A contribution to understanding the primary moult of birds

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Contents

Plagiarism declaration

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Data were made available to me from various sources specifically for the primary moult analyses in this thesis. Included in the data files was additional information which was not used for these analyses, which may be used by the owners of the data for analyses of other aspects of the species biology. Therefore, future access to the data will need to be arranged with the owners of the data. I am grateful to the data owners for entrusting these files to me for the analyses presented in this thesis.

Kobie Raijmakers ringed Red-headed Finches and provided the long-term moult dataset for analysis in Chapter 3. He also provided details of the capture sites. He owns the data and will be a co-author of the paper.

Micah Scholer provided moult data from the New Zealand Moult Record Scheme and contributed to the discussion of the biology of Silvereye in Chapter 4. He also commented on drafts of Chapters 4 and 6. He will be a co-author of these two papers. Ms Michelle Bradshaw, Banding Officer for the New Zealand National Bird Banding Scheme, assisted with access to data used in Chapter 6. The data used in Chapter 4 are owned by the New Zealand Moult Record Scheme and the data used in Chapter 6 are owned by the New Zealand Moult Record Scheme and the New Zealand National Bird Banding Scheme.

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The illustrations contained in this thesis are my own work. They can only be reproduced independently of this thesis with my consent.

Co-authors

When these chapters are submitted to journals for publication, it is envisaged that key people listed here will be co-authors, as listed below. They have been involved with data collected or assisted with gaining access to data, provided information on study sites and pointed in the direction of relevant literature. Their contributions have been central to the production of these chapters and their roles, as described in the Acknowledgements have been critical.

My responsibility has been the analysis and interpretation of data, the core component of the thesis. I performed all the data analyses and produced all the figures and tables, except the figure of the world map in Chapter 7. I wrote the Methods and Results sections of all chapters and wrote the first drafts of the Introduction and Discussion sections. After receiving feedback and insights from other co-authors I finalised all chapters. I compiled Appendix 1.

Appendix 2 is not part of the thesis but is included because it is the paper that develops a component of the methods used in Chapter 3. The paper has been submitted to a journal. It is included here because there is no published source of these methods.

Chapter	**Title**	**Co-authors**
Chapter 1	Introduction	T Scott
Chapter 2	Primary moult of adult Laughing Doves *Spilopelia senegalensis*: Introduction of the Relative Duration Index and a comparison of moult indices	T Scott, LG Underhill and GD Underhill
Chapter 3	The primary moult of adult Red-headed Finches *Amadina erythrocephala*	T Scott, K Raijmakers and LG Underhill
Chapter 4	Primary moult of Silvereye *Zosterops lateralis* in New Zealand	T Scott, M Scholer and LG Underhill
Chapter 5	Primary moult of Wrybills *Anarhynchus frontalis*	T Scott, AC Riegen and LG Underhill
Chapter 6	Primary moult of passerines introduced to New Zealand from source populations in the United Kingdom	T Scott, M Scholer, R Robinson and LG Underhill
Chapter 7	Global review of quantitative studies of primary moult of birds using the Underhill-Zucchini moult model	T Scott and LG Underhill
Appendix 1	Estimates of primary moult parameters using the Underhill-Zucchini moult model	T Scott
Appendix 2	Influence of groups of points on estimates of the parameters of moult	LG Underhill and T Scott

Abstract

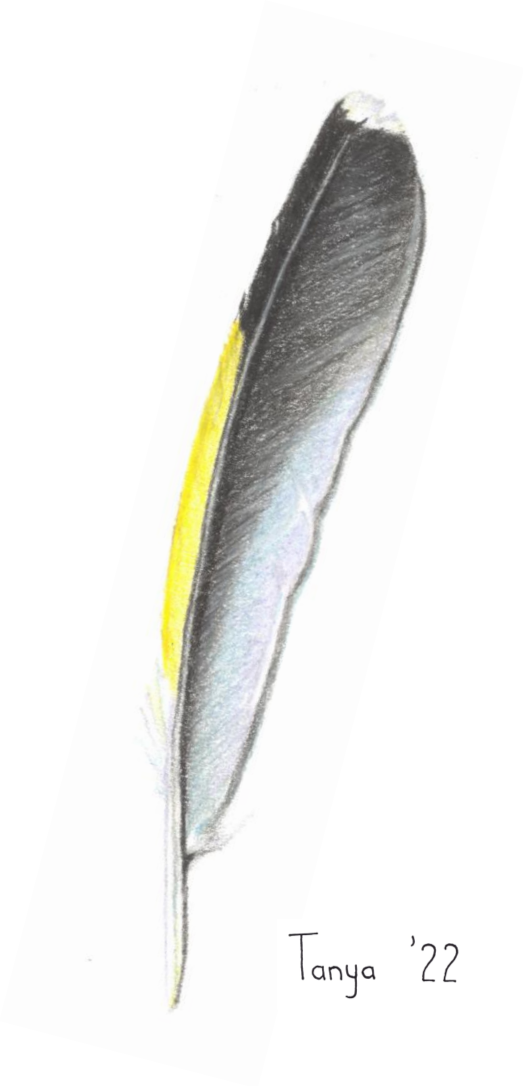
Moult is an essential component of the annual cycle of birds, along with breeding, and, if migratory, migration. The leading statistical model for the analysis of primary moult is the Underhill-Zucchini moult model. It estimates moult parameters (duration, the mean start date and its standard deviation).

An objective of this thesis was to assemble all published results which had used the Underhill-Zucchini moult and to examine the resulting database for patterns in the timing, duration and synchronisation of moult. A total of 242 analyses of 136 species were found. The initial analysis of the database generated two observations: firstly, that latitude played an important role in determining patterns of primary moult, and, secondly, that the available data were latitudinally, spatially across continents, and taxonomically not representative. These gaps in knowledge were too large to rectify within the confines of a single PhD thesis. The preliminary chapters of the thesis added 18 analyses, for 11 species, and have made a contribution towards representativity.

Two of the preliminary chapters make substantive contributions to the methods of undertaking statistical studies of moult. A new moult index, the Relative Duration Index, is introduced. Moult studies are frequently undertaken by combining datasets collected in different years (or different places). This thesis contains the first practical application of a proposed method to identify which of the individual datasets have a large influence of the estimates of the moult parameters.

Nine analyses extended the latitudinal range of studies southwards and were based on datasets assembled in New Zealand. These are the first analyses of primary moult using the Underhill-Zucchini moult model from this country. For seven species, this thesis undertakes moult studies of a species in both its original country, the United Kingdom, and the country into which it had been introduced, New Zealand. These are the first analyses of primary moult of this kind.

Preliminary patterns of moult strategies are discussed. Critical gaps in our understanding of primary moult are identified. Priorities for fieldwork and analysis are described in order that key gaps are filled and a global review of primary moult can be undertaken.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CHAPTER 1

Introduction

Chapter 1

Introduction

BIRDS, FEATHERS AND MOULT

There are approximately 10 000 species of birds worldwide (Campbell et al. 2008). Many characteristics of birds are adaptions for flight, the most obvious being their wings and feathers. Birds are the only animals which regularly replace their most important means of locomotion; the vast majority of bird species replace all the main flight feathers of their wings on an annual basis.

Birds evolved from theropods, which are bipedal saurischians. Studies of theropod fossils have revealed that several dinosaur species closely related to birds had feathers, which implies that feathers evolved before powered flight (Campbell et al. 2008). Birds are now the only extant vertebrates with feathers (Jenni and Winkler 2020).

What are feathers?

A feather consists of the calamus and the rachis which together make up the shaft. Barbs with barbules and rami radiate out from the rachis forming the vane (Jenni and Winkler 2020).

Contour feathers form the surface plumage and give a bird its colour. They consist of body feathers and flight feathers. Flight feathers can be divided further into wing (primary, secondary and tertial) feathers and tail (rectrix) feathers. Most flying birds have nine or ten primaries numbered from inside (P1) to outside (P9 or P10). Birds also have downy feathers underneath the contour feathers (Jenni and Winkler 2020).

Functions of feathers

Feathers of birds serve many functions. They protect the bird's thin skin from impact and abrasion against physical objects, exposure to UV light, water penetration and they provide thermal insulation. Feathers enable flight by helping to shape the wing like an aerofoil and streamlining the body reducing drag. Contour feathers and, for some species, ornamental feathers give a bird its shape and colour and have communicational and non-communicational functions (Jenni and Winkler 2020). These functions include assisting with foraging such as flushing out prey, interspecific signalling such as camouflage and communication with conspecifics via sexual and social signalling, which includes dominance status, breeding status and the phenotypic and genetic quality of the individual (Savalli 1995, Dale 2006, Senar 2006, Santos et al. 2011, Roulin 2016). Facial bristles function as tactile sensors and prevent unwanted particles entering the eyes, nares and ear openings (Persons and Currie 2015, Jenni and Winkler 2020). Filoplumes are hair-like structures associated with the contour and flight feathers. They have mechanoreceptors that detect sideways movement, such as feather displacement, and sense vibrations, such as air speed, and changes in feather arrangement (Necker 1985, Brown and Fedde 1993, Jenni and Winkler 2020).

There are also many specialised functions of feathers that only occur in specific groups of birds. Waterbirds use their feathers to control their buoyancy (Jenni and Winkler 2020). Flight feathers in some species are modified to produce signal sounds when in rapid or display flight and some clap their wings together to produce sound (Jenni and Winkler 2020). Others have developed feather adaptations to quieten sound production during flight, especially in nocturnal owls (Jenni and Winkler 2020). Another feather adaption in owls is specialised feathers centred around the ear openings and covering most of the face that help with and improve detection and localisation of sounds (Koch and Wagner 2002, 2009). Feathers can also be modified to provide mechanical support, as seen in species such as woodpeckers which use their tails for support when climbing trees (Jenni and Winkler 2020). Sandgrouse males have specialised body feathers on their underside for transporting water to their chicks (Cade and Maclean 1967, Rijke 1972). Feathers of some species have been found to contain toxins and unpleasant smelling odours from a variety of sources that are used as a chemical defence against predators and ectoparasites and in some cases as a form of chemical communication (Dumbacher et al. 1992, Dumbacher and Pruett-Jones 1996, Weldon and Rappole 1997, Dumbacher 1999, Dumbacher et al. 2000, 2004, 2009, Hagelin and Jones 2007, Clayton et al. 2010, Jenni and Winkler 2020). Many species use feathers as a nesting material to improve nest insulation (Møller 1984, Stephenson et al. 2009, Dawson et al. 2011). Some species consume their own feathers to help regurgitate undigested food (Piersma and van Eerden 1989) and others have special feathers that aid in the maintenance and preening of plumage using powder down (Jenni and Winkler 2020).

The need for moult

Feathers consist mainly of the protein keratin, which is a strong, durable, lightweight biological material (Rohwer and Rohwer 2013). Keratin is also found in the scales of reptiles (Campbell et al. 2008). Fully-grown feathers are non-living structures and cannot self-repair. They are subject to wear, damage or loss over time and need to be replaced by a process called moult in order to maintain their functions (Payne 1972, Jenni and Winkler 2020). Feathers wear as a result of abrasion, sunlight and parasites (Jenni and Winkler 2020). Whole feathers can be lost due to impact; physical interactions with the surrounding environment, with members of the same species and with predators; fright moult; and the formation of brood patches (Lindstrom and Nilsson 1988, Møller et al. 2006, Jenni and Winkler 2020). The extent of wear on feathers depends on the habitat and climate in which the bird lives, the season, the bird's behaviour and migratory strategy, the degree to which individual feathers are exposed or concealed and feather colour (darker feathers, which contain more melanin, are more resistant than lighter coloured feathers) (Barrowclough and Sibley 1980, Burtt 1986, Ellis 2006, Jenni and Winkler 2020). Wear leads to the loss of feather mass and changes to the feather colour and shape, which ultimately leads to changes in wing shape. Worn and missing feathers therefore impact all functions of the plumage, particularly insulation, flight and appearance (Jenni and Winkler 2020). Birds regularly maintain their feathers through behaviours such as preening, scratching, bathing and oiling with secretions from the preen gland. These are, however, time-consuming activities and there needs to be a compromise between time spent on these and other activities (Clayton et al. 2010, Bush and Clayton 2018, Jenni and Winkler 2020). Consequently, there seems to be a balance between sustained feather wear and the amount of time a bird invests in maintaining its plumage (Jenni and Winkler 2020).

Another purpose of moult, after replacing feathers that are worn or lost, is to acquire new plumage characteristics. The functions of feathers may change over time and those feathers that are no longer suitable need to be replaced so that the plumage can meet its new requirements (Jenni and Winkler 2020). The characteristics and qualities of feathers that often need to be altered are the colouration needed for either display or crypsis, insulation and flight (Jenni and Winkler 2020). Birds may change their plumage in response to age and season. Juvenile plumage is generally quite different in colour and structure to adult plumage and changes with age (Newton 1968, Tiainen and Henski 1985, Nielson 1993, Norman 1997, Alonso and Arizaga 2006, Fernández and Lank 2007, Butler et al. 2008, Mila et al. 2008, Green et al. 2009, Jenni and Winkler 2020). The relative importance of plumage for display and crypsis may vary throughout the year and the best plumage for camouflage may differ with different seasons (Jenni and Winkler 2020). This seasonal change in plumage is achieved by birds undergoing more than one moult a year (Jenni and Winkler 2020).

What is moult?

The replacement of dead epidermal structures, such as hair, skin of reptiles and growth of claws, is common. Moult occurs by a similar process in both birds and mammals and is a means of periodically replacing worn feathers and hair (Beltran et al. 2018). Moult in birds is the annually recurring planned loss and replacement of feathers of part of or the whole plumage. Moult is a process which is largely controlled by circannual rhythm in many species, especially passerines. This means that it is endogenously controlled according to a genetically programmed schedule that occurs approximately every 12 months (Guyomarc'h and Guyomarc'h 1995, Cadée et al. 1996, Gwinner 1996, 2003, Piersma et al. 2008, Karagicheva et al. 2016, Jenni and Winkler 2020). Circannual rhythm is synchronised with seasonal changes such as photoperiod (Dolnik and Gavrilov 1980, Berthold 1996, Gwinner 1996, 2003, Goymann et al. 2012) or temperature and rainfall in tropical areas that experience consistent day length year-round (Beltran et al. 2018). Photoperiod determines when moult can start, the extent of moult and the rate at which moult progresses. Moult, however, is hormonally controlled at the tissue level (Jenni and Winkler 2020), which includes the loss of old feathers and the growth of new ones, the sequence and shedding interval between feathers and the symmetry between wings (Jenni and Winkler 2020). This enables birds to adapt the duration, timing and extent of moult to environmental and biological conditions such as food availability, temperature, parasite load, stress and social behaviour (Jenni and Winkler 2020).

Along with breeding and, for many species, migration, moult is a key component and drastic event in the annual cycle and generally occurs during a specific period in the cycle that seldom overlaps with breeding or migration. For many species the moult period constrains other activities or is even a timeout from most of the other activities. Breeding, moult and migration are all time-consuming and energy-demanding activities. Moult has been studied far less than the other two (Newton 2009) and needs further research and exploration. Moult is more variable and adaptable in its timing, duration and extent compared to breeding and migration, but it is essential (Newton 2009, Kiat et al. 2018, Remisiewicz 2011). A breeding season can be missed but missing a moult reduces the bird's survival (Jenni and Winkler 2020).

The collection of moult data by bird ringers during bird ringing expeditions is relatively simple compared to collecting breeding and migration data (Newton 2009). Moult is also easier to study than the other two activities because it can be quantified and analysed using statistical methods to estimate its timing and duration (Newton 2009). In addition, precise historical data, stretching back over five decades, exists in large volumes, collected by a standard quantitative protocol which has remained unchanged.

One of the key issues in biology at present is understanding how biodiversity is responding to global climate change. More research has been devoted to finding long-term trends in relation to climate change (for example, distributional shifts of species) than to establishing how the seasonal organisation of the annual cycle is impacted. We already know that the timing of moult is responding to global climate change. Of the three key components of the annual cycle of birds, moult is the one that can be quantified with relative ease, with extensive baseline data. Research opportunities presented by the study of moult have thus far been poorly explored.

The physiology of moult

During a complete moult in birds, all feathers are replaced as well as the epidermal structures of the legs, feet, bill, claws and skin in some cases (King and Murphy 1990, Jenni and Winkler 2020). The feathers that are grown during moult consist of over 90% protein, which is about 25% of the overall protein content of a small bird (Jenni and Winkler 2020). Bone regeneration is also substantially increased during moult (Jenni and Winkler 2020). Moult is therefore a time of body restoration. When the feathers and other epidermal structures are shed, they are discarded to the environment. New feathers replace old feathers by pushing the old feather out, resulting in gaps in the plumage and a partial loss of plumage function during moult. Growing feathers develop mainly outside the body as blood quills and have a large supply of blood in the shaft to facilitate their growth and are therefore vulnerable. Feathers develop from their tip to their base. Therefore, the barbs and barbules grow first and the calamus grows last (Jenni and Winkler 2020). Feathers can only develop from feather follicles. These follicles are formed during embryonic development (Lucas and Stettenheim 1972, Prum 1999, Jenni and Winkler 2020). Feathers cannot grow continuously. Feather follicles are only active during periods of feather growth (Jenni and Winkler 2020). A developing feather grows day and night (Newton 1968, Murphy and King 1986) and must finish growth and cannot interrupt growth. Once growth is complete, the follicle becomes inactive (Yue et al. 2005). Feather growth takes place within the ring of epidermal collar cells which is situated at the base of the feather follicle (Jenni et al. 2012). A feather forms by the proliferation and differentiation of the epidermal collar cells of the follicle into keratinocytes (which form the barbs and barbules) and supporting cells (which separate the rami and barbules) (Yue et al. 2005, Widelitz et al. 2007, Alibardi and Toni 2008, Chen et al. 2015). Activation of the follicle causes growth of the circular epidermal collar into the epidermal cylinder, which fills with feather pulp and pushes the old feather out (Watson 1963a, b, Jenni and Winkler 2020). Feather pulp provides the nutrients and hormones needed for the differentiation, elongation and keratinisation of the keratinocytes. The feather cylinder develops into the feather shaft which comprises of the calamus and rachis from which the vanes radiate. The cylinder also splits into barbs, which have branches called barbules that make up the feather vanes (Campbell et al. 2008, Jenni et al. 2012). Colours are transported to the barbs and barbules via melanocytes (melanin pigments) and via fat particles (cartenoid pigments) in the blood vessels of the feather pulp (Lucas and Stettenheim 1972). The feather pulp then recedes, keratinocytes fill with β-keratin and die, the supporting cells break up and die, the feather sheath wrapped around the developing feather breaks away and the feather vane unfolds (Lucas and Stettenheim 1972, Alibardi and Toni 2008, Jenni and Winkler 2020).

In theory, birds can decrease the duration of moult by either growing feathers more quickly or growing more feathers at one time (Rohwer and Rohwer 2013). Feather growth rate, however, is limited and larger, longer feathers take disproportionately more time to grow than smaller, shorter feathers. This results in large birds needing exponentially more time to replace their flight feathers than smaller birds (Rohwer et al. 2009). The size of the feather follicle (cross-sectional area of the follicle) determines the form and structure of the feather (such as its shape, the number of barbs and the diameter of the calamus). It also determines the rate at which feather material is produced and therefore its growth rate by mass (mg/day) as the follicle size limits the rate of cell division within the epidermal collar cells situated at the base of the feather (Jenni et al. 2012, Rohwer and Rohwer 2013, Jenni et al. 2020). Feather growth rate is therefore restricted by feather form and structure. Nutrient supply to the epidermal collar cells and the growing feather may also limit growth (Jenni et al. 2012). Feather growth rate is best expressed as the mass of feather material produced per day because it increases more linearly with time than the daily increase in feather length (mm/day) (Seel 1976, Dawson 2003, Jenni and Winkler 2020). The amount of feather material laid down per unit length is termed feather massiveness or feather quality (Jenni and Winkler 2020). Since the size of the feather follicle limits the rate at which feathers can be grown, feather growth rate cannot be increased without compromising the quality of the feather produced. Therefore, for birds to reduce the time spent moulting their primary feathers, maintain feather quality and meet time constraints imposed by their annual cycle, they mostly grow more feathers simultaneously (Rohwer and Rohwer 2013).

The order in which feathers are moulted and the shedding interval between feathers is roughly predetermined (Jenni and Winkler 2020). Moult usually progresses symmetrically, especially in species which moult the corresponding primary wing feathers simultaneously on left and right wings (Jenni and Winkler 2020). The rate of increase in primary feather mass is relatively constant and there is a peak in the rate of total feather material produced during the middle of a complete moult (Newton 1966, Seel 1976, Bancroft and Woolfenden 1982, Wijnandts 1984, Dietz et al. 1992, Murphy and King 1992). Moult duration varies between species, between individuals of the same species and can vary from one year to the next within individuals (Jenni and Winkler 2020). The duration of primary moult is a good indicator of the duration of a complete moult of the entire plumage in birds that retain their ability to fly during moult because primary moult stretches over nearly the whole moult period (Rohwer and Rohwer 2013, Jenni and Winkler 2020). Moult duration is dependent on the length of the primary feathers (with length of primaries increasing with the bird's body size) and moult intensity (the number of feathers moulted simultaneously) (Rohwer et al. 2009, Jenni and Winkler 2020). Moult intensity determines the size of the feather gaps during moult (Jenni and Winkler 2020). In birds that retain their ability to fly, moult intensity is the main means by which they shorten or lengthen moult duration (Rohwer and Rohwer 2013, Jenni and Winkler 2020).

