Moult Strategies of Oystercatchers (Haematopidae) in New Zealand, Australia and South Africa

by

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Abstract

While there are a number of studies that have examined the moult strategies of migrant waders (Charadrii), only a few have focused on non-migrant waders. As part of a collection of papers that have analysed moult using the Underhill-Zucchini moult model, we used this method to observe the moult strategies of species within the family Haematopidae. Our data includes a combination of previously acquired ringing data and that which we collected, along with contributions by citizen scientists, in the form of photographic records. The first chapter provides an introduction to the study, placing it within the context of comparable research, and placing moult within the context of the birds' important life stages. Our second chapter focuses on the Australian Pied Oystercatcher *Haematopus longirostris*, of which we completed a detailed analysis of the wing and feather moult. Within chapters 3-6 we examine the wing moult strategies of the Sooty Oystercatcher *H. fuliginosus* of Australia, the South Island Pied Oystercatcher *H. finschi* and Variable Oystercatcher *H. unicolor* of New Zealand, and the African Oystercatcher *H. moquini* of South Africa. With no long-distance movements, these oystercatchers are free to devote more time and energy towards other stages in their life cycle: breeding and moult. We identified the moult parameters of start date, standard deviation in start date, duration and end date for each of the five species. We acquired the relative feather masses and used these in the conversion of the moult scores to proportion feather mass grown (PFMG). The final chapter synthesizes the work, consisting of a comparison and identification of the similarities and differences between the species' moult strategies, and possible reasons for these. We approach the conclusion that further research is needed on the strategies of moult for resident waders, and this may be achieved successfully through the use of digital photography. With an expanding knowledge of the parameters of moult, there is opportunity for even more discoveries into these birds' lives, which will have benefits for their conservation.

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Chapter One: Introduction

The shorelines and inland bodies of water of all continents, excluding Antarctica are home to a group of about 220 species of birds known as waders, classified in the order Charadriiformes, suborder Charadrii. The name describes their tendency to wade through the water for the purpose of foraging for food in the sand or mud. Birds within this group include plovers, sandpipers, ibises, herons, oystercatchers, and other similar species. Waders have characteristic long and slender legs which give them balance in deep water or mud and help with their foraging habits. Long bills are also a common feature in wader species, with the additions of sharp pointed tips or curved shapes depending on food preference (Hayman et al. 1986; van de Kam et al. 2004; Kumbhar and Mhaske 2020).

As with all other bird groups, the annual cycle of a wader has either two or three main components; for migrants these are breeding, migration and moult, and for residents are breeding and moult. The scheduling of these stages varies considerably depending on the species' habits, their geographical location, the climate and other factors. For example, Newton (2009) describes that at least eight variations in the order of these events occur in the lives of different European bird populations, and this is also visible in birds all over the world.

Many wader species migrate to suitable breeding locations where climatic and environmental conditions are more favourable than their foraging or moulting locations which may have unadaptable seasonal changes. Breeding behaviour and physiology can be correlated with a species' chosen breeding grounds. An increase in latitude of breeding areas has been associated with an increase in the growth rate of wader chicks (Tjørve 2007).

Most wader chicks are precocial, meaning that the birds are born with the ability to take care of themselves. However, there are exceptions, such as the chicks of Magellanic Plovers *Pluvianellus socialis* which are fed regurgitated food stored in the parent's crop, and oystercatchers (Family Haematopidae) which are semi-precocial – the chicks are mobile from hatching, but are fed by parents after hatching (Starck and Rickleffs 1998).

Around the stages of breeding and migration, birds must fit moult into their schedule. Moult is the replacement of a bird's old feathers with new ones. This process requires a high proportion of energy, nutrients and time within the birds' life (Alonso et al. 2009). The timing, duration and extent of moult varies between species due to factors such as environmental conditions, migration routes, and breeding periods. Birds that participate in migration have smaller windows in which to carry out their moult, as is the case for migrant waders (Jackson 2018); non-migrants have more time available than migratory species.

The quantitative study of moult

The key step in the quantitative study of moult was developed by Ashmole (1962), who devised a system of scoring old feathers a 0, new feathers a 5, and growing feathers values from 1 (a pin) to 4 (nearly fully grown). The "moult score" was then the sum of the scores for the nine or 10 individual primaries, following an ascending pattern from the innermost primary. Ginn and Melville (1983) pointed out that the statistical methods in use for the analysis of moult data were unsatisfactory. Five years later, a custom-built statistical moult model, based on the method of maximum likelihood was published (Underhill and Zucchini 1988); this paper included mathematical explanations of why the methods previously in use were biased. The Underhill-Zucchini moult model made two assumptions: the starting dates for moult had a normal distribution, i.e. a mean and a standard deviation, and a moult index that increased linearly with time through moult; in other words there was a single duration of moult for all birds. Most analyses were performed using a Fortran programme developed by Brandao (1998). Serra (2002) developed the concept of estimating the parameters of moult for individual primaries; this requires relatively large volumes of data throughout moult. Erni et al. (2013) developed a package in R (R Core Team 2020) which made the estimation of the parameters accessible to analysts in a way not achieved before. By 2022, more than 260 analyses using the Underhill-Zucchini moult model had been undertaken (Scott and Underhill submitted). In the meantime, progress had been made in the development of a moult index that increased approximately linearly with time; Underhill and Summers (1993) showed that replacing the traditional "moult score" with proportion feather mass grown (PFMG) created a moult index that increased linearly. The paper by

Remisiewicz et al (2009) provided the broad analysis template upon which the moult analyses in this dissertation are based.

Moult in migratory species

A collection of studies on moult in migratory birds have been conducted with the use of the Underhill and Zucchini (1988) moult model: three with a focus on shorebirds (Serra 2002; Barshep 2011; Jackson 2018), and one investigating passerines (Burman 2016). Timing of moult is adaptive according to the distance travelled during migration and the environmental conditions present at the non-breeding areas (Serra 2002; Barshep 2011; Jackson 2018). In a study conducted on the Curlew Sandpiper *Calidris ferruginea*, the timing of moult at the non-breeding grounds was influenced by carry-over effects from conditions at the breeding grounds which had first affected the timing of post-breeding and migration. Warm temperatures at the breeding grounds favoured early breeding and migration of males, and with low predation in addition to the warm temperatures during chick development, late migration of females was favoured. Changes in the timing of autumn migration also had an impact on the timing of moult for these birds. Moult started later in years when temperatures at the breeding grounds were high (Barshep 2011).

The moult durations of the Grey Plover *Pluvialis squatarola* differed with environmental conditions, because primary moult was of short duration in northern areas where cold winter placed a constraint on moult completion and of long duration further south, where the December-February period was warm (Serra 2002). Adults of the Lesser Sandplover *Charadrius mongolus*, the Greater Sandplover *Charadrius leschenaultia*, and the Terek Sandpiper *Xenus cinereus* adjust their initiation of moult according to the proximity to breeding grounds, with those starting moult earlier in the northern nonbreeding sites, than those with longer distances to travel to southern nonbreeding sites (Jackson 2018).

The impacts of external factors on moult as well as the specific aspects of moult, such as physiology and history have been studied in other migrant species. A study of Cory’s Shearwaters *Calonectris diomedea borealis* explored the impacts of exogenous factors on the timing of moult and the overlap with reproduction and discovered significant differences under opposing environmental conditions. Breeding status had the greatest impact on moult onset, and the individuals that failed to breed began the moult process earlier than those still rearing chicks (Alonso et al. 2009). Often there is a close relationship between the end of breeding and moult onset; a study of Common Starlings *Sturnus vulgaris* suggests that this is linked to high levels of prolactin at the start of moult (Dawson 2006). Moult has been phylogenetically analysed in Western Palearctic warblers (Sylviidae) and results suggest moult before migration at the breeding grounds as an ancestral pattern, while moult after migration has a pattern of evolving 7–10 times due to increases in migratory distances (Svensson and Hedenström 1999).

In addition to using the Underhill and Zucchini (1988) moult model on migratory shorebirds, a study used this method in an investigation of the Barn Swallow *Hirundo rustica*, a migratory passerine (Burman 2016). Global environmental factors, such as global climate change, influence processes in avian life cycles. The swallows responded to this phenomenon through changes in their phenology, with earlier migration to breeding grounds and earlier breeding onset. Resulting changes in the length of breeding subsequently affected the start of moult (Burman 2016).

Moult in resident species

In general, resident bird species moult in late summer and autumn after breeding and take their time to moult because they are not constrained by migration (but the imminent arrival of harsh winter weather can induce a rapid moult in far northern species) (Newton 2009). The primary moult of 15 species of weaverbirds (Ploceidae) in South Africa was analysed and it was discovered that earlier breeding and onset of moult occurred in the winter rainfall regions, compared to the summer regions. Moult of the primaries began almost immediately after breeding (Oschadleus 2005). The sequence of events in a bird’s lifecycle is dependent on their regional location. Non-migratory species in the temperate regions generally follow the pattern of moult after breeding, known as post-nuptual moult; while those in the tropics experience many variations, such as pre-nuptual moult, moult while breeding, moult in between the breeding season, or experience two breeding periods each followed by moult (Barta et al. 2006).

Many species of wader do not migrate, or only move short distances between breeding and non-breeding localities. Most of the resident wader species breed in tropical and subtropical habitats, where it is warm throughout the year, and include species such as avocet, stilts, dotterels, plover and oystercatchers. Non-migrants are often found among migratory species along the shore or inland bodies of water, for example, both resident and migratory species occur along all the flyways during the non-breeding season (Milton 2003). Within species, there may be populations that choose to stay resident, such as the Maio (Cape Verde) population of the Kentish Plover *Charadrius alexandrinus*, and populations of Black-winged Stilt *Himantopus himantopus* in the warmer regions. Little has been studied concerning the moult of resident wader species, but it is probable that their moult is extended over longer periods in comparison to migrants.

Why study moult?

The period of moult within the annual cycle of a bird is physiologically demanding. For example, in birds less than 100 g in mass, the mean mass of the feathers is 7.1% of body weight (range 6%–12%); this represents 18% to 39% of the lean dry body-mass, and about 25% of the total protein contained in the bird (Jenni and Winkler 2020). Replacing this material on an annual basis is an energetically challenging process. The moult period is thus important for the bird and is thus important for ornithological research. The various aspects of moult, such as duration, timing and onset may act as indicators for other factors affecting a bird’s life. The study of changes to moult strategies may shed light on global changes to the environment, such as climate change. For example, delays in the onset of moult due to a longer breeding season from climate change may have an exponential impact on the survival of Barn Swallows (Burman 2016). The aspects of moult may also have a physiological impact on a bird, for example, moult duration may determine, in part, the quality of primary feathers (Serra 2002).

Moult studies are a neglected aspect of ornithology. There is a growing need to fill gaps in knowledge, especially in an era of global climate change. Studies of moult are of both research and biodiversity conservation importance. For some species, it is easier to quantify moult than other aspects of a bird’s lifecycle. Because the protocol for collecting moult has stood the test of time, and has remained unchanged since it was developed by Ashmole (1962), there is a valuable collection of historical moult data that may be of use as a baseline for understanding changes in strategies over time. With the increasing interest in the effects of weather on bird species and the success of their breeding, it is even more vital that moult studies be conducted because of their influence in identifying the timings of fledging, breeding onset, and the end of breeding (Ginn and Melville 1983).

The strategies of moult within a species are flexible (Alonso et al. 2009), thus it is important to study the moult patterns of various populations in detail to identify characteristics specific to a species. Although this is a timely process, it is clear that the information gained is worth the effort of the study.

Methods of moult data collection

Over the decades, data has been recorded and collected for the purposes of acquiring knowledge and understanding, and to protect the earth’s fauna and flora. Since the late 1600s, information has been recorded about birds, with early studies containing illustrated works and specimens preserved in museums. In the late 1800s, bird ringing was introduced, providing a revolutionary method for collecting information which could not be gathered through observations only. Ringing has made it possible to understand orientation and population dynamics, as well as a number of other aspects within ornithology (Perdeck 1977). It is still a popular form of data collection used today, in studying birds of small resident populations or large groups of migratory species.

Advances in technology have brought about many new methods used in bird studies. Some of these include bird tracking methods such as the use of radio, satellites or geolocators, and even mobile phone networks (Fiedler 2009). Another method that is becoming increasingly popular in studies is that of photography. For the purposes of examining moult, photography has been used as early as 1982, for example, in a study of the 2-year replacement cycle of primaries of California Condors *Gymnogyps californianus*, three stages of moult were identified and discussed. Though this study covered a small sample size, it outlined the value of photography (Snyder et al. 1987).

As mentioned by Vieira et al. (2017), photography has largely been used over the years as an additional source of data, complementing that already collected through conventional methods. These scientists brought to attention that photography could be used as a stand-alone method and be just as reliable as other methods of handling birds, in studying moult. Technological advances have allowed for detailed observations of feathers in images, expanding the possibilities for moult data collection (Vieira et al. 2017; Pyle 2021).

Photography

With the use of photography as a data collection method, there is a variety of benefits to the conservation of the species as well as growth of the citizen scientist community. A camera can capture moments at different stages in a bird’s life, increasing the knowledge base of the species. In comparison with ringing, there are no nets involved with photography and this allows for less disturbance towards the species and no limitations on sample sizes.

Photography provides the opportunity for citizens to contribute to scientific studies. With this inclusivity, the knowledge as well as the concern for species and the environment grows amongst members of the public. A moult study on eight species of hummingbirds made use of data collected by citizen scientists, allowing for the interpretation and clarification of moult and plumage strategies (Pyle 2021).

This method does have limitations, we cannot record body or mass measurements or other details about the habits/characteristics of specific individuals, but for the use of this study, photographic images hold enough information to analyse and identify the parameters of moult. A limitation that is much broader in scale, is that it is only possible for photography to be used with certain species, and not others. For example, it is easy to photograph African Oystercatchers because these birds stay within a certain home range along the coastline, thus making it possible to distinguish between pairs and avoid capturing the same bird twice. Photography of moult becomes a lot more difficult when a bird may fly, for example, to any area within a forest, this is where ring identification is helpful to distinguish between individuals that are photographed.

This study

Oystercatchers are a charismatic wader species frequently found on rocky and sandy shores and bays or may have slightly extended ranges inland (Heppleston 1973; Anderson and Minton 1978; Allen et al. 2019). The birds occur in every continent except Antarctica. Most species are pied, though some are completely black in appearance, and all have characteristic bright red beaks, legs, and rings around their eyes. Their beaks are long and slender but have slight variation in shape according to their diet.

In coastal habitats, oystercatchers forage at low tide and their diet ranges from mussels to bivalves based on the coastal type, while inland species forage for earthworms and insect larvae. Most pied species tend to inhabit light-coloured sandy shores, while those completely black in colour are found on dark-coloured rocky shores. This rings true for *H. longirostris* and *H. fuliginosus* at the Furneaux Islands, the two species are adapted to the sandy and rocky shores, respectively. Their colour pattern in relation to predator evasion and their foraging ecology are possible reasons for their habitat choices. *H. longirostris* is more adapted to foraging for bivalves, gastropods and polychaete worms, while *H. fuliginosus* is adapted to feed on mussels, limpets, gastropods and chitons (Lauro and Nol 1995; Fraser and Lindsey 2018). Oystercatchers across the globe have also been found feeding on crabs, fish, and echinoderms.

H. moquini is located on both rocky and sandy shores and is thus adapted to various diets associated with its habitats. Most of its food is found on rocky shores, this previously included indigenous mussels and limpets, but has since changed after the overpopulation of the invasive mussel *Mytilus galloprovincialis*, which has had a positive impact on the population sizes and breeding productivity of *H. moquini* (Zardi et al. 2018). Only a few prey species are preyed upon on sandy shores, namely bivalves and amphipods (Hockey and Underhill 1984).

A collection of works outlining the conservation assessments of all known species of oystercatcher was established by Ens and Underhill (2014), and describes the species' biology, habitat, distribution, conservation status and threats. We aim to add to this body of knowledge, to contribute research on moult strategies of oystercatchers.

For this study, we chose five of the six species in South Africa, Australia and New Zealand. The Chatham Island Oystercatcher *H. chathamensis* has its entire population of c. 300 birds on one island in New Zealand, and is Endangered; the five species included in this dissertation are all Least Concern (Ens and Underhill 2014).

In this study we examine, compare, and discuss the moult strategies of five species of oystercatcher. These species (and their distributions) are the African Oystercatcher *Haematopus moquini* of South Africa (Figure 1), the Australian Pied Oystercatcher *Haematopus longirostris* and Sooty Oystercatcher *Haematopus fuliginosus* of Australia (Figures 2 and 3), and the South Island Pied Oystercatcher *Haematopus finschi* and Variable Oystercatcher *Haematopus unicolor* of New Zealand (Figures 4 and 5). We aim to develop accounts of the timing, duration, and extent of the moult periods of these species, and identify the similarities and differences of their strategies and possible reasons for these.

The birds chosen for this study have distributions located at similar distances south of the equator (Figures 1 to 5) This facilitates comparison and identification of factors affecting aspects of the birds' annual cycles. The birds differ in the timing of breeding and moult in their annual cycles. Of the five species, four are essentially resident as adults. The exception is the South Island Pied Oystercatcher; almost all adults migrate between their breeding grounds in the interior of the South Island and their non-breeding areas in the North Island (Figure 4) (Ens and Underhill 2014).

To determine their moult strategies, previously collected ringing data were provided for the four Australian and New Zealand species, and photographic data were collected for the African Oystercatcher to supplement a small volume of ringing data.

This study is part of a collection of papers which uses the moult model of Underhill and Zucchini (1988) to analyse primary moult and the results have been included in Scott and Underhill (submitted). We aim to contribute to the knowledge base for the purposes of having an improved understanding and implementation of conservation efforts towards the protection of these charismatic waders.

Thesis structure

The species with the best quality data was Australian Pied Oystercatcher. What set the species apart was the fact that there was the large volume of data available for the analysis of moult; it was also the species for which it was feasible to follow the "template" for primary moult studies, established by Remisiewicz et al. (2009). It was therefore selected as the lead species for this dissertation. It is reported on in Chapter 2, and it is done in the most detail. The bulk of the African Oystercatcher data were collected by an innovative method, digital photography, and therefore this species was selected for Chapter 3. This is followed by chapters on each of the three remaining species for which data were available: Chapter 4, Sooty Oystercatcher; Chapter 5 South Island Pied Oystercatcher; Chapter 6, Variable Oystercatcher. Each of these species presented different analysis issues, and it was deemed appropriate to turn each into a chapter. *It is intended that the chapters relating to each species will be submitted to a journal (for example, Emu*, *Ostrich* (the chapter on the moult of the African Oystercatcher has been submitted to the issue of this journal focused on moult), *Notornis and Wader Study).* There is thus some repetition in the Introduction and Methods, but it is kept to a minimum. Comparisons between the five species are postponed to Chapter 7, which provides a synthesis of the results for all the species.

References

Allen AM, Ens BJ, Van de Pol M, van der Jeugd H, Frauendorf M, Oosterbeek K, Jongejans E. 2019. Seasonal survival and migratory connectivity of the Eurasian Oystercatcher revealed by citizen science. *The Auk: Ornithological Advances* 136: 1–17.

Alonso H, Matias R, Granadeiro JP, Catry P. 2009. Moult strategies of Cory’s Shearwaters *Calonectris diomedea borealis*: the influence of colony location, sex and individual breeding status. *Journal of Ornithology* 150: 329–337.

Anderson K, Minton C. 1978. Origins and movements of Oystercatchers on the Wash. *British Birds* 71: 439–447.

Ashmole NP. 1962. The Black Noddy *Anous tenuirostris* on Ascension Island. Part 1. General Biology. Ibis 103: 235–273.

Barshep Y. 2011. Migration and moult strategy of the Curlew Sandpiper. PhD thesis, University of Cape Town.

Barta Z, Houston AI, McNamara JM, Welham RK, Hedenström A, Weber TP, Feró O. 2006. Annual routines of non-migratory birds: optimal moult strategies. *Oikos* 112: 580–593.

Brandao A 1998. A comparative study of stochastic models in biology. PhD thesis, University of Cape Town.

Burman MS. 2016. Citizen science reveals complex changes in Barn Swallow phenology in South Africa over three decades. PhD thesis, University of Cape Town.

Dawson A. 2006. Control of molt in birds: association with prolactin and gonadal regression in Starlings. *General and Comparative Endocrinology* 147: 314–322.

Ens BJ, Underhill LG. 2014. Synthesis of oystercatcher conservation assessments: general lessons and recommendations. *International Wader Studies* 20: 5–22.

Erni B, Bonnevie BT, Oschadleus H-D, Altwegg R, Underhill LG. 2013. moult: an R package to analyse moult in birds. *Journal of Statistical Software* 52: 1–23.

Fiedler W. 2009. New technologies for monitoring bird migration and behaviour. *Ringing & Migration* 24: 175–179.

Fraser N, Lindsey A. 2018. Some observations of Australian Pied Oystercatcher on Worimi Conservation Lands. *The Whistler* 12: 35–42.
Ginn H, Melville D. 1983. *Moult in birds*. Tring: British Trust for Ornithology.
Hayman P, Marchant J, Prater T. 1986. Shorebirds. London: Croom Helm.
Heppleston P. 1973. The distribution and taxonomy of oystercatchers. *Notornis* 20: 102–112.
Hockey P, Underhill L. 1984. Diet of the African Black Oystercatcher *Haematopus moquini* on rocky shores: spatial, temporal and sex-related variation. *African Zoology* 19: 1–11.
Jenni L, Winkler R. 2020. *The biology of moult in birds*. London: Helm.
Jackson C. 2018. The moult and migration strategies of Lesser Sand Plover, Greater Sand Plover and Terek Sandpiper. PhD thesis, University of Cape Town.
Kumbhar D, Mhaske D. 2020. Study of waders diversity in the catchment area of Ujani Reservoir, Solapur District (MS), India. *International Journal of Biological Innovations* 2: 287–294.
Lauro B, Nol E. 1995. Patterns of habitat use for Pied and Sooty Oystercatchers nesting at the Furneaux Islands, Australia. *The Condor* 97: 920–934.
Milton D. 2003. Threatened shorebird species of the East Asian-Australasian Flyway: significance for Australian wader study groups. *Wader Study Group Bulletin* 100: 105–110.
Newton I. 2009. Moult and plumage. *Ringing & Migration* 24: 220–226.
Oschadleus H-D. 2005. Patterns of primary moult in the weavers, Ploceidae. PhD thesis, University of Cape Town.
Perdeck A. 1977. The analysis of ringing data: pitfalls and prospects. *Vogelwarte* 29: 33–44.
Pyle P. 2021. Examination of digital images from Macaulay Library to determine avian molt strategies: A case study on molts and plumages in eight species of North American hummingbirds. *bioRxiv* 2021.02.03.429637
R Core Team. 2020. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.
Remisiewicz M, Tree AJ, Underhill LG, Gustowska A, Taylor PB. 2009. Extended primary moult as an adaptation of adult Wood Sandpipers *Tringa glareola* to their freshwater habitats in southern Africa. *Ardea* 97: 271–280.
Scott T, Underhill, LG. submitted. Global review of quantitative studies of primary moult of birds using the Underhill-Zucchini moult model.
Serra L. 2002. Cold winters vs long journeys: adaptations of primary moult and body mass to migration and wintering in the Grey Plover *Pluvialis squatarola*. PhD thesis, University of Cape Town.
Snyder NF, Johnson EV, Clendenen DA. 1987. Primary molt of California Condors. *The Condor* 89: 468–485.
Starck JM, Ricklefs RE. 1998. Patterns of development: the atricial-precocial spectrum. In: Starck JM, Ricklefs RE (eds). *Avian growth and development. Evolution within the altricial-precocial spectrum.* Oxford: Oxford University Press. pp 3–30.
Svensson E, Hedenström A. 1999. A phylogenetic analysis of the evolution of moult strategies in Western Palearctic warblers (Aves: Sylviidae). *Biological Journal of the Linnean Society* 67: 263–276.
Tjørve K. 2007. Does chick development relate to breeding latitude in waders and gulls? *Wader Study Group Bulletin* 112: 12–23.

