nature of white-fronted tern colonies at a given site; the movement of birds between colonies; the variability of the onset of nesting; extends the longest within-New Zealand distance at which a bird has been recovered away from its natal area to 593 km; and gives examples of long-lived birds, up to 25.1 years.

ACKNOWLEDGEMENTS

This study was carried out under permits issued by the, then, Wildlife Branch of the Department of Internal Affairs, a forerunner of the Department of Conservation, to Ken Rowe and Lindsay Rowe. Comments from an anonymous reviewer have led to improvements in this note.

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Keywords: White-fronted tern, *Sterna striata*, Kaikoura, New Zealand, recoveries, sightings, dispersal

SHORT NOTE

The Ornithological Society of New Zealand's iconic 1951 takahē drawing by Charles Tunnickliffe

B.J. GILL

Auckland War Memorial Museum*, Auckland, New Zealand

The Ornithological Society of New Zealand (OSNZ) was inaugurated in 1940 (Gill & Heather 1990). A decade later, its committee resolved to change the name of its journal from *New Zealand Bird Notes* to *Notornis*. The first issue with the new name was Volume 4, Part 1, published in July 1950. The journal was growing in size and importance and the new name was in line with the tradition of the world's ornithological societies to name their journals after high-profile birds. The South Island takahē or notornis (*Porphyrio* [*Notornis*] *hochstetteri*) had become well known, both locally and world-wide, following its dramatic rediscovery in Fiordland in 1948 by Dr Geoffrey Orbell.

Since 1952, the OSNZ has used as a design on the covers of *Notornis*, and a few of its other publications, an exquisite drawing of a takahē

(Fig. 1; Heather 1990). Its first use was on the cover of *Notornis* Volume 5, Part 1 (July 1952). The only published explanation of the drawing (same issue; p. 1) was: "The society is pleased to be able to present a new cover design of a notornis, executed by the eminent English artist C. F. Tunnickliffe". How the society obtained the drawing was not reported at the time.

To research background details of the drawing I consulted the OSNZ archive (MS-2003-75), which is housed in the library of Auckland War Memorial Museum. The inventory of the archive (completed by Michael Taylor in 2011) indicates that Box 10, Folder 2 (correspondence 1950–1960), holds letters between Tunnickliffe (CFT) and John Cunningham (JC), the OSNZ Secretary. I examined this folder in 2023, finding two letters from CFT (September 1951 and August 1952) and four letters from JC to CFT (1951–1952). I came across another letter from JC to CFT (December 1950) in Box 10, Folder 1. Besides correspondence, I checked the AGM and Committee minutes for this period (Box 10).

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Correspondence: adiantum@outlook.co.nz

*retired

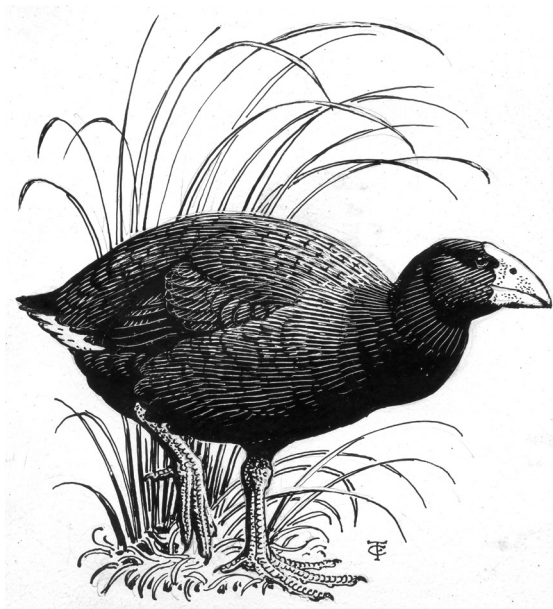


Figure 1. High-resolution scan of C.F. Tunnicliffe's original ink drawing of a South Island takahē (110 x 100 mm). Image: B. Gill.

C.F. Tunnicliffe O.B.E., R.A. (1901–1979)

Charles Frederick Tunnicliffe was born in Cheshire, England, in December 1901 (Niall 1979). He studied at Manchester Academy of Fine Art, and at the Royal College of Art (London). He was elected R.A. in 1954 and received an O.B.E. in 1977. Tunnicliffe died in Anglesey, Wales, in February 1979.

Charles Tunnicliffe had a great affinity with the British countryside and became a notable wildlife artist (Niall 1980). Birds were his special focus. He made detailed portraits of birds in life and painted birds in their habitat. He made field sketches and also post-mortem paintings of limp birds with their wings and legs extended. His bird paintings were used on covers of British bird magazines. He illustrated many books, and there are several books devoted to selections of his art work (e.g. Niall 1979, 1980; Gillmor 1981).

Obtaining the drawing

How Tunnicliffe and the OSNZ came to discuss a drawing remains uncertain, because I cannot find in the OSNZ archives the earliest letters between the parties, or the AGM or Committee minutes for 1949, 1950 or 1951.

Surviving correspondence comes later in the chain of events. JC wrote to CFT on 14 December 1950 acknowledging a letter from CFT dated 4 October (not seen). JC undertook to obtain one or

more photographs of the takahē, and drawings of topographical details of the bird, to send to CFT as reference material for a drawing. He would also send a copy of the society's special publication on the takahē which would include photographs. (A collection of articles from *Notornis* Vol. 4, Part 5, July 1951, was reissued and repaginated as a booklet entitled "The Takahe".) JC asked if CFT could send a rough sketch that could be shown to members who know the bird well, rather than going "right ahead with the scraper board drawing".