The overall cost per unit time of moult is strongly dependent on the extent of moult, the intensity of moult and compensations made during moult. Moult is an energetically and nutritionally expensive process in terms of energy and nutrients needed to grow new feathers and in terms of the loss of plumage function while the new feathers grow (Jenni and Winkler 2020). Of the energy required during the moult process, only a small portion is converted into feather mass. This indicates there are many other physiological processes occurring within the body than just the replacement of feathers during moult, including rejuvenation of many integumentary structures (Hoye and Buttemer 2011, Jenni and Winkler 2020). The physiological adaptations that occur during moult are an increase in the body's network of blood vessels and blood volume, mainly plasma volume, along with increases in total body water and water intake and loss (Chilgren and deGraw 1977, deGraw and Kern 1985, Jenni and Winkler 2020). Protein synthesis and protein breakdown is notably enhanced throughout the entire body during moult, not just in the growing feathers (Dolnik and Gavrilov 1979, Cherel et al. 1994, Murphy and Tarusio 1995, Tarusio and Murphy 1995, Pearcy and Murphy 1997). Body temperature and resting metabolic rate are also higher (Jenni and Winkler 2020). Increased thermoregulatory costs occur as a result of decreased plumage insulation (Newton 1968, Lustick 1970). Flight ability and efficiency are reduced due to wing gaps, which leads to increased energetic costs and predation risk (Slagsvold and Dale 1996, Lind 2001, Hedenström 2023) and decreased foraging ability and efficiency (Jenni and Winkler 2020, Hedenström 2023). Protection from water and effectiveness of display and signalling are costs that have not yet been investigated.

Birds can balance out, at least partly, the increased energetic costs through physiological and behavioural compensations and adaptations, such as decreasing other body system functions, decreasing activity levels or by altering their behaviour and becoming more inconspicuous (Jenni and Winkler 2020). During moult certain components of the immune system are reduced, while others are enhanced (spleen and thymus) (Jenni and Winkler 2020). During fast and intense moults, birds may reduce their body's physiological response to stress (reduce heart rate and release of the hormone corticosterone). This is generally not seen when moult is slow and over an extended period (Jenni and Winkler 2020). Their body mass is also generally lower during moult than during other times of the year (Newton 1969, Seel 1976, Hall et al. 1987), which helps to reduce the costs of activities, especially flight, and reduces their basal metabolic rate. Maximum metabolic rate or maximum aerobic capacity is also reduced and therefore maximum performance is reduced during moult (Jenni and Winkler 2020). Changes in body composition occur and organs that are not used during moult are reduced, for example ducks and geese reduce the mass of their breast muscle but increase leg muscle mass during moult for more time spent on the water than in flight (Jenni and Winkler 2020). Most birds reduce their activities (locomotion, reproduction, migration, foraging and display) during moult (Ben-Hamo et al. 2016, Jenni and Winkler 2020) which may decrease their predation risk and injury risk (especially to the vulnerable blood quills) (Jenni and Winkler 2020) and decrease their energy expenditure. Moult of flight feathers resulting in wing gaps affects flight capabilities and flight costs (Hedenström 2023). Birds can mitigate the costs of wing gaps as best as possible by altering the sequence in which flight feathers are moulted, increasing the mass of flight muscles and changing their flight dynamics, such as wing beat frequency and take-off angle (Holmgren et al. 1993, Chai 1997, Swaddle et al. 1999, Lind and Jakobsson 2001, Jenni and Winkler 2020, Hedenström 2023). Small wing gaps can be compensated for but at some additional energetic costs, while large gaps decrease flight capability.

Consequently, a paradox exists in that the moult process is energetically costly, but the moult period is usually a low-cost period for free-living birds, mainly because most or all moult costs are compensated or overcompensated for. Therefore, the energetic costs of moult do not appear to be their main constraint (Hoye and Buttemer 2011, Jenni and Winkler 2020). A bird in intensive moult is restricted in terms of flight, thermoregulation, behaviour and physiology. From an ecological perspective, moult is not a time of high energy expenditure but a time of constraints of other activities and processes. The degree of these constraints is dependent on moult intensity (Jenni and Winkler 2020).

Factors affecting feather quality

The conditions experienced during moult affect the quality of the feathers produced. They influence the size, structure and colour of the new feathers produced, and the extent of moult. When time for moult is limited or conditions are poor the speed of moult is increased, which results in lower quality feathers being grown. Moult speed is the moult intensity, which is the number of simultaneously growing feathers and therefore the number of gaps in the plumage. It is not the growth rate of the individual feathers. Generally, a fast moult, as opposed to a slow moult, will result in poorer quality body and flight feathers and body feathers of poorer colour. Feather quality is likely to be dependent on migratory behaviour. Migratory species generally produce feathers of poorer quality than sedentary conspecifics. Feather quality is also influenced by the moult-breeding overlap as overlapping moult with breeding can reduce feather quality in some species. Stress events, food availability, parasite load, exposure to pollutants and infection during moult all have an impact on the quality of the feathers grown (Jenni and Winkler 2020). Moult that produces plumage of decreased quality affects the fitness and survival of the individual (Dawson et al. 2000, Brommer et al. 2003, Jenni and Winkler 2020). Feather quality affects all feather properties and therefore functions of the plumage, including flight performance, insulation and signalling (Dawson et al. 2000, Jenni and Winkler 2020).

Because the conditions during moult impact feather quality, feather quality and appearance can be modified with each moult. It is therefore important to moult under favourable conditions to obtain a high-quality plumage. These include abundant and predictable food supplies (Newton 1966, Snow 1976), warm ambient temperatures (Buttemer et al. 2015, Jenni and Winkler 2020), end of the rainy season and dry conditions (Miller 1961), long day lengths and low predation risk (Newton 1966, Vega Rivera et al. 1999, Jenni and Winkler 2020).

Moult strategies

The study of moult gives insight into the moult strategies used by birds. Moult strategy explains how birds fit moult into their annual cycle along with breeding and migration (Jenni and

Winkler 2020). The order, timing and duration, and degree of overlap of these three events are related to the environmental and ecological conditions in which a population lives. Moult should occur after times of substantial feather deterioration or before life stages that will benefit the most from new feathers and when it is preferably not in conflict with another activity in the annual cycle (Jenni and Winkler 2020). The best time for moulting is usually after breeding when offspring become independent and conditions are favourable (Kiat et al. 2018, Jenni and Winkler 2020).

Most birds undergo one complete moult each year, but some moult two or three times a year, while larger birds can take more than a year to complete a full moult. A bird's moult strategy is determined by the length and growth rate of the longest primary feathers, which sets the minimum moult duration, the level of flight ability that needs to be conserved during moult, the timing of other events during the annual cycle that cannot occur at the same time as moult, and food abundance and accessibility (Jenni and Winkler 2020).

Moult and migration, and moult and breeding should ideally be separated because they compete in terms of time, energy and nutritional requirements, as well as in terms of flight and reproductive success (Jenni and Winkler 2020). Long distance migrants generally have a shorter moult duration than short-distance migrants and residents (de la Hera et al. 2009, 2011, 2012, Repenning and Fontana 2016). Breeding activity usually delays the start of moult and not breeding enables moult to commence earlier (Dietz et al. 2013). Because moult is essential, breeding time may be restricted, pushed earlier or omitted (Jenni and Winkler 2020). Competition between moult and breeding usually has the following outcome: if the birds breed early or only produce one brood, then they can moult slowly and produce high quality plumage (Jenni and Winkler 2020); if the birds breed late or have two broods, then they are forced to start moult late, moult fast resulting in low quality plumage and have shorter moult durations (Johnson and Minton 1980, Morrison et al. 2015, Jenni and Winkler 2020). When breeding and moult do overlap, moult usually progresses more slowly resulting in a longer moult duration (Johnson et al. 2012). The moult-breeding overlap generally occurs in species that have a long or late breeding season (Morton and Morton 1990, Svensson and Nilsson 1997, Newton and Rothery 2005) and when there is plenty of food available during the breeding season but not outside the breeding season (Payne 1965, Foster 1975, Hunter 1984, de Swardt 1992, Espie et al. 1996, Barbraud and Chastel 1998, Bridge 2006, Bond et al. 2013).

Small birds show a variety of moult strategies if they are limited for time during the annual cycle. They may increase moult speed and become nearly flightless by moulting many flight feathers simultaneously but this sacrifices plumage quality and flight performance (Kiat et al. 2018, Jenni and Winkler 2020, Mumme et al. 2021). They may overlap moult with breeding (or migration, but this is more unusual) (Kiat et al. 2018, Jenni and Winkler 2020). If migratory, they may moult in their breeding areas once breeding is complete; they may moult at a stopover site during migration or at their wintering grounds; others undergo a split moult, moulting part of their plumage in one area, suspending moult during migration and completing it in another (Niles 1972, Newton 2009, Kiat et al. 2018, Jenni and Winkler 2020). Under rare circumstances small birds may stop moult and retain their feathers for another year (Jenni and Winkler 2020). Medium-sized birds generally have longer moult durations and breeding seasons than smaller birds and therefore often struggle to fit both events into the annual cycle separately. For this reason, a moult-breeding overlap occurs quite regularly (Payne 1972, Boddy 1981, Bancroft and Woolfenden 1982, Kjellen 1994). Large birds, such as large birds of prey, have a big problem when it comes to moult. Their large flight feathers require a long time to grow. If they need to maintain flight ability during moult, they can only tolerate small wing gaps as wing gaps have a larger impact on flight capability in large birds than in small birds. These birds also have long breeding seasons due to the long time it takes to raise a brood (Jenni and Winkler 2020). They therefore regularly overlap breeding and moult, but some are still unable to fit moult into the annual cycle and therefore only moult some of their flight feathers each year (Langston and Rohwer 1996, Zuberogoitia et al. 2018). In large birds that do not overlap breeding and moult, and are unable to fit moult into the annual cycle, they may skip breeding one year to catch up on moult (Langston and Rohwer 1996, Rohwer et al. 2011). Another strategy used by large birds, especially waterbirds, but also seen in some smaller birds, is that they moult all their flight feathers simultaneously and become flightless until close to the completion of moult (Jenni and Winkler 2020). Juvenile birds of most species undergo a different moult to adults during their first year and then they adopt the adult moult from their second year onwards. In some species it takes several years for juveniles to assume the adult plumage (Jenni and Winkler 2020).

The focus of this thesis is not on the purpose, physiology, energetic costs or control of moult underlying all the processes and patterns but rather on the statistical approaches of analysing moult and assessing patterns and differences in the timing and duration of primary moult. Only birds that undergo a continuous sequential moult annually are considered in these analyses.

THE STATISTICAL METHODS DEVELOPED FOR THE STUDY OF MOULT

The statistical challenge in the study of primary moult in wild birds is that we do not observe it starting or finishing. The birds which are sampled, usually obtained during bird ringing operations or by photography of birds in flight, are either “in moult”, “not yet started moult” or “completed moult”. It is from these indirect observations that we need to estimate the timing and duration of moult.

The standard field method for recording primary moult in birds is to examine the primary feathers of one wing and score each feather from 0 to 5 based on the state of the feather. Old feathers are given a score of 0 and new, fully-grown feathers 5. Growing feathers are assigned a score of 1 to 4: 1 = missing feather or feather pin, 2 = growing feather up to one-third of its final length, 3 = feather is one to two-thirds grown, 4 = feather is more than two-thirds grown but not its final length. The primary moult score, which is a numerical indicator of the bird’s state of moult, is then calculated by summing the scores of the individual primaries (Ashmole 1962, Ginn and Melville 1983). The majority of birds have either nine or 10 primary feathers per wing (maximum moult score of 45 or 50 respectively) and primary moult usually starts from the innermost primary (P1) and continues sequentially to the outermost (P9 or P10). The sequence of moult scores, 5555411000, means that the four innermost primaries are new, the fifth is almost fully grown, the sixth and seventh are either missing or feather pins and the outer three are old feathers. The sum of moult scores for this wing gives an overall moult score of 26. The Traditional Moult Score referred to in later chapters is the proportion of the total moult score.

Most passerines have moult scores that increase linearly through time (Ginn and Melville 1983) but for some species, such as waders, moult scores do not increase at a constant rate. It is more realistic to assume that feather material is grown at a constant rate for these species. Subsequently proportion feather mass grown was developed as an alternate moult index (Summers et al. 1983).

Moult scores can be converted to proportion feather mass grown (Summers et al. 1983, Underhill and Zucchini 1988, Underhill and Summers 1993). The mass of individual primaries is recorded by drying fresh feathers in good condition in a convection oven at 60°C for 24–48 hours and weighing them to the nearest 1 mg or 0.1 mg. To obtain the relative mass of each primary, the percentage mass that each feather contributes to the total mass of all primaries is calculated. This percentage mass is averaged across the number of birds from which feathers were taken (Summers et al. 1983, Underhill and Summers 1993). Moult scores for the individual primaries are then converted to proportion feather mass grown by multiplying the relative mass of each primary by factors as recommended in Underhill and Zucchini (1988) and Underhill and Summers (1993): relative mass of a primary with moult score of 0, 1, 2, 3, 4 or 5 is multiplied by 0, 0.125, 0.375, 0.625, 0.875 or 1 respectively and summed over the primaries to obtain an estimate of proportion feather mass grown.

The easiest and most obvious way of analysing moult data is to do a simple linear regression of moult score on date using only birds in active moult. The start and end dates of moult and the duration of moult are estimated from the regression equation. Pimm (1976) noted that this method gives inaccurate results because it overestimates duration of moult for the average bird. The reason for the incorrect moult estimates from linear regression is that the variance of the residuals of the response variable (moult score) is not constant. There is less variability in moult score at the beginning and end of moult than during the middle stages of moult (Underhill 1985, Underhill and Zucchini 1988). The data therefore violates one of the key assumptions of linear regression, homoscedasticity. When the moult scores are plotted against date, the scatter of points is shaped as a parallelogram. The regression line fitted to this data tends to run diagonally along the long axis of the parallelogram thus estimating the start and end dates of the population rather than the individual (Pimm 1976, Summers et al. 1983). Pimm (1976) suggested regressing date on moult score to obtain more accurate estimates. This method treats moult score as the explanatory variable (x) and date as the response (y) variable. Underhill and Zucchini (1988) demonstrated this approach to be biased, as it does not meet the assumptions of linear regression.

Other methods which have been used to analyse moult data include curvilinear regression of mean and median moult score against date, curvilinear regression of moult scores against mean dates, linear regression of date against percentage feather mass grown and curvilinear regression of 5% increases in feather mass grown against mean dates (Summers et al. 1983).

Underhill and Zucchini (1988) present an alternative method, the Underhill-Zucchini moult model, to analyse the timing of primary moult. This mathematical model has become the leading model for the statistical analysis of moult. The model uses maximum likelihood estimation to estimate moult parameters (duration of moult, mean start date of moult and standard deviation of the mean start date of moult) for the average bird in the sampled population. The standard deviation of start date is a measure of variation of start date in the population. The model requires a moult index that increases at a constant rate. The moult index used is dependent on the moult characteristics of the studied species. It might be overall moult score, proportion feather mass grown or some other measure that increases linearly through time and is scaled to range from 0 (moult not yet started) to 1 (moult completed). In addition to the assumption that the moult index increases linearly, the moult model has three other key assumptions. The first is that the duration of moult is the same for all birds in the population. The model is therefore not suitable for analysing moult in species where some birds in the population have arrested, suspended or partial moult. The second is that the start date of moult of individuals is normally distributed about the estimated mean start date of the population. And the third is that the birds caught on each sampling occasion are a random sample from the population and the probability of capture is independent of moult stage.

Developments of the moult model

The parameters of the moult model could initially be estimated using one of three data types (Underhill and Zucchini 1988). Data type 1 and 2 are used when all birds in the population have an equal probability of capture independent of their moult stage. Type 1 data simply classifies birds into one of three categories: “moult not yet started”, “in moult” or “completed moult” whereas type 2 data consists of a moult index value assigned to each bird that indicates their state of moult. Type 3 data is used when the sampled population consists only of birds in active and their moult indices are recorded (Underhill and Zucchini 1988, Underhill et al. 1990). The model was later extended to include two additional data types (type 4 and 5) to accommodate populations when only a portion of the population is available for sampling. Type 4 data is used when birds migrate into the sampling area and start moult shortly after arrival and then remain in the area once moult is complete for the duration of the sampling period. It is therefore assumed that type 4 data consists of moult indices of birds that are “in moult” and “completed moult”. Type 5 data is used when birds are present in the sampling area before they start moult and during moult but once they have completed moult, they depart. Type 5 data therefore consists of moult indices of birds “not yet started moult” and “in moult” (Underhill et al. 1990).

The model developed by Underhill and Zucchini (1988) was intended to be applied to the full tract of primary feathers. Serra (2002) developed the idea of applying the model to individual primary feathers. From this and using proportion feather mass grown as the moult index, a cumulative curve of feather growth could be plotted (Remisiewicz et al. 2009). The cumulative growth curve allows one to check the assumption of linear feather mass increase (Underhill and Zucchini 1988) through moult and to model moult when the accumulation of feather mass is not linear.

The moult model was initially not widely used because it was not easy to implement to analyse data. The development of the definitive software, the package “moult” in R (Erni et al. 2013), to do the actual calculations to estimate the parameters of moult made implementing the model user-friendly and broadly available. Extensions of the moult model allow the parameters of moult to depend on explanatory variables and allow one to investigate how some of the parameters might differ in different situations (Erni et al. 2013).

THESIS OUTLINE

This thesis aims to expand upon the current developments of the Underhill-Zucchini moult model in Chapters 2 and 3. Chapter 2 introduces a new moult index, the Relative Duration Index, to quantify progress through moult. It uses the Laughing Dove *Spilopelia senegalensis* as a case study. Chapter 3 focuses on the Red-headed Finch *Amadina erythrocephala* which is a poorly studied species with little known about its biology. This chapter quantifies one aspect of its life history, the primary moult of adult Red-headed Finches. It also illustrates a strategy for handling the potential problem that data from a single year (or a single site) are influential in the analysis of primary moult.

Latitude is known to play an important role in determining moult patterns but, apart from Africa, moult studies in the southernmost limits of the continents are lacking. Little is also known about the moult of New Zealand's endemic, native and introduced bird species. Chapter 4 focuses on the moult of the self-introduced Silvereye *Zosterops lateralis* and how it compares to that of other *Zosterops* species. Chapter 5 focuses on Wrybill *Anarhynchus frontalis*, which is a species of plover endemic to New Zealand. It is classified as a Vulnerable species and as such its population dynamics and breeding are well described. However, there is a gap in knowledge in the understanding of its moult and this chapter fills that gap and compares its moult with that in other closely related species.

Moult strategies are flexible, and the timing and duration of moult are adapted to local conditions. When considering introduced resident species, no papers have compared their moult patterns in their original range to locations where they have been introduced, especially where the original range and the introduced range are in separate hemispheres separated by c. 90 degrees of latitude. In Chapter 6 the primary moult of seven European passerines introduced to New Zealand is compared to birds of the same species in United Kingdom populations from where they originated. We are interested in how the change of hemispheres and 160 years of elapsed time since introduction has affected their moult patterns.

The thesis concludes, in Chapter 7, with the creation of a database of studies that included estimates of primary moult parameters obtained using the Underhill-Zucchini moult model. Relationships between the estimated moult parameters and a series of explanatory variables are explored. Chapter 7 points out the deficiencies in the available information, which consist mainly of critical gaps in knowledge. Priorities for fieldwork and analysis are described so that key gaps are filled and a global review of primary moult can be undertaken.