Underhill LG, Summers R. 1993. Relative masses of primary feathers in waders. *Wader Study Group Bulletin* 71: 29–31.
Underhill LG, Zucchini W. 1988. A model for avian primary moult. *Ibis* 130: 358–372.
Van de Kam J, Ens B, Piersma T, Zwarts L. 2004. *Shorebirds: An illustrated behavioural ecology.* The Netherlands: KNNV Publishers.
Vieira BP, Furness RW, Nager RG. 2017. Using field photography to study avian moult. *Ibis* 159: 443–448.
Zardi G, McQuaid C, Jacinto R, Lourenço C, Serrão E, Nicastro K. 2018. Re-assessing the origins of the invasive mussel *Mytilus galloprovincialis* in southern Africa. *Marine and Freshwater Research* 69: 607–613.

Figures

Figure 1: Distribution map of the African Oystercatcher in South Africa, with distribution indicated in yellow.

Figure 2: Distribution map of the Australian Pied Oystercatcher in Australia, with distribution indicated in yellow.

Figure 3: Distribution map of the Sooty Oystercatcher in Australia, with distribution indicated in yellow.

Figure 4: Distribution map of the South Island Pied Oystercatcher in New Zealand, with distribution indicated in yellow.

Figure 5: Distribution map of the Variable Oystercatcher in New Zealand, with distribution indicated in yellow.

Chapter 2: Primary moult in the annual cycle of adult Australian Pied Oystercatchers *Haematopus longirostris*

Abstract: The Australian Pied Oystercatcher *Haematopus longirostris* is a short distance migrant that resides along the coastlines of Australia. Adult birds will travel to the breeding grounds, laying their first clutches between October and November. Moult takes place after breeding, followed by a few months in-between for survival through the winter. Our estimated moult start and completion dates using the Underhill-Zucchini moult model for the ten primaries as a tract are 19 December to 25 May, respectively. The start date for the first primary was estimated as 20 December, and the completion date for the tenth primary was 2 June. With a short-distance migration, the birds allocate more time to their moult period to produce good quality feathers. However, the birds have a large wing gap of 0.11 during moult, which comes at a cost to their flight ability.

Introduction

In the monograph covering the 11 oystercatcher species (Ens and Underhill 2014), the phenomenon of moult is barely mentioned. As Goss-Custard (2014) pointed out, there are many gaps in knowledge even for the best-known species in this genus. Moult is one of these knowledge gaps. The importance of moult to a bird is related to the fact that its long-term survival is dependent on the maintenance of the ability to fly efficiently, and this is achieved through the replacement of feathers (Jenni and Winkler 2020).

The oystercatcher genus *Haematopus* is the only one in the family Haematopidae, which in turn is in the suborder Charadrii. There have been multiple studies of the primary moult of many species in two families in this suborder, the plovers Charadriidae and the sandpipers Scolopacidae; these are summarized by Jackson and Underhill (2022). The remaining families, including the Haematopidae, have been neglected.

In this paper we consider the primary moult of one member of the Haematopidae, the Australian Pied Oystercatcher *Haematopus longirostris*. The structure of the paper broadly follows that of Remisiewicz et al. (2009). We assembled the available data on the primary moult of this species, and used the moult model of Underhill and Zucchini (1988) to estimate the parameters of moult of the 10 individual primaries and the feather tract as a whole. We assessed the internal consistency of the model by calculating the cumulative relative feather growth of the primaries using both sets of estimates.

Methods

Data collection

The Australian Pied Oystercatcher is a wader species that inhabits sandy shores, foraging for bivalves and other marine invertebrates along the coastlines of Australia, mainly on ocean beaches, in estuaries and other coastal embankments (Taylor et al. 2014).

The knowledge acquired through conducting this study will build upon the research conducted on the Australian Pied Oystercatcher by wader study groups in Australia. Much information has been collected on their habitat, food preferences, their distribution, life history, and the natural and anthropogenic factors that threaten their conservation, though less is known about their moult patterns (Taylor et al. 2014)

Australian Pied Oystercatchers have been caught and banded at around 20 locations on the south-east and north-west Australian coastline since 1976 by the Victorian Wader Study Group (VWSG) and Australasian Wader Study Group (AWSG). Birds were captured at high-tide roost sites in flocking areas during the non-breeding season (usually February through to August) using cannon nets. Further details on catching and banding can be found in Kraaijeveld-Smit et al (2001 stilt 40), Kraaijeveld-Smit et al (2004) and Hansen et al (2009).

The age classes were based on bill, leg and eye colour (Kraaijeveld-Smit et al 2001). In this analysis, we only used the primary moult scores of birds banded in Victoria and South Australia which were classified as adults.

Primary moult scores were provided following the standard method of representation which includes one wing with primaries characterized by 10 digits, with old feathers scored as 0, new feathers as 5, and numbers in between representing intermediate stages of growth (Ginn and Melville 1983; Underhill and Zucchini 1988). To refer to the days from date of capture, the capture date was chosen as 1 October, and we combined records from all years in the dataset to analyse moult over the timeframe of a single year.

Data Analysis

We used the moult model of Underhill and Zucchini (1988) to estimate the three parameters of primary moult. This method assumes that moult duration is a single parameter; and that the starting dates of moult of individual birds have a normal distribution with a mean and standard deviation. The three parameters are estimated using the method of maximum likelihood (Underhill and Zucchini 1988); Erni et al. (2013) provided an algorithm that implements the estimation of the parameters using the method of maximum likelihood in the moult package in R (R Core Team 2020). We approached analysis with the strategy to estimate the moult parameters of the 10 primaries as a tract, and to estimate the parameters of moult for each of the 10 individual primary feathers, as first described by Serra (2002).

The moult model requires a moult index that increases linearly with time (Underhill and Zucchini 1988). A standard approach to achieve such an index is to use Proportion Feather Mass Grown (PFMG) (Underhill and Zucchini 1988; Underhill and Joubert 1995). When estimates of the moult parameters of the individual primaries are available, as here, the assumption of the linearity of the chosen moult index can be evaluated, using an approach devised by Remisiewicz et al. (2009), described below. We calculated PFMG using the method developed by Underhill and Summers (1993). The relative masses of primary feathers are required for this calculation (Underhill and Joubert (1995). We used published relative masses of the 10 primary feathers of adult Australian Pied Oystercatcher (Table 1) (Meissner et al. 2018) who had used the method described by Underhill and Joubert (1995) to obtain them.

For the primary moult analyses we used 1 October as Day 1 because it was earlier than any date on which primary moult was observed and later than any observed date of completion of moult. We used data type 2 of Underhill and Zucchini (1988) because all birds were available for capture throughout the sample period. We used the algorithm of Erni et al. (2013) to estimate the primary moult parameters: mean start date, standard deviation in start date, and duration of primary moult, along with their standard errors. This also enabled the calculation of a completion date.

To estimate the parameters of moult for individual primaries we used the approach described by Serra (2000). The feather-by-feather analysis was achieved through separation of the moultscore values to individual primary feather columns for primary one (innermost; P1) to primary 10 (outermost; P10). A moult index for each primary feather was obtained by allocating a relative feather mass grown of 0 to old feathers which had been scored 0 and 1 to new feathers which had been scored 5 and growing feathers with scores 1, 2, 3 and 4 were allocated the values 0.125, 0.375, 0.625 and 0.875 respectively (Serra 2002). For growing feathers, the complements of these values were allocated in the calculation of the proportion feather mass missing (PFMM); each feather was then multiplied by the percentage relative feather mass. Feathers scored 0 and 5 contributed 0 to PFMM. We added the values for the growing feathers to obtain PFMM; this represents the size of the gap in the primary feathers (Remisiewicz et al. 2009). We used the dates whereby the first primary began moult and the last primary ended moult as those for the start and completion dates for the overall moult period of the feather analysis.

Following the method devised by Remisiewicz et al. (2009), we checked the assumption that the chosen moult index increased linearly by calculating the cumulative PFMG curve. We used the start and completion dates of each primary and their relative masses, and calculated the daily contribution of each primary to PFMG during its moult. We summed these daily increments for each individual day from the starting date of P1 until the ending date of P10, and cumulated them through this period. Given that this cumulative curve is based on relative feather masses, the result must be linear if the assumptions underlying use of PFMG in the moult model are correct. Furthermore, the cumulative curve should lie close to a straight line joining the estimated start and completion dates from the moult model (Underhill and Zucchini 1988) applied to the full primary feather tract.

Results

A total of 3580 Australian Pied Oystercatchers were available for this analysis. 94% originated from the states of Victoria and South Australia, 5% had been banded in Western Australia and 1% in Tasmania. Due to the sample size availability, the 3356 birds residing in Victoria and South Australia were chosen for this analysis.

Birds were observed to undertake a continuous moult. This means that, once the bird begins to moult, there will always be feather growth taking place (scores of 1, 2, 3 and 4 within the moult formula). No suspension of moult was observed, and thus, once a bird commenced moult, the bird has completed moult for all of its primary feathers.

The mean starting date for the primary moult of adult Australian Pied Oystercatchers in Victoria and South Australia was estimated to be 19 December. The estimated standard deviation in starting date for the primary wing was 22 days. The duration was estimated to be 157 days, and the end date was therefore estimated to be 25 May (Table 2, Figure 1).

The relative masses of oystercatcher primary feathers increased steadily from 4.7% for primary 1 (P1) to 15% for primary 10 (P10) (Table 1). This pattern was not reflected in the durations of moult of individual feathers (Table 3, Figure 2). It was P4 and P5 which were estimated to have the shortest durations of moult, both 33 days (Table 3). The estimated duration of P1 was 50 days, but it needs to be noted that the standard error (SE) of the duration for P1 was 7 days and that the SE of the starting date was 5 days (Table 3). Thus, the parameters of moult of P1 cannot be treated as reliably estimated; this is a consequence of the small volumes of data at the time of start of moult of P1 (Figure 1) and note that the same contains only nine birds which were processed before the start of primary moult (Table 3). The duration of moult for P10, the heaviest feather, was 60 days, and that the SEs of the three parameters of moult for this feather were small, and that it can therefore be treated as reliably estimated.

The estimated gap between the starting dates of moult of P1 and P2 was 23 days (Table 3). The gaps between the next four successive pairs of feathers were either 9 or 10 days (Table 3). This tends to confirm the observation in the paragraph above that the parameters of moult are poorly estimated. It is tentatively suggested that the starting date of P1 be taken as 10 days prior to the starting date of P2, i.e. 20 December. In relation to the gaps between completion dates of subsequent primaries, the estimate for P1 of 26 January seems satisfactory and is left unaltered; this yields an estimated duration of 37 days, which in turn is compatible with the estimated durations of subsequent primaries. These values are inserted into Table 3 as adjusted values for P1.

The original estimated growth period for P1 was between 7 December to 26 January. Primary feather growth duration decreased from P1 to P5 and then increased to P10. The adjusted moult period for P1 is 20 December to 26 January. The growth period for P10 was estimated to be between 3 April and 2 June (Table 3).

The starting date of moult of P1 was estimated to be 7 December (Table 3); from the analysis of the primary feather tract as a whole was 19 December (Table 2). The difference is likely to be a reflection of the reality of the poor estimates of the parameters of moult of P1, as discussed above. The adjusted starting date for P1 was 20 December (Table 3), close to the estimate for the primary feathers (Table 2). The estimated completion dates for the primary tract (25 May) and for P10 (2 June) differed by eight days (Tables 2 and 3).

The feather growth periods overlapped by various numbers of days (Figures 3 & 4), with the shortest overlap of 22 days for P7 and P8, and the longest being 41 days for P9 and P10. The primary feathers had a consecutive growth rate which correlated with their relative feather masses (Figure 3). The number of simultaneously growing primaries had an overall decrease with an increase in relative feather mass (Figure 4), with the first five primaries growing alongside at least two other primaries, and the last five primaries growing with less than two other primaries simultaneously.

Over the course of the moult period, the birds were missing an average of 0.11 of their primary feather mass (Figure 5). The largest values were 0.33 of the total percentage feather mass missing, recorded in two individuals: one bird at the start of moult growing its first five primaries simultaneously (a moultscore of 1111100000 on 29 January), and a second bird towards the end of its moult stage growing its last four primaries simultaneously (a moultscore of 5555553221 on 24 April). We calculated the correlation coefficient between PFMG and PFMM as -0.6522.

The cumulative Percentage Feather Mass Grown makes use of the growth rates from Table 3, including the adjusted values for P1. The assumptions about the cumulative PFMG are correct because the result shows a uniform growth rate (Figure 6) which is closely alongside the estimated start and completion dates of moult of 19 December to 25 May.

Discussion

In a year of life of an adult Australian Pied Oystercatcher, the birds breed and moult; there is no evidence of regular migration for this species. However, local movements occur with some populations shifting to estuaries and bays in Tasmania and parts of Victoria that are more sheltered during the winter season. There is evidence that pairs within the more sheltered Corner Inlet remain on their territories throughout the year. A few long-distance movements of immature or adult birds have been recorded from southern Victoria to Tasmania, South Australia (River Murray mouth) and New South Wales (Ballina), though it is undetermined whether this is a return to natal territories or a movement to breeding areas (Taylor et al. 2014).

Without migration, the birds are able to devote more time and energy towards their other life stages, the timing of which varies with latitude. The egg-laying season of first clutches for Australian Pied Oystercatchers in Victoria (and Tasmania) is between October and November (Taylor et al. 2014). These populations will then go through winter. Our estimated dates for the moult period of Australian Pied Oystercatchers in Victoria are from December to late May/early June (Table 2 & 3; Figure 1), which correspond with their main laying season, leaving a few months in-between for winter (Taylor et al. 2014).

In analysing moult using the two approaches of the wing and feather-by-feather models, there was a difference of 20 days between the two estimated moult durations. This relatively small difference validates that the dates of moult are well estimated by the moult model.

The observed growth rate of the primary feathers of the birds in this study (Figure 3) confirms our assumption that the moult index increases linearly. The cumulative percentage feather mass grown illustrated alongside the start and completion dates of moult for this species (Figure 6) further confirms that the growth rate is uniform.

The timing of individual feather growth highlighted three feathers growing simultaneously for the first five primaries, and two growing simultaneously thereafter. Although the innermost primary had the smallest mass, it was primaries 4 and 5 that had the shortest growth duration, while the outermost primary had the longest growth duration. Thus, mass was not the determining factor for duration of growth. The feathers grew consecutively from P1 to P10, lightest to heaviest. It can be observed that with the heavier primary feathers, less feathers are grown simultaneously, this may be due to a possible increase in the amount of energy required for production of a heavier feather. It was interesting to discover that the longest duration of growth overlap was between the two heaviest feathers, P9 and P10, while the shortest was between P7 and P8.

The average percentage feather mass missing of 0.11 (Figure 5) is slightly larger than the value of 0.10 for the Wood Sandpiper *Tringa glareola* (Remisiewicz et al. 2009). A larger wing gap during moult means a more limited flight ability for the Australian Pied Oystercatcher, because the size of the wing gap generally impacts flight energetics (Hedenström and Sunada 1999).

In conclusion, Pied Oystercatchers have more time available without migration and thus spend a longer period during moult than migratory species of waders. The Underhill-Zucchini moult model provides a useful formula to analyse moult, giving a good estimate of the timing of moult as it corresponds with the timing of other life stages. Their primary feathers follow a uniform growth rate, with more overlap for lighter feathers in comparison to heavy. This species has quite a large wing gap and thus has more impaired flight ability during moult.

Acknowledgements

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References

Ens BJ, Underhill LG. 2014. Synthesis of oystercatcher conservation assessments: general lessons and recommendations. *International Wader Studies* 20: 5–22.

Erni B, Bonnevie BT, Oschadleus H-D, Altwegg R, Underhill LG. 2013. Moult: an R package to analyse moult in birds. *Journal of Statistical Software* 52: 1–23.

Ginn H, Melville D. 1983. *Moult in birds*. Tring: British Trust for Ornithology.

Goss-Custard J. 2014. Foreword. *International Wader Studies* 20: 4.

Hedenström A, Sunada S. 1999. On the aerodynamics of moult gaps in birds. *Journal of Experimental Biology* 202: 67–76.

Jackson CH, Underhill LG. 2022. Primary moult strategies in adult migrant waders (Charadrii). *Wader Study* 129: 126–137.

Jenni L, Winkler R. 2020. *The biology of moult in birds*. Bloomsbury Publishing.

Meissner W, Zaniewicz G, Gogga P, Pilacka L, Klaassen M, Minton C. 2018. Relative mass of flight feathers in waders – an update. *Wader Study* 125: 205–211.

R Core Team. 2020. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Remisiewicz M, Tree AJ, Underhill LG, Gustowska A, Taylor PB. 2009. Extended primary moult as an adaptation of adult Wood Sandpipers *Tringa glareola* to their freshwater habitats in southern Africa. *Ardea* 97: 271–280.

Serra L. 2002. Cold winters vs long journeys: adaptations of primary moult and body mass to migration and wintering in the Grey Plover *Pluvialis squatarola*. Unpubl. PhD thesis, University of Cape Town, South Africa.

Summers RW. 1980. On the rate of change of moult scores in waders. Wader Study Group Bulletin 28: 24.

Summers RW, Swann RL, Nicoll M. 1983. The effects of methods on estimates of primary moult duration in the Redshank Tringa totanus. *Bird Study* 30: 149−156.

Taylor IR, Newman OMG, Park P, Hansen B, Minton CD, Harrison A, Jessop R. 2014. Conservation assessment of the Australian Pied Oystercatcher *Haematopus longirostris*. *International Wader Studies* 20: 116–128.

Underhill LG. 2003. Within ten feathers: Primary moult strategies of migratory waders (Charadrii). In: Avian Migration. Berthold P, Gwinner E, Sonnenschein E (eds). *Avian Migration*. Berlin: Springer: 187–197.

Underhill LG, Joubert A. 1995. Relative masses of primary feathers. *Ringing & Migration* 16: 109–116.

Underhill LG, Summers R. 1993. Relative masses of primary feathers in waders. *Wader Study Group Bull* 71: 29–31.

Underhill LG, Zucchini W. 1988. A model for avian primary moult. *Ibis* 130: 358–372.

Plots and Figures

Table 1: Relative masses (%) of the primary feathers of eight Australian Pied Oystercatchers; data from Meissner et al. (2018).

Primary	**P1**	**P2**	**P3**	**P4**	**P5**	**P6**	**P7**	**P8**	**P9**	**P10**
Relative mass (%)	4.7	5.9	7.0	8.3	9.6	10.8	12.2	12.9	13.6	15.0

Table 2: Estimated moult parameters for the Australian Pied Oystercatcher from Victoria and South Australia. The parameters include start date, SD in start date, duration, end date and their corresponding standard errors in brackets, as well as the % PFMG per day and the sample sizes for the stages of moult.

Start date	SD start date	Duration (days)	End date	PFMG per day	Pre-moult	In-moult	Post-moult
19 December (1.7)	21.9 (1.4)	157.3 (2.9)	25 May	0.0064	9	1780	1567

Table 3: Estimated moult parameters for the primary feathers (1-10) of the Australian Pied Oystercatcher from Victoria and South Australia. The three parameters of the model are start date, standard deviation of start date and duration; the end date is computed as start date plus duration. Standard errors of the estimated parameters are given in brackets. The Proportion Feather Mass Grown (PFMG) per day is calculated as the relative feather mass divided by duration, and is used in the production of Figure 6. The sample sizes for the three stages of moult are given. The gap is the estimated time interval between the primary in the row and the following row. For an explanation of P1 adjusted, see text.

Primary	Feather mass	Start date	SD start	Duration (days)	End date	PFMG per day	Pre-moult	In-moult	Post-moult	Gap
P1	4.7	07 December (4.1)	28.8 (4.9)	49.6 (7.4)	26 January	0.0009	9	124	3223	23
P1 adjusted		20 December		37.0	26 January	0.0012				
P2	5.9	30 December (2.8)	20.0 (2.9)	37.5 (5.0)	05 February	0.0016	18	148	3190	9
P3	7.0	08 January (2.4)	21.7 (2.4)	35.1 (5.0)	12 February	0.002	39	179	3138	10
P4	8.3	18 January (2.0)	20.5 (1.9)	33.1 (4.5)	20 February	0.0025	74	204	3078	9
P5	9.6	27 January (1.7)	19.1 (1.5)	33.1 (3.9)	01 March	0.0029	113	235	3008	10
P6	10.8	06 February (1.5)	18.7 (1.3)	36.9 (3.5)	15 March	0.0029	183	301	2872	15
P7	12.2	21 February (1.4)	19.2 (1.2)	36.6 (3.4)	30 March	0.0033	289	354	2713	17
P8	12.9	09 March (1.3)	21.1 (1.1)	41.0 (3.4)	19 April	0.0031	449	504	2403	13
P9	13.6	22 March (1.3)	22.7 (1.1)	51.7 (3.3)	13 May	0.0026	616	790	1950	12
P10	15.0	03 April (1.2)	22.4 (0.9)	59.8 (3.1)	02 June	0.0025	741	1044	1571	

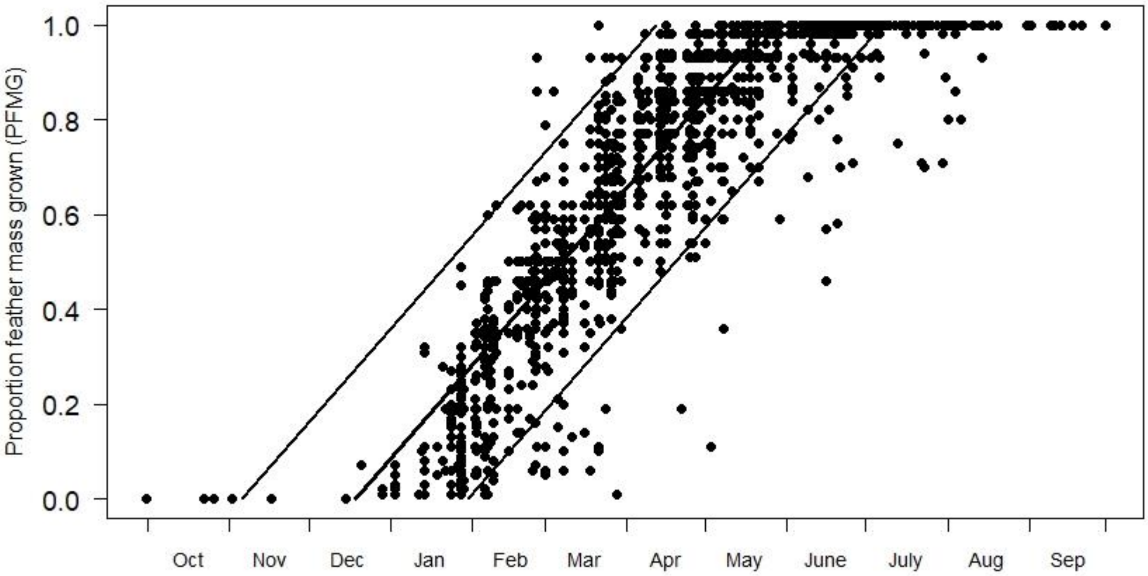

Figure 1: Scatter plot of Proportion Feather Mass Grown (PFMG) for the Australian Pied Oystercatcher in the states of Victoria and South Australia. The points represent the PFMG scores for individual birds plotted against date. The centre line represents the average timing of moult for a bird, and the two outer lines indicate the 95% confidence intervals of birds in moult (see text).

