

*Notornis*, 2024, Vol. 71: 37-45

0029-4470 © The Ornithological Society of New Zealand Inc.

## 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.

McArthur, N.J.; Krouse, S.K.; Thomas, D.; Thompson, H.; Melville, D.S.; Williams, E.M.; Walker, S.; Schlesselmann, A-K.V. 2024. Using egg floatation to estimate the age and hatching dates of South Island pied oystercatcher (*Haematopus finschi*) eggs. *Notornis* 71(2): 37–45.

**Keywords:** Charadriiformes, egg age, egg floatation, Haematopodidae, hatching success, nest survival, South Island pied oystercatcher

Received 24 May 2023; accepted 24 June 2024

\*Correspondence: [nikki.mcarthur.101@gmail.com](mailto: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

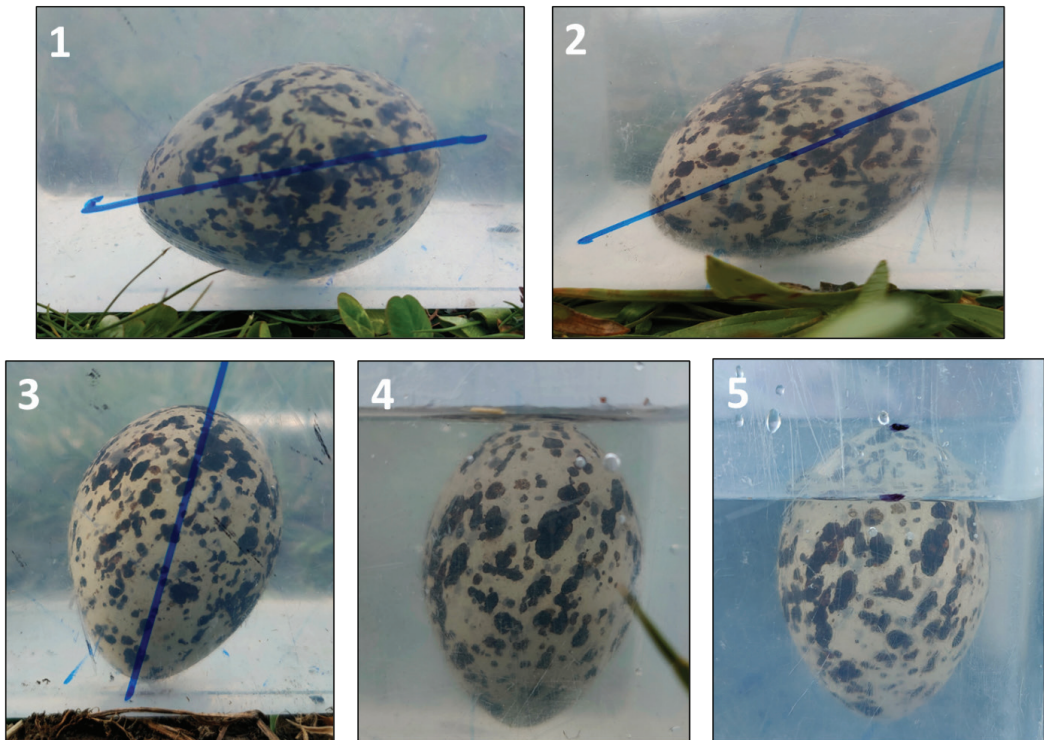
capture and banding of incubating parents; e.g. to maximise the number of adults caught for banding during a given breeding season.

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  $2.0 \pm 0.23$  (*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 ( $\pm 0.20$  *se*) and a 90<sup>th</sup> 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  $\leq 4.9$  days of true egg age when using this regression equation.