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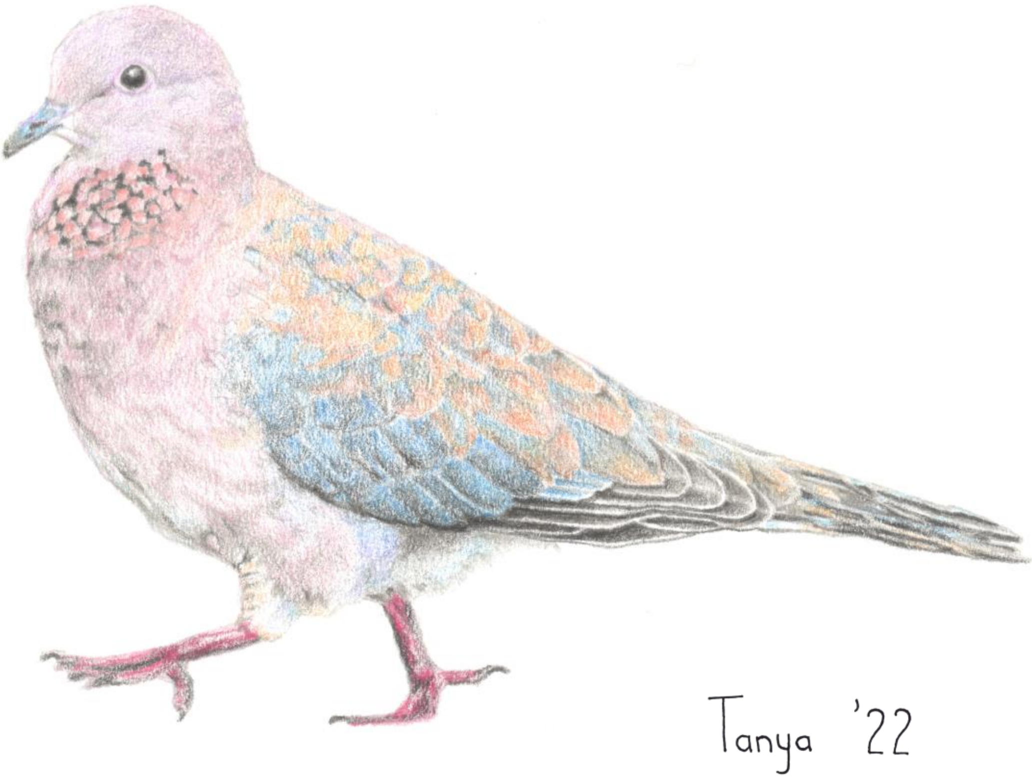

CHAPTER 2

Primary moult of adult Laughing Doves *Spilopelia senegalensis*: Introduction of the Relative Duration Index and a comparison of moult indices

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Abstract: A new moult index, the Relative Duration Index (RDI), to quantify progress through moult using the Underhill-Zucchini moult model was developed, using the Laughing Dove *Spilopelia senegalensis* as a case study. RDI weights individual primaries in accordance with their estimated relative moult durations in the same way as PFMG weights primaries in accordance with their relative masses. A sample of 1,893 moult records of adult Laughing Doves was used to study their primary moult. Moult parameters were estimated for three moult indices: Traditional Moult Score (TMS), Proportion Feather Mass Grown (PFMG) and Relative Duration Index (RDI), and for each of the 10 primaries. Comparing the moult parameter estimates of each of the three indices to their respective cumulative growth curves obtained from the progression of moult of individual primaries, PFMG had the closest fit. However, any of the three moult indices would give satisfactory results for the Laughing Dove. Laughing Doves had an estimated primary moult duration of 215 days, with a mean start date of 3 November and a mean completion date of 6 June. The standard deviation parameter was 66 days, which implies a lack of synchronisation of moult in adult doves. It was hypothesised that RDI might be an appropriate moult index for species which moult one feather at a time and for which the individual moult durations are not proportional to their mass, as seen in Laughing Doves. However, this was not the case as PFMG provided the best fit. RDI might also prove to be an appropriate moult index for species which moult multiple feathers simultaneously during part of the moult period and these feathers grow more slowly than when fewer feathers are moulting simultaneously. The best practice for the analysis of primary moult using the Underhill-Zucchini moult model is to include adequate information, so that validity of analysis can be independently assessed; a primary-by-primary analysis, if there is sufficient data; evenly distributed data throughout the whole moult period; and appropriate tables and figures to assess the quality of results.

Keywords: Doves, pigeons, Underhill-Zucchini moult model

INTRODUCTION

The statistical challenge in the study of primary moult in wild birds is that we do not observe the dates on which it starts or finishes. The birds which are sampled, usually obtained during bird ringing or by photography of birds in flight, are either “in moult”, “not yet started moult” or “completed moult”. It is from these indirect observations that we need to estimate the timing and duration of moult. From a statistical perspective, there are five key milestones in the study of primary moult: (1) the recording system used mainly by bird ringers (Ashmole 1962); (2) the ideas behind the concept of “proportion feather mass grown” (Summers 1980); (3) the statistical model developed by Underhill and Zucchini (1988); (4) the idea of applying this model to individual primary feathers (Serra 2000, Underhill et al. 2006); and (5) the extensions of the model developed by Erni et al. (2013) and implemented in R so that the analysis is broadly available. This chapter blends these advances to develop a new moult index to quantify progress through moult. It uses the Laughing Dove *Spilopelia senegalensis* as a case study to illustrate the concepts.

The Laughing Dove is widely distributed in Africa (except for deserts and tropical forests), southwestern Asia and Western Australia. It is commensal with man, and the range is expanding due to both expansions and introductions (del Hoyo et al. 1997). It is an obligate drinker, so it has expanded its range into areas where agriculture and suburban development have provided water (Rowan 1983, Colahan and Harrison 1997). Despite its abundance, substantive studies of Laughing Doves are scarce. In northern Africa, for example, it is described by Brahmia et al. (2015) as a poorly documented species. In southern Africa, the most recent major studies were done four decades ago: Stellenbosch, Western Cape (Siegfried 1971a, b; Siegfried et al. 1972, Heÿl 1976, 1982); Barberspan, North West Province (Dean 1977, 1979a, b, 1980); and eastern Botswana (Irving and Beesley 1976, Beesley 1978). Heÿl’s (1976, 1982) studies were motivated by the potential for Laughing Doves to be classified as gamebirds and the studies in Botswana by the dove reaching pest status in cereal crops. Siegfried et al. (1972) considered that, because of their sedentary habits and their abundance in urban, suburban and rural habitats, Laughing Doves had potential for use as environmental indicators, such as the uptake of lead into their bones. These factors make the Laughing Dove a species of considerable anthropogenic importance.

This chapter considers the primary moult of adult Laughing Doves in Cape Town, South Africa, near the southern limit of its range. The statistical analysis of primary moult requires the use of a “moult index” (Underhill and Zucchini 1988); this chapter compares the outcomes using three different indices, one of which is new. A set of the three moult parameters (Underhill and Zucchini 1988) was estimated for each of the three indices and sets of moult parameters for each of the 10 primaries were estimated, as done by Underhill et al. (2006). The chapter places emphasis on the development of best practice methods for the analysis of primary moult using the Underhill and Zucchini (1988) moult model (1988).

METHODS

Laughing Doves were trapped by George D. Underhill using a zap net (Underhill and Underhill 1987) on the lawns of two gardens (12 and 14 Muswell Hill Road, 33.949° S, 18.483° E) in Mowbray, a suburb 6 km from the centre of Cape Town, South Africa. A walk-in trap was used for a short period. In addition, Laughing Doves were captured incidentally in mistnets during ringing studies at various localities within 50 km of Cape Town between June 1983 and January 1994. Birds were ringed with SAFRING rings (de Beer et al. 2000).

Doves were aged on the basis of plumage characteristics into two classes, juvenile or adult (Hunter 1973). The sexes of the birds were unknown. The state of primary moult was recorded for one wing as a moult formula comprising 10 digits, one digit for each primary. Each primary feather was scored a value from 0(=old) to 5(=new) indicating the stage of moult of that primary (Ginn and Melville 1983). Data from birds aged as adults were used in this analysis.

For most species, there is a period of the year during which no birds are in active primary moult. Conventionally, moult analyses are done by first choosing a date within this period and treating birds with "no moult" immediately after this date as "no moult old" and those immediately prior as "no moult new" (implicit in, for example, Oschadleus and Underhill 2006). A cut-off date like this for Laughing Doves was not possible because there was no period in the year when no birds are in primary moult. This was also the case with Ring-necked Doves *Streptopelia capicola* (Underhill et al. 1999) and Speckled Pigeons *Columba guinea* (Underhill and Underhill 1997). The strategy used to resolve this problem with the Laughing Dove was the same as that used by Underhill and Underhill (1997) and Underhill et al. (1999). A diagonal line parallel to the mean moult line was positioned visually to pass through the area with the fewest data points. The x-axis of the plot then needed to be extended so that additional months are repeated at the end of the axis and the records above the diagonal line shifted to the extended x-axis (see Results).

The three parameters of primary moult (duration, starting date and standard deviation of starting date) were estimated using the model of Underhill and Zucchini (1988). It was estimated that 95% of birds start moult in the period given by the estimated mean start date ± 1.96 × estimated standard deviation parameter. Models were fitted using the package 'moult' (v. 2.1.0) (Erni et al. 2013) in R (v. 3.6.2) (R Core Team 2019). Day 1 was set as 1 September. Data type 2 of the moult model requires data from birds in all stages of moult (Underhill and Zucchini 1988), therefore we used it because entire population of adult Laughing Doves was present on each sampling date and it can be assumed that each member of the population had equal chance of being sampled regardless of its moult stage. The moult model assumes that the modelled index increases linearly with time. The choice of index needs to be carefully considered in relation to this model assumption. The assumption of linear increase in moult index would not be met if Laughing Doves undertook suspended moult. Both Siegfried (1971b) and Dean (1979b) specifically mentioned that they did not observe suspended moult in this species.

Three moult indices, using the data from the 10 feathers forming the primary tract of the Laughing Dove, were calculated. Let s_i, $i = 1, \ldots, 10$, denote the score allocated to the ith primary. (1) The Traditional Moult Score (TMS) is the sum of the moult scores of the individual primaries (Ashmole 1962). To transform to a moult index lying between 0 and 1, the sum was divided by 50, which is the moult score corresponding to all 10 primaries being new:

$$\text{TMS} = \left(\sum_{i=1}^{10} s_i\right)/50$$

(2) The Proportion Feather Mass Grown (PFMG) was calculated as in Underhill and Zucchini (1988) and Underhill and Summers (1993):

$$\text{PFMG} = \sum_{i=1}^{10} m_i \, p(s_i)$$

where $p(0) = 0$, $p(1) = 0.125$, $p(2) = 0.375$, $p(3) = 0.625$, $p(4) = 0.875$, $p(5) = 1$, as in Underhill and Zucchini (1988) and where m_i is the relative mass of the ith primary feather. Relative masses of primary feathers of Laughing Doves were obtained from Underhill and Joubert (1995). (3) The Relative Duration Index (RDI) is a new index that weights individual primaries in accordance with their estimated individual moult durations. These individual moult durations were obtained from the moult parameters estimated for each individual primary (described below). The "relative duration" of the moult of each primary was calculated by adding the durations of the 10 primaries and dividing the duration of each primary by this sum. Let d_i denote the relative duration of moult of the ith primary. Then the Relative Duration Index (RDI) is defined as:

$$\text{RDI} = \sum_{i=1}^{10} d_i p(s_i)$$

The Underhill-Zucchini moult model assumes that once moult starts, the moult index increases linearly with time until moult is completed. TMS gives each feather equal weight in the moult index, PFMG gives each feather weight in proportion to its mass, and RDI gives each feather weight in proportion to its observed duration of moult. Moult models using any of these three indices are known as the full tract models because they describe moult of the 10 primary feathers as an entity.

Because sample sizes were large and because the dataset was fairly uniformly distributed throughout the year, it was feasible to estimate the three parameters of primary moult for each individual primary feather, also using data type 2. This was done as described in Serra (2000) and Underhill (2003) where a moult index was created for each primary by transforming scores of 0 to 5 in the moult formula to 0, 0.125, 0.375, 0.625, 0.875 and 1 respectively. The estimated moult durations for each individual primary were used in the calculation of RDI, as described above. We plotted the progress of moult for individual primaries, as first done by Underhill (2003). The x-axis represents date. The line for each feather starts on the x-axis on the date of start of moult. The endpoint for the line is directly above the date of completion of moult on the x-axis. The height to which the line for each feather rises varies with the choice of moult index. For PFMG, the heights on the y-axis are the relative feather masses; for RDI, the heights are the relative durations of moult for each primary; and for TMS the heights are all 0.10, because each of the 10 feathers is given equal weight. The slopes of the lines represent the rate of increase of the moult index. If the moult index is increasing at the same rate for each primary feather, then the 10 lines will be parallel. By design, the lines for RDI are parallel. For the other two indices we can assess departure from parallelness by calculating the coefficient of variation (CV) of the 10 slopes in each plot. The moult index with the smaller CV is then a strong candidate for being the best moult index. Another criterion for assessing the moult indices is to compare the estimated dates of the start of moult of the first primary and the end of moult of the 10th primary with the equivalent results from the full tract moult model for the 10 primaries. The preferred moult index will have dates that closely coincide.

For each moult index (TMS, PFMG and RDI), the plots described above were used to assess the assumption of a linear increase in moult index by calculating the daily cumulative proportions of primary feather growth and plotting them to form a curve, as described by Remisiewicz et al. (2009). For each of the three moult indices, this cumulative growth curve was calculated using the relative primary weighting appropriate for that moult index (Remisiewicz et al. 2009). In the cumulative curve for TMS each primary is given equal weighting. For PFMG, the cumulative curve is calculated giving each primary weight according to its relative mass and for RDI, it is calculated giving each primary weight according to its relative moult duration. If there is an exactly linear increase in the moult index, then the cumulative growth curve is also linear. We compared the cumulative growth curves for each of the three indices with the results of the associated full tract model. For each cumulative growth curve we also plotted a straight line, joining the estimated dates of start and completion of primary moult for the 10 primaries. The closer the cumulative growth curve is to this straight line, the better the assumption that the moult index increases linearly with time is met. Our final choice of moult index is based on this assessment. If there is large deviation from a straight line in the cumulative curves for all indices, then none of the indices are appropriate and the results must be treated with caution.

Two auxiliary measures relating to primary moult were computed. Both provide insight into the direct and indirect energetic costs of moult.

Firstly, the average number of simultaneously growing primaries is defined as moult intensity and is a proxy for the energetic costs of feather production (Remisiewicz et al. 2009, Jenni and Winkler 2020b). The average number of primaries growing simultaneously while each of the 10 primaries was in moult was calculated (Remisiewicz et al. 2009). The 95% confidence intervals were also calculated and plotted.

Secondly, Proportion Feather Mass Missing (PFMM), as described by Remisiewicz et al. (2009), was plotted. PFMM quantifies the relative size of the wing gap created when primary feathers are being moulted, taking into account the relative mass of the primaries. PFMM helps to quantify an important component of the more subtle costs of moult, this being that the larger the wing gap the greater the impairment to flight capabilities, such as speed of flight and manoeuvrability (Jenni and Winkler 2020a, 2020b, Hedenström 2023). PFMM is a development of the concept of "raggedness" developed by Haukioja (1971). This original definition failed to take relative feather masses into account.

One assumption of the moult model of Underhill and Zucchini (1988) is that the date of start of moult of individuals is normally distributed. To date, no progress has been made on a strategy to examine this assumption. The plot proposed here makes progress towards examining one property of the normal distribution, its symmetry. The PFMG scores of actively moulting adults were projected back to their start dates of moult. These starting dates were plotted as a histogram with 25-day class intervals. Because of the truncation of moult scores resulting from birds classified as "not yet started" and "completed", there is no theoretical reason why this histogram should have a normal distribution. However, if birds were sampled consistently through the moult season, the distribution of starting dates should be unimodal and symmetric.

We hypothesise that the most likely departure from symmetry will be a heavy tail to the right. This would point to most birds starting primary moult as soon as possible in the moult period, for example shortly after breeding, and a substantial minority starting late, for reasons such as extended breeding attempts or poor health condition. This departure from the assumptions of the moult model has not previously been considered.

Another assumption of the moult model is that birds are available to be sampled, independent of their stage of moult. A method which enables this assumption to be assessed visually is developed here. A histogram of PFMG scores of birds in active moult was constructed. Class intervals of 0.1 were used but alternative class intervals might also be appropriate. It is anticipated that, provided birds have been sampled consistently through the moult season, the histogram will be approximately that of a uniform distribution. Although Mumme et al. (2021) did not produce these plots in their analysis of the moult of 13 North American warbler species, it is clear from their results that moult intensity was so large in the middle stages of moult that birds became reluctant to fly and were underrepresented in the moult samples. With their data, the histogram suggested here would have been strongly U-shaped, indicating that this assumption of the Underhill-Zucchini moult model had been violated. If the Underhill-Zucchini moult model had been applied to the data of Mumme et al. (2001), the results would have needed to be qualified by reporting that there had been a departure from the assumption of equal catchability.

RESULTS

A total of 1,893 captures of adult Laughing Doves was made in the Cape Town area: 252 were pre-moult, 939 were in active moult and 702 were post-moult. The moult of the 10 primary feathers was sequential, commencing with the innermost primary, P1, and ending with the outermost, P10. As with Siegfried (1971b) and Dean (1979b), we did not record suspended moult.

Moult of the individual primary feathers

We present first the results for the individual primaries (Table 1). The estimate of the mean start date of moult of P1 was 4 November and the estimate of the completion date of P10 was 3 June, both with standard errors of 3 days. This implies an overall moult duration for the Laughing Dove of 212 days (SE 4 days). The relative masses of the primaries increased monotonically from 6.7% for P1 to 14.2% for P10, so that the outermost primary was 2.1 times the mass of the innermost (Table 2). The estimates of the duration of moult of individual primaries averaged 20.4 days but fell into two clusters: the duration of moult for P1 to P6 varied between 16.1 days (P3) and 19.6 days (P1), and for P7 to P10 varied between 22.8 days (P10) and 26.4 days (P8). The correlation between the moult duration and primary mass was 0.84 ($P<0.003$) (Figure 1). However, the durations did not increase monotonically from P1 to P10, and the ratio between the longest and shortest durations was 1.64, suggesting that moult duration of individual primaries was not proportional to their masses (Tables 1 and 2). It was this lack of proportionality that motivated the development of the Relative Duration Index (Equation 3). The coefficient of variation (CV) of the slopes for the primaries in the progression of moult in relation to their relative masses was 15.4% (Figure 2). This was similar to the CV of the slopes

(16.9%) when each primary was given equal weight (Figure 3), implicit in the calculation of the Traditional Moult Score (Equation 2). Figure 4 shows the progression of moult in relation to the relative durations; these lines are parallel, so the CV of the slopes is zero. The Relative Duration Index (Equation 3) is motivated by the notion that if growth rates of primaries are not proportional to their masses, as appears to be the case here, the RDI (Equation 3) might perform better then PFMG or TMS.

The feather shedding interval, which is the period between the dropping of the successive primary feathers, was obtained by subtracting the start date of moult of one primary from the start date of moult of the previous primary (Table 1). The average interval was 20 days, with a generally increasing pattern (the average of the first three feather shedding intervals was 16 days, and of the final three was 30 days) (Table 1). The average feather shedding interval was thus similar to the average individual feather duration (Table 1).

Apart from P1 and P10, which have only a single adjacent primary, the mean number of simultaneously growing primaries averaged 1.4 for P2 to P9 (Figure 5). Excluding the first and last primaries, the number of primary feathers growing simultaneously decreased from P2 to P9 (Pearson's $r = -0.84$, $P=0.005$) and decreased as the mass of the primary increased ($r = -0.78$, $P<0.012$) (Figure 5, Table 2).

Moult of the entire primary tract

Using 1 September as the cut-off date, the plot of, for example, PFMG against date (Figure 6) is problematic for analyses using the Underhill-Zucchini moult model, in that the points in the top left corner of the plot are clearly birds which made a considerably later start to moult than the majority of the birds. Subsequently we produced a series of three plots (Figure 7 for TMS, Figure 8 for PFMG and Figure 9 for RDI) with adjusted dates as described in Figure 6. The estimates of the mean starting date of moult using the three moult indices spanned 14 days (20 October to 3 November) and the estimates of the completion date were within nine days of each other (26 May to 6 June) (Table 3). The duration parameter estimates for TMS, PFMG and RDI were within five days of each other; 220, 215 and 218 days respectively and the standard deviations were 65.1, 65.5 and 65.1 days respectively. The large standard deviation parameters imply a lack of synchronisation of moult in adult Laughing Doves, with the length of the period during which an estimated 95% of doves start (or complete) moult being 255 days (eight months) for TMS and RDI, and 257 days for PFMG. The mean starting and completion dates for primary moult estimated using the PFMG moult index (Table 3) provided the closest fit to the estimated mean starting date for P1 and completion date for P10 (Table 1). The red lines in Figures 7, 8 and 9 depict the cumulative proportions of primary feather growth. Visual evaluation of the deviation of the cumulative curve for each moult index from its associated straight line, derived from the moult model using that index, assists in selection of the best index for the chosen species. In the case of Laughing Doves, the cumulative growth curve for TMS is a poor fit to the line derived from the moult model using TMS (Figure 7). The cumulative growth curve for PFMG fits the line derived from the PFMG moult model more closely than that for RDI (Figures 8 and 9). PFMG is therefore the preferred moult index for this species. The focus of the results from this point on uses PFMG index of moult progress.

Wing gap size during primary moult

For birds in moult, the average size of the wing gap as described by PFMM was 4.9% with a standard deviation of 4.6%. This provides a quantitative measure of moult intensity. This means that at any given time during active moult birds were missing 4.9% of their primary feather mass (Figure 10). The largest wing gap was 22.5% (for a dove with moult score recorded as 55555 55421) and there were times during active moult when no wing gap was present (Figure 10).