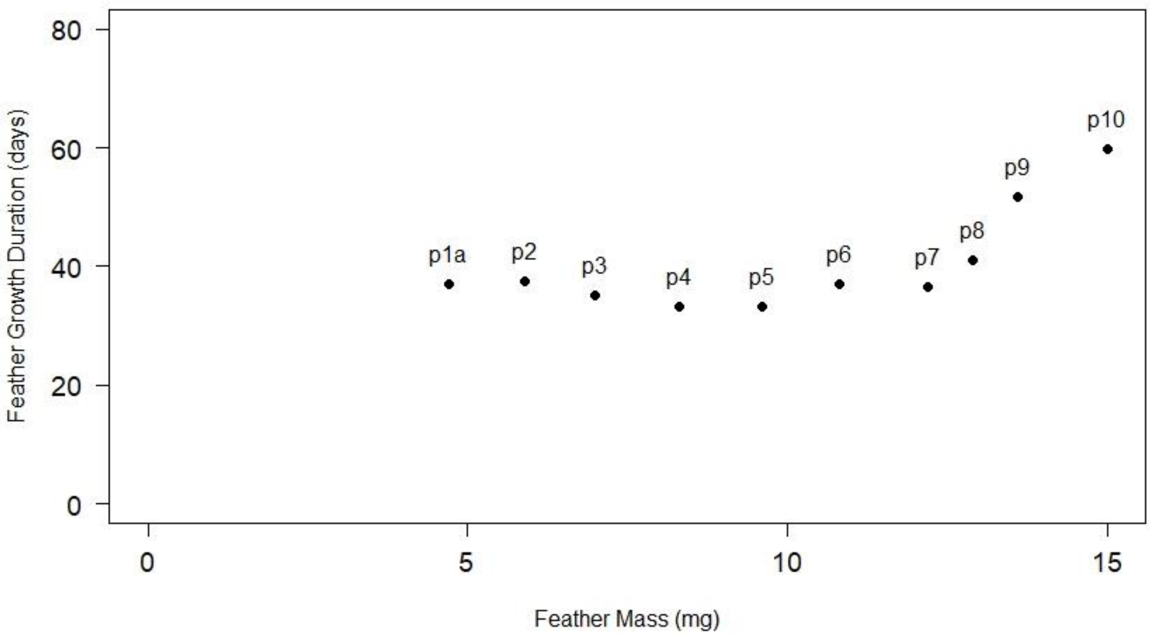

Figure 2: Growth duration (days) of primary feathers (P1-P10) relative to their relative mass for the Australian Pied Oystercatcher in Victoria and South Australia.

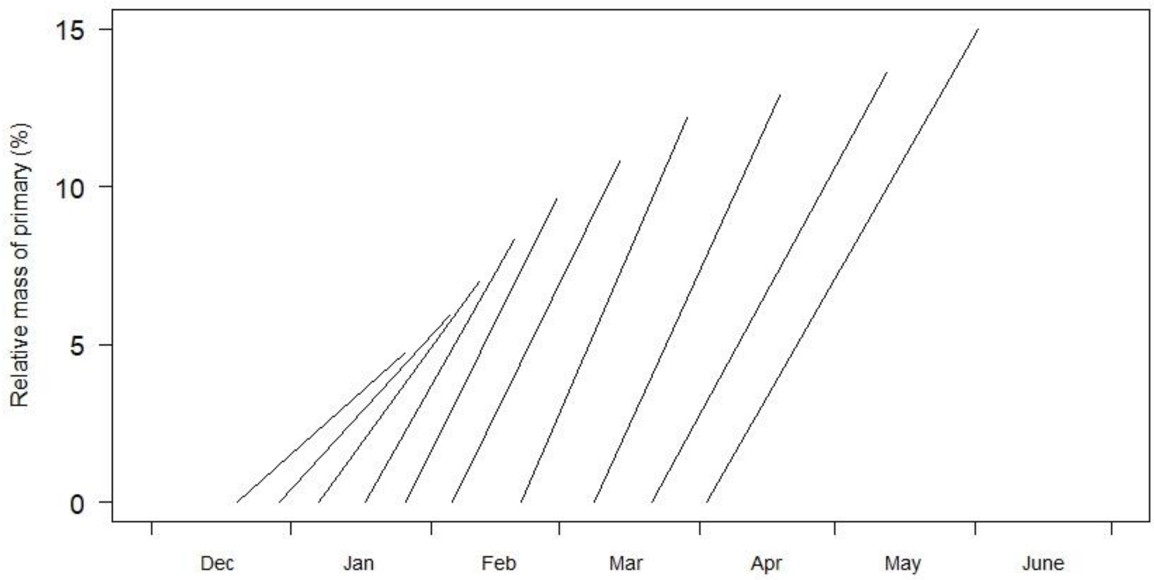

Figure 3: Estimated growth rates of the 10 primary feathers relative to their relative mass (%) for the Australian Pied Oystercatcher in Victoria and South Australia.

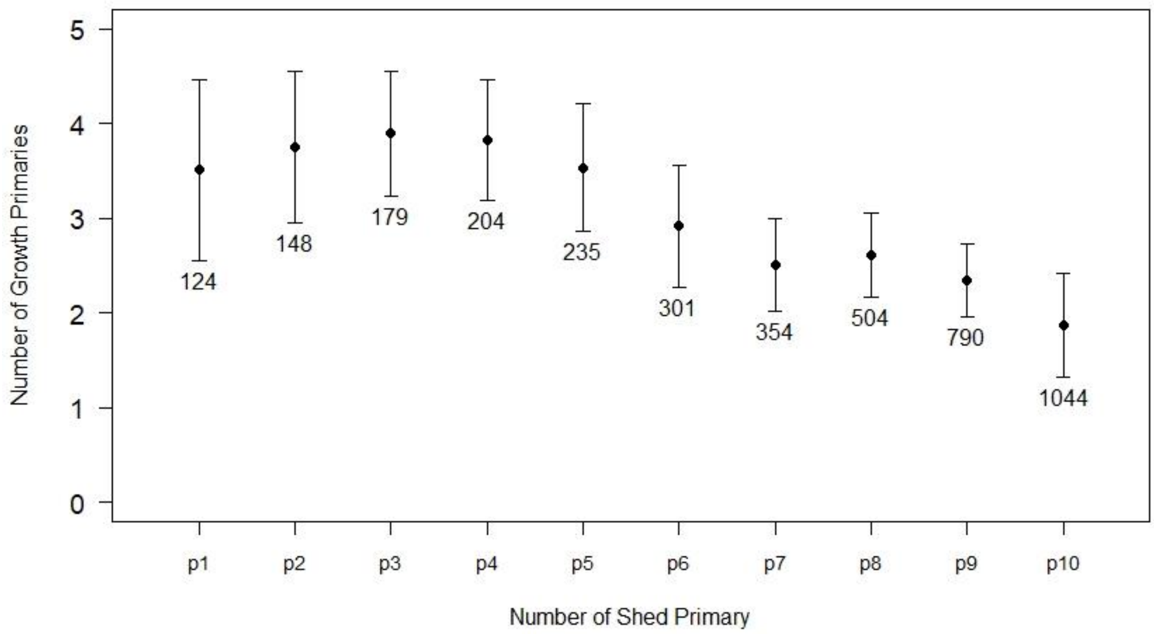

Figure 4: Mean number of simultaneously growing primary feathers for the Australian Pied Oystercatcher in Victoria and South Australia. Sample sizes are given.

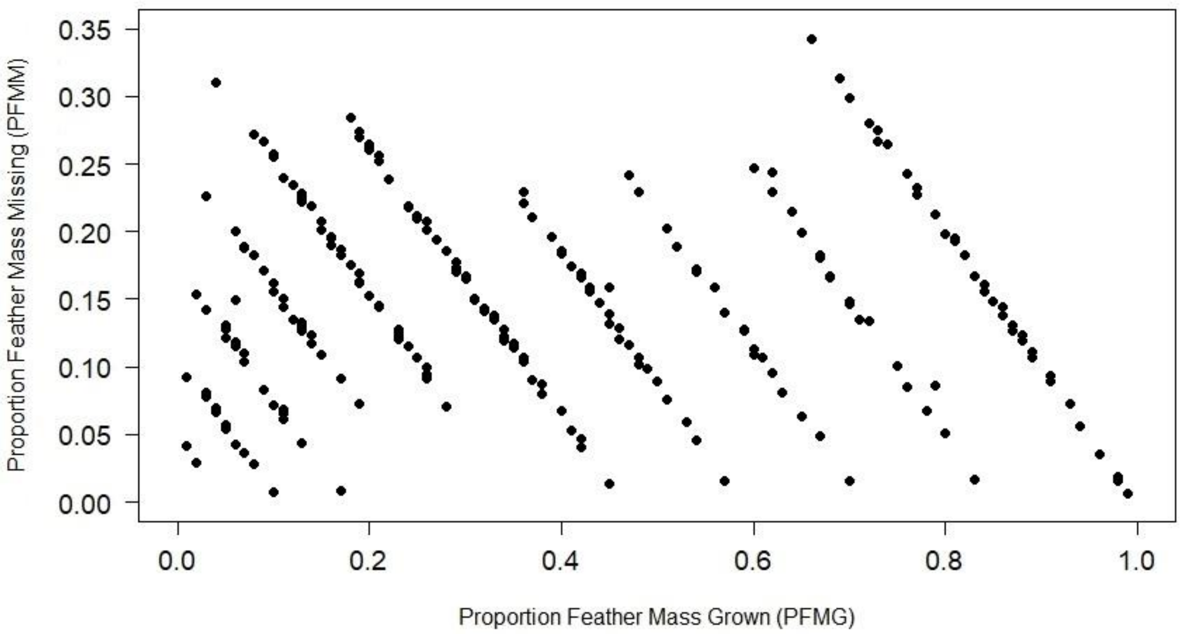

Figure 5: Scatter diagram of Proportion Feather Mass Missing (PFMM) plotted against Proportion Feather Mass Grown (PFMG) for the Australian Pied Oystercatcher in Victoria and South Australia. The lines formed by the points are an artefact of the data collection protocol.

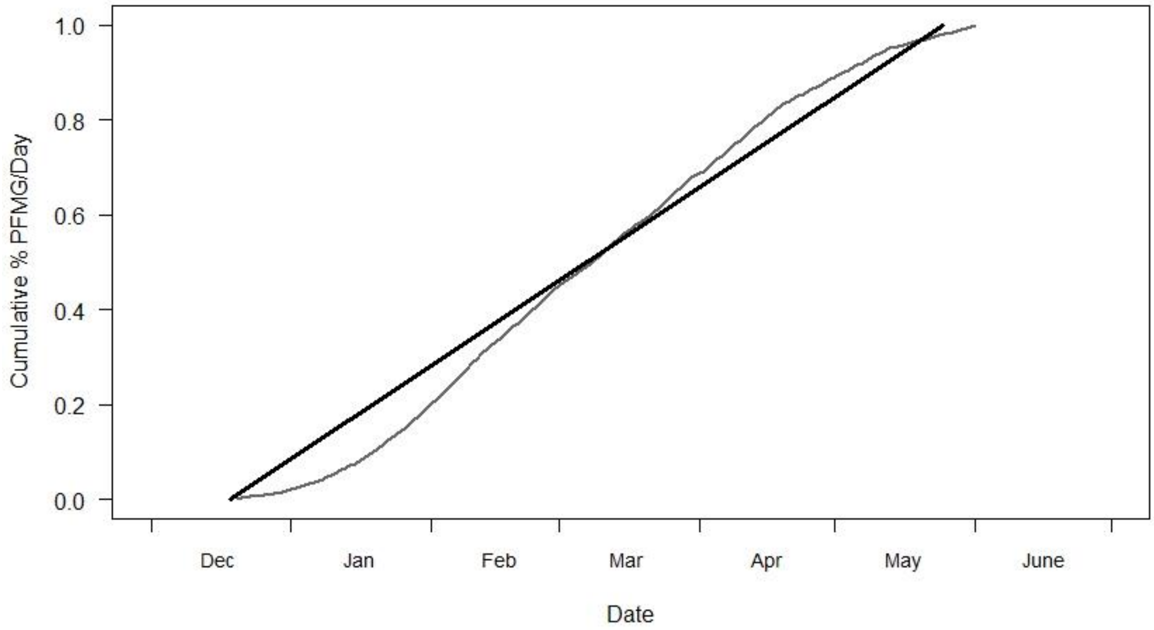

Figure 6: The cumulative Proportion Feather Mass Grown (PFMG) during primary moult is plotted alongside the average timing of moult for the Australian Pied Oystercatcher in Victoria and South Australia. The cumulative curve is calculated using the method described in Remisiewicz et al. (2009). The individual feather growth rates from Table 3 were used to plot the cumulative curve, and the adjusted values for P1 were used (see text).

Chapter 3: Primary moult in the annual cycle of adult African Oystercatchers *Haematopus moquini*

Abstract: African Oystercatchers *Haematopus moquini* are sedentary; the annual schedule has two components, breeding and moult. The Underhill-Zucchini moult model estimated a primary moult duration of 154 days, and mean start and completion dates of 1 April and 2 September. 90% of eggs are laid between mid-November to mid-February; thus, on average, oystercatchers have two to three months between moult completion and egg laying. The completion date confirms an overlap between moult and the period of post-fledging dependence of juveniles on their parents The 154-day primary moult duration spreads the energetic demands of feather production to cope with this overlap and with the fact that primary moult extends through winter when storms make inter-tidal areas inaccessible for days. There are c. 50 quantitative studies of primary moult for migrant waders (Charadrii), this is the third for a resident wader. The other two are in south-eastern Australia: Hooded Dotterel *Thinornis rubricollis* and Sooty Oystercatchers *Haematopus fuliginosus*. The Hooded Dotterel has one of the longest estimated moult durations (203 days); moult and breeding overlap. The annual schedules for Sooty and African Oystercatchers are similar, as is the estimated moult duration: 149 days. Studies of the primary moult of Eurasian Oystercatchers *Haematopus ostralegus* are not fully quantitative, but the duration is estimated to be 100 days, two-thirds of that of the two sedentary oystercatchers. This is likely a consequence of Eurasian Oystercatchers having migration and harsh winter conditions as additional components of the annual schedule, and thus a limited period for primary moult. This study was based largely on photographic records of African Oystercatchers in flight, with contributions by citizen scientists. This paper has two key conclusions: the need for more studies of the moult strategies of Haematopidae and of resident waders; digital photography can be used successfully to study primary moult.

Introduction

Bird species have up to five energy demanding activities to fit into their annual schedules, not necessarily undertaken in this order: breeding, moult, survival through harsh weather conditions, migration from breeding area to non-breeding area, and migration from non-breeding area to breeding area (Prater 1981; Jenni and Winkler 2020; Jackson and Underhill 2022). There is variation in the number, order and timing of these activities, and birds generally undertake moult when and where its energetic costs can be accommodated into the annual schedule and with key exceptions, these activities do not overlap (Jenni and Winkler 2020). Many species do not migrate or move short distances; others migrate away from the breeding area, to places closer to the equator, where harsh winter weather does not occur (Jenni and Winkler 2020). The African Oystercatcher *Haematopus moquini* represents an extreme along this continuum; adults only undertake two of the five activities, breeding and moult. Not only do they not migrate, pairs remain continuously on their breeding territories and defend them aggressively through the non-breeding season (Underhill 2014).

There have been extensive studies of the primary moult of migrant waders (Charadrii). Jackson and Underhill (2022) reviewed the primary moult of 24 species of migrant waders, based on 57 studies which had made use of the moult model of Underhill and Zucchini (1988). In contrast, this is the third study on a resident wader; the others being the Sooty Oystercatcher *Haematopus fuliginosus* in south-eastern Australia and the Hooded Dotterel *Thinornis rubricollis* in Victoria, Australia (Hansen et al. 2009, Rogers et al. 2014, Scott and Underhill submitted this issue). Hooded Dotterels extensively overlap all stages of breeding and primary moult (Rogers et al. 2014). In contrast, African Oystercatchers do not undergo primary moult during incubation and during the period between hatching and fledging of chicks, but their primary moult overlaps the long period, of c. 100 days, of post-fledging dependence of young birds on their parents (Summers and Cooper 1977; Underhill 2014).

Traditionally, studies of primary moult have been based on data collected during bird ringing exercises or from museum specimens. The first studies of primary moult using digital photography were done on Sooty Shearwaters *Puffinus griseus* at sea

(Keijl 2011), on Bar-tailed Godwits *Limosa lapponica* (Conklin and Battley 2012) and on Black Skimmers *Rynchops niger* (Vieira et al. 2017).

In this paper, we use a combination of records obtained using digital photography and traditional methods to estimate the parameters of moult of adult African Oystercatchers using the moult model of Underhill and Zucchini (1988). We compare the results with those of other oystercatchers and Hooded Dotterel.

Methods

African Oystercatchers breed on rocky and sandy shores along the southern African coastline stretching from Ichaboe Island, southern Namibia, to KwaZulu-Natal, South Africa (Underhill 2014). Juveniles, once independent move to nursery areas largely outside the range of breeding adults and return to their natal areas two or more years later, in adult plumage (Hockey et al. 2003; Rao 2005). Many of these birds do not immediately secure breeding territories becoming ("floaters"), but are indistinguishable from adults (Quintana et al. 2021).

African Oystercatchers feed exclusively in the intertidal zone; on rocky shores during low-tide cycles, but on sandy shores they can potentially feed throughout the tide cycle (Parsons 2006). They are expanding in both range and abundance (Kemper et al. 2007; Brown et al. 2019), largely due to the introduction, and subsequent expansion, of the alien mussel *Mytilus galloprovincialis* at the iron-ore terminal at Saldanha Bay where the first ore-carriers arrived in 1977 (Quintana et al. 2021).

Part of the primary moult data were obtained during ringing of adult oystercatchers on Robben Island, Western Cape, South Africa, between 2001 and 2006. We also obtained primary moult data from the ringing records of the Western Cape Wader Study Group (Underhill 1979), and the South African Bird Ringing Unit (SAFRING) .

The bulk of our data were derived from photographs of adult oystercatchers in flight, both our own records and those received from citizen scientists. Our records were made in July to October of 2020 and 2021. We walked along coastlines at Muizenberg, Kommetjie, Soetwater, Bettys Bay and Robben Island at low tide, while the birds were foraging, on clear and sunny days with the wind blowing towards the observer. We each used digital cameras at a fast shutter speed to obtain clear pictures of the birds as they flew.

The photographic strategy was to locate one or more oystercatchers on the shoreline. The photographer focused on the birds, while an assistant walked slowly towards them until they took flight. The photographer attempted to get images of the wings with the 10 primary feathers visible. Multiple photographs were taken of each bird in the group, before moving to the next bird so that individual birds were distinguishable later when the moult was scored.

Adult oystercatchers are readily distinguished from juveniles by their eye-rings and bill colour; this is clear for both birds in the hand and photographic records. Adults have bright orange eye-rings and red bills; whereas juveniles have dull eye-rings and brownish markings on the end of the bill (illustrated in Hockey and Douie 1995). The moult status of the primary feathers of one wing was recorded as a sequence of 10 digits, one for each primary, numbered from proximal to distal, following the standard approach of Ashmole (1962) and Ginn and Melville (1983). Moult scores of 0 and 5 indicate old and new feathers respectively and moult scores of 1–4 indicate the varying stages of growth. This was done for both birds in the hand and for photographs of wings. The date of ringing or photography was recorded as well as the number of days since 1 January. The birds were not sexed.

Estimation of the parameters of primary moult using the Underhill-Zucchini moult model requires a knowledge of the relative masses of the primary feathers. We followed the techniques described by Underhill & Summers (1993) to estimate the relative primary masses. We transformed the moult scores for the 10 primary feathers of each bird into Proportion Feather Mass Grown (PFMG) calculated from the moult sequence and the relative masses of the 10 primary feathers (Underhill and Summers 1993; Underhill and Joubert 1995). We used the Underhill and Zucchini (1988) moult model with data type 2 to estimate the parameters of primary moult, as implemented by Erni et al. (2013). The statistical analyses were conducted in R 4.0.3 (R Core Team 2020).

We also calculated Proportion Feather Mass Missing (PFMM) (Ward et al. 2007; Remisiewicz et al. 2009). PFMM describes the size of the wing gap in the primary feather tract during moult and it takes into consideration the relative masses of the missing primaries. We plotted PFMM against PFMG.

Results

The relative mass of the innermost (smallest) primary was 5.7%, and that of the outermost (heaviest) was 14.8% (Table 1), a ratio of 2.6.

Our data consisted of 588 records of primary moult: 362 were our own photographic records, 72 records were photographic contributions made by citizen scientists from KwaZulu-Natal, the Northern Cape, Eastern Cape and Western Cape and 154 were records made directly from birds.

The sample of 588 adult moult protocols included 150 birds prior to moult (all primaries old), 273 in moult and 165 after moult completion (all primaries new) (Table 2). Figure 1 demonstrates that the data are well scattered through the moult period. The duration of moult was estimated to be 154 days, the mean starting date of moult to be 1 April, and the mean completion date to be 2 September (Table 2). The estimate of the standard deviation of starting date was 28 days, so that the estimated period during which 95% of birds start moult was from 55 days (=1.96×27.9) before the starting date to 55 days after it (from 5 February to 22 May); the equivalent period for completion date was from 9 July to 27 October) (Figure 1, Table 2).

The Proportion Feather Mass Missing (PFMM) was uniform through moult, so that the size of the wing gap did not vary systematically. The average, for birds in moult, was 0.076 (so that on average 7.6% of the feather mass was missing) (Figure 2).

Discussion

Primary moult in the annual schedule of African Oystercatchers

Adult African Oystercatchers have two components to their annual schedules: breeding and moult (Underhill 2014). Detailed quantitative analyses of the timing of breeding at Koeberg Nuclear Power Station (Parsons 2006) and at Robben Island (Braby and Underhill 2007; Tjørve and Underhill 2008a; Quintana et al. 2021) indicate that the period during which 90% of eggs are laid is from mid-November to mid-February, with a median date in late-December. With a mean completion date for moult in early September (Table 2), oystercatchers thus have on average a period of two to three months after primary moult and before egg laying, some of which is occupied by pre-breeding activities, mostly on territories which have been continuously occupied during moult.

Eggs laid late in the breeding season have a smaller probability of hatching and producing fledglings than early eggs (Tjørve and Underhill 2008b), and most chicks have fledged by March (Parsons 2006). Thus, the 95% confidence interval of the date of moult, 5 February to 22 May, with a mean start date of 1 April, coincides well with the end of the breeding season. The earliest birds to moult are potentially failed breeders or from the adult-plumaged population of “floaters” which have not secured breeding territories. Parsons (2006) observed final departure dates from adult territories of 12 fledglings; the median period between hatching and departure was 93 days, with a median departure date of 2 May (and latest observed date was 6 July). The median post-fledging dependence period was 49 days. Thus, as noted by Summers and Cooper (1977) there is substantial overlap between the start of moult and post-fledging dependence on parents.