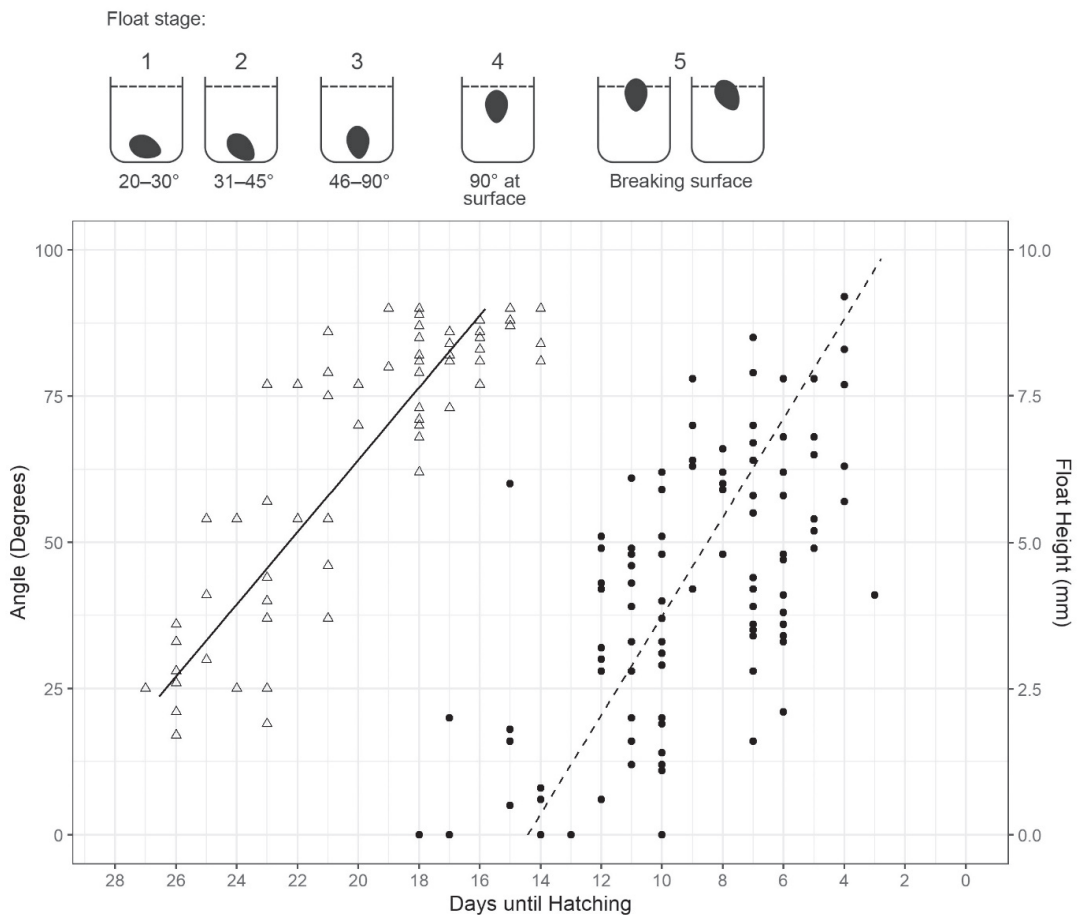
### Late incubation

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:

$$\begin{aligned} \text{No. days until hatching} \\ = & 260.49 + (-2.74 \times \text{Mean egg angle of clutch}) \\ & + (-1.13 \times \text{Mean egg float height of clutch}) \end{aligned}$$

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 90<sup>th</sup> 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  $\leq 4.9$  days during early incubation and  $\leq 5.0$  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  $90^\circ$ ), whereas egg float heights progress more gradually through a narrower range of values (0 mm to  $\sim 10$  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 90<sup>th</sup> 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.

#### ACKNOWLEDGEMENTS

A special thank you to Colin O'Donnell and Paul Sagar for their advice regarding project design and field methodology and for their assistance in the field. We would also like to thank Archie MacFarlane, Morgan Coleman, Grant Morriss and Department of Conservation staff from the Raukapuka / Geraldine Office for their logistical support and assistance in the field, and Nicolette Faville for her assistance with creating Figure 2. Thank you to Malcolm and Sue Prouting of Mesopotamia Station and to Ricky Sinclair and James Wright of Forest Creek station for their permission to access private land and for assistance with accommodation and fieldwork logistics. We are grateful to Te Rūnanga o Arowhenua for supporting this work. This project was funded by MBIE's Science and Innovation Group Strategic Science Investment Funding for Crown Research Institutes, and all field procedures were undertaken according to animal ethics approval No. AEC 363 (Department of Conservation). Lastly, we would like to give our thanks to Paul Sagar, Craig Symes and two anonymous reviewers for taking the time to review and comment on an earlier draft of this paper.