Examining the assumptions of the moult model

The histogram of estimated start dates of Laughing Doves in active moult peaked at the end of October and beginning of November and had a positive skewness of 1.10 (Figure 11). The mean predicted start date was 15 November, with a standard deviation of 65 days. The median start date was 1 November. In Figure 12, observed PFMG scores were approximately uniformly distributed, indicating that the trappability of the doves during sampling appeared to be independent of stage of moult. These two histograms (Figures 11 and 12) only included birds in active moult.

DISCUSSION

Primary moult of the Laughing Dove

The differences between the estimates of the moult parameters were relatively small when comparing the three moult indices. This suggests that, for the Laughing Dove, the moult model is fairly robust in terms of choice of moult index. Although different moult indices did produce varying results, they would not be misleadingly different in, for instance, a meta-analysis of primary moult results using the model. The transformation of moult scores to Proportion Feather Mass Grown is vital in the analysis of the migrant shorebirds and terns. For example, in the Common Redshank *Tringa totanus*, the outermost primary, P10, is 3.2 times heavier than P1 (Summers et al. 1983) and in the Common Tern *Sterna hirundo*, the ratio is 8.0 (Underhill and Joubert 1995). The PFMG transformation is less imperative in the Laughing Dove, for which the heaviest primary is 2.1 times the mass of the lightest (Table 2). This observation almost certainly applies to other species with similar mass ratios between the heaviest and lightest feathers.

The Proportion Feather Mass Grown (PFMG) index was our preferred moult index because it most closely reflected the per-primary model; the estimates for the start and end date of primary moult (3 November and 6 June respectively) coincided best with the P1 start date (4 November) and P10 end date (3 June) (Tables 1 and 3). However, to estimate the parameters of moult for each individual primary large samples of sets of moult scores, spread fairly evenly throughout the period of primary moult, are needed.

Because the Laughing Doves moulted, on average, c 1.5 feathers at a time (Figure 5) and because the durations of moult of individual feathers were not proportional to their masses (Figure 1), the Relative Duration Index (RDI) was potentially a moult index which increased more linearly through time than Proportion Feather Mass Grown (PFMG). This proved not to be the case. However, there might well be species which moult a single feather at a time, and for which the individual moult durations are not proportional to their mass. For such species, the RDI might be the appropriate moult index. RDI might also prove to be an appropriate moult index for species which moult multiple feathers simultaneously during part of the moult period and these feathers grow more slowly than when fewer feathers are moulting simultaneously.

Even when the moult model assumption that starting dates are normally distributed is met perfectly, there is no theoretical reason why the distribution of projected start dates through time (Figure 11) should have a normal distribution. This is because of the truncation of the pre-moult and post-moult records. However, if the data were collected evenly through time, as in this situation, the distribution is expected to be symmetric. We observed positive skewness (coefficient 1.10). In words, this means that there were many birds making a late start to moult and few making an early start to moult (Figures 7–9, 11). This finding has both statistical and biological implications. Statistically, it raises the question of what impact departure from the model assumption, that starting dates are normally distributed, would have on the results. The standard way to tackle this problem is through an extensive simulation study. However, in other contexts where a normal distribution is assumed, skewness values between –2 and +2 are regarded as acceptable (Hair et al. 2010).

Biologically, the implication is that, although the overwhelming majority of Laughing Doves follow an annual cycle which involves moult starting between September and December, there appears to be a substantial minority which start moult later than this, so the histogram of starting dates is positively skewed (Figure 11). The timing of breeding in the Western Cape is also positively skewed, with a peak in October (Colahan and Harrison 1997), about a month earlier than the start of primary moult. The period from egg-laying to fledging of chicks is close to one month for Laughing Doves (Hockey et al. 2005). A suggested research project would be to relate timing of breeding for individual doves to the timing of start of moult. This would include an investigation of the extent to which Laughing Doves overlap breeding and primary moult and of whether or not they suspend moult during breeding. This would confirm Dean's (1979b) comment that because moult was slow it was not physiologically demanding and therefore the birds could moult and breed simultaneously without stopping moult.

Primary moult of doves analysed using the Underhill-Zucchini moult model

The estimated durations of primary moult of adult Laughing Doves were 215 days (PFMG estimate) and 212 days (per primary estimate) which were nearly 100 days longer than the 120-day duration Dean (1979b) estimated using regression analysis. Siegfried (1971b) suggested a 164-day duration for the completion of primary moult in adults based on re-examination of birds that were re-trapped on more than three occasions. The most intensive period of active primary moult of Laughing Doves is during the summer months, December to April, with two thirds of active moult recorded during this five-month period, which is in agreement with Siegfried (1971b). Focusing on studies of populations in South Africa and that have used the Underhill-Zucchini moult model, so that differences between species are due to biology and not latitude or analysis method, the duration of primary moult for Ring-necked Doves is 192 days (Underhill et al. 1999) and for Rock Pigeons is 218 days (Underhill and Underhill 1997). Compared to the Laughing Dove PFMG duration estimate and per primary overall duration estimate, the duration of moult in Ring-necked Doves is 23 days and 20 days shorter respectively. The duration of moult in Rock Pigeons is three and six days longer respectively.

The moult of Ring-necked Doves and Rock Pigeons is more synchronised than that of Laughing Doves. 95% of Ring-necked Doves and Rock Pigeons are estimated to have started primary moult within 176 days (Underhill et al. 1999) and 118 days (Underhill and Underhill 1997) respectively of their mean start dates. The corresponding value for Laughing Doves was 257 days, which shows a lack of seasonality in the timing of moult.

Using the PFMG estimate of start date of moult, Laughing Doves started moult 20 days earlier than Ring-necked Doves and 53 days earlier than Rock Pigeons (3 November compared to 23 November and 26 December respectively) (Underhill and Underhill 1997, Underhill et al. 1999). Using the start date of moult of P1, Laughing Doves commenced moult 19 days earlier than Ring-necked Doves and 52 days earlier than Rock Pigeons. Laughing Doves ended moult on 6 June (PFMG estimate) and 3 June (per primary estimate). This is the same end date as that of Ring-necked Doves (2 June) and is two months earlier than Rock Pigeons (2 August) (Underhill and Underhill 1997, Underhill et al. 1999).

There are no hypotheses to explain these differences. The commonality between them is that, in the three species, the duration of primary moult is 6–7 months. Of the species which undertake a continuous annual moult, for which the Underhill-Zucchini moult model is appropriate, these durations are among the longest recorded (Chapter 7).

Best practice for studies of primary moult

One of the by-products of this chapter has been an attempt at a demonstration of best practice approaches to the analysis of primary moult. In studies of primary moult we recommend that analysts include adequate information so that the validity of the analysis can be independently assessed. If there is sufficient data to undertake a primary-by-primary analysis this should be undertaken. It is not feasible to provide a guideline for numbers of records required to achieve this. The most important consideration is that records need to be fairly evenly distributed from before moult commences to after moult is completed. The tables and figures as appropriate to the particular moult index employed should be included in the results, either in the paper itself or alternatively in the supplementary information. This will enable an assessment of the quality of the results to be made.

When choosing the best moult analysis method, the choice is essentially between using either the primary-by-primary analysis and the starting date for P1 and the end date for P10 or using the full tract analysis based on a moult index. The standard errors when using the primary-by-primary analysis are invariably larger than when using a full tract analysis. Therefore, there is no clear-cut answer and each situation needs to be judged on its merits.

Recommendations for further studies

In most previous applications of the moult model it was a simple exercise to find a date on which no birds were in primary moult and to use this as the reference date. This strategy was not possible in this analysis because there was no time of the year when no doves were in moult (Figure 6). To make use of the current version of the moult model it was necessary to generate a diagonal line through the part of the data with the least values, which resulted in the development of Figure 8. As moult data becomes available for species in the tropics this difficulty is likely to become commonplace (pers. obs). The mathematical statistical approach to resolving this problem is to use circular statistics (Mardia and Jupp 2000) and to replace the assumption that the starting dates of moult have a normal distribution with the assumption that they have one of the circular distributions, such as the Von Mises distribution or the wrapped normal distribution (Mardia and Jupp 2000) (Birgit Erni *in litt*.). This development would entirely overcome the problems revealed by Figure 6 and would enable routine moult analysis on other species which exhibit the same pattern.

Although the Relative Duration Index seemed likely to be an improvement on Proportion Feather Mass Grown in this study, this was not the case. This alternative moult index needs to be explored with other species.

The concept of Proportion Feather Mass Missing (Figure 10) remains relatively novel. Their usefulness needs to be evaluated once similar plots are available for a substantial sample of species. The availability of PFMM plots for species which undergo a moult of short duration with several primaries in moult simultaneously would assist this process.

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Table 1. Estimated moult parameters for each of the 10 primary feathers of Laughing Doves in Cape Town, using the same approach as Serra (2000).

Primary	**Moult parameters**				**Sample sizes**		
	Mean start date (SE)	**Duration (SE)**	**Standard deviation of start date (SE)**	**End date (SE)**	**Not yet moulted**	**In moult**	**Moult complete**
P1	4 Nov (3.0)	19.6 (2.3)	49.1 (2.4)	23 Nov (2.8)	252	65	1576
P2	19 Nov (3.0)	16.6 (2.1)	53.3 (2.4)	6 Dec (2.8)	310	58	1525
P3	5 Dec (3.1)	16.1 (2.0)	59.8 (2.6)	21 Dec (3.0)	369	58	1466
P4	22 Dec (3.2)	17.8 (2.1)	64.4 (2.6)	9 Jan (3.0)	440	69	1384
P5	11 Jan (3.2)	18.8 (2.0)	68.7 (2.6)	30 Jan (3.0)	522	78	1293
P6	30 Jan (3.1)	18.0 (2.0)	70.2 (2.6)	17 Feb (3.0)	606	78	1209
P7	18 Feb (3.0)	23.6 (2.2)	70.2 (2.5)	14 Mar (2.9)	693	106	1094
P8	12 Mar (3.0)	26.4 (2.3)	71.7 (2.5)	8 Apr (2.9)	796	122	975
P9	12 Apr (2.9)	24.3 (2.2)	73.1 (2.6)	6 May (2.9)	942	114	837
P10	11 May (2.9)	22.8 (2.1)	72.1 (2.7)	3 Jun (2.9)	1083	108	702

Table 2. Relative masses of the 10 primaries of the Laughing Dove (Underhill and Joubert 1995), and the relative durations of moult of each primary (see text). The relative masses are used for the calculation of Proportion Feather Mass Grown (PFMG) and the relative durations are used for the Relative Duration Index (RDI).

Primary	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
Relative mass (%)	6.7	7.3	7.6	8.2	8.9	9.7	11.3	12.6	13.6	14.2
Relative duration (%)	9.6	8.1	7.9	8.7	9.2	8.8	11.6	12.9	11.9	11.2

Table 3. Estimated moult parameters for the whole primary tract of adult Laughing Doves for three moult indices in Cape Town (TMS=Traditional Moult Score, PFMG=Proportion Feather Mass Grown, RDI=Relative Duration Index; see text). Day 1 was 1 September. The sample sizes of birds which were pre-moult, in moult and post-moult were 252, 939 and 702, respectively.

Moult Index	Duration (SE)	Start day (SE)	Start day standard deviation (SE)	Start date (SE)	End date (SE)
TMS	220.4 (4.5)	49.9 (3.3)	65.1 (1.5)	20 Oct (3.3)	28 May (2.5)
PFMG	215.1 (4.4)	64.1 (3.1)	65.5 (1.5)	3 Nov (3.1)	6 Jun (2.6)
RDI	218.0 (4.4)	57.0 (3.2)	65.1 (1.5)	27 Oct (3.2)	2 Jun (2.5)

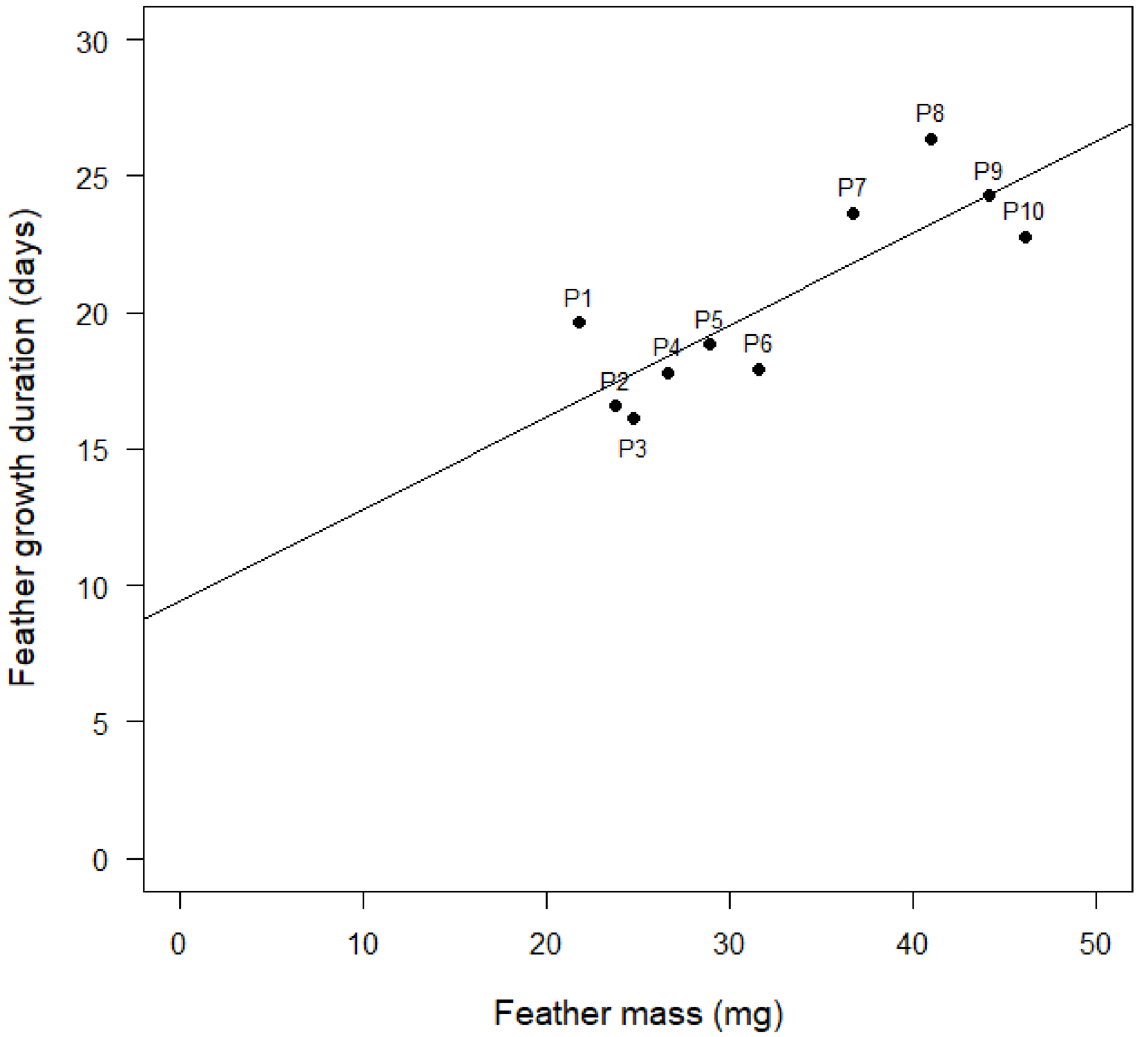


Figure 1. Plot of the duration of growth of each Laughing Dove primary feather versus its mass. The constant in the regression line is significantly different from zero (P=0.007), indicating that the estimated duration of moult for each feather was not proportional to its mass.

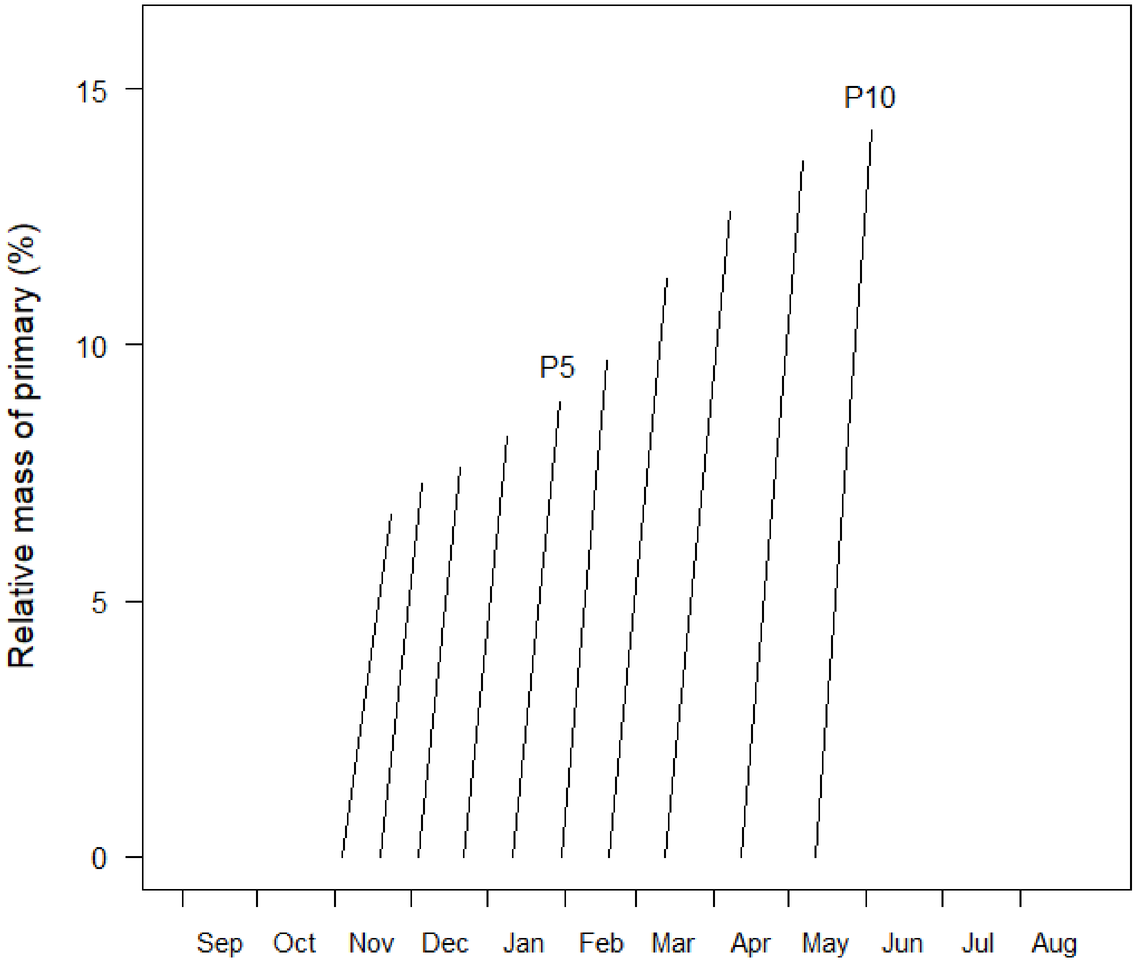


Figure 2. The progression of moult of individual primaries (P1–P10) of adult Laughing Doves. The gradient of the line of each primary represents the growth rate of the primary relative to its mass. The mean (and standard deviation) of the slopes of these 10 lines were 0.490 (0.0755) relative mass units per day, yielding a coefficient of variation (CV) of 15.4%. This is the weighting of primaries involved in the calculation of Proportion Feather Mass Grown (PFMG) (Equation 2).