In the Western Cape, the moult period extends through winter, when storm conditions can make the intertidal area inaccessible for periods of several days.

The overall primary moult period, taken from the lower to upper limits of the estimated 95% confidence interval of primary moult is from 5 February to 27 October, 264 days (8.7 months), essentially the non-breeding period. However, individual birds have an estimated moult duration of 154 days (5.1 months), so they have a “buffer” of 110 days (3.6 months) within the population moult period.

The estimated moult duration of 154 days enables high-quality feathers to be grown (Serra 2001). It is also sufficiently long that the energetic demands of feather production are well spread out, enabling birds to cope with the feeding of post-fledging dependents, and with the risks of winter storms which making food in the inter-tidal zone inaccessible, forcing birds to fast.

The overall timing of moult in the population, 8.7 months from early February to late October, means that the core breeding period is excluded. Breeding in African Oystercatchers is energetically demanding. Females produce an average of 3.5 eggs (27% of their body mass) during the breeding season (range 1–8 eggs, 8–61% of body mass). In spite of incubating eggs for a relatively long period (30 days) to produce nominally precocial chicks, they need to feed them for the next 93 days. During the 40-day period from hatching to fledging, the estimated growth efficiency of oystercatcher chicks is 16.5%; the fledging mass is 470 g, suggesting that each chick needs a total of 2.8 kg of food during the period up to fledging (Tjørve et al. 2007; Tjørve and Underhill 2009). This excludes the period of post-fledging dependence of chicks, when their demands decrease, which likely enables adults to invest some energy in replacing primaries.

The mean Percentage Feather Mass Missing was 0.076 (Figure 2), smaller than the values of 0.10 for the Wood Sandpiper *Tringa glareola* and 0.081 for the Kelp Gull *Larus dominicanus* (Ward et al. 2007, Remisiewicz et al. 2009). The size of the wing gap impacts flight energetics (Hedenström and Sunada 1999); the likely advantage of the relatively small wing gap of the African Oystercatcher is that flight ability is little impaired during the extended moult period.

Primary moult in the African Oystercatcher in relation to other oystercatcher species and the Hooded Dotterel

The estimated primary moult duration of the Sooty Oystercatcher was 149 days, using the Underhill and Zucchini (1988) moult model with PFMG (Hansen et al. 2009), similar to the 154 days for the African Oystercatcher (Table 2). Apart from the fact that Sooty Oystercatchers are less sedentary than African Oystercatchers, with many moving from the offshore islands where they breed to the adjacent mainland (Hansen et al. 2014), the annual schedules of the two species are similar.

The annual schedule of the Eurasian Oystercatcher *Haematopus ostralegus* contrasts sharply with that of the African and Sooty Oystercatchers. Over most its range, the annual schedule includes all five components described above; breeding is followed by migration and then moult, which needs to be completed before the onset of harsh winter weather, and then a return to the breeding grounds (van der Pol et al. 2014). Although there are no analyses of primary moult of the Eurasian Oystercatcher using the moult model of Underhill and Zucchini (1988), several good quality analyses all provide similar results, which converge on a primary moult duration of c. 100 days (Wilson and Morrison 1981; Ginn and Melville 1983). Figure 1 of Dare and Mercer (1974) and Figure 3 of Hulscher (1977) both show that moult start dates of adult Eurasian Oystercatchers lie close to the end of July at sites in Wales and the Netherlands, respectively. Mean completion date is in October, early autumn. Dare and Mercer (1974) described the period of moult in their study area as the period of maximum available food supply of the oystercatchers' two main prey species, cockles *Cerastoderma edule* and mussels *Mytilus edulis*, and described how food supplies shrank as winter approached, with the flesh content of equivalent-sized cockles and mussels in winter being up to 40% less than their autumn values. The duration of moult of the migratory Eurasian Oystercatcher is two-thirds that of the two almost sedentary species; this is likely a consequence of the additional components of the annual schedule.

Hooded Dotterels occur in southern Australia, and breed along the shores of the ocean and inland lakes. Nest failure rates are large, due to predation and disturbance, and repeat nesting is frequent and persistent (Elson and Singor 2008, Rogers et al. 2014). Breeding has been recorded in all months but rarely in winter; however, the peak breeding season is in the austral summer from November to February (Elson and Singor 2008). This peak is subsumed into the average period of primary moult duration (estimated as 19 October to 10 May) (Rogers et al. 2014). The estimated duration of primary moult, 203 days, is one of the longest of 139 species which have been analysed using the Underhill and Zucchini (1988) moult model, and reviewed by Scott and Underhill (submitted this issue). Rogers et al. (2014) suggested that the long duration enables the energetic demands of moult to be sufficiently small that re-nesting is continuously feasible.

From these examples, it is clear that there is considerable variation in moult strategies of the Haematopidae and of the resident waders, likely to be comparable with the diversity of strategies for migrant waders (Jackson and Underhill 2022). It will be of great interest and value to increase the numbers of species from both groups with quantitative moult analyses (Newton 2009).

The use of digital photography to study primary moult

This paper confirms the main finding of Vieira et al. (2017) that systematic photography in the field can be used in the study of primary moult. The points that they made were all applicable to this study. African Oystercatchers are difficult and time-consuming to catch outside the breeding season; digital photography constituted a successful approach to rapidly obtaining a large sample of records. Gently disturbing birds to take flight is far less invasive than the processes involved in trapping and bird ringing, the source of most primary moult data (Vieira et al. 2017).

In terms of the actual scoring process, the most difficult decisions when examining a photograph are to decide whether to allocate a primary moult score of 1 (missing feather or pin) or 2 (when the feather has the appearance of a small brush). This decision is easier with the bird in the hand. The current version of the Erni et al. (2013) algorithm, implemented in R, enables scores of 0, 0.5, 1, 1.5, …, 4.5 and 5 to be allocated to individual primary feathers. We recommended that in these cases, a score of 1.5 be allocated.

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References

Ashmole, N. 1962. The Black Noddy *Anous tenuirostris* on Ascension Island Part 1. General Biology. *Ibis* 103: 235–273.
Braby J, Underhill LG. 2007. Was poor breeding productivity of African Black Oystercatchers on Robben Island in 2004/05 caused by Feral Cats, Kelp Gulls, Mole Snakes or the Sumatra tsunami? *Wader Study Group Bulletin* 113: 66–70.
Brown M, Arendse B, Mels B, Lee AT. 2019. Bucking the trend: the African Black Oystercatcher as a recent conservation success story. *Ostrich* 90: 327–333.
Dare PJ, Mercer AJ. 1974. The timing of wing-moult in the Oystercatcher *Haematopus ostralegus* in Wales. *Ibis* 116: 211–214.
Elson SJ, Singor MJC. 2008. The Hooded Plover breeding data from Western Australia. *Stilt* 53: 6–12
Ens BJ, Underhill LG. 2014. Synthesis of oystercatcher conservation assessments: general lessons and recommendations. *International Wader Studies* 20: 5–22.
Erni B, Oschadleus HD, Bonnevie BT, Altwegg R, Underhill LG. 2013. Moult: An R package to analyse moult in birds. *Journal of Statistical Software* 52: 1−23.
Ginn H, Melville D. 1983. *Moult in birds*. Tring: British Trust for Ornithology.
Hansen BD, Minton CDT, Jessop R, Collins P. 2009. Biometrics, sexing criteria, age-structure and moult of Sooty Oystercatchers in south-eastern and north-western Australia. *Emu* 109: 25–33.
Hansen BD, Minton CDT, Harrison AE, Jessop R. 2014. Conservation assessment of the Sooty Oystercatcher *Haematopus fuliginosus*. *International Wader Studies* 20: 161–172.
Hedenström A, Sunada S. 1999. On the aerodynamics of moult gaps in birds. *Journal of Experimental Biology* 202: 67–76.
Hockey PAR, Douie C. 1995. *Waders of southern Africa*. Cape Town: Struik Winchester.
Hulscher JB. 1977. The progress of wing-moult of Oystercatchers *Haematopus ostralegus* at Drachten, Netherlands. *Ibis* 119: 507–512.
Jackson CHW, Underhill LG. 2022. Primary moult strategies in adult migrant waders (Charadrii). *Wader Study* 129: 126–137.
Jenni L, Winkler R. 2020. *The biology of moult in birds*. London: Helm.
Kemper J, Underhill LG, Crawford RJM, Roux J-P. 2007. Revision of the conservation status of seabirds and seals in the Benguela Ecosystem. In: Kirkman SP (ed), *Final report of BCLME (Benguela Current Large Marine Ecosystem) project on Top Predators as Biological Indicators of Ecosystem Change in the BCLME*. Cape Town: Avian Demography Unit. pp 325–342.
Newton I. 2009. Moult and plumage. *Ringing & Migration* 24: 220–226.
Parsons NJ. 2006. Quantifying abundance, breeding and behaviour of the African Black Oystercatcher *Haematopus moquini*. Unpubl. PhD thesis, University of Cape Town, South Africa.
Prater AJ. 1981. A review of the patterns of primary moult in Palaearctic waders. In: Cooper J (ed), *Proceedings of the symposium on birds of the sea and shore*. Cape Town: African Seabird Group. pp 393–409
Quintana I, Button R, Underhill LG. 2021. African Oystercatchers on Robben Island, South Africa: The 2019/2020 breeding season in its two decadal context. *Wader Study* 128: 209–219.

R Core Team. 2020. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Remisiewicz M, Tree AJ, Underhill LG, Gustowska A, Taylor PB. 2009. Extended primary moult as an adaptation of adult Wood Sandpipers *Tringa glareola* to their freshwater habitats in southern Africa. *Ardea* 97: 271–280.

Rogers KG, Rogers DL, Weston MA. 2014. Prolonged and flexible primary moult overlaps extensively with breeding in beach-nesting Hooded Plovers *Thinornis rubricollis*. *Ibis* 156, 840–849.

Scott A, Underhill LG. submitted. Global review of quantitative studies of primary moult of birds using the Underhill-Zucchini moult model. *Ostrich*.

Serra L. 2001. Duration of primary moult affects primary quality in Grey Plovers *Pluvialis squatarola*. *Journal of Avian Biology* 32: 377–380.

Summers RW, Cooper J. 1977. The population, ecology and conservation of the Black Oystercatcher *Haematopus moquini*. *Ostrich* 48: 28–40.

Tjørve KMC, Underhill LG. 2008a. Breeding phenology of African Black Oystercatchers *Haematopus moquini* on Robben Island, South Africa. *Ostrich* 79: 141–146.

Tjørve KMC, Underhill LG. 2008b. The influence of disturbance and predation on the breeding success of the African Black Oystercatcher, *Haematopus moquini*, on Robben Island, South Africa. *Waterbirds* 31: 83–96.

Tjørve KMC, Underhill LG. 2009. Growth and its relationship to fledging success of African Black Oystercatcher *Haematopus moquini* chicks. *Zoology* 112: 27–37.

Tjørve KMC, Underhill LG, Visser GH. 2007. Energetics of growth in semi-precocial shorebird chicks in a warm environment: the African Black Oystercatcher, *Haematopus moquini*. *Zoology* 110: 176–188.

Underhill LG. 1979. The Western Cape Wader Study Group. *Bokmakierie* 31: 82–85.

Underhill LG. 2014. Assessment of the conservation status of African Black Oystercatcher *Haematopus moquini*. *International Wader Studies* 20: 97–108.

Underhill LG, Joubert A. 1995. Relative masses of primary feathers. *Ringing & Migration* 16: 109–116.

Underhill LG, Summers RW. 1993. Relative masses of primary feathers of waders. *Wader Study Group Bulletin* 71: 29–31.

Underhill LG, Zucchini W. 1988. A model for avian primary moult. *Ibis* 130: 358–372.

Van de Pol M, Atkinson P, Blew J, Crowe O, Delany S, Duriez O, Ens BJ, Hälterlein B, Hötker H, Laursen K, Oosterbeek K, Petersen A, Thorup O, Tjørve K, Triplet P, Yésou P. 2014. A global assessment of the conservation status of the nominate subspecies of Eurasian Oystercatcher *Haematopus ostralegus*. *International Wader Studies* 20: 47–61.

Vieira BP, Furness RW, Nager RG. 2017. Using field photography to study avian moult. *Ibis* 159: 443–448.

Ward VL, Oschadleus HD, Underhill LG 2007. Primary moult of the Kelp Gull *Larus dominicanus vetula* in the Western Cape, South Africa. In: Kirkman SP (ed), *Final report of BCLME (Benguela Current Large Marine Ecosystem) project on Top Predators as Biological Indicators of Ecosystem Change in the BCLME*. Cape Town: Avian Demography Unit. pp 201–204.

Wilson JR, Morrison RIG. 1981. Primary moult in Oystercatchers in Iceland. *Ornis Scandinavica* 12: 211–215.

Tables and Figures

Table 1: Relative masses of primary feathers of African Black Oystercatcher based on both wings of two adult birds. The total mass of the primary feathers of each wing were 3.6 g for each wing of a large bird which had just completed primary moult, and 2.5 g for each wing of a small bird with worn primaries. The relative feather masses of the four wings were computed first and were then averaged for the four available primaries. The coefficients of variation of the relative feather masses were all 3% or less.

Primary	**P1**	**P2**	**P3**	**P4**	**P5**	**P6**	**P7**	**P8**	**P9**	**P10**
Relative mass (%)	5.65	6.69	7.59	8.45	9.37	10.61	11.30	12.14	13.44	14.76

Table 2: Estimated moult parameters for the wing of the African Oystercatcher. The parameters include start date, SD in start date, duration, end date and their corresponding standard errors in brackets, as well as the % PFMG per day and the sample sizes for the stages of moult.

Start date	**SD start**	**Duration (days)**	**End date**	**PFMG per day**	**Pre-moult**	**In-moult**	**Post-moult**
1 April (3.9)	27.9 (2.9)	154.1 (5.6)	2 September	0.0065	150	273	165

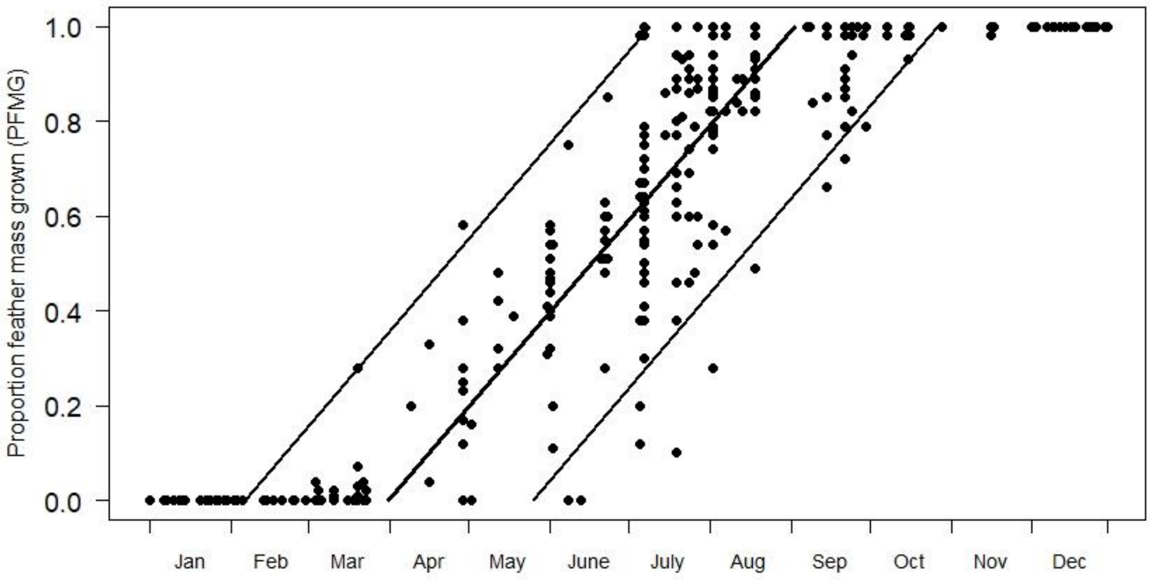

Figure 7: Scatter plot of Proportion Feather Mass Grown (PFMG) for the African Oystercatcher. The points represent the PFMG scores for individual birds plotted against date. The centre line represents the average timing of moult for a bird, and the two outer lines indicate the 95% confidence intervals of birds in moult (see text).

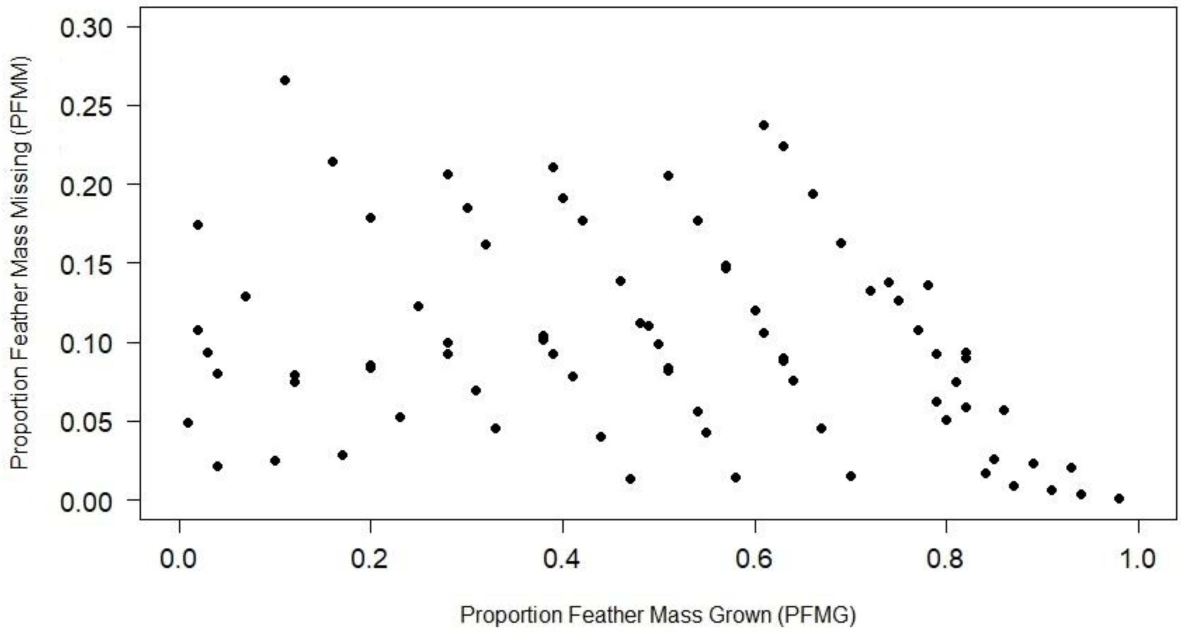

Figure 8: Scatter diagram of Proportion Feather Mass Missing (PFMM) plotted against Proportion Feather Mass Grown (PFMG) for the African Oystercatcher. The lines formed by the points are an artefact of the data collection protocol.

Figure 3: Examples of photographs of African Oystercatchers used in this study. A. Robben Island, Western Cape, South Africa, 14 August 2021. Photographer: Taylyn C Bate. B. Muizenberg, Western Cape, South Africa. 6 July 2020. Photographer: Peter G Ryan.

Photograph A

Photograph B

Chapter 4: Primary moult in the annual cycle of adult Sooty Oystercatchers *Haematopus fuliginosus*

Abstract: The Sooty Oystercatcher *Haematopus fuliginosus* is a largely sedentary wader widespread at low densities along the coasts and offshore islands of Australia. Without the expense of migration, these birds prolong the period of moult within their annual schedule. An analysis of their primary feathers as a tract reveals that adults in the states of Victoria and South Australia moult from 26 December to 10 June as estimated by the Underhill-Zucchini moult model. We also analysed the individual primary feathers, the start date of moult for the first primary was 25 December, while the completion date for the tenth primary was 20 June. Our results correspond with previous studies on moult strategies and also show that there is overlap between breeding and moult, as the birds breed between October and February.

Introduction

This chapter is the first of three secondary chapters in this dissertation dealing with the primary moult of a species of oystercatcher Haematopidae. The Sooty Oystercatcher *Haematopus fuliginosus* is endemic to Australia. In tropical Australia the subspecies *opthalmicus* occurs, and the nominate species occurs in the south, extending to Tasmania.

The Sooty Oystercatcher is widespread along the coast and offshore islands of Australia at low densities. It prefers coastlines with a rock component to entirely sandy shores, and it frequently breeds on offshore islands. It is largely sedentary wader, maintaining territories throughout the year. Breeding is mainly from October to January in the southeast of Australia; those in the northwest breed from July to early September (Marchant and Higgins 1993; Johnstone and Storr 1998; Hansen et al. 2014).

Hansen et al. (2014) presented information on the biometrics of the Sooty Oystercatcher and included a discussion of the primary moult. Using a different approach to the modelling method adopted in this paper, they estimated that the mean start date of primary moult in southeastern Australia was 1 January, and that the duration was between 150 and 180 days. Based on limited data, Hansen et al. (2014) suggested that primary moult in northwestern Australia was about two months earlier than that in southeastern Australia.

In this chapter, using a larger dataset than that available to Hansen et al. (2014), we performed an analysis of the timing of primary moult of adult Sooty Oystercatchers in southeastern Australia and in northwestern Australia. We used the Underhill and Zucchini (1988) moult model, and estimated the timing and duration of primary moult, Our analysis focused on the primary feathers as a tract, and also on the individual primary feathers.

Methods

Data collection

Sooty Oystercatchers have been caught and banded at coastal sites in southeastern and northwestern Australia since 1976. Birds were captured at high-tide roost sites in flocking areas during the non-breeding season using cannon nets. Further details on catching sites and banding methods can be found in Kraaijeveld-Smit et al. (2001, 2004) and Hansen et al. (2009). The age classes were based on bill, leg and eye colour (Hansen et al. 2001). In this analysis, we only used the primary moult scores of adults. Moult scores of Sooty Oystercatchers were represented using the standard method, which describes the 10 primaries of one wing as strings of 10 digits; old feathers are scored as 0, new feathers as 5, and numbers 1–4 representing intermediate stages of growth (Ginn and Melville 1983; Underhill and Zucchini 1988).

Data Analysis

All birds were in continuous moult, without pausing or suspending growth of any primary feathers; thus there was continuous feather growth from moult onset to completion, and the moult model; of Underhill and Zucchini (1988) is therefore appropriate. Our strategy for analysis, described by Serra (2002), focused on estimating the moult parameters of the 10 primary feathers as a tract, as well as those for the 10 individual primary feathers. We estimated the three parameters of primary moult of the model of Underhill and Zucchini (1988): duration, mean starting date and the standard deviation of mean starting date. The estimates are calculated using the moult package developed by Erni et al. (2013), available in R (R Core Team 2020).

The moult model assumes that the progression of moult is quantified by an index that increases linearly with time. This is achieved, at least approximately by converting the moult scores to Proportion Feather Mass Grown (PFMG) (Underhill and Zucchini 1988; Underhill and Joubert 1995). We calculated PFMG using the method developed by Underhill and Summers (1993), which makes use of the relative masses of the primary feathers (Underhill and Joubert 1995). Due to the unavailability of relative masses for the Sooty Oystercatcher, we substituted published relative masses of the 10 primary feathers of eight adult Australian Pied Oystercatchers (Meissner et al. 2018).