#### LITERATURE CITED

- Ackerman, J.T. and Eagles-Smith, C.A. 2010. Accuracy of egg floatation throughout incubation to determine embryo age and incubation day in waterbird nests. *The Condor* 112: 438-446.
- Alberico, J.A.R. 1995. Floating eggs to estimate incubation stage does not affect hatchability. *Wildlife Society Bulletin* 23: 212-216.
- Baker, A.J. 1969. *The comparative biology of New Zealand oystercatchers*. Unpubl. Master of Science thesis, University of Canterbury, Christchurch.
- Bassett, S. 2012. Operation Nest Egg incubation and chick rearing best practice protocols. Oralis Ltd, Wellington. <https://www.doc.govt.nz/globalassets/documents/conservation/native-animals/birds/operation-nest-egg-protocols.pdf>
- Bobeková, I. 2022. *The secret life of wader chicks: Understanding the ontogeny of behaviours towards independence in Eurasian oystercatchers (Haematopus ostralegus)*. Unpubl. Master of Resource Management thesis, University of Akureyri, Akureyri, Iceland. <http://hdl.handle.net/1946/42002>
- Cruz, J.; Pech, R.P.; Seddon, P.J.; Cleland, S.; Nelson, D.; Sanders, M.D.; Maloney, R.F. 2013. Species-specific responses by ground-nesting Charadriiformes to invasive predators and river flows in the braided Tasman River of New Zealand. *Biological Conservation* 167: 363-370.
- Dinsmore, S.J.; White, G.C.; Knopf, F.L. 2002. Advanced techniques for modelling avian nest survival. *Ecology* 83: 3476-3488.
- Ellis, K.S.; Cavitt, J.F.; Larsen, R.T.; Koons, D.N. 2018. Using remote cameras to validate estimates of nest fate in shorebirds. *Ibis* 160: 681-687.
- Gale, S.; Welch, J.; Nelson, D. 2020. *Project River Recovery Annual Report 1<sup>st</sup> July 2019 to 30<sup>th</sup> June 2020*. Project River Recovery Internal Report 2020/02, Department of Conservation, Twizel.
- Hansen, J.; Schmidt, N.M.; Reneerkens, J. 2011. Egg hatchability in high Arctic breeding wader species Charadriiformes is not affected by determining incubation stage using the egg floatation technique. *Bird Study* 58: 522-525.
- Hebbali, A. 2020. *olsrr: Tools for Building OLS Regression Models*. R package version 0.5.3. <https://CRAN.R-project.org/package=olsrr>
- Hughey, K.F.D. 1985. *Hydrological factors influencing the ecology of riverbed breeding birds on the plains' reaches of Canterbury's braided rivers*. Unpubl. PhD thesis, Lincoln University, Lincoln.
- Jamieson, I.G. and Ryan, C.J. 2000. Increased egg infertility associated with translocating inbred takahe (*Porphyrio hochstetteri*) to island refuges in New Zealand. *Biological Conservation* 94: 107-114.
- Johnson, D.H.; Jones, S.; Geupel, G. 2007. Estimating nest success: A guide to the methods. *Studies in Avian Biology* 34: 65-72.
- Kearvell, J.C. 2011. Causes of breeding failure in banded dotterel (*Charadrius bicinctus*) breeding on Ashley Spit, North Canterbury, New Zealand. *Notornis* 58: 43-45.
- Liebezeit, J.R.; Smith, P.A.; Lanctot, R.B.; Schekkerman, H.; Tulp, I.; Kendall, S.J.; Tracy, D.M.; Rodrigues, R.J.; Meltotte, H.; Robinson, J.A.; Gratto-Trevor, C.; McCaffery, B.J.; Morse, J.; Zack, S.W. 2007. Assessing the development of shorebird eggs using the floatation method: Species-specific and generalised regression models. *The Condor* 109: 32-47.
- Mabee, T.J.; Wildman, A.M.; Johnson, C.B. 2006. Using egg floatation and eggshell evidence to determine age and fate of Arctic shorebird nests. *Journal of Field Ornithology* 77: 163-172.
- Maloney, R.F.; Keedwell, R.J.; Wells, N.J.; Rebergen, A.L.; Nilsson, R.J. 1999. Effect of willow removal on habitat used by five birds of braided rivers, MacKenzie Basin, New Zealand. *New Zealand Journal of Ecology* 23: 53-60.
- Marchant, S.; Higgins, P.J. 1993. *Handbook of Australian, New Zealand & Antarctic birds: Volume 2 Raptors to Lapwings*. Oxford University Press, Melbourne.