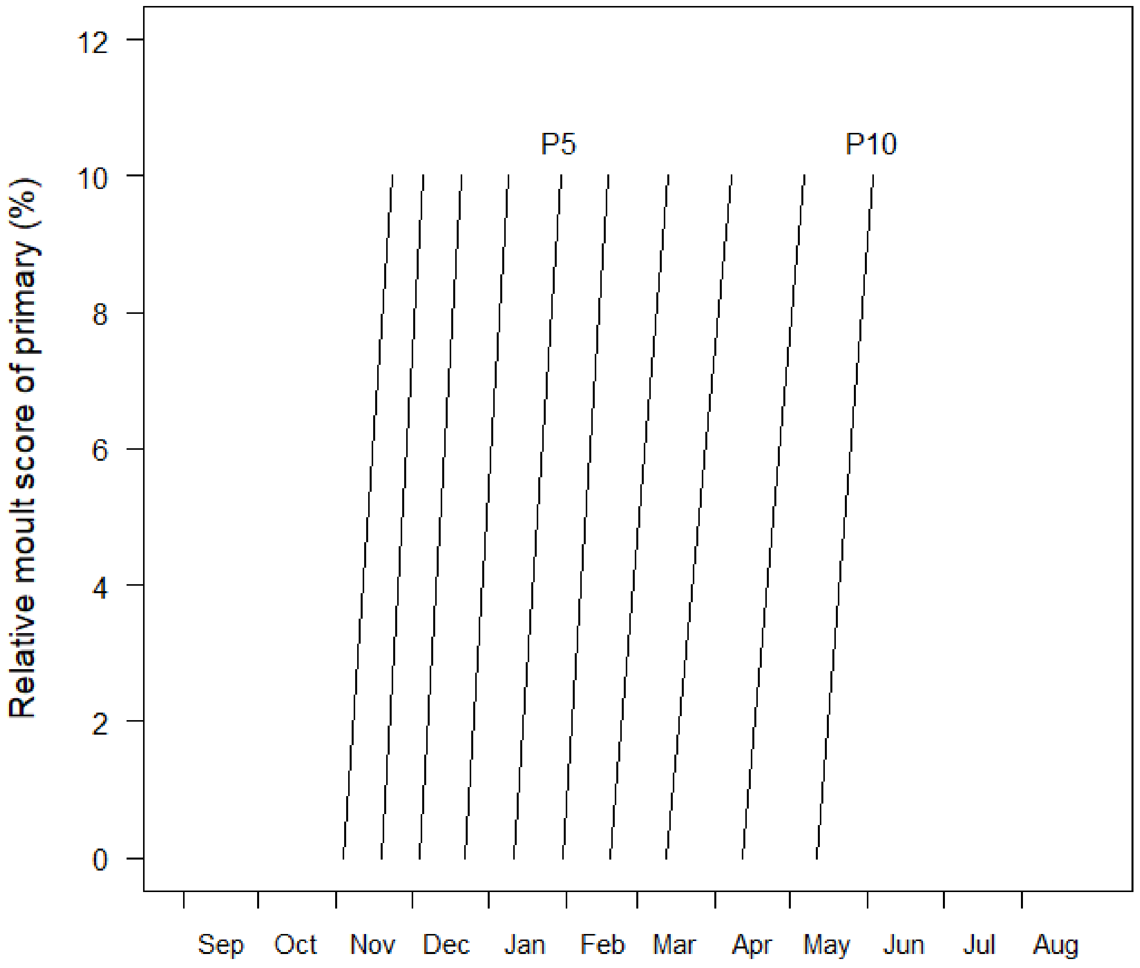


Figure 3. The progression of moult of individual primaries (P1–P10) of adult Laughing Doves. The gradient of the line of each primary represents the growth rate of the primary assuming that each primary has equal mass, as is done in the calculation of the Traditional Moult Score (Equation 1). The mean (and standard deviation) of the slopes of these 10 lines were 0.505 (0.0853) relative moult units per day, yielding a coefficient of variation (CV) of 16.9%.

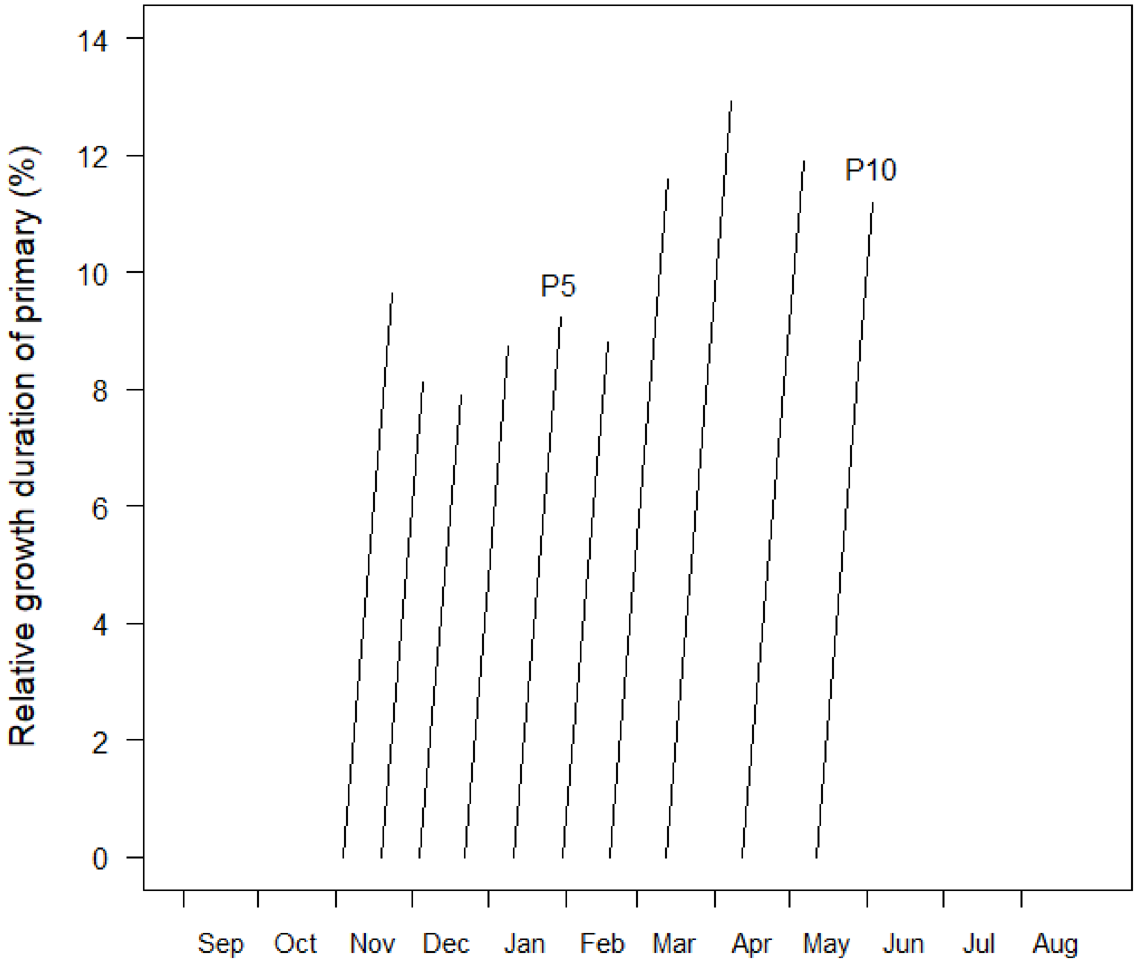


Figure 4. The progression of moult of individual primaries (P1–P10) of adult Laughing Doves. The gradient of the line of each primary assumes that the growth rate of the primary is proportional to its relative duration (Table 2). The mean of the slopes of these 10 lines was 0.487 relative duration units per day. The lines are exactly parallel by design, thus the CV is 0%. This is the weighting given to feathers in the new Relative Duration Index (Equation 3).

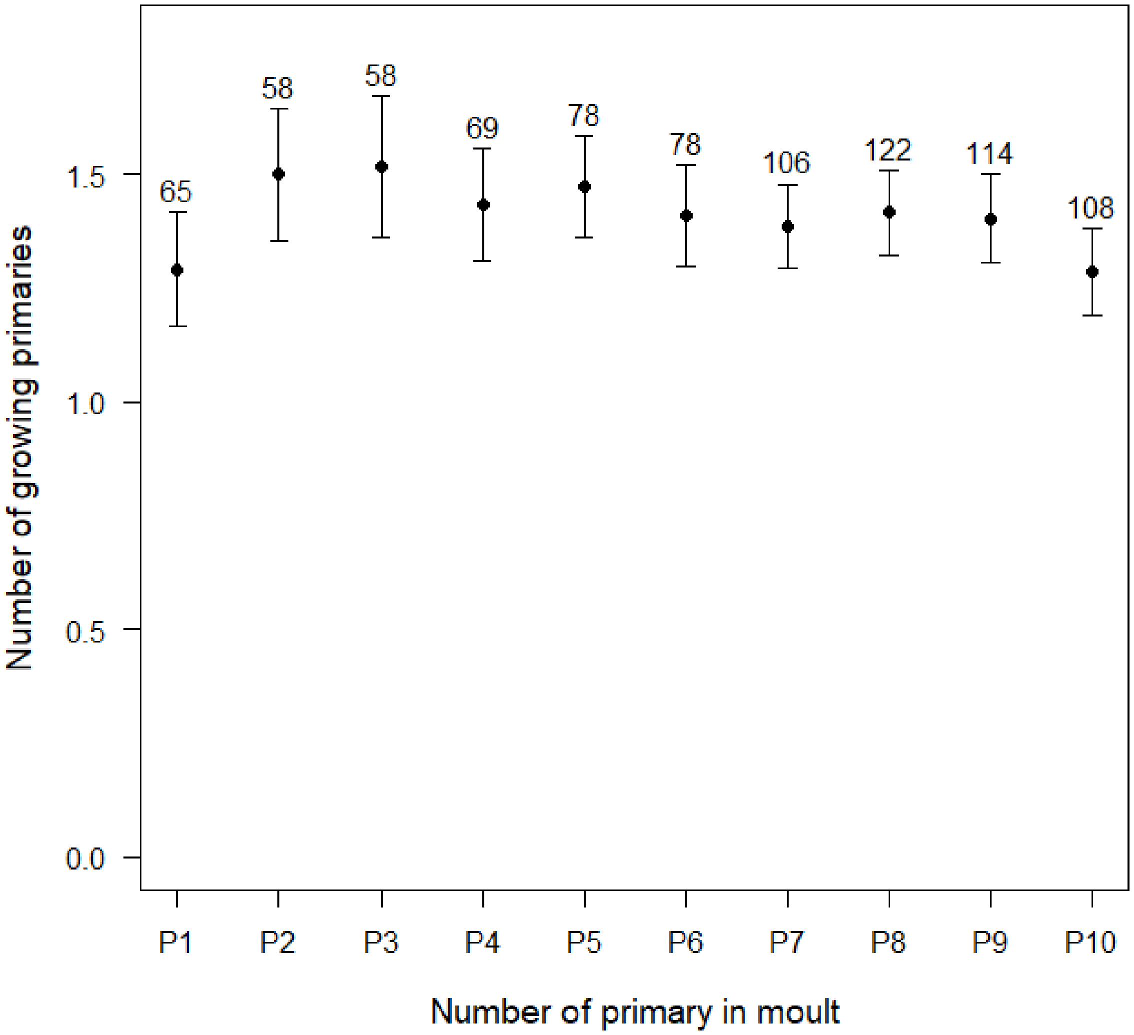


Figure 5. The mean number of primaries growing simultaneously while each of the 10 primaries of adult Laughing Doves was in moult. The 95% confidence intervals for the mean and the sample sizes are shown.

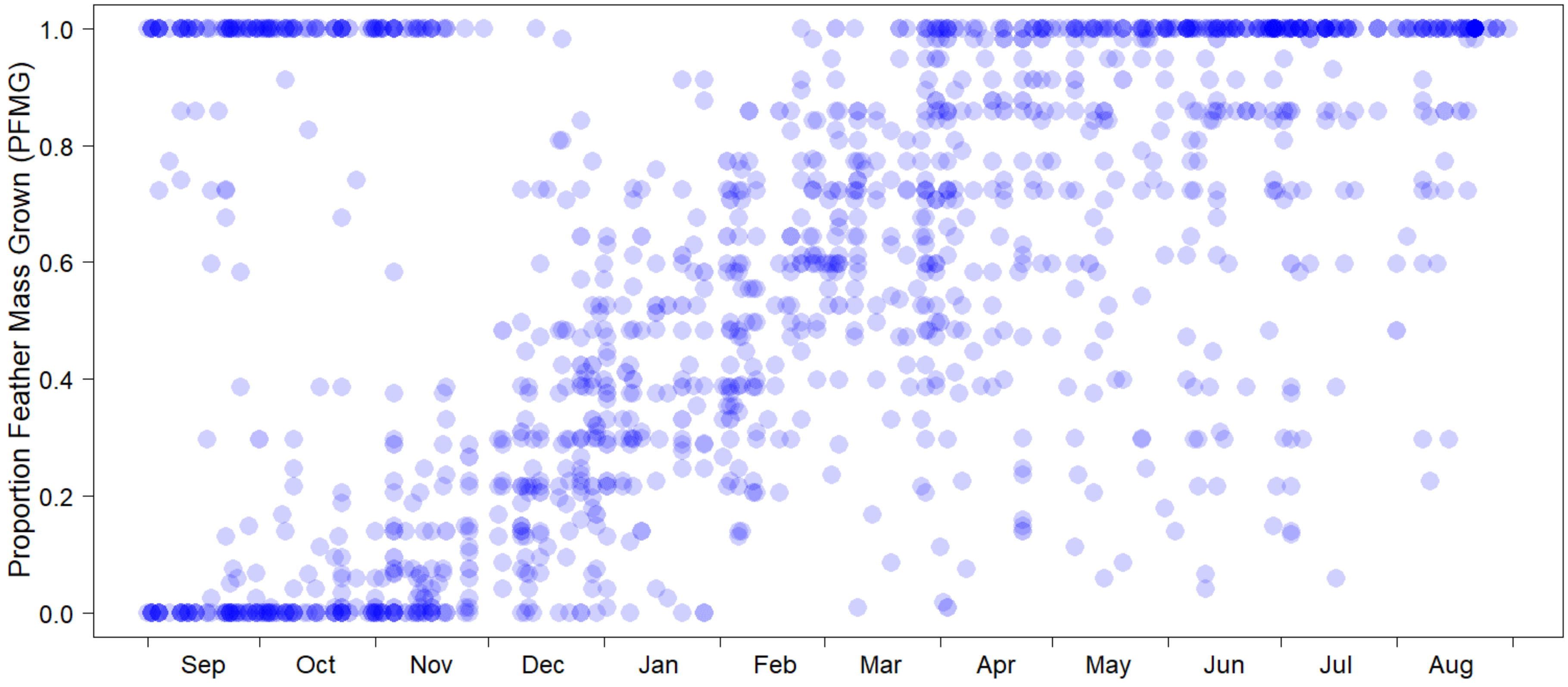


Figure 6. Modified scatter diagram* of PFMG and calendar date for adult Laughing Doves in Cape Town, using 1 September as the cut off date. It is obvious that the records in the top left corner represent birds that started moult relatively late, after about February. The solution to this is to use a diagonal line parallel to the mean moult line and positioned visually to pass through the region with the fewest data points. The x-axis of the plot then needs to be extended so that additional months are repeated at the end of the axis, and the records above the diagonal line shifted to the extended x-axis. See Methods. Comparison of this figure with Figure 8 indicates that the operation of shifting points only needs to be done once as no further points need to be shifted in Figure 8.

* Moult scores are recorded on a discrete scale (each primary is allocated an integer score between 0 and 5). A consequence of this is that conventional scatter plots of moult scores in relation to dates are misleading because there is no representation of the number of records represented by a single symbol in the plot. In this modification of the scatter diagram, the data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade refers to one data point and the darkest shade refers to 30 overlapping data points.

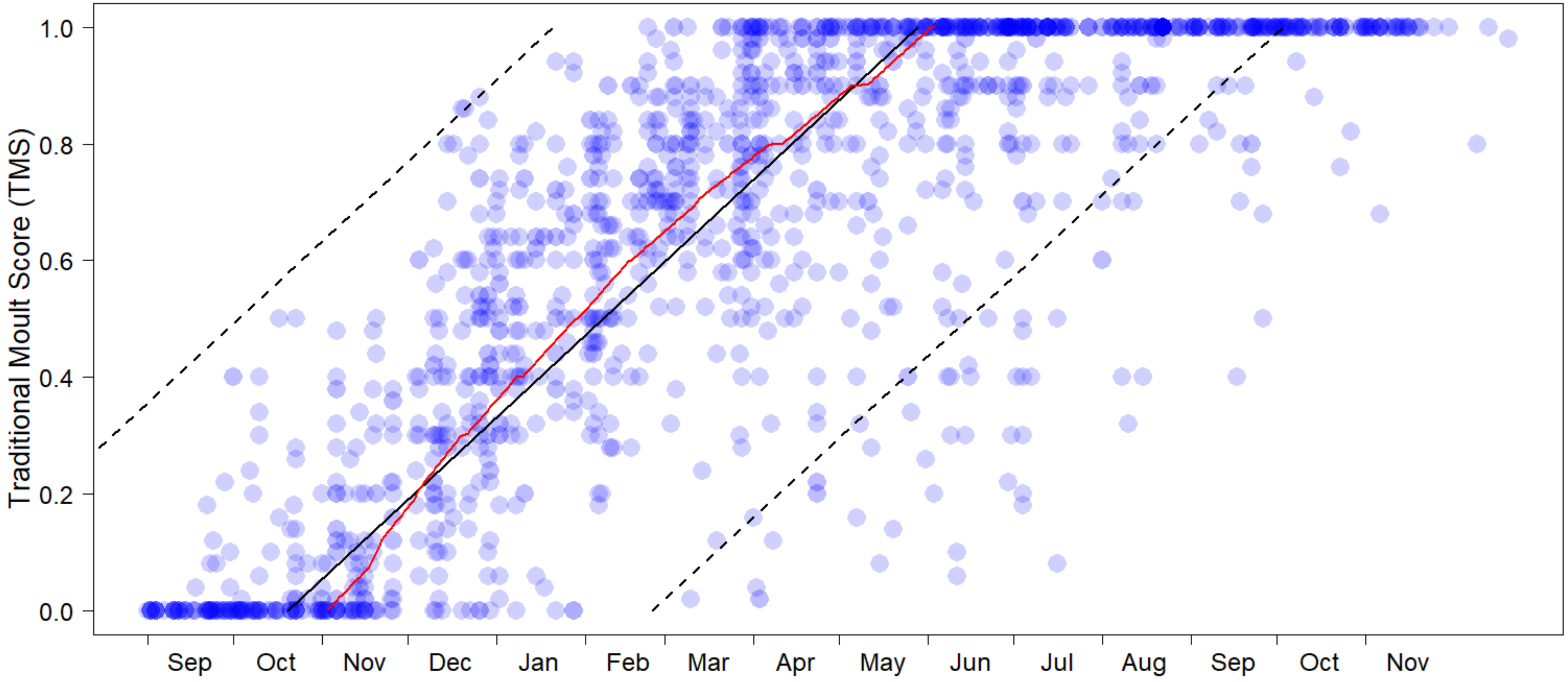


Figure 7. Modifed scatter diagram* of TMS and adjusted day for adult Laughing Doves in Cape Town. The straight line links the estimated starting date with the estimated completion date using TMS as the moult index. The dashed lines are the 95% intervals derived from the standard deviation of the start date. The curved line was computed from the moult durations of the individual primaries giving each primary equal weight (see text).

* See comment to Figure 6

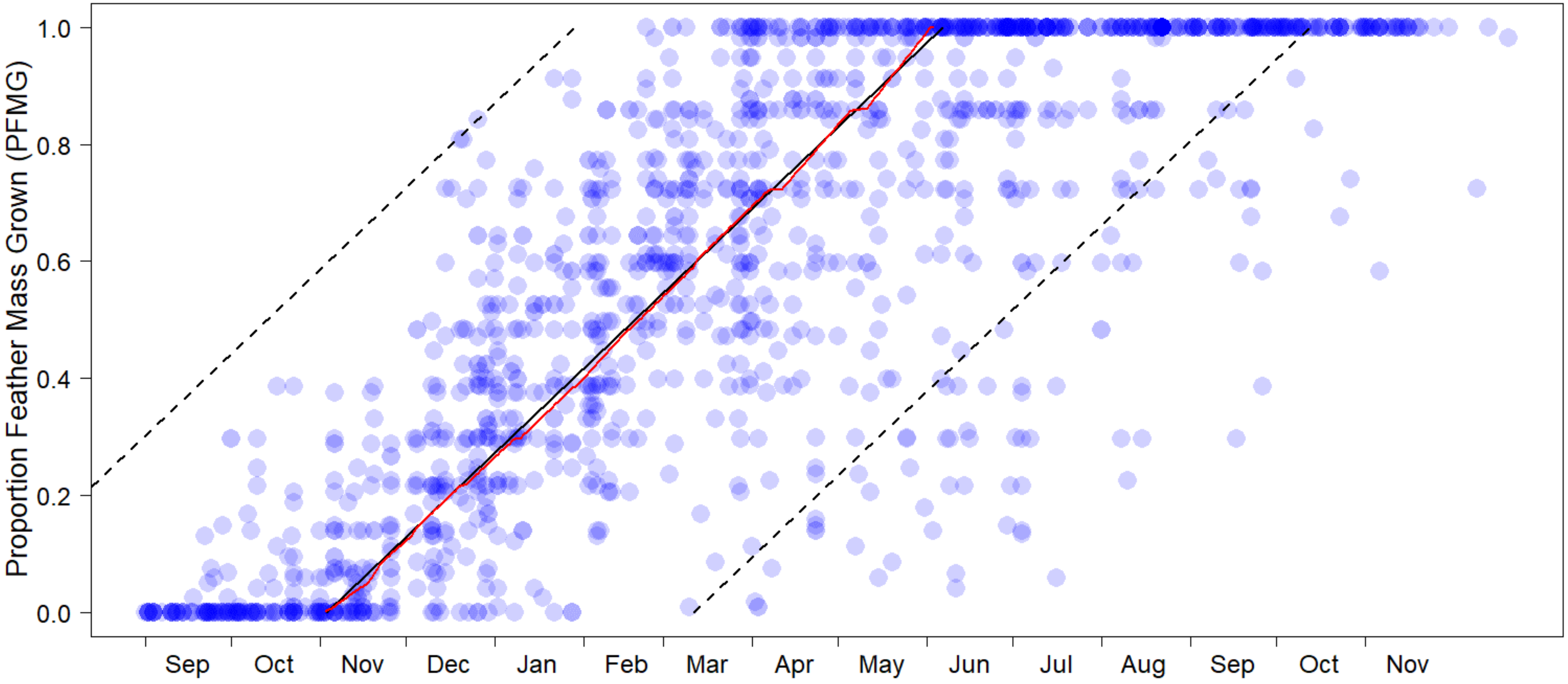


Figure 8. Modified scatter diagram* of PFMG and adjusted day for adult Laughing Doves in Cape Town. The straight line links the estimated starting date with the estimated completion date using PFMG as the moult index. The dashed lines are the 95% intervals derived from the standard deviation of the start date. The curved line was computed from the moult durations of the individual primaries giving each primary weight relative to its mass (see text).