We chose 1 October as the reference date in analyses, so that calendar dates were transformed into days since 1 October. Annual records were combined to analyse the data over the timeframe of a single year. The choice of reference date was chosen to be earlier than any observed date for moult onset, and later than any observed date of moult completion. Throughout the sample period, all birds were available for capture, and thus we used data type 2 of Underhill and Zucchini (1988). The moult parameters, estimated using the algorithm developed by Erni et al. (2013), include: mean start date, standard deviation in start date, and duration of primary moult, along with their standard errors. We calculated a completion date based on the mean start date and duration estimates.

The method described by Serra (2002) was used in the estimation of the moult parameters for the individual primary feathers. We achieved the feather-by-feather analysis by dividing the moultscore values into separate columns for primary one (innermost; P1) to primary ten (outermost; P10). We created moult indices for each primary through the allocation of relative feather mass grown. Old feathers scored as 0 were allocated the value of 0, while new feathers scored as 5 were allocated the value of 1, feathers of intermediate growth scored as 1, 2, 3 and 4 were allocated the values 0.125, 0.375, 0.625 and 0.875 respectively (Serra 2002). Complements of the values given to feathers of intermediate growth were allocated for the calculation of the proportion feather mass missing (PFMM), with the value for each feather then being multiplied by the percentage relative feather mass. Moultscore values of 0 and

5 for the feathers were both allocated as 0 for the PFMM calculation. PFMM was determined by summing up the values for feathers of intermediate growth, which quantified the size of the gap in the primaries (Remisiewicz et al. 2009). The overall moult period used for feather analysis comprised of the dates for moult onset of the first primary and moult completion of the last primary.

Remisiewicz et al. (2009) devised an approach to evaluate the linearity of the moult index, requiring the availability of moult parameters for the individual primary feathers.To verify the assumption that the moult index increases linearly, we used the method devised by Remisiewicz et al. (2009) and calculated the cumulative PFMG curve. With the primary relative masses available, and the estimates of the start and completion dates for each feather, we were able to determine the daily contribution of each primary to PFMG during its moult. We created cumulative values using the sum of the daily contributions from the starting date of P1 to the completion date of P10. If the assumptions about the use of PFMG are correct, the relative feather masses will cause the cumulative curve to be linear. The curve should also follow closely against the straight line that joins the start and completion dates for the primary feather tract that are estimated by the moult model (Underhill and Zucchini 1988).

Results

Records for 1071 and 85 adult Sooty Oystercatchers from southeastern and northwestern Australia respectively were available for this analysis (Table 1). The model estimated a mean starting date of 26 December for the primary moult of the Sooty Oystercatchers in southeastern Australia. The standard deviation in starting date for the primary wing was estimated at 22 days. Moult duration was estimated to be 168 days; thus the estimated end date was 10 June (Table 1, Figure 1). For northwestern Australia, the model estimated a mean starting date of 4 October and a standard deviation was estimated to be 26 days. Moult duration was estimated to be 185 days; thus the estimated end date was 6 June (Table 1, Figure 2). The parameter estimates for northwestern Australia had large standard errors, as a result of the small sample size.

For the individual primaries, the shortest estimated duration of moult was 39 days for P3, and P2 and P4 have similar values (Table 2). It was unexpected for P1 to have a estimated duration of 65 days; the lack of reliability in this value is reflected by the standard error (14 days), and also the large standard error of the estimated start (10 days) (Table 2). We infer that the estimated moult parameters for P1 are not reliable, and this is largely due to small sample sizes near the start of moult (Figure 1, Table 2). We can compare these results to the estimates of the parameters of moult for, say, P10, which had small standard errors, and thus can be considered reliable estimate.

It is also clear from the difference in starting dates between P1 and P2 in comparison to differences between starting dates for the rest of the feathers, that the estimates for P1 is not reliable (Table 2). There are 44 days between the starting dates of P1 and P2, while the time between the moult onset of the next four successive feathers was between 10–13 days (Table 2). We tentatively propose an alteration to the estimations for P1, for the purpose of making it compatible with the other more reliable results. We suggest a starting date taken as 12 days prior to the starting date of P2, which is 6 January. This gives a starting date for P1 as 25 December. The average moult duration for P1–P4 is 40 days; thus we suggest that the end date for P1 would be 40 days to the adjusted starting date, 3 February. These adjusted moult parameters seem satisfactory for placement in the context of the rest of the primary moult parameters. Table 2 includes these adjusted values for P1.

With the adjusted dates, the feather growth period for P1 is between 25 December and 3 February. The growth durations (Table 2, Figure 3) are similar values between P1 and P3, from which they increase steadily to P10, with a now close pattern to their relative feather masses. The feather growth period for P10 is estimated as 15 April to 20 June (Table 2).

The starting date for P1 estimated by the model was 23 November, which has a substantial difference of 33 days to that estimated for the primary tract as a whole of 26 December (Table 1). Thus, our adjustment to P1 can be further supported, as the new date of 25 December (Table 2) differs by one day to the estimated starting date for the primary feather tract (Table 1). There was a difference of 10 days between the completion dates estimated for the primary tract (10 June; Table 1) and P10 (20 June; Table 2).

The individual primary feathers overlapped their growth periods by between 20–44 days (Figures 4 and 5). Feathers P1 and P2 had the shortest overlap of 21 days, while P9 and P10 had the longest overlap of 43 days. With the adjustment made to P1 as mentioned above, the primary feathers followed a uniform growth rate which corresponds to their relative feather masses (Figure 4). An increase in relative feather mass corresponds with a decrease in the number of primaries growing simultaneously. During the growth of P1 to P5 the birds can grow slightly over four feathers simultaneously, while for P6 to P8 this drops to between 3–4 feathers simultaneously, and for P9 and P10 the birds grow less than three feathers at the same time (Figure 5).

With our adjustment to the start date, duration, and completion date for P1, the moult periods for the primary tract and the feather-by-feather analysis differ by five days in duration; the duration implicit in the analysis of the individual primary feathers was 173 days, while that of the full primary tract was 168 days. The standard errors in the model with the full primary tract (Table 1) are smaller than those of the individual feathers (Table 2) and it therefore is appropriate to use the estimates from the full tract model as first choice for the results, and regard the results from Table 2 as confirmatory.

An average proportion of 0.11 of the primary feather mass was missing from the Sooty Oystercatchers during their moult period (Figure 6). The largest percentage of feather mass missing (PFMM) was identified as 0.39 in a bird towards the end of moult growing its last five primaries simultaneously (a moult score of 5555542221 on 25 April). The second and third largest values for PFMM were 0.35 (a bird with moult score 5555554211 on 7 May) and 0.31 (a bird with moult score 5555554311 on 25 April), respectively. The correlation coefficient between PFMG and PFMM was calculated to be -0.5894.

It is clear that the cumulative Proportion Feather Mass Grown (PFMG) has a fairly uniform growth rate (Figure 7), which corresponds with the estimated start and completion dates of moult of 26 December to 10 June (Table 1). The cumulative PFMG calculation makes use of the primary feather growth rates, which include the adjusted parameters for P1 (Table 2).

Discussion

Without the expense of migration within their annual schedules, Sooty Oystercatchers, a resident, can devote more time and energy, in comparison to migrant waders, towards the annual cycle stages of breeding and moult. The breeding season for birds in southeastern Australia is between October and January, rarely extending into February (Marchant and Higgins 1993; Hansen et al. 2014). However, the mean starting date of moult of adults was 26 December (Table 1), suggesting that some adults commence moult before chicks fledge. This should be checked through fieldwork.

The estimated duration in southeastern Australia was 168 days, generating an average end date for primary moult of 10 June. However, breeding does not commence until October, so that there is an almost five-month period when the Sooty Oystercatchers are neither breeding nor moulting. It needs to be investigated whether there is some constraint, for example, a food shortage in this region during this period.

Our results suggest that primary moult in northwestern Australia is approximately three months earlier than is southeastern Australia (Table 2), a month longer than the provisional suggestion of two months made by Hansen et al. (2009). Unlike in southeastern Australia, there appears to be little overlap between the end of breeding (early September) and the mean moult start date (4 October) (Table 2). The estimated duration in northwestern Australia was 185 days, yielding a mean end date for primary moult of 6 April. Breeding commences three months later (rather than almost five, as it does in southeastern Australia).

These observations about the differences in the annual cycle of the Sooty Oystercatcher between the two subspecies in southeastern and northwestern Australia are tentative. They deserve further attention.

Acknowledgements

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References

Erni B, Bonnevie BT, Oschadleus H-D, Altwegg R, Underhill LG. 2013. Moult: an r package to analyse moult in birds. *Journal of Statistical Software* 52: 1–23.
Ginn H, Melville D. 1983. *Moult in birds*. Tring: British Trust for Ornithology.
Hansen BD, Minton CD, Harrison AE, Jessop R. 2014. Conservation assessment of the Sooty Oystercatcher *Haematopus fuliginosus*. *International Wader Studies* 20: 161–172.
Hansen BD, Minton CD, Jessop R, Collins P. 2009. Biometrics, sexing criteria, age-structure and moult of Sooty Oystercatchers in south-eastern and north-western Australia. *Emu-Austral Ornithology* 109: 25–33.
Hedenström A, Sunada S. 1999. On the aerodynamics of moult gaps in birds. *Journal of Experimental Biology* 202: 67–76.
Johnstone RE, Storr GM. 1998. *Handbook of western Australian birds*, vol. 1. Perth: Western Australian Museum.
Marchant S, Higgins P (eds). 1993. *Handbook of Australian, New Zealand and Antarctic Birds*. Melbourne: Oxford University Press.
Meissner W, Zaniewicz G, Gogga P, Pilacka L, Klaassen M, Minton C. 2018. Relative mass of flight feathers in waders–an update. *Wader Study* 125: 205–211.
R Core Team. 2020. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.
Remisiewicz M, Tree AJ, Underhill LG, Gustowska A, Taylor PB. 2009. Extended primary moult as an adaptation of adult Wood Sandpipers *Tringa glareola* to their freshwater habitats in southern Africa. *Ardea* 97: 271–280.
Serra L. 2002. Cold winters vs long journeys: adaptations of primary moult and body mass to migration and wintering in the Grey Plover *Pluvialis Squatarola.* PhD thesis, University of Cape Town, South Africa.
Underhill LG, Joubert A. 1995. Relative masses of primary feathers. *Ringing & Migration* 16: 109–116.
Underhill LG, Summers R. 1993. Relative masses of primary feathers in waders. *Wader Study Group Bull* 71: 29–31.
Underhill LG, Zucchini W. 1988. A model for avian primary moult. *Ibis* 130: 358–372.

Tables and Figures

Table 1: Estimated moult parameters for the Sooty Oystercatcher from southeastern and northwestern Australia. The three parameters of the model include start date, standard deviation of start date and duration; the end date is computed as start date plus duration. Standard errors of the estimated parameters are given in brackets. The Proportion Feather Mass Grown (PFMG) per day is calculated as the relative feather mass divided by duration, and is used in the production of Figure 7 for the birds from southeastern Australia. The sample sizes for the three stages of moult are given.

State	Start date	SD start da te	Duration (days)	End date	PFMG per day	Pre-moult	In-moult	Post-moult
Southeastern Australia	26 December (3.2)	22 (2.7)	167.7 (3.8)	10 June	0.006	1	732	338
Northwestern Australia	4 October (9.2)	26 (5.7)	184.9 (7.9)	6 April	0.0054	0	77	8

Table 2: Estimated moult parameters for the primary feathers (1-10) of the Sooty Oystercatcher from southeastern Australia. The three parameters of the model are start date, standard deviation of start date and duration; the end date is computed as start date plus duration. Standard errors of the estimated parameters are given in brackets. The Proportion Feather Mass Grown (PFMG) per day is calculated as the relative feather mass divided by duration, and is used in the production of Figure 7. The sample sizes for the three stages of moult are given. The gap is the estimated time interval between the primary in the row and the following row, for an explanation of P1 adjusted, see text.

Primary	Feather mass	Start date	SD start	Duration (days)	End date	PFMG per day	Pre-moult	In-moult	Post-moult	Gap
P1	4.7	23 November (9.7)	43.6 (13.0)	64.5 (14.0)	26 January	0.0007	1	38	1032	11
P1 adjusted		25 December		40	3 February	0.0012				
P2	5.9	06 January (5.7)	22.8 (6.1)	39.4 (7.7)	14 February	0.0015	4	38	1029	13
P3	7.0	19 January (4.2)	17.4 (3.8)	38.8 (5.4)	27 February	0.0018	10	52	1009	10
P4	8.3	28 January (3.4)	18.4 (3.0)	39.6 (5.0)	08 March	0.0021	17	65	989	11
P5	9.6	08 February (3.0)	18.8 (2.6)	40.2 (4.7)	19 March	0.0024	37	73	961	11
P6	10.8	20 February (2.7)	19.1 (2.4)	42.5 (4.5)	02 April	0.0025	56	100	915	13
P7	12.2	04 March (2.5)	20.8 (2.3)	42.6 (4.7)	15 April	0.0029	80	148	843	14
P8	12.9	18 March (2.4)	23.7 (2.2)	48.0 (4.9)	05 May	0.0027	121	253	697	14
P9	13.6	01 April (2.2)	22.8 (1.8)	56.2 (4.3)	27 May	0.0024	178	381	512	14
P10	15.0	15 April (2.0)	21.9 (1.4)	66.2 (4.0)	20 June	0.0023	252	481	338	

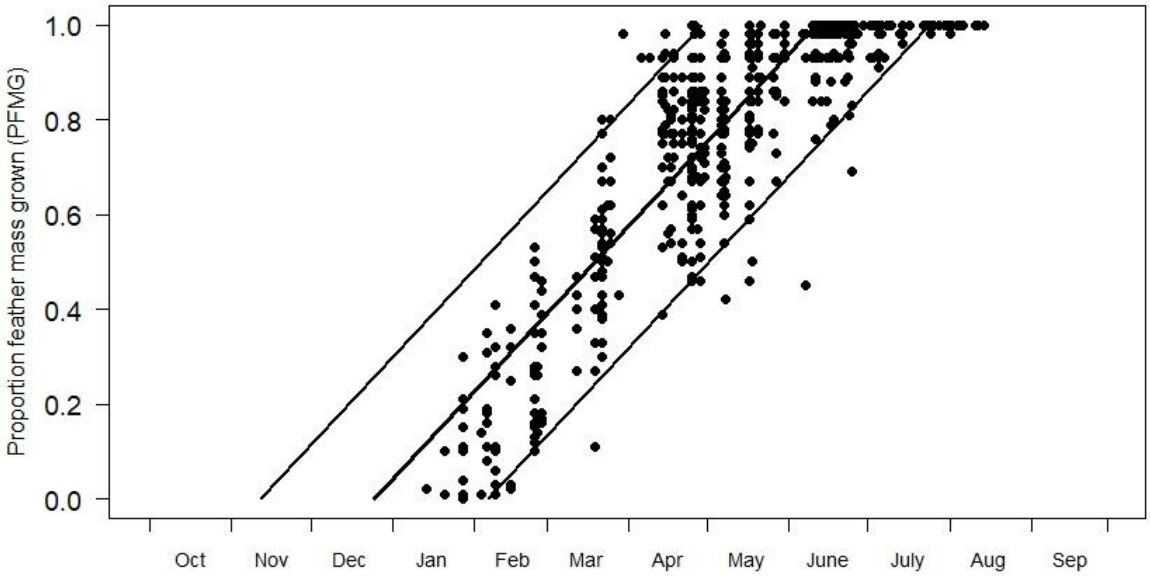

Figure 1: The Proportion Feather Mass Grown (PFMG) distributed against the timeframe of one year for the Sooty Oystercatcher from southeastern Australia. The center line represents the average timing of moult for a bird, and the two outer lines indicate the 95% confidence intervals of birds in moult. The points represent the individual PFMG scores for the three stages of moult.

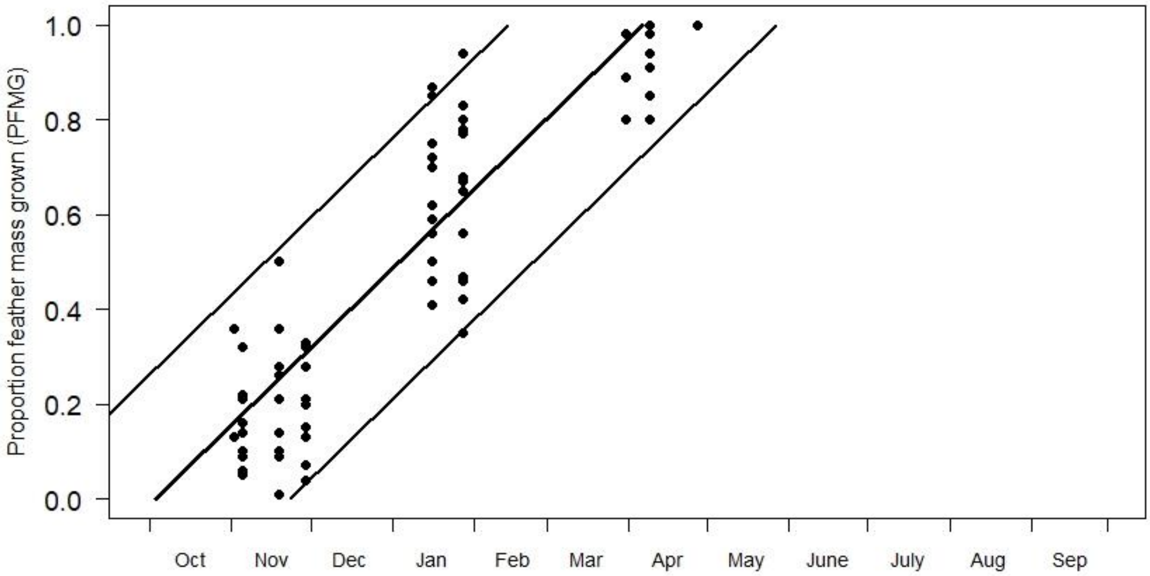

Figure 2: The Proportion Feather Mass Grown (PFMG) distributed against the timeframe of one year for the Sooty Oystercatcher from northwestern Australia. The center line represents the average timing of moult for a bird, and the two outer lines indicate the 95% confidence intervals of birds in moult. The points represent the individual PFMG scores for the three stages of moult.

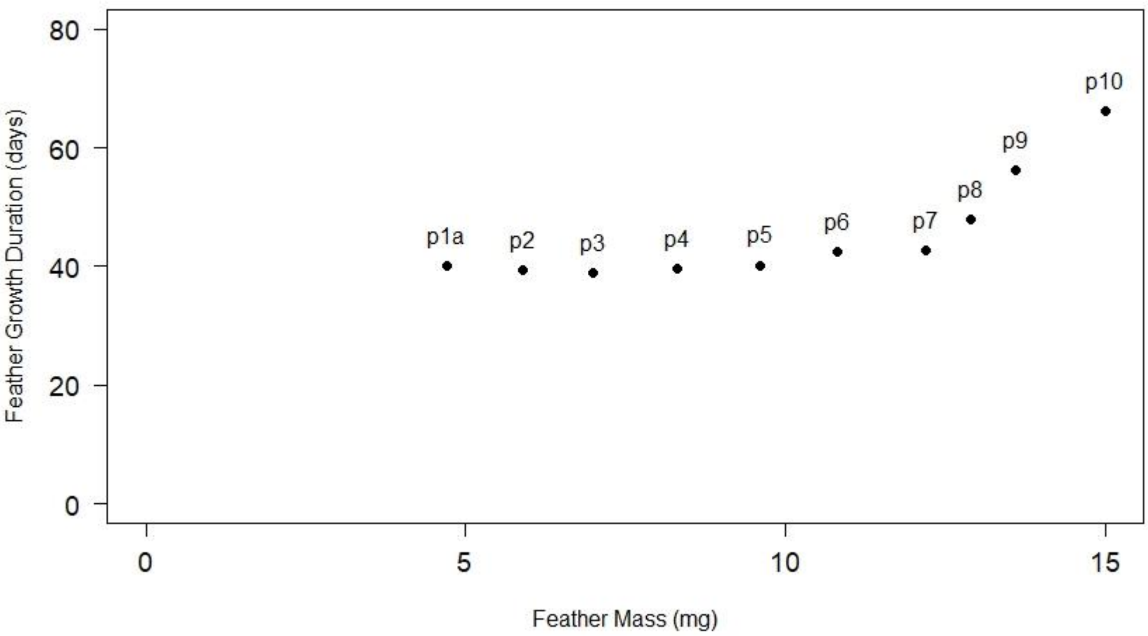

Figure 3: Growth duration (days) of primary feathers (P1-P10) relative to their relative mass for the Sooty Oystercatcher from southeastern Australia. The adjusted value for P1 is used (P1a).

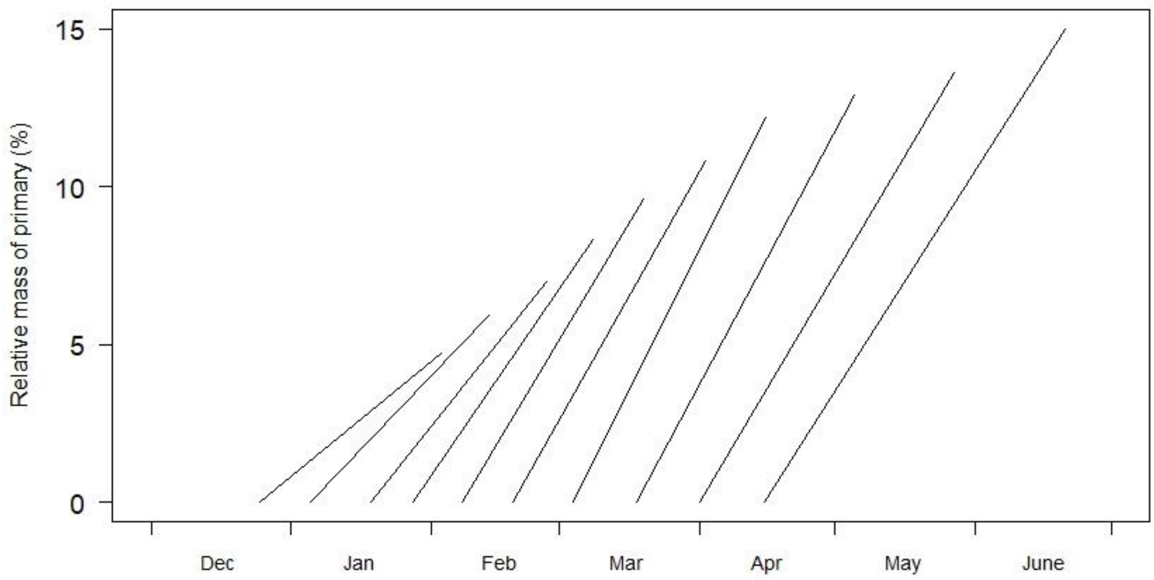

Figure 4: Estimated growth rates of the 10 primary feathers relative to their relative mass (%) for the Sooty Oystercatcher from southeastern Australia. The adjusted value for P1 is used.