JC sent the society's special takahē publication with a letter dated 21 July 1951. He also referred CFT to Plate 28 of Buller (1882) for "a splendid drawing [of the takahē], in which all the scutellations on the legs and feet are correct, and in addition the bird is in quite a good stance". JC added: "Dr [Robert] Falla says if you bear in mind that the bird reminds him of a moorhen [*Gallinula chloropus*] you will get the drawing right".

CFT replied from his home in Anglesey on 21 September 1951. "I enclose two finished drawings as I think the time saved by doing finished work as against rough sketches makes the gamble worth while. There is no extra charge for the second drawing, I merely wanted you to have at least one alternative." Instead of "a money payment", he requested to "have copies of 'Notornis' as they are issued until you consider the debt discharged". This letter establishes 1951 as the year that Tunnicliffe drew the takahē.

JC acknowledged receipt of the "fine drawings" (letter, 4 February 1952). "I am very impressed with the drawings, and so are the one or two members so far privileged to see them. As they are rather valuable, I have not sent them round to each of our committee, but have made rough photographic copies to show the committee. I rather think that the bird in the stooping attitude will meet with general approval from those who know the bird in life."

On 28 June 1952, JC wrote to advise CFT that *Notornis* Volume 5, Part 1, had just been printed with the Tunnicliffe takahē on the cover. The committee had resolved to make CFT a life member of the OSNZ in lieu of payment for the drawing. JC wrote again on 23 July 1952, asking if the takahē drawing could be used on the cover of the checklist of New Zealand birds that the OSNZ was shortly to publish (Fleming 1953). In reply (letter, 6 August 1952) CFT stated: "You may use the drawing, or drawings, of *Notornis* as you wish ...".

The takahē drawing

The original drawing is currently in an acid-free envelope in Box 22, Folder 1, of the OSNZ archive. It is a pen and ink drawing, with black ink, measuring about 110 mm tall by 100 mm wide (Fig. 1).

The drawing is on a rectangle of white card measuring 140 x 120 mm. The card is mounted, as required for its initial printing, on a larger piece of rough, yellow-brown cardboard. This is annotated "Masterton Printing Co." and "1 line block 3½ wide" (3.5 inches = 89 mm).

The drawing comprises an elegant and accurate depiction of a takahē with its head held low and the right leg raised. There is a background of tussock grass. Close examination shows faint pencil marks, in among the inked areas, from the artist's preparatory sketch. Tunnicliffe's cipher (CFT) is drawn in at lower right. The drawing makes a nice composition, well suited as a cover design. As such it was presumably intended to be printed at full size or with slight reduction. Because the drawing is highly detailed it looks poor when greatly reduced in an attempt to make a logo.

Discussion

Until the early correspondence (or the OSNZ meeting minutes for the relevant years) are found, we have to wonder why Tunnicliffe, in Britain, drew a takahē for a New Zealand ornithological group. He may have had a connection to someone in New Zealand, on account of which he offered to make the drawing or somebody in the OSNZ requested it. Certainly he would have been known to New Zealand ornithologists from his art work in British nature books and magazines. But why did the OSNZ not ask a local artist? People like E. Mervyn Taylor (1906–1964) could have done the job. Taylor was an accomplished nature artist (James 2006) and he had drawn birds for Falla's school journal on the subject (Falla & Taylor 1949).

Whatever the circumstances, acquiring an exquisite drawing of a South Island takahē by such an internationally acclaimed bird artist as Charles Tunnicliffe is a significant event in the OSNZ's history. The society has used the drawing regularly as cover art on its publications for 70 years. This is the legacy of Tunnicliffe's artistry and the effort of OSNZ office-holders to obtain the drawing.

The fate of Tunnicliffe's second takahē drawing is not known to me and I have seen no representation of it. It is presumably a black ink drawing of similar size to the surviving drawing but showing a takahē in a different attitude. It was probably signed "CFT". It may be lost, or it may turn up in the OSNZ archive. It may even have found its way, erroneously, into another archive.

ACKNOWLEDGEMENTS

I thank staff of the Auckland Museum library for providing access to the OSNZ archive collection, and Richard Wolfe for helpful comments on a draft of this note.

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Keywords: bird art, cover design, history, archives

CORRIGENDUM

Holdaway, R.N.; Allentoft, M. E. 2022. A basic statistical approach to determining adult sex ratios of moa (Aves: Dinornithiformes) from sample series, with potential regional and depositional biases. *Notornis* 69: 158-173.

RICHARD N. HOLDAWAY

Palaeocol Research Ltd, P.O. Box 16569, Hornby, Christchurch 8441, New Zealand

In this article, the callouts to panels in the caption to Figure 4 in this paper are incorrect. The caption should read:

Figure 4 Binomial distributions for sex ratios of *Euryapteryx curtus* from Tokerau Beach, Northland, and *E. curtus* and *Pachyornis germanoides* from Tangatupura Swamp, northern Wairarapa, by numbers of leg elements assigned to sex by length by Worthy (1987). **A-C**, *E. curtus*, Tokerau Beach: **A**, femora; **B**, tibiotarsi; **C**, tarsometatarsi. **D**, *E. curtus*, Tangatupura. **E-G**, *P. germanoides*, Tangatupura: **E**, femora; **F**, tibiotarsi; **G**, tarsometatarsi. Black, 1♀/1♂; light blue, 1.1♀ / 1♂; light blue dashed, 1.4♀ / 1♂; blue, 2♀ / 1♂; green, 3♀ / 1♂; orange, with symbols, 4♀ / 1♂. Vertical blue dotted line, number of females in sample; horizontal blue dotted line, critical value $\alpha = 0.05$.

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