* See comment to Figure 6

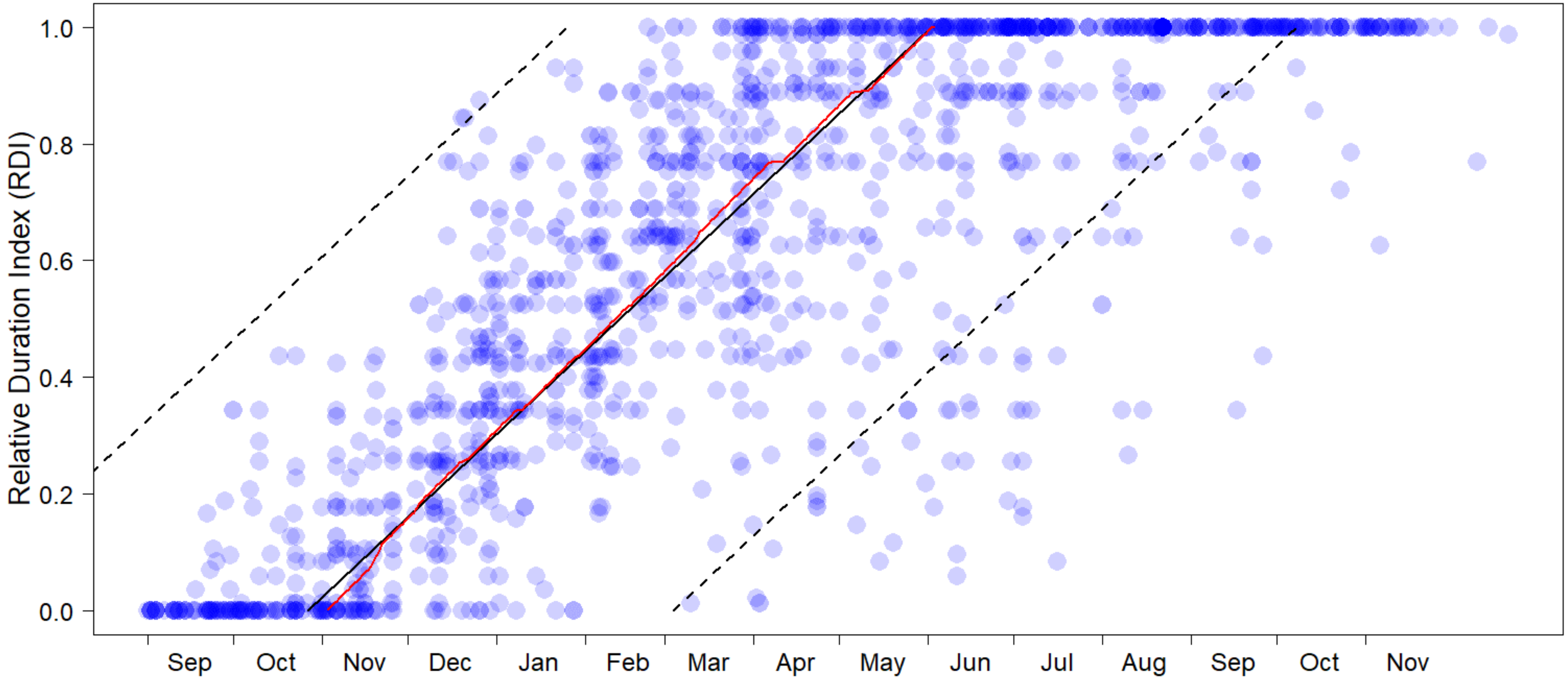


Figure 9. Modified scatter diagram* of RDI and adjusted day for adult Laughing Doves in Cape Town. The straight line links the estimated starting date with the estimated completion date using RDI as the moult index. The dashed lines are the 95% intervals derived from the standard deviation of the start date. The curved line was computed from the moult durations of the individual primaries giving each primary weight relative to its moult duration (see text).

* See comment to Figure 6

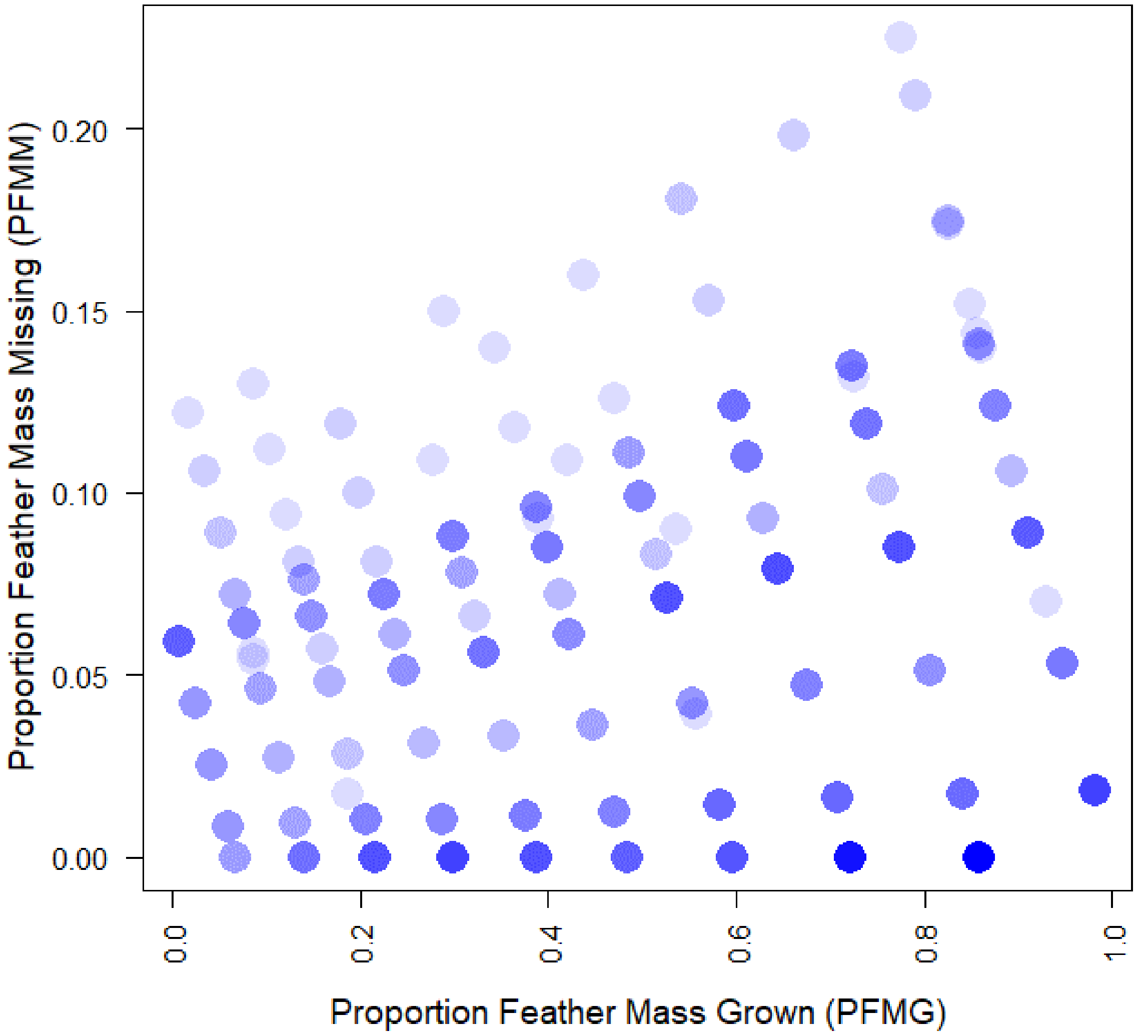


Figure 10. For adult Laughing Doves in moult, the relationship between proportion feather mass missing (PFMM) and proportion feather mass grown (PFMG) is represented by a modified scatter diagram*. The pattern of parallel lines is an artefact of the protocol for the recording of the moult stage of each primary as an integer between 0 and 5. As a result, each point in this scatter diagram can represent multiple records.

* In this modification of the scatter diagram, the data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade refers to one data point and the darkest shade refers to 54 overlapping data points.

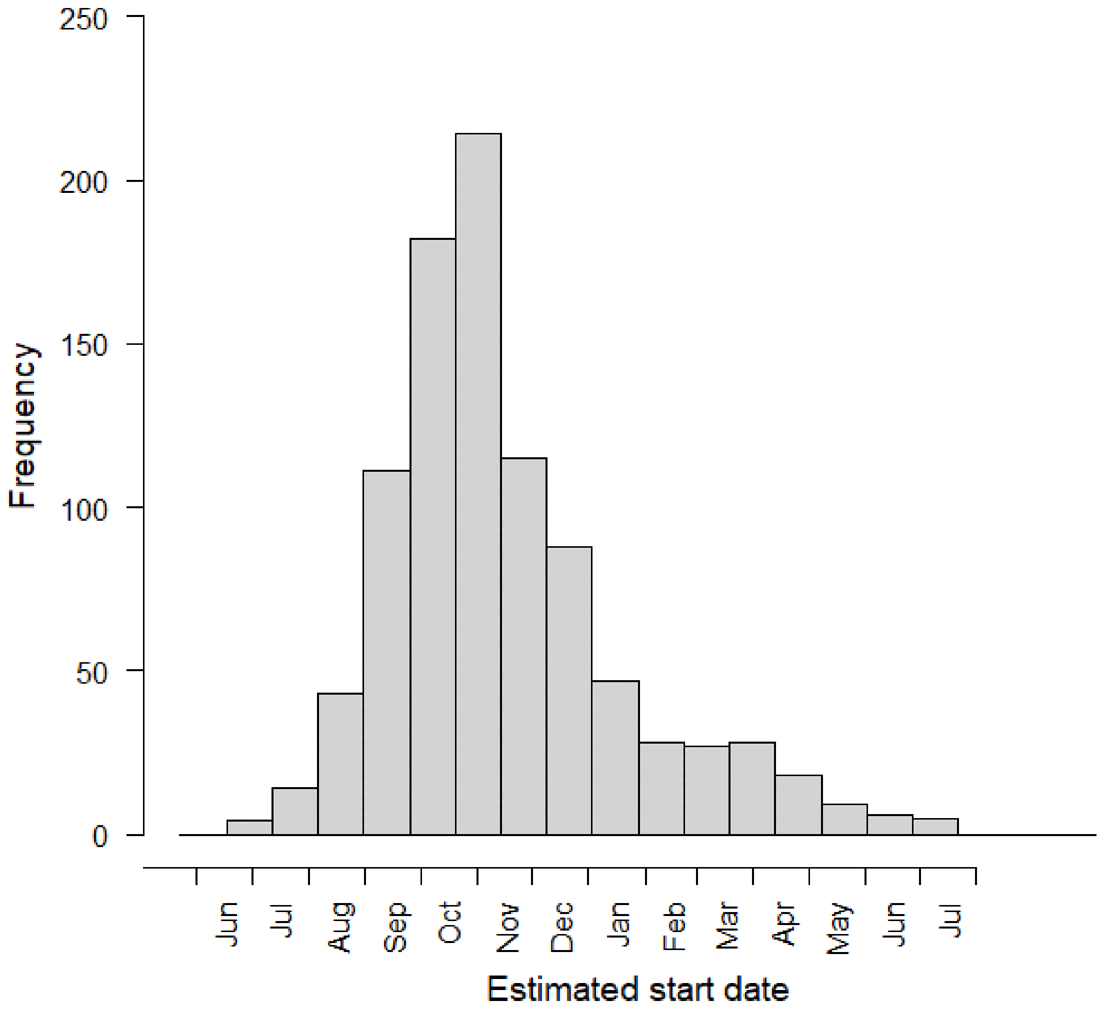


Figure 11. Histogram of estimated start day of moult of 939 adult Laughing Doves in active moult, based on Figure 8. The start day of moult for birds in active moult were projected using the result that the PFMG increases by 0.00465 units per day (1/215.1). The skewness of the histogram was 1.10. The class interval was 25 days. In reality, the data for the repeated months should be combined. This points to the need to make use of circular statistics. This concept is expanded upon further in the Discussion, in the section on Recommendations for Further Research.

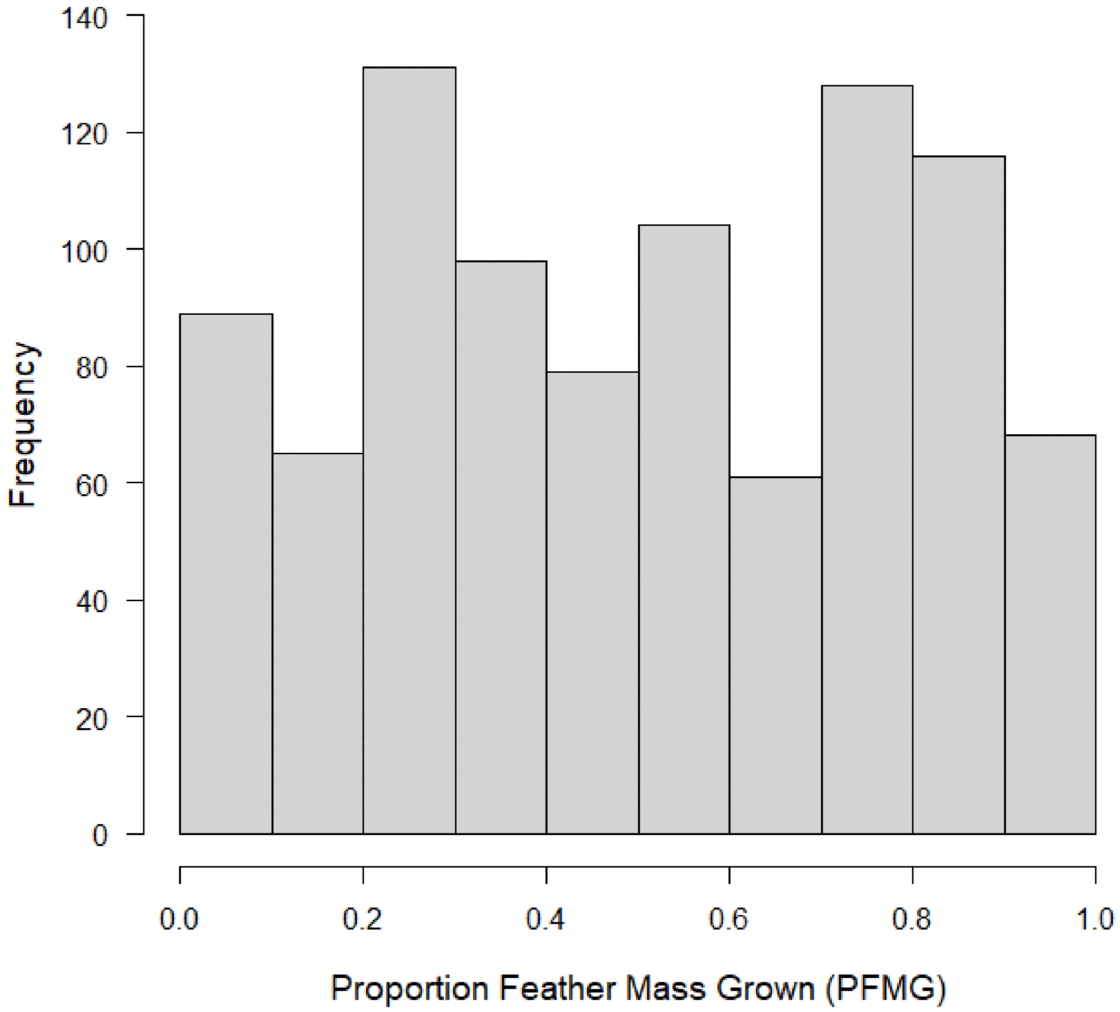
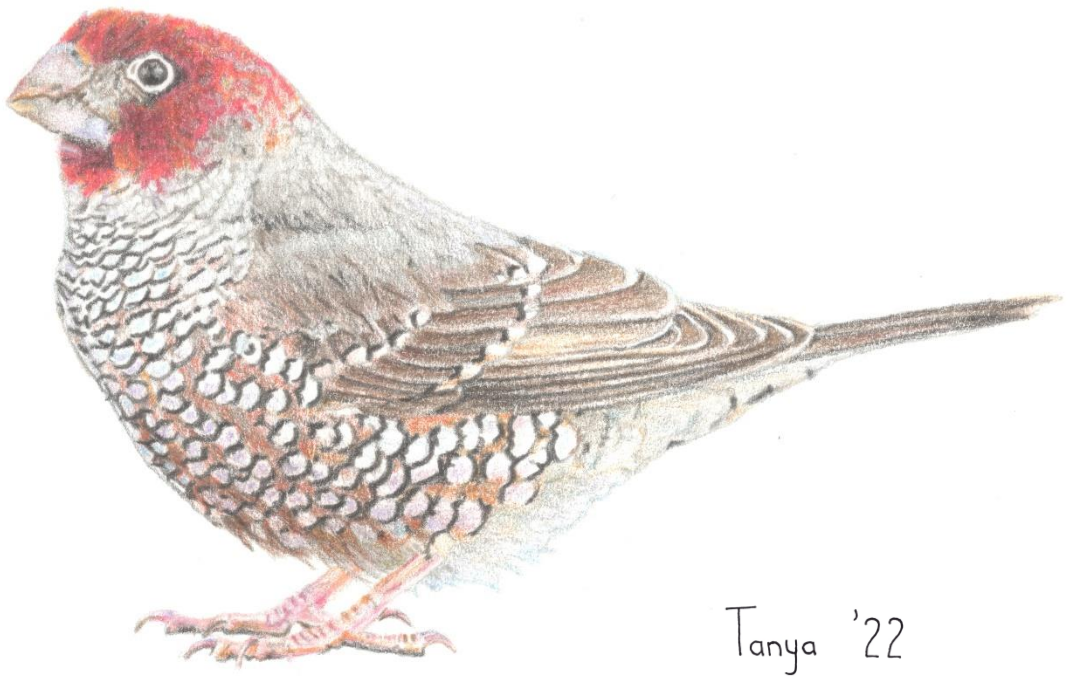


Figure 12. Histogram showing frequency of occurrence of PFMG scores of Laughing Doves in active primary moult with class intervals of 0.1 PFMG units.



CHAPTER 3

The primary moult of adult Red-headed Finches *Amadina erythrocephala*

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Abstract: Little is known about the biology of Red-headed Finches *Amadina erythrocephala*. This study investigates its primary moult, which is the first aspect of its life history to be looked at in depth. Additionally, it uses a modified Cook's distance algorithm to explore the influence of individual years on the moult parameter estimates. Lastly the primary moult of Red-headed Finches is compared to that of other passerines resident in the Highveld region of South Africa. Red-headed Finches breed through the Highveld winter and start moult on 22 August on average. Moult extends through spring and most of summer, reaching completion on 22 February, on average. However, in the moult years of 1988, 2005, 2008 and 2019 moult started unusually early whereas in 2017 moult started unusually late. The duration of moult was estimated to be 185 days. The majority of other passerines resident in the central Highveld of South Africa breed through summer, undergo primary moult in autumn and complete moult before the regular frosts start to occur during the Highveld winter. The moult duration of the Red-headed Finch was also substantially longer than that for the other resident passerines.

Keywords: Underhill-Zucchini moult model, Estrildidae, Cook's distance, passerine, South African HIghveld

INTRODUCTION

The Red-headed Finch *Amadina erythrocephala* is a poorly studied species. The total number of references to the species in Hockey et al. (2005) is 12 and all except one of these are to a multispecies book or paper. The exception is a preliminary guide for bird ringers (Raijmakers 1992). It is an intrinsically interesting bird species in at least two ways: (1) it is one of four species classified as a near-obligate nest adopter of weaver nests (Oschadleus 2018); (2) within its range, it is one of the only species with a peak breeding period in the dry, cold winter period of the summer-rainfall region of southern Africa (Herremans 1997, Harrison et al. 1997). This chapter focuses on one aspect of the biology of the Red-headed Finch: the primary moult of adults. It is based on a dataset collected between 1987 and 2020 at Secunda in southern Mpumalanga and at sites within 30 km of Vanderbijlpark in southern Gauteng, South Africa. It is likely that this is one of few species for which the first aspect of its biology to be studied in depth is primary moult.