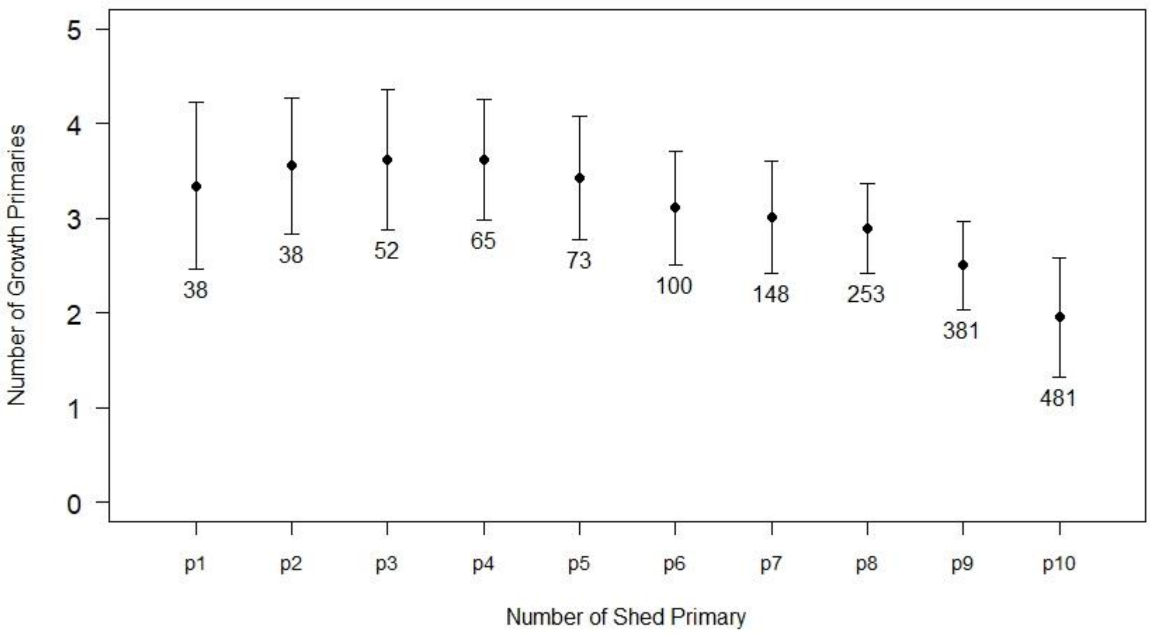

Figure 5: Mean number of simultaneously growing primary feathers for the Sooty Oystercatcher from southeastern Australia. Sample sizes are given.

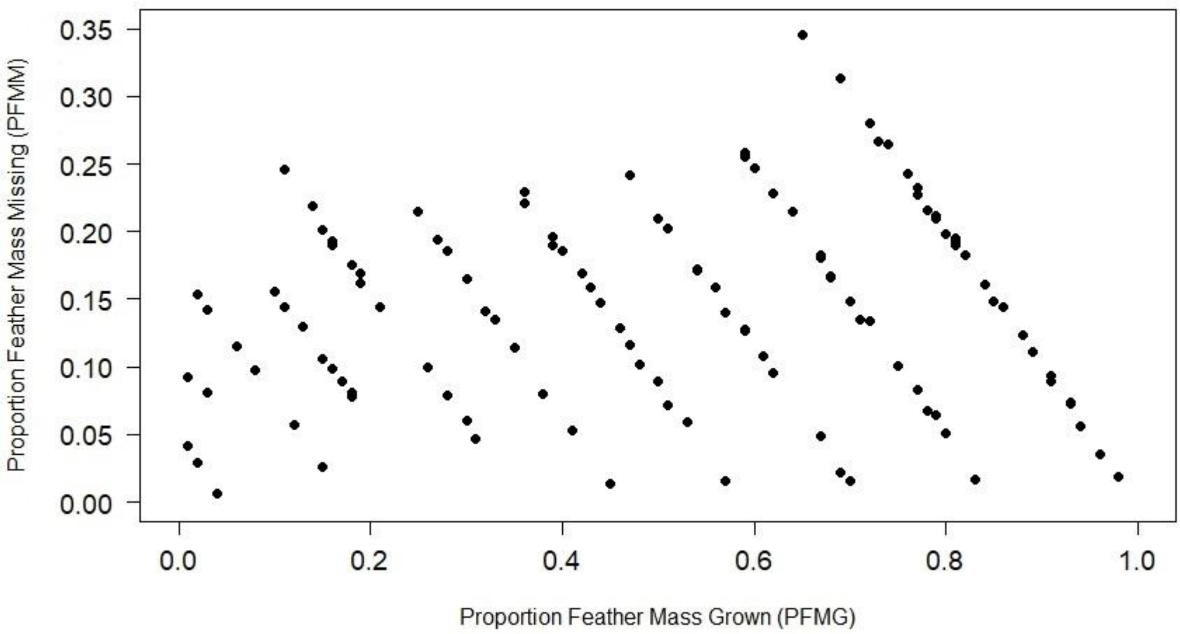

Figure 6: Scatter diagram of the proportion feather mass missing (PFMM) plotted against proportion feather mass grown (PFMG) for the Sooty Oystercatcher from southeastern Australia. The lines formed by the points are an artefact of the data collection protocol.

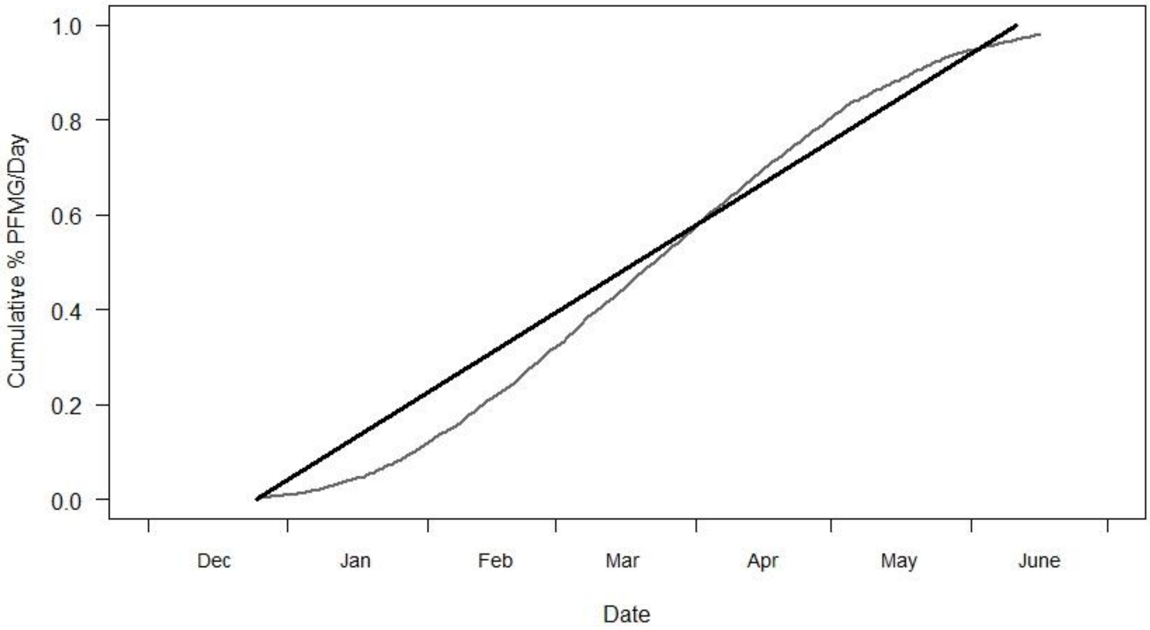

Figure 7: The cumulative proportion feather mass grown (PFMG) during primary moult is plotted alongside the average timing of moult for the Sooty Oystercatcher from southeastern Australia. The cumulative curve is calculated using the method described in Remisiewicz et al. (2009). The individual feather growth rates from Table 2 were used to plot the cumulative curve, and the adjusted values for P1 were used (see text).

Chapter 5: Primary moult of the South Island Pied Oystercatcher *Haematopus finschi*

Abstract: The South Island Pied Oystercatcher *Haematopus finschi* is a migratory species endemic to New Zealand. The birds breed exclusively inland in the spring and early summer, with peak egg-laying from mid-August to mid-September. Migration takes place after breeding between December and early February as the birds fly to large tidal bays in the North Island. An estimate of the start and completion of moult suggests that 95% of adult birds moult between 8 December to 8 February, which confirms earlier studies that moult follows breeding. This two-month period is long enough to produce good quality feathers, but possibly represents a constraint on their annual cycle. Birds return to the breeding grounds from early June to early August. Juveniles are estimated to moult between 22 September to 24 March, while second-year birds are estimated to moult between 22 November to 29 May. Juveniles do not migrate with the adults, but some second-year birds join them. As the birds mature, their annual schedules align with that of the adults.

Introduction

This chapter is the second of three secondary chapters in this dissertation dealing with the primary moult of a species of oystercatcher Haematopidae. Of the five species considered here, the South Island Pied Oystercatcher *Haematopus finschi* is the only one that can be described as a migrant and the only one that breeds almost exclusively inland (Marchant and Higgins 1993; Sagar and Veitch 2014). It is endemic to New Zealand, breeding in spring and early summer, mostly on the braided river systems east of the Southern Alps, to an altitude of 1800 m. After breeding, birds leave these inland breeding areas and most migrate to the large tidal bays in the Auckland area of the North Island.

Knowledge of primary moult is limited (Baker 1975; Marchant and Higgins 1993; Sagar and Veitch 2014). Prior to this study, published information stated that adults moulted after their breeding season and northwards migration from about January to

April, that the primary moult of second-year birds was about two months earlier than that of adults, and that first year birds moulted their primaries in spring (Baker 1975; Marchant and Higgins 1993).

The aim of this paper is to improve and refine our knowledge of the timing of primary moult of this species. We also place the timing of moult into the context of the other two main events in the annual cycle, breeding and migration.

Methods

Data collection

The South Island Pied Oystercatcher dataset contains 935 records, mostly collected between the years 2020–2022 by members of the wader study group based in Auckland. The data included a rich set of observations from each bird; the two of interest to this analysis were primary moult and age category. Three age categories were used in this analysis: juveniles (284), second-year birds (179) and adults (472).

The banders followed the standard method of data collection for moult scores which was devised by Ashmole (1962) and has been in use continuously since then: the status of the primary feathers of one wing of each bird handled were summarized by 10 digits, with old feathers scored as 0, new feathers scored as 5, and growing feathers represented by 1–4, based on their stage of growth (Ginn and Melville 1983; Underhill and Zucchini 1988).

Data Analysis

Birds were observed to be in continuous moult; no suspension or pausing of feather growth took place during the moult period; The date of capture was chosen as 1 August, and we analysed moult over the timeframe of a single year. We approached analysis using the method of maximum likelihood to analyse the 10 primaries as a tract (Underhill and Zucchini 1988; Serra 2002; Erni et al. 2013). Our study made use of the Underhill and Zucchini (1988) moult model from the moult package in R (R Core Team 2020) to estimate the three parameters of moult. In this method, moult duration is assumed as a single parameter, and the starting dates of moult follow a normal distribution and have a mean and standard deviation.

We used Proportion Feather Mass Grown (PFMG) as the moult index so that the moult index may increase linearly with time (Underhill & Joubert 1995). PFMG was calculated using the estimated moult parameters for the individual primary feathers (Underhill and Summers 1993; Remisiewicz et al. 2009). Relative feather masses for the South Island Pied Oystercatcher were provided for this calculation (Table 1).

Data analysis was conducted using the Underhill and Zucchini (1988) moult model for estimation of the three moult parameters for each of the three age categories. The algorithm developed by Erni et al. (2013) in R (R Core Team 2020) was used to estimate the parameters using the method of maximum likelihood. In this model, moult duration is treated as a single parameter, and the moult starting dates follow a normal distribution, with a mean and standard deviation. We analysed the 10 primary feathers as a tract, as described by Serra (2002).

Proportion Feather Mass Grown (PFMG), calculated in the standard way, was used as the moult index (Underhill and Joubert 1995). The PFMG calculation required the relative feather masses for the Variable Oystercatcher (Table 1). Data type 2 was used in the models because all birds were available for capture throughout the period of sampling.

During moult, the size of the gap in the primary feathers is represented by the Proportion Feather Mass Missing (PFMM). This was calculated for all birds in moult as described by Remisiewicz et al. (2009). PFMM was plotted against PFMG.

Results

The Underhill-Zucchini Moult model estimated the mean start date for juvenile SIPO birds as 22 September, with the standard deviation in start date as 28 days. The duration was estimated to be 185, so that the estimated end date was 24 March (Table 2, Figure 1). Second-year birds were estimated to have a mean starting date of 22 November, with a standard deviation in start date of 32 days, an estimated duration of 188 days, and a mean end date of 29 May (Table 2, Figure 2). For adults, the estimated mean start date was 8 January, with a standard deviation of 16 days and an estimated moult duration of 126 days, so that the mean end date was 13 May (Table 2, Figure 3). From these results it follows that the mean start date estimations for juveniles was 62 days earlier than that of second-years, and that second-year birds started moult, on average 47 days earlier than adults.

During the moult period, the average proportion of feather mass missing was 0.12 (Figure 4). The largest proportion of feather mass missing were two values of 0.29: one had its primary moult recorded as 1111100000 on 31 January, and the second as 3222210000 on 6 February. The correlation between percentage feather mass missing and percentage feather mass grown was –0.127, which is not significant.

Discussion

These results confirm, quantify and refine the broad patterns of primary moult described by Baker (1975) and Marchant and Higgins (1993). Adults breed inland in the South Island as well as Hawkes Bay and Wairarapa in the North Island; the peak egg-laying period is early spring, from mid-August to mid-September; most clutches laid later in spring and into early summer are replacement clutches (Sagar et al. 2000). Breeding adults leave their inland territories between December and early February and most migrate directly to their coastal non-breeding areas, settling in the northern South Island and northern North Island. A large proportion move to the northern part of the North Island, which lies at a distance of 600–1000 km from the breeding range.

From Table 2, the estimated mean start date and standard deviation suggested that the period during which 95% of adults commence primary moult is the two-month period from 8 December to 8 February, confirming earlier observations that moult takes place after breeding (Baker 1975; Marchant and Higgins 1993). The moult model suggests that primary moult is completed in the relative short time period of 126 days (see Chapter 7 for a comparison of moult durations of the five species considered in this dissertation), so that half the oystercatchers have completed moult by 13 May (and 97.5% by 13 June). This fits neatly with the period of southward migration, the return to the breeding grounds, starting in early June, peaking in late July and continuing into early August (Marchant and Higgins 1993). We conclude that adult South Island Pied Oystercatchers utilize most of the period on the non-breeding grounds to undertake primary moult, and that this possibly represents a constraint on their annual cycle. On the other hand, the estimated primary moult duration of 126 days is adequate to produce high-quality primaries (Serra 2001; Jackson and Underhill 2022).

Juveniles arrive from the breeding grounds from midsummer onwards, and form steadily increasing proportions in the populations in non-breeding areas. They do not migrate south when the breeding adults depart in late winter. They start their first primary moult soon after the adults leave. The estimated mean start date is 22 September (Table 2). The estimated standard deviation parameter is 28 days, implying that the moult of juveniles is not synchronized; these results suggest that 95% of juveniles commence primary moult between 30 July and 16 November; there are no time constraints on this moult, and it is estimated to take 185 days, finishing on average on 24 March of the following year, after the adults have returned from the breeding areas, followed by the new cohort of juveniles. The juveniles from the previous breeding season become classified as second-year birds.

Some second-year birds migrate southwards with the adults, but a proportion remain on the non-breeding areas. These birds undertook a second primary moult, with an estimated mean start date of 22 November, prior to the return of the breeding adults. This start date is 47 days before the estimated starting date of primary moult of adults. This difference provides a more precise quantification than the “two months” suggested by Baker (1975) between the start of moult of second-year birds and adults; Baker’s (1975) estimate was based on a minimal volume of data, and is remarkably close to the result obtained here. The moult of second-year birds has an estimated duration of 188 days, but with a relatively large standard error. It is likely that the end date of this moult is more similar to the end date of the primary moult of adults than the results in Table 2 suggest (13 May for adults 29 May for second-year birds). This pattern then enables the second-year birds to merge their annual cycles with that of breeding adults.

The juvenile birds begin moult the earliest, starting in late September and completing in late March (Table 2, Figure 1). About two months after the juveniles start, the second-year birds will begin moulting from late November to late May (Table 2, Figure 2). Both groups spend a significantly longer time (about two months longer) in moult in comparison to the adults. As the birds mature, moult is started later and later to prepare for the breeding stage of their lives. The adult birds in this study start moult in early January and complete in mid-May (Table 2, Figure 3). It is probable that the adult moult timing and duration is due to preparation for their next stage of life, as they will need to devote less time and energy towards moult and make space for migration and the breeding period.

There is a clear pattern of the schedules of the non-breeding birds in this study slowly aligning with the moult period of breeding adults as the birds mature. Adults are known to moult between January and April, then migrate between early June and December to the breeding grounds. Pre-breeding (pre-alternate) moult takes place from August to September, and egg-laying will start sometime from early August to mid-November. Adults will also undertake a post-breeding (pre-basic) moult (Baker 1974, 1975; Marchant and Higgins 1993; Sagar and Veitch 2014).

During the moult period, the wing gap is an important indicator of the limitations placed on the individual bird that affect flight ability (Hedenström and Sunada 1999). The wing gap varies in size depending on the species. For the South Island Pied Oystercatchers, the wing gap of 0.12 during moult is larger in comparison to another resident wader species, the Wood Sandpiper *Tringa glareola* of which studies reveal a wing gap of 0.10 during moult (Remisiewicz et al. 2009). It would be interesting to discover if the large wing gap for the young group of birds in our study is also consistent among breeding adults for this species.

References

Ashmole N. 1962. The Black Noddy *Anous tenuirostris* on Ascension Island Part 1. General Biology. *Ibis* 103: 235–273.

Baker AJ. 1974. Criteria for aging and sexing New Zealand oystercatchers. *New Zealand journal of marine and freshwater research* 8: 211–221.

Baker AJ. 1975. Morphological variation, hybridization and systematics of New Zealand oystercatchers (Charadriiformes: Haematopodidae). *Journal of Zoology* 175: 357–390.

Erni B, Bonnevie BT, Oschadleus H-D, Altwegg R, Underhill LG. 2013. Moult: an r package to analyse moult in birds. *Journal of Statistical Software* 52: 1–23.

Ginn H, Melville D. 1983. *Moult in birds*. Tring: British Trust for Ornithology.

Hedenström A, Sunada S. 1999. On the aerodynamics of moult gaps in birds. *Journal of Experimental Biology* 202: 67–76.

Jackson CH, Underhill LG. 2022. Primary moult strategies in adult migrant waders (Charadrii). *Wader Study* 129: 126–137.

Marchant S, Higgins P (eds). 1993. *Handbook of Australian, New Zealand and Antarctic Birds*. Melbourne: Oxford University Press.

R Core Team 2020. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.
Remisiewicz M, Tree AJ, Underhill LG, Gustowska A, Taylor PB. 2009. Extended primary moult as an adaptation of adult Wood Sandpipers *Tringa glareola* to their freshwater habitats in southern Africa. *Ardea* 97: 271–280.
Sagar P, Geddes D, Banks JC, Howden P. 2000. Breeding of South Island pied oystercatchers (Haematopus ostralegus finschi) on farm land in mid-Canterbury, New Zealand. *Notornis* 47: 71–81.
Sagar P, Veitch D. 2014. Conservation assessment of the South Island oystercatcher *Haematopus finschi*. *International Wader Studies* 20: 155–160.
Serra L. 2001. Duration of primary moult affects primary quality in Grey Plovers *Pluvialis squatarola*. *Journal of Avian Biology* 32: 377–380.
Serra L. 2002. Cold winters vs long journeys: adaptations of primary moult and body mass to migration and wintering in the Grey Plover *Pluvialis Squatarola.* PhD thesis, University of Cape Town, South Africa.
Underhill LG, Joubert A. 1995. Relative masses of primary feathers. *Ringing & Migration* 16: 109–116.
Underhill LG, Summers R. 1993. Relative masses of primary feathers in waders. *Wader Study Group Bull* 71: 29–31.
Underhill LG, Zucchini W. 1988. A model for avian primary moult. *Ibis* 130: 358–372.

Tables and Figures

Table 1: Relative masses of the primary feathers for the South Island Pied Oystercatcher from New Zealand. These results were provided by David Melville and Phil Battley (*in litt.*), and were obtained using the method described in Underhill and Joubert (1995). The sample size was two birds.

Primary	**P1**	**P2**	**P3**	**P4**	**P5**	**P6**	**P7**	**P8**	**P9**	**P10**
Relative mass (%)	4.44	5.43	6.41	7.73	9.16	10.72	11.99	13.36	14.23	16.53

Table 2: Estimated moult parameters for the wing of the South Island Pied Oystercatcher from New Zealand, categorised by age class (juveniles, second-year birds, and adults). The parameters include start date, SD in start date, duration, end date and their corresponding standard errors in brackets, as well as the % PFMG per day and the sample sizes for the stages of moult.

Age class	**Start date**	**SD start date**	**Duration (days)**	**End date**	**PFMG per day**	**Pre-moult**	**In-moult**	**Post-moult**
Juveniles	22 September (5.7)	28.2 (2.7)	184.5 (6.5)	24 March	0.0054	62	189	33
Second-year birds	22 November (10.9)	31.5 (5.0)	188.2 (8.3)	29 May	0.0053	59	96	24
Adults	8 January (6.3)	16.0 (3.0)	126.0 (3.4)	13 May	0.0079	75	265	132

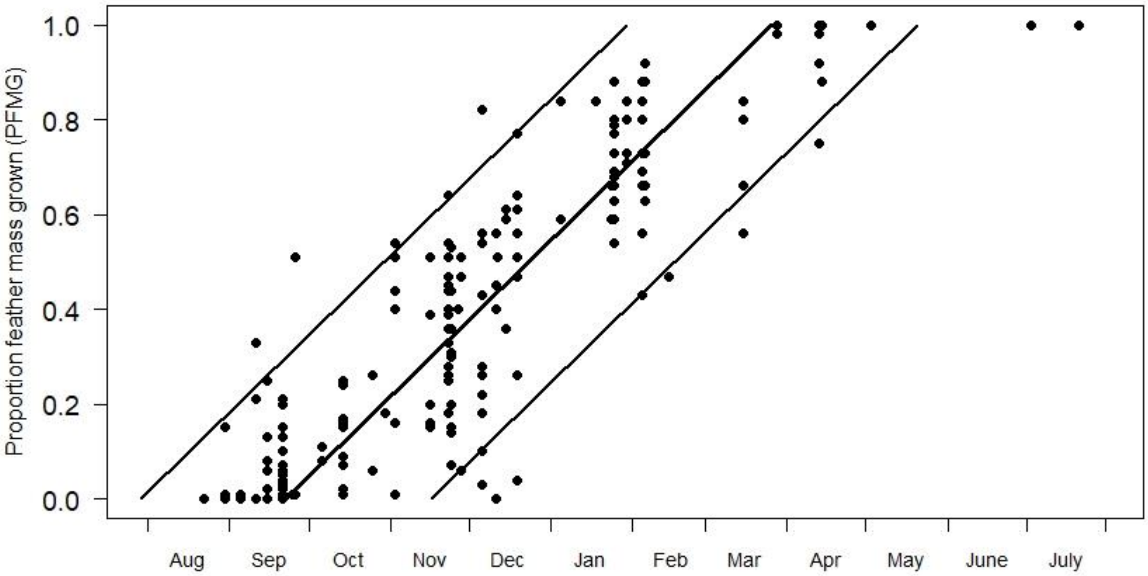

Figure 9: The Proportion Feather Mass Grown (PFMG) for juvenile South Island Pied Oystercatchers from New Zealand. The centre line represents the average timing of moult for a bird, and the two outer lines indicate the 95% confidence intervals of birds in moult. The points represent the individual PFMG scores.