- McArthur, N.; Jones, P. and Lees, D. 2021. *Eastbourne – Wainuiomata coastline tūturiwhatu / banded dotterel management strategy 2021-2026*. Mainland Island Restoration Organisation (MIRO), Eastbourne. <https://miro.org.nz/dotterels/>
- McNew, L.B.; Gregory, A.J.; Wisely, S.M.; Sandercock, B.K. 2009. Estimating the stage of incubation for nests of greater prairie-chickens using egg floatation: a float curve for grouse. *Grouse News* 38: 12-14.
- Mendez, V.; Alves, J.A.; Gill, J.A.; Pórisson, B.; Carneiro, C.; Pálsdóttir, A.E.; Vignisson, S.R.; Gunnarsson, T.G. 2022. Effects of pair migratory behaviour on breeding phenology and success in a partially migratory shorebird population. *Ecology and Evolution* 12, e9184.
- Morse, J.A.; Powell, A.N.; Tetreau, M.D. 2006. Productivity of black oystercatchers: Effects of recreational disturbance in a national park. *The Condor* 108: 623-633.
- Norbury, G.; Heyward, R. 2008. Predictors of clutch predation of a globally significant avifauna in New Zealand's braided river ecosystems. *Animal Conservation* 11: 17-25.
- Norbury, G.L.; Price, C.J.; Latham, M.C.; Brown, S.J.; Latham, D.M.; Brownstein, G.E.; Ricardo, H.C.; McArthur, N.J.; Banks, P.B. 2021. Misinformation tactics protect rare birds from problem predators. *Science Advances* 7: eabe4164.
- O'Donnell, C.F.J.; Hoare, J.M. 2011. Meta-analysis of status and trends in breeding populations of black-fronted terns (*Chlidonias albostrriatus*) 1962-2008. *New Zealand Journal of Ecology* 35: 30-43.
- O'Donnell, C.F.J.; Sanders, M.; Woolmore, C.; Maloney, R.F. 2016. *Management and research priorities for conserving biodiversity on New Zealand's braided rivers*. Department of Conservation, Wellington.
- R Core Team 2019. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>.
- Riegen, A.C.; Sagar, P.M. 2020. Distribution and numbers of waders in New Zealand, 2005-2019. *Notornis* 67: 591-634.
- Robertson, H.A.; Baird, K.A.; Elliott, G.P.; Hitchmough, R.A.; McArthur, N.J.; Makan, T.D.; Miskelly, C.M.; O'Donnell, C.F.J.; Sagar, P.M.; Scofield, R.P.; Taylor, G.A.; Michel, P. 2021. Conservation status of birds in Aoteoroa New Zealand, 2021. *New Zealand Threat Classification Series* 36, Department of Conservation, Wellington.
- Robertson, H.A.; Heather, B.D. 1999. Effect of water levels on the seasonal use of Lake Wairarapa by waders. *Notornis* 46: 79-88.
- Sagar, P.M.; Geddes, D.; Banks, J.; Howden, P. 2000. Breeding of South Island pied oystercatchers (*Haematopus ostralegus finschi*) on farmland in mid-Canterbury, New Zealand. *Notornis* 47: 71-81.
- Sanders, M.D.; Maloney, R.F. 2002. Causes of mortality at nests of ground-nesting birds in the Upper Waitaki Basin, South Island, New Zealand: a 5-year video study. *Biological Conservation* 106: 225-236.
- Savage, J.L.; Crane, J.M.S.; Kākāpō Recovery Team; Hemmings, N. 2022. Low hatching success in the critically endangered kākāpō is driven by early embryo mortality not infertility. *Animal Conservation* 25: 352-360.
- Schlesselmann, A.-K.V.; O'Donnell, C.F.J.; Monks, J.M.; Robertson, B.C. 2018. Clearing islands as refugia for black-fronted tern (*Chlidonias albostrriatus*) breeding colonies in braided rivers. *New Zealand Journal of Ecology* 42: 137-148.
- Schlesselmann, A. 2021. *Review of 6-year upper Rangitata River predator control project*. Contract report LC5001, Manaaki Whenua Landcare Research, Dunedin.
- Shaffer, T.L. 2004. A unified approach to analysing nest success. *The Auk* 121: 526-540.
- Spiegel, C.S. 2008. *The incubation patterns, parental roles and nest survival of black oystercatchers (Haematopus bachmani): Influences of environmental processes and potential disturbance stimuli*. Unpublished Master of Science thesis, Oregon State University, Corvallis, Oregon.
- Steffens, K.E.; Sanders, M.D.; Gleeson, D.M.; Pullen, K.M.; Stowe, C.J. 2012. Identification of predators at black-fronted tern *Chlidonias albostrriatus* nests, using mtDNA analysis and digital video recorders. *New Zealand Journal of Ecology* 36: 48-55.
- Van Heezik, Y.; Lei, P.; Maloney, R.; Sancha, E. 2005. Captive breeding for reintroduction: influence of management practices and biological factors on survival of captive kaki (black stilt). *Zoo Biology* 24: 459-474.
- van Paassen, A.G.; Veldman, D.H.; Bientema, A.J. 1984. A simple device for determination of incubation stages in eggs. *Wildfowl* 35: 173-178.
- Vega-Ruiz, I.I.; Castillo-Guerrero, J.A.; Fernández, G. 2021. Drivers of the breeding success of American oystercatchers (*Haematopus palliatus frazari*) at a critical site in Sinaloa, Mexico. *Journal of Field Ornithology* 92: 18-29.
- Walker, S.; Monks, A.; Innes, J. 2020. National changes in occupancy for New Zealand-breeding Charadriiformes, 1969-1979 to 1999-2004. *Notornis* 67: 677-691.
- Wei, T.; Simko, V. 2021. *R package 'corrplot': Visualization of a Correlation Matrix (Version 0.91)*. <https://github.com/taiyun/corrplot>
- Wills, D.E.; Murray, J.; Powlesland, R.G. 2003. Impact of management on the breeding success of northern New Zealand dotterel (*Charadrius obscurus aquilonius*) on Matakana Island, Bay of Plenty. *Notornis* 50: 1-10.