Within the discipline of statistics, there is a precise definition to the concept of “influence” (Belsey et al. 1980). A point, or group of points, are said to be influential if their inclusion in a statistical analysis has a disproportionately large impact on the results of an analysis. The identification of influential observations is regarded as a particularly difficult problem within statistics. Once influential observations are located, decisions about how to deal with them are based on careful thinking rather than automated processes. A particular manifestation of “influence” arises in the analysis of primary moult. When primary moult datasets from multiple years (or also locations) are pooled and the moult analysis is performed on the combined dataset, it is possible that data from individual years unduly influence the estimates of the parameters. For example, suppose that primary moult in a particular year was unusually early. Further, suppose that the sample of moult records for that year was large and that all the data were collected near the start of moult. Then, in the statistical analysis the data from that year would be influential in biasing the estimated starting date to be early. It would also bias the duration to be misleadingly long. In the statistical sense, the data from that year would be classified as influential. Underhill and Scott (submitted) developed an approach to measuring the influence of the dataset from individual years (or potentially locations). Their approach was based on the concepts underpinning Cook’s distance in multiple regression (Cook 1977, 1979) in which the statistical influence of each point in the regression model is estimated. This chapter provides an application of this method.

Accordingly, this chapter has two objectives. The first is to quantify the primary moult of adult Red-headed Finches using the analysis guidelines recommended in Chapter 2. The second objective is to illustrate a strategy for handling the potential problem associated with data from a particular year being influential, in the statistical sense, in an analysis of primary moult in which data from multiple years are combined.

METHODS

Fieldwork

Targeted data collection for Red-headed Finches was done by JMH (Kobie) Raijmakers between 1987 and 2020. Ringing took place in Secunda, Mpumalanga (26°32’S 29°13’E) from 1987 to 1990 and thereafter at two localities in Vanderbijlpark, Gauteng (26°43’S 27°52’E from 1990 to 2019 and at 26°46’S 27°51’E from 2019 to 2020). Most ringing was done in suburban gardens. Initially mainly mist nets were used and subsequently feeding table traps and drop traps were utilised together with the mist nets. Red-headed Finches were also incidentally mistnetted during general ringing operations in the Vredefort Dome area where the habitat consisted of dry bankenveld. Ringing sites were near Parys, northern Free State (26°56’S 27°14’E); Fochville, south-eastern Northwest Province (26°42’S 27°33’E); and Vanderbijlpark (26°43’S 27°38’E) and Vereeniging (26°36’S 27°52’E) in south-eastern Gauteng. Birds were ringed with 2.8 mm rings (aluminium alloy, stainless steel or incoloy) supplied by the South African Bird Ringing Unit (SAFRING), with appropriate permits issued by the provincial conservation departments.

The birds were aged and sexed as described by Raijmakers (1992) and the moult stage of the primary feathers of one wing was recorded as a moult formula consisting of a sequence of nine digits. This sequence comprises one digit (moult score) 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. For birds not in active moult, the decision whether the primary feathers are "all old" or "all new" is subjective, largely because the process of feather wear is gradual.

Statistical analysis

For most species, it is possible to develop the concept of the "moult year" unambiguously. A reference date is chosen during the period of the year in which no birds are in active moult. This date is decided after data collection and the decisions made in the field about whether the primaries are "all old" or "all new" are revisited. Primaries which were classified as "all new" in the period after the reference date until moult starts are assigned the status of "all old", and those classified as "all old" in the period after moult is completed and before the reference date are assigned "all new" status. The Results demonstrate how this process is performed, and how, for the Red-headed Finch, it fails.

The reason for failure was that it was not possible to choose a reference date in this way because there was no period in the year when the birds are not actively moulting their primary feathers. Provisionally we used 1 June as the reference date, because it was the time of the year with the fewest birds in moult, and we reallocated birds not in moult as "all old" or "all new" relative to this date (see Results). However, there were birds near the end of moult in the months after June and birds near the start of moult in the months before June. This problem was also found in the data for Laughing Doves *Spilopelia senegalensis* (Chapter 2). The approach used there to solve this problem was to find a diagonal line, parallel to the mean moult line, and positioned visually to go through the area with the fewest data points. The x-axis was then extended in both directions. For birds in moult, data points above the top diagonal line were moved to the end of the extended x-axis and those below the bottom diagonal line were moved to the beginning of the extended x-axis (see Results).

However, birds not moulting remained as classified into the main June to May section of the x-axis, so there were no birds not in moult along the extended sections of the x-axis. To assign pre- and post-moult birds to the extended sections would have involved guesswork. In addition, in the algorithm for the method of maximum likelihood for the moult model, data points relating to birds not in moult which are distant in time from the start date and completion date of primary moult ought to have minimal influence on the results. We checked this by also doing the analysis using both 16 May and 16 June as reference dates.

The steps used for this analysis of primary moult followed the approach recommended in Chapter 2. The three parameters of primary moult (duration, mean start date and standard deviation of start date) were estimated in R (v. 3.6.2) (R Core Team 2019) using the Underhill and Zucchini (1988) moult model as fitted by the package "moult" (Erni et al. 2013). It was estimated that 95% of birds start moult in the period given by the estimated mean start date ± 1.96 x estimated standard deviation parameter of start date. Data type 2 was used in the moult model because the population contained pre-moult, in-moult and post-moult birds and it is assumed that birds in each moult category had an equal probability of capture (Underhill and

Zucchini 1988). The moult model assumes that the moult index increases linearly through time. Careful thought with regards to this model assumption is therefore needed when choosing an index.

The three parameters of moult were estimated for the full primary tract using three moult indices: Traditional Moult Score (TMS), Proportion Feather Mass Grown (PFMG) (Underhill and Summers 1993) and the Relative Duration Index (RDI) (Chapter 2). TMS is the proportion of the total moult score (Table 1). PFMG, as defined by Underhill and Summers (1993), was calculated from the moult formula and the mean relative masses of the nine primary feathers for the Estrildidae (Table 1). RDI (Chapter 2) was calculated using the moult formula and the relative moult durations of the nine primary feathers obtained from the primary-by-primary analysis (described below).

Because the sample sizes were large and the data were spread fairly evenly throughout the year, it was possible to estimate the moult parameters for each of the nine primary feathers using the Underhill-Zucchini moult model (Serra 2000, Underhill 2003). Moult scores 0–5 for each primary were transformed to values 0, 0.125, 0.375, 0.625, 0.875 and 1 respectively to create a moult index (Underhill and Zucchini 1988). The estimated moult duration for each primary was used in the calculation of RDI, as described above. The mean start date of moult of the first, innermost primary (P1) and the end date of moult of the ninth, outermost primary (P9) were taken as estimates of the start and completion dates of primary moult. If there is enough data to enable this method to be used, then it becomes the standard against which the results for the full primary tract can be evaluated.

The progress of moult of the individual primary feathers in relation to the relative mass of the primaries was plotted as done in Underhill (2003) and Chapter 2. The gradients of the lines represent the rate of increase in relative feather mass. If the relative feather mass is increasing at the same rate for each primary feather, then the nine lines will be parallel. The coefficient of variation (CV) of the gradients of the nine lines was calculated to evaluate their departure from parallelness.

The daily growth rate (PFMG/day) of each primary was calculated by dividing its relative mass by its estimated duration of growth (Table 2). Using these daily growth rates and the estimated mean start and end dates of moult of each primary, the daily increases in PFMG for each primary were estimated. These increments in PFMG were summed together for each calendar day resulting in an estimate of the amount of new feather material produced each day for an average bird. From this, the cumulative growth curve during the moult of an average bird was plotted. In a similar way, the daily increases in TMS (which gives each primary equal weight) and RDI (which gives each primary weight in proportion to its duration of growth) were estimated and respective cumulative curves were plotted. The Underhill-Zucchini moult model assumes that moult progresses at a constant rate (Underhill and Zucchini 1988) and consequently the moult index increases linearly through time. Therefore, if the cumulative curve is a straight line, then growth was linear for that moult index (Remisiewicz et al. 2009). The cumulative curves for each moult index were compared to their respective mean moult lines. If the model assumption is met, then they should coincide.

Two additional measures that relate to primary moult were explored. They provide insight into the energetic costs of moult, both direct and indirect. The first measure is the average number of primaries growing simultaneously and is a proxy for the energetic costs of growing new feathers (Remisiewicz et al. 2009, Jenni and Winkler 2020). The mean number of simultaneously growing primaries when each of the nine primaries was in moult was calculated along with the 95% confidence limits of the mean (mean ± 1.96 x standard error) (Remisiewicz et al. 2009). The second measure is raggedness developed by Haukioja (1971) and describes the size of the gap in the primary wing feathers during moult. Wing gaps reduce flight performance (Hedenström 2023) and raggedness therefore assists in quantifying this indirect cost of moult. The larger the wing gap, the greater the impairment to flight capabilities, such as lift, flight speed, manoeuvrability and foraging efficiency (Jenni and Winkler 2020, Hedenström 2023). Raggedness was estimated using a method that is complementary to the calculation of TMS. To calculate raggedness, primary feathers with a moult score of 1, 2, 3 and 4 were converted to 4, 3, 2 and 1 respectively to represent the missing moult score of each primary. Moult scores of 0 and 5 were taken as representing 0 (i.e. no missing primary). These values were summed across all primaries (P1–P9) and divided by 45 for each bird.

One assumption of the Underhill-Zucchini moult model is that the birds sampled are a random sample from the population and that their probability of capture is independent of moult stage (Underhill and Zucchini 1988). This assumption was assessed as in Chapter 2. A histogram of TMS scores of birds in active moult was constructed using class intervals of 0.05 TMS units. The histogram is expected to display an approximately uniform distribution if sampling took place consistently throughout the moult period (Chapter 2).

The algorithm of Underhill and Scott (submitted) was applied to examine the influence of each moult year on the moult parameter estimates. This algorithm is an extension of Cook's distance used in multiple regression to identify influential observations (Cook 1977, 1979). It successively calculates the estimates of the moult parameters with the data for each moult year removed and uses the same concepts as in Cook's distance to identify the moult years that were influential in estimating the moult parameters. The impact of the influential or outlier years was considered and a new moult model was constructed allowing those years identified as outliers by the modified Cook's distance algorithm to have different starting dates.

RESULTS

Moult of the entire primary tract

A total of 5586 captures of adult Red-headed Finches were made between November 1987 and October 2020. 97% of these were made during the fieldwork targeting Red-headed Finches in the suburban gardens and 3% during incidental mistnetting in the surrounding areas. The nine primaries were moulted sequentially, starting with the innermost primary (P1) and finishing with the outermost (P9), and the dataset is thus suitable for analysis by the Underhill-Zucchini moult model.

There are two difficulties with the original dataset. These are illustrated in the plot of, for example, PFMG against date (Figure 1).

Firstly, at the time of ringing far more birds had primaries which had been classified as "all old" (3395) than as "all new" (121) (Figure 1). This was prior to the observer knowing that the analysts would choose 1 June as the reference date (day 1). Inspection of Figure 1 suggests birds ought to be completing moult by the beginning of December. We therefore reclassified birds recorded, at the time of ringing, as "all old" after the beginning of December as "all new" (Figure 2). After 1 June was imposed as reference date, 25% (1403) were in pre-moult, 37% (2070) were in active moult and 38% (2113) had completed moult (Figure 2, Table 3).

Secondly, Figure 1 has clusters of data points in the top left and bottom right corners of the plot which are clearly birds which made a substantially later and earlier start to moult respectively than the majority of birds. The diagonal line of Figure 1, passing through the region with the fewest observations, illustrates this. The strategy for dealing with these clusters was to extend the x-axis in both directions by three months to the left and by two months to the right. The clusters of observations above the diagonal line in June and July of Figure 1 are shifted to the extended x-axis on the right and the clusters below the diagonal line in March to May of Figure 1 are shifted to the extended x-axis on the left. We constructed a plot for each moult index (Figure 2 for TMS, Figure 3 for PFMG and Figure 4 for RDI). In relation to birds in active moult these plots appear to be satisfactory for analysis by the moult model.

However, in Figures 2 to 4, there is a conspicuous lack of pre-moult (0s) and post-moult (1s) records along the extended portions of the x-axis. As described in the Methods, we therefore repeated the procedure for each moult index using reference dates half a month earlier than 1 June and half a month later. It is clear from the results in Table 3 that the choice of reference date does not have a substantial impact on the moult parameters for any of the three moult indices. We therefore chose 1 June as final reference date and thus focus on the results in the first three lines of Table 3 in the comparison of the three moult indices.

The estimates of the mean starting dates of moult using the three moult indices (TMS, PFMG and RDI) were within five days of each other (19 August to 24 August) and the estimates of mean end dates of moult spanned six days (17 February to 23 February) (Table 3). The estimates for duration of moult were within three days of each other and were 185, 183 and 182 days respectively (approximately six months) (Table 3). The standard deviation of the mean start dates of moult was 54 days for the three moult indices, which means that the period during which 95% of the population of adult finches started (and ended) moult was 212 days (7 months) (Table 3). This implies that primary moult in adult Red-headed Finches is not synchronous.

Moult of the individual primary feathers

The results of the individual primaries are presented in Table 2. The estimated mean starting date of moult of the first primary (P1) was 20 August (day 81) and the estimated mean completion date of moult of the last primary (P9) was 18 February (day 263). The period between the start of moult of P1 and the end of moult of P9 was 182 days. The relative masses of the primaries increased from 8.35% for P1 through to 13.65% for P9 so that the outermost primary is 1.6 times the mass of the innermost primary (Table 1, Figure 5). The average moult duration of the individual primaries was 26.3 days, but they can be grouped into two groups with the duration of moult of P1, P8 and P9 varying from 20 days (P1) to 22 days (P8) and the duration of moult of P2 to P7 varying from 27 days (P2) to 31 days (P4). The Pearson's correlation coefficient between the duration of moult of the primaries and their relative mass was -0.16 (P=0.68) (Figure 5). The moult durations of the nine primaries did not increase from P1 through to P9 as their relative masses did and the ratio between the shortest (P9) and longest (P4) durations was 1.53. The duration of moult of the primaries was therefore not proportional to their mass (Table 1, Figure 5). The daily growth rate of the primaries (PFMG/day) was relatively constant from P1 to P7 ranging from 0.33 to 0.46. It then increased through to P9. The growth rate for P9 was about twice as fast as that of P2, P3 and P4 (Table 2). This is shown by the slightly steeper growth lines for the outer primaries (Figure 6). The coefficient of variation (CV) of the slopes of the primaries in the plot depicting the progression of moult was 26.9% (Figure 6).

The estimated feather shedding interval between primaries, defined as the period between the start of moult of successive primaries, ranged from 16 days (between P1 and P2) to 22 days (between P5 and P6, and P7 and P8). The mean shedding interval for all primaries was 20 days and the standard deviation was 2.2 days (Table 2, Figure 6).

During the replacement of the middle seven primaries (P2–P8), there was a mean number of 1.6 (standard deviation 0.09) feathers growing simultaneously compared to 1.2 feathers during the replacement of the innermost (P1) and outermost primaries (P9), which had only one adjacent primary (Figure 7). The number of simultaneously growing primaries increased from P1 to P4 and then decreased from P4 through to P9 (Figure 7). Viewing Figure 5 in conjunction with Figure 7, it can be stated that when there are fewer feathers moulting simultaneously, as in the beginning and end of primary moult they grow quicker, but when there are several moulting at one time, as in the middle stages of moult, they grow slower.

Cumulative growth curves

Using the daily increases in TMS, PFMG and RDI of each primary feather and the duration of simultaneous growth of adjacent primaries, the plots of cumulative increase in each of the three moult indices during moult were almost linear (Figures 2, 3 and 4). When considering where the mean moult line (black line) for each moult index lies in relation to its cumulative curve (red line), it becomes apparent that TMS is the best moult index because its cumulative growth curve is most linear and therefore best satisfies model assumptions. TMS is therefore the preferred moult index for this species and the rest of the results from this point forward use it as the index of moult progress (Figure 2).

Wing gap size during primary moult

The mean size of the gap in the primaries of birds in active moult, as described by raggedness, was 0.07 with a standard deviation of 0.03. This means that on average birds were missing 7% of their primaries during moult (Figure 8). The smallest wing gap estimated was 0.02 and the largest was 0.18 (Figure 8).

Examining the assumption that capture was independent of moult stage

Observed TMS scores were approximately uniformly distributed (Figure 9). The probability of capture during sampling therefore appeared to be independent of moult stage.

Influential moult years

Moult years 1988, 2008, 2005, 2019 and 2017 had the largest modified Cook's distances: 5.68, 5.09, 4.78, 4.75 and 2.66 respectively, in order of magnitude (Table 4). We stopped at five years in Table 4 because the sixth largest value lay on the edge of the spread of the bulk of the modified Cook's distance values. The distance algorithm takes into account not only the differences between the estimates of the parameters with individual years omitted but also the correlations between the estimates of the parameters. For example, in this analysis the correlation between the estimate of the duration parameter and the estimate of the start date parameter was −0.963 and it frequently has similar large values in most analyses (pers. obs.). What this means in practice is that the likelihoods associated with multiple pairs of estimates of these two parameters have values close to the maximum likelihood. The negative correlation provides the information that these pairs of values have slightly earlier start dates and slightly longer durations or slightly later start dates and slightly shorter durations. Because there were multiple "outlier years" and because there was correlation between the estimates of the parameters, the actual parameter estimates with individual years omitted were not informative (Table 4). Initially we attempted to use the information about the "outlier years" by leaving them out successively, resulting in a steadily decreasing sample size (Table 5). Our second approach was to enable the start dates in each of the five identified years to differ, treating them as factor levels in the moult model. This strategy allowed each of these years to have a separate start date, while the remaining years had a common start date, which we call the baseline start date (Table 6). Because of the correlation between the estimates of duration and start date, it was not feasible to treat both as factor variables. The duration of moult in this latter model was estimated to be 185 days with a baseline mean start date of 22 August and end date of 22 February. In the moult years 1988, 2005, 2008 and 2019, moult was estimated to start 12, 4, 13 and 7 days earlier than the baseline start date respectively (Table 6). Figures 10 and 11 highlight the data for moult years 1988 and 2017. They show that in 1988 moult started 12 days earlier than the baseline and in 2017 started 10 days later than the baseline (Table 6). The standard deviation of the mean start date was 54 days.

DISCUSSION

Primary moult of Red-headed Finches

Moult of the primary feather tract in adult Red-headed Finches was continuous. For this species, the differences in the moult parameter estimates when using the three moult indices were sufficiently small that they did not make a real difference from a biological perspective (Table 3). In terms of choice of moult index, these small differences demonstrate that, for this finch, the moult model is robust, in spite of the fact that the relative weightings given to the primaries for the three moult indices varied substantially (Table 1). It was therefore unexpected that the choice of moult index made a relatively small difference to the moult parameter estimates

(Table 3) and that the final choice of moult index was not clear-cut. These results suggest that, for this species, the moult model is robust, in that the choice of moult index does not make a large difference to the results. The extent to which this is true for other species needs investigation.

The Traditional Moult Score (TMS) was the preferred index for two reasons. Firstly, it closely matched the primary-by-primary model. The mean start and end dates of moult of the full primary feather tract (19 August and 19 February respectively) corresponded well with the start date of moult of P1 (20 August) and the end date of moult of P9 (18 February) (Tables 2 and 3). However, large volumes of data spread evenly throughout the moult period are needed to undertake a primary-by-primary moult analysis. The second reason for TMS being the preferred index is because the TMS mean moult line fitted its cumulative curve the best (Figure 2).

Modified Cook's distance algorithm

This study represents the first application, to non-simulated data, of the algorithm to identify years in which the timing of moult was exceptional in relation to the norm (Underhill and Scott submitted). The purpose of the algorithm is to help guard against the situation in which pooling of data from different years to produce a sample of data points large enough for meaningful analysis by the moult model of Underhill and Zucchini (1988) produces seriously misleading results. Therefore, we evaluate the performance of the algorithm in relation to this dataset on Red-headed Finches.

The algorithm was based on the concepts of Cook's distance, designed for multiple linear regression (Cook 1977, 1979). These original papers suggested that the number of values highlighted as outliers and the action taken as a result of this identification should be considered on an individual basis. Every situation should be treated on its merits. We justified our decision to consider five years in Table 4 as outliers because the smaller values did not lie far outside the distribution of the remaining modified Cook's distance values. We tried two strategies for dealing with the identified years. One was to omit them and the other was to treat them as having different starting dates. In this context, it appears that the latter strategy was the better of the two, since it provides a better insight into the structure of the data. In other situations, alternative approaches might be useful. Ultimately, the decisions taken need to be motivated and guided by the biological interpretability of the results.

In this first application of the modified Cook's distance algorithm, we identified those years in which moult was earlier or later than the norm. This is valuable insight in its own right. On top of that, we have the confidence that our results were not biased by pooling data across years. In other circumstances, the decisions taken as a result of identifying years as outliers will be different. There will undoubtedly be datasets in which the appropriate decision will be to completely exclude an outlier year from the moult model calculations.