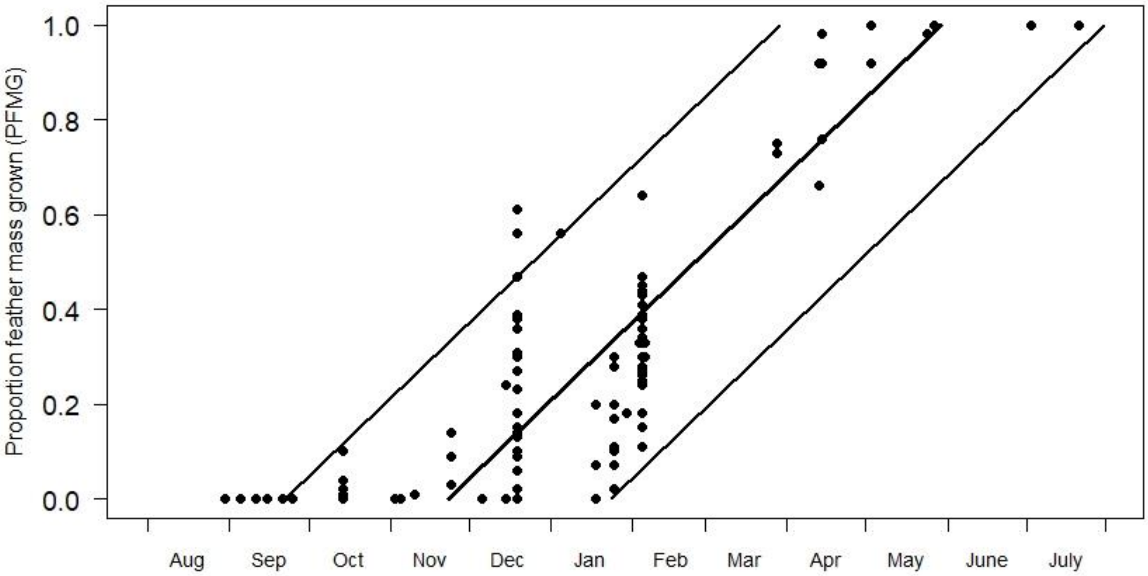

Figure 10: The Proportion Feather Mass Grown (PFMG) for second-year South Island Pied Oystercatchers from New Zealand. The centre line represents the average timing of moult for a bird, and the two outer lines indicate the 95% confidence intervals of birds in moult. The points represent the individual PFMG scores.

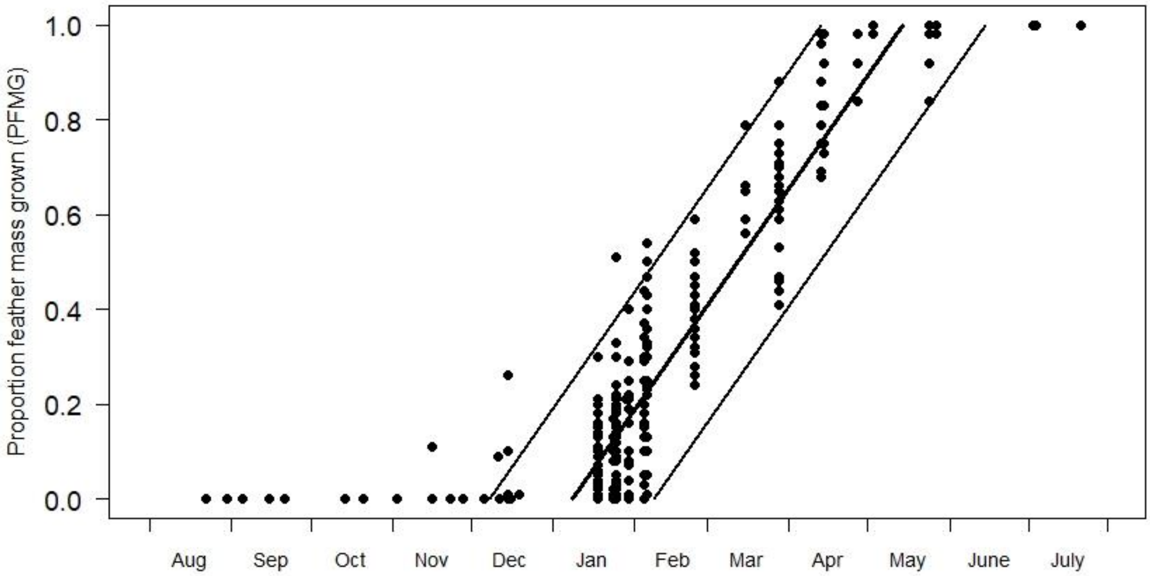

Figure 11: The Proportion Feather Mass Grown (PFMG) for adult South Island Pied Oystercatchers from New Zealand. The centre line represents the average timing of moult for a bird, and the two outer lines indicate the 95% confidence intervals of moult. The points represent the individual PFMG scores.

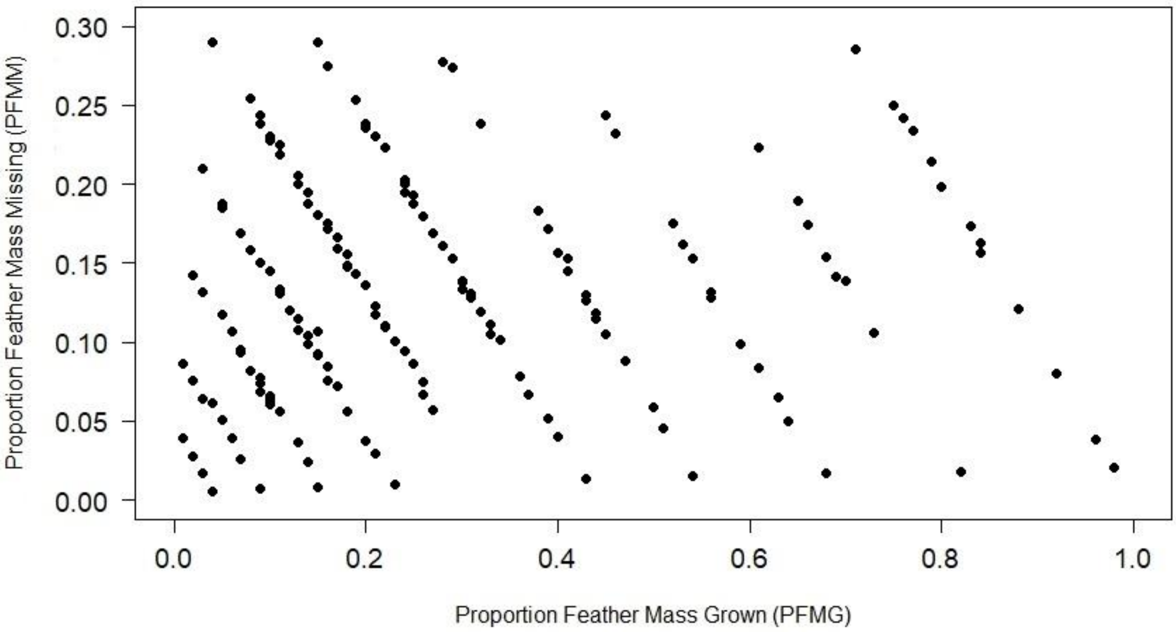

Figure 12: Scatter diagram of Proportion Feather Mass Missing (PFMM) plotted against Proportion Feather Mass Grown (PFMG) for the South Island Pied Oystercatcher from New Zealand. The lines formed by the points are an artefact of the data collection protocol.

Chapter 6: Primary moult in the annual cycle of the Variable Oystercatcher *Haematopus unicolor*

Abstract: The Variable Oystercatcher *Haematopus unicolor* is endemic along the coastlines of New Zealand's islands. The birds are mostly sedentary, undergoing only local movements between natal/feeding territories. Their annual schedules change as they mature, with juveniles moulting the earliest in the year, from 29 October to 12 April, as estimated by the Underhill-Zucchini moult model, second-years from 16 December to 3 July, and adults from 3 January to 6 June. Egg-laying takes place from mid-September to February, with peak fledging from January to February. Our results support the claim by Dowding (2014) that "moult may overlap with chick rearing", and suggests that overlap between breeding and moult is a common occurrence for the Variable Oystercatcher.

Introduction

This chapter is the third of three secondary chapters in this dissertation dealing with the primary moult of a species of oystercatcher Haematopidae. This chapter deals with the moult of the Variable Oystercatcher *Haematopus unicolor*.

The Variable Oystercatcher is endemic to New Zealand. It is confined to the coastline of the North Island, South Island, Steward Island and their offshore islands, and unlike the South Island Pied Oystercatcher *Haematopus finschi* does not occur inland. Two-thirds of the population is found in the North Island, especially the northeastern coastline. The Variable Oystercatcher is the only polymorphic species in the family Haematopidae; its plumage is on a continuous spectrum from a black-and-white pied morph to an all-black morph, with intermediate stages in between (Baker 1975; Marchant and Higgins 1993; Hockey 1996; Dowding and Moore 2006; Dowding 2014). Adults are sedentary, and move locally to feed, distances of 10 km are known (Dowding and Moore 2006). Juveniles often move from their natal sites in early August to join flocks. Flocks are generally young, non-breeding individuals. Dowding and Moore (2006) suggested that these "nursery flocks" parallel those observed in southern Africa for the African Oystercatcher *Haematopus moquini*.

Eggs are laid in nests, a little above the spring high tide line from mid-September to early February, with a peak in November; second or third clutches are laid after loss, and chicks fledge as late as February or March (Dowding 2014).

Based on an assessment of 30 museum specimens, primary moult of the Variable Oystercatcher was limited to the period of December and July (Marchant and Higgins 1993). Data available to Dowding (2014) suggested that breeding adults commence primary moult between mid-January and late February.

In this chapter, we undertake an analysis of primary moult data of Variable Oystercatchers from New Zealand. We aim to provide a clearer picture of the timing, duration, and extent of moult for this species. Our analysis separates juveniles, second-year birds and adults in determination of three moult parameters for each group, using the Underhill and Zucchini (1988) moult model.

Methods

Data collection

The data used for this species includes 159 records of Variable Oystercatchers from New Zealand, collected between during 2000–2022 by the South Island Wader Study Group. Members of the group made a full set of measurements of each bird and aged them into three categories, juveniles (29 birds), second-year birds (42) and adults (88). One of the sets of measurements was primary moult observations, using the standard method, with a single wing’s primary feathers characterized by 10 digits: old feathers are scored as 0, new feathers as 5, and growing feathers numbered 1–4 based on their growth stage (Ginn and Melville 1983; Underhill and Zucchini 1988).

Data Analysis

The oystercatchers were observed to follow continuous moult, without suspension, or pausing feather growth; feathers continued growing from the moult starting date to the moult completion date. We chose 1 August as Day 1 because no birds were observed to be in primary moult prior to this date.

Data analysis was conducted using the Underhill and Zucchini (1988) moult model for estimation of the three moult parameters for each of the three age categories.

The algorithm developed by Erni et al. (2013) in R (R Core Team 2020) was used to estimate the parameters using the method of maximum likelihood. In this model, moult duration is treated as a single parameter, and the moult starting dates follow a normal distribution, with a mean and standard deviation. We analysed the 10 primary feathers as a tract, as described by Serra (2002).

Proportion Feather Mass Grown (PFMG), calculated in the standard way, was used as the moult index (Underhill and Joubert 1995). The PFMG calculation required the relative feather masses for the Variable Oystercatcher (Table 1). Data type 2 was used in the models because all birds were available for capture throughout the period of sampling.

During moult, the size of the gap in the primary feathers is represented by the Proportion Feather Mass Missing (PFMM). This was calculated for all birds in moult as described by Remisiewicz et al. (2009). PFMM was plotted against PFMG.

Results

We estimated the mean start date for the 29 juveniles to be 29 October, the standard deviation of start date to be 23 days and the moult duration to be 166 days, yielding an estimated completion date of 12 April (Table 2, Figure 1). The equivalent results for the 42 second-year birds were estimated to be start date, 16 December, standard deviation, 29 days and a moult duration of 200 days, and thus an estimated completion date of 3 July (Table 2, Figure 2). For 88 adults the estimated start date was 3 January, standard deviation of start date, 23 days, moult duration of 154 days, and thus an estimated completion date of 6 June (Table 2, Figure 3). The estimated start date for second-year birds was 48 days later than first-year birds, and that for adults 18 days later than second-year birds. Because of the small sample sizes, the standard errors of the moult parameters were relatively large (Table 2).

An average of 0.09 primary feather mass was estimated to be missing from the birds during their moult period (Figure 4). We observed the two highest values of PFMM, both on 29 March, with the highest as 0.34 with moult score 5555554211 and the second highest as 0.25 with moult score 5555543210. The correlation between percentage feather mass missing and percentage feather mass grown was 0.057 (n.s.).

Discussion

The egg-laying component of the breeding season of the Variable Oystercatcher is from mid-September to early February, with a peak in the laying of first clutches in October and November (Marchant and Higgins 1993; Dowding 2014). Clutches laid after mid-December are mostly replacements of lost clutches (Marchant and Higgins 1993). Given incubation and fledging periods of approximately four and seven weeks respectively, the peak fledging period takes place three months after egg-laying, in January and February (Marchant and Higgins 1993, Dowding 2014).

The estimated mean starting date of primary moult of adult Variable Oystercatchers was 3 January (Table 2). Remarkably, Dowding (2014) noted that “moult may overlap with chick-rearing (and occasionally with incubation in the case of late clutches)”. Our results provide strong quantitative confirmation to this observation, and suggest that the overlap between primary moult and the later stages of breeding is of common occurrence in the Variable Oystercatcher.

The duration of adult moult was estimated to be 155 days (Table 2), so that the mean end date was 6 June. This suggests that Variable Oystercatchers do not extend primary moult to a date close to the start of the next breeding season; in fact there is a period of approximately four months (June to September) in which the average adult is neither breeding nor moulting. The fact that the end of breeding and the start of primary moult are overlapped suggests that there must be some biological condition at play during winter and early spring, such as a food shortage, underlying the need for a period during which only maintenance activities are undertaken.

As with the African Oystercatcher, fledglings remain with their parents for several months before being evicted from their natal territories in autumn or winter, with early August as the latest date (Dowding 2014; Underhill 2014). Juveniles then join flocks of pre-breeding oystercatchers and reside near their natal site or disperse widely, some travelling as far as 310 km (for example from Dunedin to Christchurch). Adults are generally sedentary and remain on their natal territories, whether on the mainland or offshore islands of New Zealand, throughout the year. The estimated mean start date of the first primary moult of juveniles is 29 October (Table 2), which is approximately the same time as the adults commence their next breeding season.

This first primary moult is estimated to be completed on 12 April on average (Table 2), and these young oystercatchers are now classified as second-year birds. These second-year birds commence their next primary moult on 16 December, on average. The estimated duration of this moult is 201 days, but with a large standard deviation. It is probable that the end date of primary moult of second-year birds (currently 3 July, Table 2) enables a smooth transition into the adult annual cycle (end date 6 June, Table 2).

The hypothesis that there is a four-month period from midwinter to spring during which some resource constraint is occurring receives further support from the fact that none of the three age classes moults with it (Table 2). This period should receive further investigation.

Comparison of the primary moult of the Variable Oystercatcher with other oystercatcher species is deferred to Chapter 7.

References

Baker AJ. 1975. Morphological variation, hybridization and systematics of New Zealand oystercatchers (Charadriiformes: Haematopodidae). *Journal of Zoology* 175: 357–390.

Dowding JE. 2014. Conservation assessment of the Variable Oystercatcher *Haematopus unicolor*. *International Wader Studies* 20: 182–190.

Dowding J, Moore S (eds). 2006. *Habitat networks of indigenous shorebirds in New Zealand*. Science & Technical Pub., Department of Conservation Report No. 0478140444. Wellington, New Zealand.

Erni B, Bonnevie BT, Oschadleus H-D, Altwegg R, Underhill LG. 2013. Moult: an r package to analyse moult in birds. *Journal of Statistical Software* 52: 1–23.

Ginn H, Melville D. 1983. *Moult in birds*. Tring: British Trust for Ornithology.

Hedenström A, Sunada S. 1999. On the aerodynamics of moult gaps in birds. *Journal of Experimental Biology* 202: 67–76.

Hockey, PAR. 1996. *Haematopus ostralegus* in perspective: comparison with other Oystercatchers. In: Goss-Custard, JD (ed), *The Oystercatcher: From Individuals to Populations*. Oxford: Oxford University Press. pp 251–285.

Marchant S, Higgins P (eds). 1993. *Handbook of Australian, New Zealand and Antarctic Birds*. Melbourne: Oxford University Press.

R Core Team 2020. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Remisiewicz M, Tree AJ, Underhill LG, Gustowska A, Taylor PB. 2009. Extended primary moult as an adaptation of adult Wood Sandpipers *Tringa glareola* to their freshwater habitats in southern Africa. *Ardea* 97: 271–280.

Serra L. 2002. Cold winters vs long journeys: adaptations of primary moult and body mass to migration and wintering in the Grey Plover *Pluvialis Squatarola.* PhD thesis, University of Cape Town, South Africa.

Underhill LG, Joubert A. 1995. Relative masses of primary feathers. *Ringing & Migration* 16: 109–116.
Underhill LG, Zucchini W. 1988. A model for avian primary moult. *Ibis* 130: 358–372.

Tables and Figures

Table 1: Relative masses of the Primary feathers for the Variable Oystercatcher from New Zealand. Based on a sample of two birds, and provided by Phil Battley and David Melville, following the method of Underhill and Joubert (1995).

Primary	**P1**	**P2**	**P3**	**P4**	**P5**	**P6**	**P7**	**P8**	**P9**	**P10**
Relative mass (%)	4.62	5.74	6.91	8.49	10.06	11.23	11.95	12.99	13.2	14.8

Table 2: Estimated moult parameters for the wing of the Variable Oystercatcher from New Zealand, categorised by age class (juveniles, second-year birds, and adults). The parameters include start date, SD in start date, duration, end date and their corresponding standard errors in brackets, as well as the % PFMG per day and the sample sizes for the stages of moult.

Age class	Start date	SD start	Duration (days)	End date	PFMG per day	Pre-moult	In-moult	Post-moult
Juveniles	29 October (20.6)	22.7 (8.1)	166.3 (9.6)	12 April	0.0060	1	24	4
Second-year birds	16 December (25.0)	28.7 (14.1)	200.8 (11.3)	3 July	0.0050	5	18	19
Adults	3 January (23.4)	25.9 (9.7)	154.7 (8.6)	6 June	0.0065	44	39	5

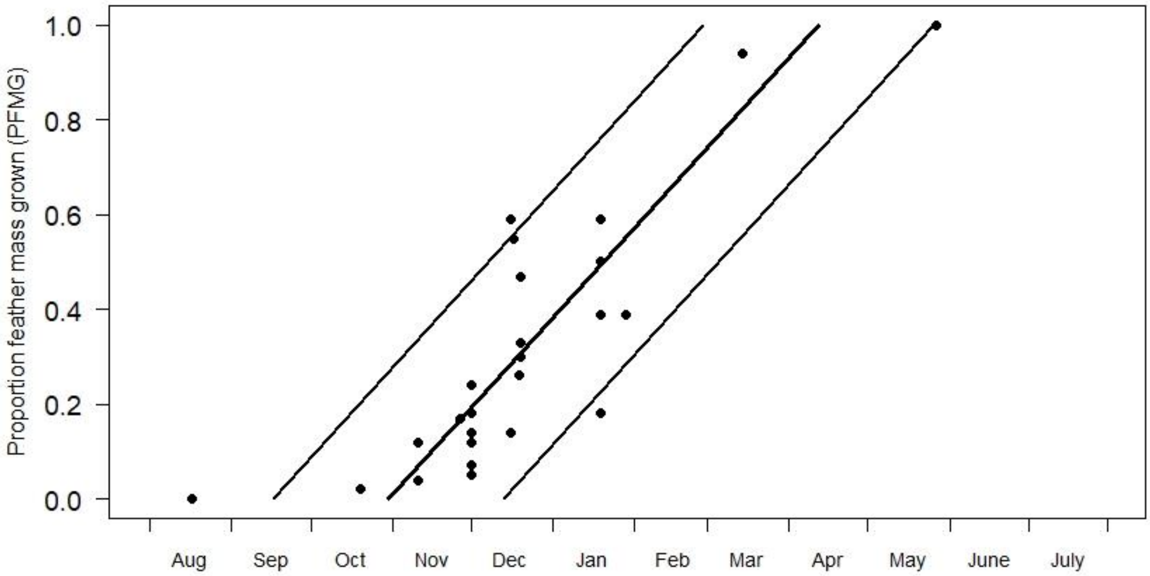

Figure 13: The Proportion Feather Mass Grown (PFMG) for juvenile Variable Oystercatchers from New Zealand. The centre line represents the average timing of moult for a bird, and the two outer lines indicate the 95% confidence intervals of birds in moult. The points represent the individual PFMG scores.

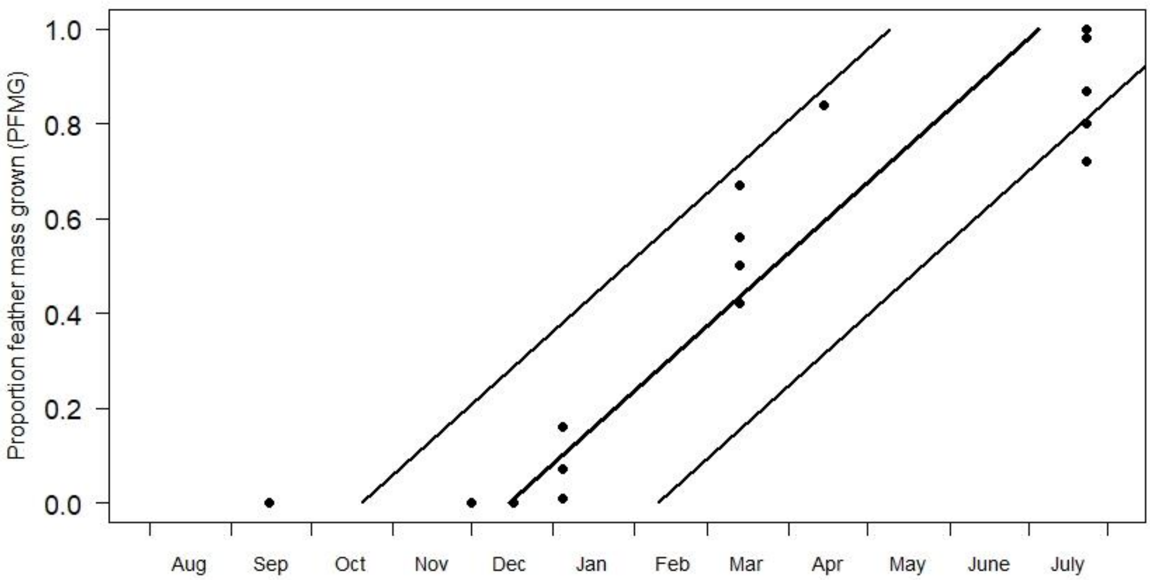

Figure 14: The Proportion Feather Mass Grown (PFMG) for second-year Variable Oystercatchers from New Zealand. The centre line represents the average timing of moult for a bird, and the two outer lines indicate the 95% confidence intervals of birds in moult. The points represent the individual PFMG scores.

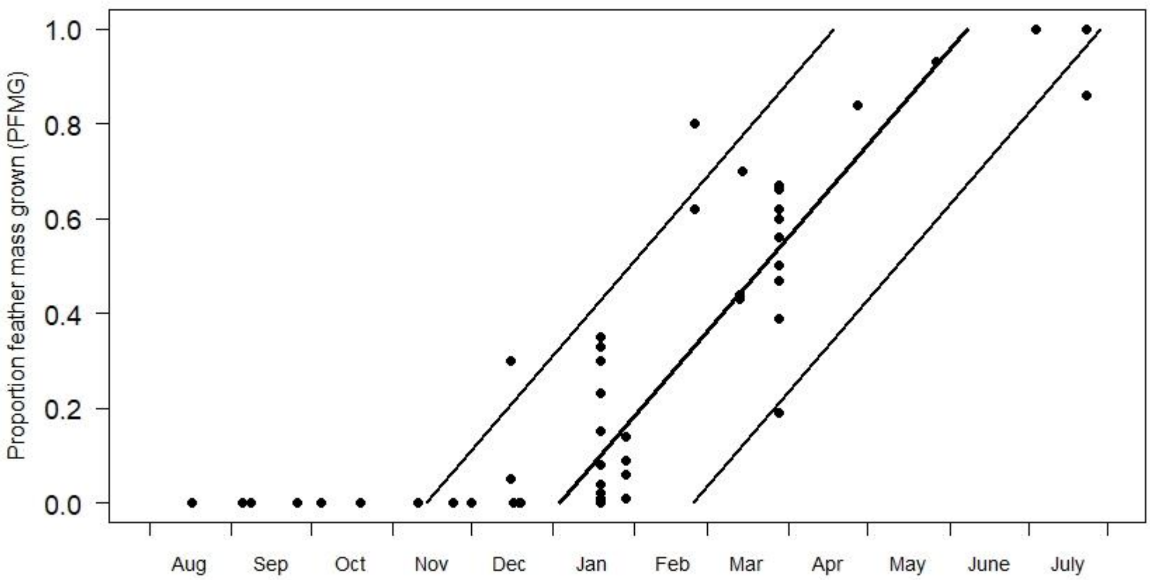

Figure 15: The Proportion Feather Mass Grown (PFMG) for adult Variable Oystercatchers from New Zealand. The centre line represents the average timing of moult for a bird, and the two outer lines indicate the 95% confidence intervals of moult. The points represent the individual PFMG scores.

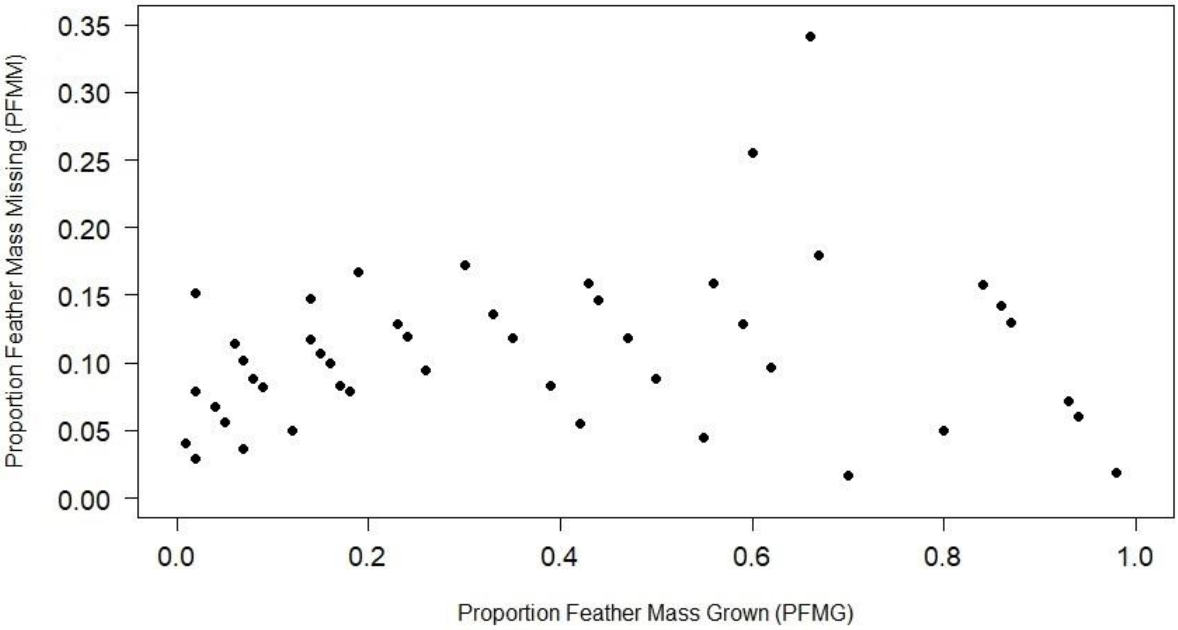

Figure 16: Scatter diagram of Proportion Feather Mass Missing (PFMM) plotted against Proportion Feather Mass Grown (PFMG) for the Variable Oystercatcher from New Zealand. The lines formed by the points are an artefact of the data collection protocol.

Chapter 7: Synthesis

In the study of birds, three main life events stand out: breeding, migration, and moult. As Newton (2009) describes, within European bird populations alone, the order of these life events occur in at least eight variations, and this can also be observed in birds across the globe. In gaining knowledge of the order of life stages for specific birds, conservation management plans can be implemented with ease, because this information highlights the time of the bird’s life in which it is most vulnerable and in need of protection and support.

The life event of moult consists of the replacement of all main flight feathers, which takes a great deal of time and energy for the bird to carry through (Alonso et al. 2009). In comparison to other life stages, moult is easily quantifiable which makes it of great use in ornithological studies. In addition to determining the timing, extent, and duration of moult itself, moult studies can highlight the timings of fledging, breeding onset, and the completion dates of breeding in a bird’s life (Ginn and Melville 1983).

Within this chapter, we focus on a study conducted on the moult strategies of five species within the group of waders known as oystercatchers (Haematopidae). Our main research questions are centered around determining the moult strategy variations among species: are there distinct patterns that emerge in the timing of moult? Do oystercatchers follow the same moult strategies? Are there differences in moult among migrant and resident oystercatchers? To answer these questions, we have used the Underhill and Zucchini (1988) moult model to estimate the moult parameters for five species of oystercatcher. Our hope is that our discoveries will provide greater understanding of these birds, and ultimately make a contribution to their conservation.

The Australian species

Two of the species chosen for this study are endemic to Australia: the Australian Pied Oystercatcher *H. longirostris* and the Sooty Oystercatcher *H. fuliginosus*. In southeastern Australia, the parameters of moult for both species were similar: the estimated mean starting dates differed by seven days (19 and 26 December), with the Sooty Oystercatcher one week later than the Australian Pied Oystercatcher

(Table 1, Figure 1). The standard deviations in start date for both species was 22 days. The moult duration estimates differed by 11 days (157 and 168 days). The estimated completion dates of primary moult differed by 16 days (25 May and 10 June, for the Australian Pied Oystercatcher and Sooty Oystercatcher, respectively) (Table 1, Figure 1). The inescapable conclusion from these results is that the timing of primary moult for these two species in southeastern Australia is remarkably similar.

Timing of breeding is also similar: Australian Pied Oystercatchers between October and November (Taylor et al. 2014) and Sooty Oystercatchers between October and February (Hansen et al. 2014) (Figure 1), although Sooty Oystercatchers sometimes overlap their breeding season with the start of moult, which reflects specific timing differences between individuals in the population. Both species appear to avoid moult in winter, between July and September. The shared order and timing of life stages for these two species is possibly due to their geographical location and thus the similar climatic conditions that both species experience.

The annual cycle of the Sooty Oystercatcher in northwestern Australia is timed about three months earlier than in southeastern Australia (Table 1). The duration of moult was estimated to be 18 days longer in the northwest than in the southeast, and the period between the completion of moult and the start of the new breeding season appeared to be shorter (Table 1).

The New Zealand species

We studied two oystercatcher species from New Zealand, the South Island Pied Oystercatcher *H. finschi* and the Variable Oystercatcher *H. unicolor*. It was feasible to undertake the analyses with three age classes: juveniles, second-year birds, and adults. There are strong contrasts between these two species. The South Island Pied Oystercatcher is a migrant between two habitat types, breeding inland in an ephemeral freshwater habitat between August and November in the interior of the South Island, and migrating to a muddy inter-tidal habitat in the coastal regions of the North Island for the remainder of the year; in contrast the Variable Oystercatcher is coastline resident (Dowding 2014; Sagar and Veitch 2014). In spite of their contrasting annual cycles, adults of both species commence moult in early January, within five days of each other (Tables 1 and 2, Figure 1). However, adult South

Island Pied Oystercatchers have a relatively short moult, 126 days, completing on average on 13 May; in contrast, adult Variable Oystercatchers have an estimated moult duration of 155 days, comparable with that of the two Australian species which are also residents along the coastline (Table 1, Figure 1).

The Underhill and Zucchini (1988) moult model estimated the moult period for juvenile South Island Pied Oystercatchers (SIPO) as between September to March. Juvenile Variable Oystercatchers (VO) started and completed moult about one month later between October to April. Second years had a similar difference in timing among species, with SIPOs in moult from November to late May, and VOs in moult from December to early July. Pre-breeding oystercatchers of both species followed a similar pattern in their moult strategy as they mature, Juveniles begin moult first, followed by second-year birds, and last, adults. The duration of moult for adults was shorter than that of juveniles and second-year birds (Table 2). This is probably because more time is available in their annual cycle, because they are not yet breeding.

The African Oystercatcher in comparison with the Australian and New Zealand species

The striking difference between the African Oystercatcher and the other four species considered here (Figure 1) is the timing of breeding and moult. African Oystercatchers in the Western Cape, the area from which the bulk of the moult data were collected, breed from November to February, the midsummer period (Parsons 2006; Braby and Underhill 2007; Tjørve and Underhill 2008; Quintana et al. 2021). In contrast, the other four species breed mostly in spring (Table 1). Likewise, primary moult of the African Oystercatcher covers the entire winter period (April to August), when stormy conditions occur periodically, and probably make access to the intertidal impossible for periods of several days. For the other four species, the completion date of primary coincides with the beginning of the winter period (13 May to 6 June, excluding the Sooty Oystercatcher in subtropical northwestern Australia) (Table 1). Apart from the short duration of the migrant South Island Pied Oystercatcher (126 days) and the long duration of the subtropical Sooty Oystercatcher (186 days), the duration for the African Oystercatcher (154 days) was similar to that of the other three resident coastal species (155, 157 and 168 days) (Table 1).

The wing gap

The proportion feather mass missing (PFMM) quantifies the size of the wing gap in the primaries (Remisiewicz et al. 2009). As described by Hedenström and Sunada (1999), the size of the wing gap indicates the limitations placed on flight ability for the bird during its moult period. For the five species considered here, the plots of PFMM vs proportion feather mass grown were similar. There are not yet many examples of these plots; and the PFMM vs PFMG plot for Wood Sandpiper *Tringa glareola* is similar to that of the five oystercatchers (Remisiewicz et al. 2009). These are likely to provide insights into the moult process once they become available for the species with short moult durations, such as the waders that moult in autumn in the northern hemisphere (Jackson and Underhill 2022).

Moult strategies

Through observation of the moult strategies of the resident species of oystercatchers within our study, there is a conceivable pattern that oystercatchers moult after breeding, which sometimes involves an overlap of the two stages. Of the various orders of events that species potentially undergo their life stages, as explained by Newton (2009), most of the species within our study followed a similar order. All of the species in our study reside in the Southern Hemisphere and thus experience winter between July and August. We observed that the Australian and New Zealand species complete moult around a similar time of year, ranging from September/December to March/June. These four species first survive through winter, then enter the breeding season, and end off with moult. However, this pattern does not ring true for all species. The African Oystercatcher has completely different timing, moult takes place between April and September, thus stretching over the winter season, and moult is followed by breeding.

In light of our research, there is a pattern of the order of life events for at least four species of resident oystercatcher. This pattern may be visible in another mostly sedentary New Zealand species, the Chatham Island Oystercatcher *H. chathamensis*, although there is little information on their moult, the birds breed around the same time with first breeders starting in October, and replacement clutches in February (Moore 2014). There is greater chance that this species has a similar order of life events because it occurs in New Zealand.

Also in the southern hemisphere, in South America, both the Magellanic Oystercatcher *H. leucopodus* and the Blackish Oystercatcher *H. ater* breed around a similar period, between September to January/February, and October/November to January, respectively (Escudero et al. 2014; Woods 2014). Thus, we can assume that the breeding season for oystercatchers within the southern hemisphere takes place during the same period.

The two South American species mentioned above both take part in migration, with the exception of resident species of Blackish Oystercatcher at the Falkland Islands. These birds follow a different order of events in their annual schedule. Immature Magellanic Oystercatchers moult between October and February, while adults moult from January to April. Before moult, the birds will migrate from the breeding grounds to the coast between January and February and remain there until August. Little is known about the moult of the Blackish Oystercatcher, but it is clear that the Magellanic Oystercatcher spends much less time in moult than resident oystercatchers, probably because of migration (Escudero et al. 2014; Woods 2014).

Most species of oystercatcher within the northern hemisphere are migrants, with the exception of some resident populations of the Black Oystercatcher *H. bachmani* in North America (Clay et al. 2014; Melville et al. 2014; Sarychev and Mischenko 2014; Tessler et al. 2014; van de Pol et al. 2014). There is less known concerning the timing of life events for these species. With the Far Eastern Oystercatcher *H. ostralegus osculans*, immature birds were found to be in active moult in late April, while adults are known to complete moult by mid-November. These birds undergo a northward and southward migration, and breeding is from mid-March to late June (Melville et al. 2014). Further studies are required to identify patterns in the timing of life events and the variations in moult strategies for the migrant species.

Recommendations for further research

This approach has proved fruitful, and it is recommended that the analyses of primary moult be undertaken for the oystercatcher species of Eurasia, North America and South America. For the sake of investigating the diversity of life histories, the next priority should be given to species which migrate. For those oystercatcher species for which the opportunities to catch and handle birds in moult during ringing operations are limited or not feasible, this project has demonstrated that photographic records of birds throughout the moult period are adequate to quantify the parameters of moult, as has been achieved here for the African Oystercatcher.

References

Alonso H, Matias R, Granadeiro JP, Catry P. 2009. Moult strategies of Cory's Shearwaters *Calonectris diomedea borealis*: the influence of colony location, sex and individual breeding status. *Journal of Ornithology* 150: 329–337.

Braby J, Underhill L. 2007. Was poor breeding productivity of African black oystercatchers on Robben Island in 2004/05 caused by feral cats, kelp gulls, mole snakes or the Sumatra tsunami? *Bulletin-Wader Study Group* 113: 66.

Clay RP, Lesterhuis AJ, Schulte S, Brown S, Reynolds D, Simons TR. 2014. A global assessment of the conservation status of the American Oystercatcher *Haematopus palliatus*. *International Wader Studies* 20: 62–82.

Dowding JE. 2014. Conservation assessment of the Variable Oystercatcher *Haematopus unicolor*. *International Wader Studies* 20: 182–190.

Escudero G, Ferrari S, Albrieu C, Matus R, Imberti S, Stoyanoff P, Webb A, Castro M, Abril M, Benegas R. 2014. Conservation assessment and ecology of the Magellanic Oystercatcher *Haematopus leucopodus*. *International Wader Studies* 20: 173–181.

Ginn H, Melville D. 1983. *Moult in birds*. Tring: British Trust for Ornithology.

Hansen BD, Minton CD, Harrison AE, Jessop R. 2014. Conservation assessment of the Sooty Oystercatcher *Haematopus fuliginosus*. *International Wader Studies* 20: 161–172.

Hedenström A, Sunada S. 1999. On the aerodynamics of moult gaps in birds. *Journal of Experimental Biology* 202: 67–76.

Jackson CH, Underhill LG. 2022. Primary moult strategies in adult migrant waders (Charadrii). *Wader Study* 129: 126–137.

Melville DS, Gerasimov YN, Moores N, Yat-Tung Y, Bai Q. 2014. Conservation assessment of far eastern oystercatcher *Haematopus [ostralegus] osculans*. *International Wader Studies* 20: 129–154.

Moore P. 2014. Conservation assessment of the Chatham Island oystercatcher *Haematopus chathamensis*. *International Wader Studies* 20: 23–32.

Newton I. 2009. Moult and plumage. *Ringing & Migration* 24: 220–226.

Parsons NJ. 2006. Quantifying abundance, breeding and behaviour of the African black oystercatcher.

Quintana I, Button R, Underhill LG. 2021. African Oystercatchers on Robben Island, South Africa: The 2019/2020 breeding season in its two decadal context. *Wader Study* 128: 209–219.

Remisiewicz M, Tree AJ, Underhill LG, Gustowska A, Taylor PB. 2009. Extended primary moult as an adaptation of adult Wood Sandpipers *Tringa glareola* to their freshwater habitats in southern Africa. *Ardea* 97: 271–280.

Sagar P, Veitch D. 2014. Conservation assessment of the South Island oystercatcher *Haematopus finschi*. *International Wader Studies* 20: 155–160.
Sarychev V, Mischenko A. 2014. Conservation assessment of *Haematopus ostralegus longipes*. *International Wader Studies* 20: 33–40.
Taylor IR, Newman OMG, Park P, Hansen B, Minton CD, Harrison A, Jessop R. 2014. Conservation assessment of the Australian Pied Oystercatcher *Haematopus longirostris*. *International Wader Studies* 20: 116–128.
Tessler DF, Johnson JA, Andres BA, Thomas S, Lanctot RB. 2014. A global assessment of the conservation status of the Black Oystercatcher *Haematopus bachmani*. *International Wader Studies* 20: 83–96.
Tjørve KC, Underhill L. 2008. Influence of disturbance and predation on breeding success of the African Black Oystercatcher, *Haematopus moquini*, on Robben Island, South Africa. *Waterbirds* 31: 83–96.
Underhill LG, Zucchini W. 1988. A model for avian primary moult. *Ibis* 130: 358–372.
van de Pol M, Atkinson P, Blew J, Crowe O, Delany S, Duriez O, Ens BJ, Hälterlein B, Hötker H, Laursen K, Oosterbeek K, Petersen A, Thorup O, Tjørve K, Triplet P, Yésou P. 2014. A global assessment of the conservation status of the nominate subspecies of Eurasian Oystercatcher *Haematopus ostralegus ostralegus*. *International Wader Studies* 20: 47–61.
Woods RW. 2014. Conservation assessment of the Blackish Oystercatcher *Haematopus ater*. *International Wader Studies* 20: 109–115.

Tables and Figures

Table 1: Estimated moult parameters for the adults of five species of oystercatchers (Haematopidae) observed in this study. The three parameters of the model include start date, standard deviation of start date and duration; the completion date is computed as start date plus duration. The extent of movement and breeding seasons are mentioned.

Species	Mean date of start	Standard deviation parameter	Duration (days)	Mean date of completion	Extent of movement of adults	Breeding season (egg-laying period)
Australian Pied Oystercatcher *H. longirostris*	19 December	22	157	25 May	Local movements between breeding and non-breeding areas	October to November
Sooty Oystercatcher *H. fuliginosus fuliginosus* (southeastern Australia)	26 December	22	168	10 June	Local movements between breeding and non-breeding areas	Mid-September to early February, peak November
Sooty Oystercatcher *H. f. opthalmicus* (northwestern Australia)	4 October	26	186	6 April	Local movements between breeding and non-breeding areas	July to early September
South Island Pied Oystercatcher *H. finschi*	8 January	16	126	13 May	Migrant between North Island and South Island	August to November
Variable Oystercatcher *H. unicolor*	3 January	26	155	6 June	Resident, local movements	October to March
African Oystercatcher *H. moquini*	1 April	28	154	2 September	Resident	November to February

Table 2: Estimated moult parameters for the South Island Pied Oystercatcher and Variable Oystercatcher from New Zealand. The birds are separated into three age classes: juveniles, second-year birds, and adults. The three parameters of the model include start date, standard deviation of start date and duration; the end date is computed as start date plus duration.

Species	**Age class**	**Start date**	**SD start**	**Duration (days)**	**End date**
South Island Pied Oystercatcher *H. finschi*	Juveniles	22 September	28	185	24 March
	Second-year birds	22 November	32	188	29 May
	Adults	8 January	16	126	13 May
Variable Oystercatcher *H. unicolor*	Juveniles	29 October	23	166	12 April
	Second-year birds	16 December	29	201	3 July
	Adults	3 January	26	155	6 June

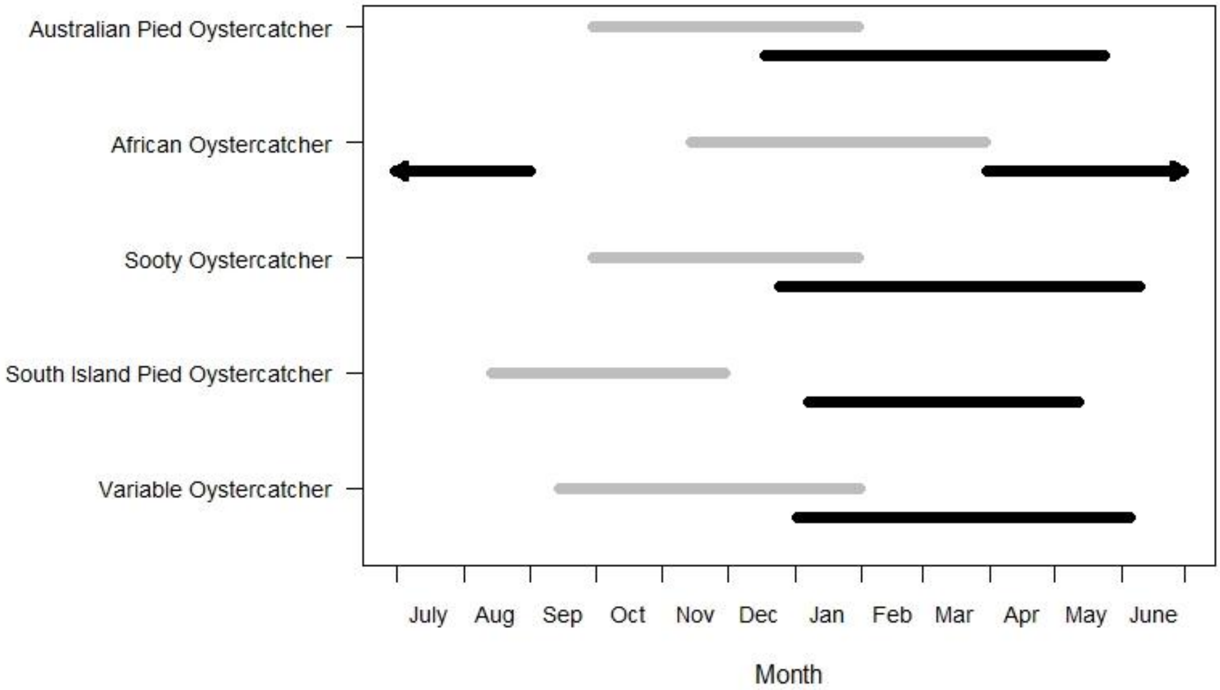

Figure 1: Calendar diagram representing the timeframe of breeding (grey) and moult (black) within the annual schedule of each oystercatcher species within this study.