Primary moult of Red-headed Finches in relation to other resident passerines in the region

There are quantitative primary moult analyses that used the Underhill-Zucchini moult model available for a fairly representative sample of 15 passerine species that are resident in the central Highveld of South Africa (Table 7). The Red-headed Finch is strikingly different in several ways. At 185 days, it has the longest primary moult duration of the sample of species. The primary moult duration of the Red-headed Finch is 53% longer than of the Green-winged Pytilia's 121 days. The median duration for the 15 species in Table 7 is 78 days, the Red-headed Finch has a duration 2.4 times longer than this. For each species, primary moult closely follows the breeding season of the summer rainfall region of South Africa, as given by Hockey et al. (2005) (Figure 12). The Red-headed Finch breeds through winter and its estimated mean starting date of moult is 22 August, 149 days later than the median starting date of 26 March for the 15 species (Table 7). The median moult completion date for the 15 species is 20 May. This coincides with the time of the year when regular frosts start to occur during the Highveld winter. The Red-headed Finch finishes moult 278 days after this median completion date.

This is further evidence that the annual cycle of the Red-headed Finch is an outlier compared with most resident passerines within its range, as identified by Herremans (1997). Further studies of other aspects of the biology of this remarkable species are thus likely to make a decisive contribution to our understanding of avian biology.

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Table 1. Relative feather masses for the Estrildidae (obtained from a feather mass database compiled by PG Ryan and LG Underhill). These values are similar to those estimated for the "average passerine" by Bonnevie (2010), given in the second line of the table. The third line provides the relative durations of moult of the nine primaries of the Red-headed Finch (derived from Table 2). The fourth line gives the relative moult scores of the nine primaries. The relative masses are used for the calculation of Proportion Feather Mass Grown (PFMG), the relative durations for the Relative Duration Index (RDI) and the relative moult scores for the Traditional Moult Score (TMS).

Primary	P1	P2	P3	P4	P5	P6	P7	P8	P9
Estrildidae relative mass (%)	8.35	9.19	9.64	10.29	11.37	11.90	12.65	12.95	13.65
Average passerine relative mass (%)	8.0	8.6	9.2	10.0	11.4	12.4	13.0	13.5	14.0
Relative duration (%)	8.59	11.45	12.16	13.19	12.79	12.16	11.62	9.25	8.79
Relative moult score (%)	11.11	11.11	11.11	11.11	11.11	11.11	11.11	11.11	11.11

Table 2. Estimated moult parameters for each of the nine primary feathers of adult Red-headed Finches.

Primary	Moult parameters				Sample sizes			Growth rate (PFMG /day)
	Mean start date (SE)	Duration (SE)	Standard deviation of start date (SE)	End date (SE)	Pre-moult	In-moult	Post-moult	
1	20 Aug (1.4)	20.3 (1.2)	48.2 (1.3)	9 Sep (1.4)	1403	278	3905	0.41
2	5 Sep (1.4)	27.1 (1.3)	49.7 (1.2)	2 Oct (1.5)	1616	344	3626	0.34
3	24 Sep (1.5)	28.8 (1.4)	50.1 (1.2)	23 Oct (1.6)	1863	345	3378	0.33
4	15 Oct (1.6)	31.2 (1.5)	52.3 (1.1)	15 Nov (1.6)	2111	341	3134	0.33
5	4 Nov (1.6)	30.3 (1.5)	53.9 (1.1)	4 Dec (1.7)	2328	314	3944	0.38
6	26 Nov (1.7)	28.8 (1.5)	54.6 (1.1)	25 Dec (1.6)	2567	291	2728	0.41
7	18 Dec (1.7)	27.5 (1.5)	55.1 (1.1)	14 Jan (1.6)	2789	282	2515	0.46
8	9 Jan (1.7)	21.9 (1.3)	57.2 (1.2)	31 Jan (1.6)	3018	233	2335	0.59
9	28 Jan (1.7)	20.8 (1.2)	58.3 (1.3)	18 Feb (1.6)	3227	246	2113	0.66

Table 3. Estimated moult parameters for the whole primary tract of adult Red-headed Finches for three moult indices (TMS=Traditional Moult Score, PFMG=Proportion Feather Mass Grown, RDI=Relative Duration Index) using data type 2. Results are presented for three reference dates: 1 June (Figures 2, 3 and 4), 16 May and 16 June (not shown). Note how the sample sizes of pre-moult and post-moult birds vary with the choice of reference date.

Moult index	Duration (SE)	Start date (SE)	Start date standard deviation (SE)	End date (SE)	Sample sizes		
					Pre-moult	In-moult	Post-moult
Reference date 1 June							
TMS	184.6 (2.0)	19 Aug (1.4)	54.1 (0.7)	19 Feb (1.4)	1403	2070	2113
PFMG	183.2 (2.0)	24 Aug (1.4)	53.8 (0.7)	23 Feb (1.4)	1403	2070	2113
RDI	182.0 (2.0)	19 Aug (1.4)	53.8 (0.7)	17 Feb (1.3)	1403	2070	2113
Reference date 16 May							
TMS	184.5 (2.0)	21 Aug (1.4)	54.1 (0.7)	21 Feb (1.4)	1960	2070	1556
PFMG	183.9 (2.0)	26 Aug (1.3)	54.0 (0.7)	26 Feb (1.4)	1960	2070	1556
RDI	181.8 (2.0)	21 Aug (1.3)	53.8 (0.7)	19 Feb (1.4)	1960	2070	1556
Reference date 16 June							
TMS	187.2 (2.1)	16 Aug (1.5)	54.9 (0.7)	19 Feb (1.4)	995	2070	2521
PFMG	185.0 (2.1)	22 Aug (1.4)	54.4 (0.7)	23 Feb (1.4)	995	2070	2521
RDI	184.7 (2.1)	16 Aug (1.5)	54.6 (0.7)	17 Feb (1.3)	995	2070	2521

Table 4. Calculations for the implementation of the modified Cook's distances (see text). Each line of the table has the data for the given moult year removed and contains the estimated primary moult parameters of adult Red-headed Finches for the remaining moult years using TMS as the moult index and data type 2. Day 1 was 1 June. The five moult years with the highest modified Cook's distances are highlighted in bold and are consider outliers.

Moult year omitted	Moult parameters for all years when the year is removed			Modified Cook's distance	Number of records omitted
	Duration (SE)	Mean start day (SE)	Standard deviation (SE) of mean start day		
None	184.6 (2.0)	79.9 (1.4)	54.1 (0.7)	–	0
1987	184.2 (2.1)	80.1 (1.4)	54.3 (0.7)	0.18	23
1988	**182.0 (2.1)**	**81.7 (1.4)**	**55.0 (0.7)**	**5.68**	**167**
1989	183.1 (2.1)	81.1 (1.4)	54.2 (0.7)	1.49	49
1990	184.3 (2.1)	79.9 (1.4)	54.1 (0.7)	0.09	25
2000	185.5 (2.1)	79.9 (1.4)	54.2(0.7)	1.21	260
2001	185.1 (2.1)	79.6 (1.4)	53.7 (0.7)	0.57	246
2002	184.4 (2.1)	80.5 (1.4)	53.5 (0.7)	0.76	491
2003	185.1 (2.1)	79.4 (1.4)	54.1 (0.7)	0.22	76
2004	184.0 (2.0)	79.9 (1.4)	53.8 (0.7)	0.59	19
2005	**186.1 (2.3)**	**79.7 (1.5)**	**55.5 (0.8)**	**4.78**	**980**
2006	185.9 (2.1)	78.2 (1.4)	53.7 (0.7)	1.33	364
2007	186.2 (2.1)	78.1 (1.5)	54.2 (0.8)	1.64	629
2008	**182.0 (2.1)**	**82.4 (1.5)**	**53.4 (0.7)**	**5.09**	**458**
2009	183.3 (2.1)	80.9 (1.4)	54.1 (0.7)	1.07	116
2010	184.9 (2.1)	79.7 (1.4)	54.0 (0.7)	0.13	75
2011	185.0 (2.1)	79.9 (1.4)	54.2 (0.7)	0.21	119
2012	184.7 (2.1)	79.9 (1.4)	54.0 (0.7)	0.04	109
2013	184.4 (2.1)	80.2 (1.4)	53.9 (0.7)	0.07	35
2014	185.5 (2.1)	79.4 (1.4)	54.2 (0.7)	0.72	103
2015	185.2 (2.1)	79.9 (1.4)	54.1 (0.7)	0.50	109
2016	184.4 (2.1)	80.0 (1.4)	54.0 (0.7)	0.05	24
2017	**186.6 (2.1)**	**78.2 (1.5)**	**54.3 (0.7)**	**2.66**	**370**
2018	185.5 (2.1)	78.9 (1.4)	53.6 (0.7)	0.92	321
2019	**182.4 (2.1)**	**81.2 (1.5)**	**54.9 (0.8)**	**4.75**	**287**
2020	184.4 (2.1)	79.7 (1.4)	54.4 (0.7)	0.29	127

Table 5. Moult parameters using TMS as the moult index for all moult years and for when each of the five moult years with the highest Cook's distances (1988, 2005, 2008, 2017 and 2019) are progressively omitted.

Years	Duration (SE)	Mean start day (SE)	Standard deviation (SE) of mean start day	Samples progressively omitted	Sample size
All	184.6 (2.1)	79.9 (1.4)	54.1 (0.7)	0	5586
Minus 1988	182.0 (2.1)	81.7 (1.4)	55.0 (0.7)	−167	5419
Minus 1988, 2008	179.2 (2.2)	84.4 (1.5)	54.3 (0.8)	−458	4961
Minus 1988, 2008, 2005	179.6 (2.5)	85.1 (1.7)	56.0 (0.9)	−980	3981
Minus 1988, 2008, 2005, 2019	175.3 (2.6)	87.9 (1.9)	57.3 (1.0)	−287	3694
Minus 2008, 2008, 2005, 2019, 2017	174.9 (2.8)	91.1 (2.0)	58.5 (1.0)	−370	3324

Table 6. Estimated moult parameters for the whole primary tract of adult Red-headed Finches using the Traditional Moult Score (TMS) and data type 2. The five years identified by the modified Cook's distance algorithm as outliers (Tables 4 and 5) were allowed to have different starting dates. For these five years, the estimates are presented as offsets in relation to the baseline starting date for the remaining years (negative offsets for earlier and positive offsets for later starting dates than the baseline).

Parameter	Estimate (SE)	Start date	End date
Duration (SE)	184.8 (2.1)	–	–
Baseline starting day (SE)	82.6 (1.7)	22 Aug	22 Feb
1988	–11.6 (4.4)	10 Aug	11 Feb
2005	–3.8 (2.5)	18 Aug	18 Feb
2008	–12.6 (3.5)	9 Aug	10 Feb
2017	10.4 (3.7)	1 Sep	5 Mar
2019	–7.3 (3.7)	14 Aug	15 Feb
Standard deviation of mean starting day (SE)	53.8 (0.7)	–	–

Table 7. Parameters of moult for passerines on the South African Highveld, estimated using the moult model of Underhill and Zucchini (1988).

English name	Species name	Start date	End date	Duration	SD of start	Source
Red-headed Finch	*Amadina erythrocephala*	22 Aug	22 Feb	185	54	This study
Orange-breasted Waxbill	*Amandava subflava*	30 Nov	22 Feb	85	46	Bonnevie and Oschadleus 2012
Thick-billed Weaver	*Amblyospiza albifrons*	20 Feb	2 May	71	24	Oschadleus 2005; Oschadleus and Underhill 2006a
Levaillant's Cisticola	*Cisticola tinniens tinniens*	18 Mar	16 May	61		Herremans et al. 1999
Common Waxbill	*Estrilda astrild*	15 Feb	4 May	79	44	Bonnevie and Oschadleus 2012
White-winged Widowbird	*Euplectes albonotatus*	18 Apr	3 Jun	47	26	Oschadleus 2005; Oschadleus and Underhill 2006b
Red-collared Widowbird	*Euplectes ardens*	5 Apr	3 Jun	60	31	Oschadleus 2005; Oschadleus and Underhill 2006b
Southern Red Bishop	*Euplectes orix*	23 Mar	3 Jun	72	35	Oschadleus 2005; Oschadleus and Underhill 2006b
Long-tailed Widowbird	*Euplectes progne*	26 Mar	25 May	61	21	Oschadleus 2005; Oschadleus and Underhill 2006b

English name	Species name	Start date	End date	Duration	SD of start	Source
Southern Masked Weaver	*Ploceus velatus*	11 Feb	28 Apr	76	19	Oschadleus 2005
Black-chested Prinia	*Prinia flavicans*	1 Feb	20 May	108		Herremans 1999
Green-winged Pytilia	*Pytilia melba*	6 Jul	3 Nov	121	67	Bonnevie and Oschadleus 2012
Red-billed Quelea	*Quelea quelea*	23 Apr	2 Aug	101	33	Oschadleus 2005
Pin-tailed Whydah	*Vidua macroura*	28 Mar	10 Jul	105	43	Bonnevie and Oschadleus 2012
Orange River White-eye	*Zosterops pallidus*	30 Jan	19 Apr	78	28	Hulley et al. 2004

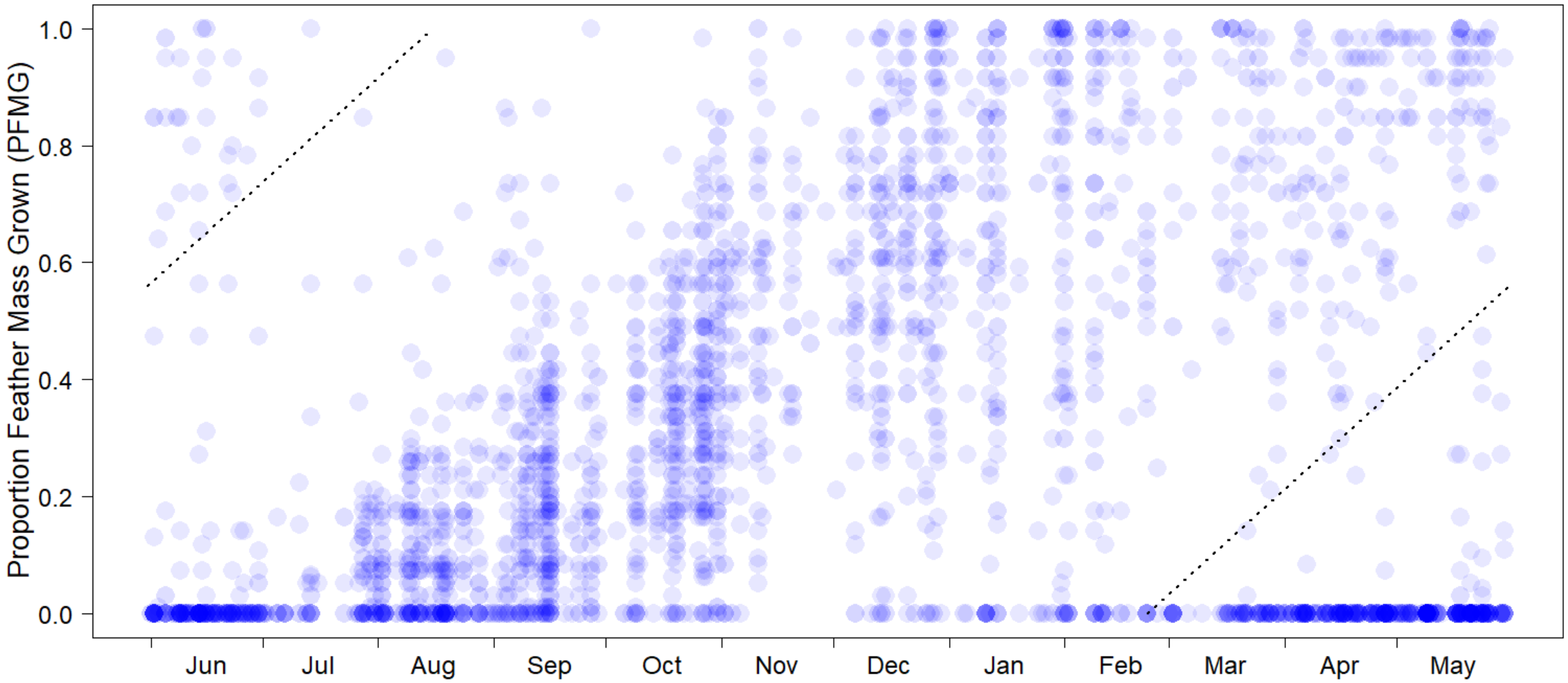

Figure 1. Modified scatter diagram* of PFMG and calendar date for adult Red-headed Finches, using 1 June as day 1. It is obvious that the records in the top left corner represent birds that started moult relatively late and those in the bottom right corner represent birds that started moult relatively early. The solution to this is to use a diagonal line (dotted), parallel to the mean moult line, and positioned visually to pass through the region with the fewest data points. The diagonal line is continuous but split between the left and right sides of the plot because the year is split at 1 June.

* Moult scores are recorded on a discrete scale (each primary is given an integer score between 0 and 5). A consequence of this is that conventional scatter plots of moult scores in relation to dates are misleading because there is no representation of the number of records represented by a single symbol in the plot. In this modification of the scatter diagram, the data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade refers to one data point and the darkest shade refers to 116 overlapping data points.

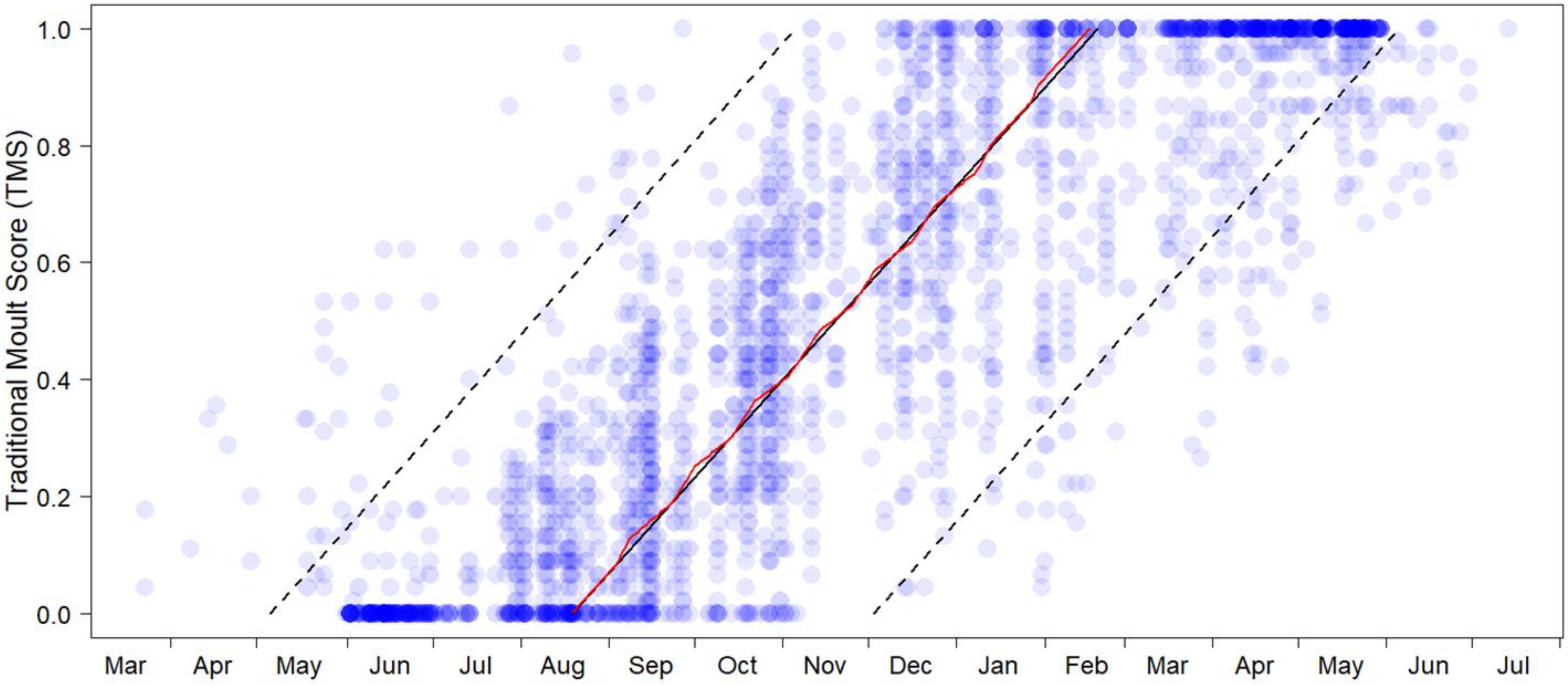

Figure 2. Modified scatter diagram of TMS and adjusted day for adult Red-headed Finches. The straight line links the estimated starting date with the estimated end date using TMS as the moult index. The dashed lines are the 95% intervals derived from the standard deviation of the start date. The red curved line was computed from the moult durations of the individual primaries giving each primary equal weight (see text). The modification to the scatter plot is described in the caption to Figure 1. The data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade refers to one data point and the darkest shade refers to 116 overlapping data points.

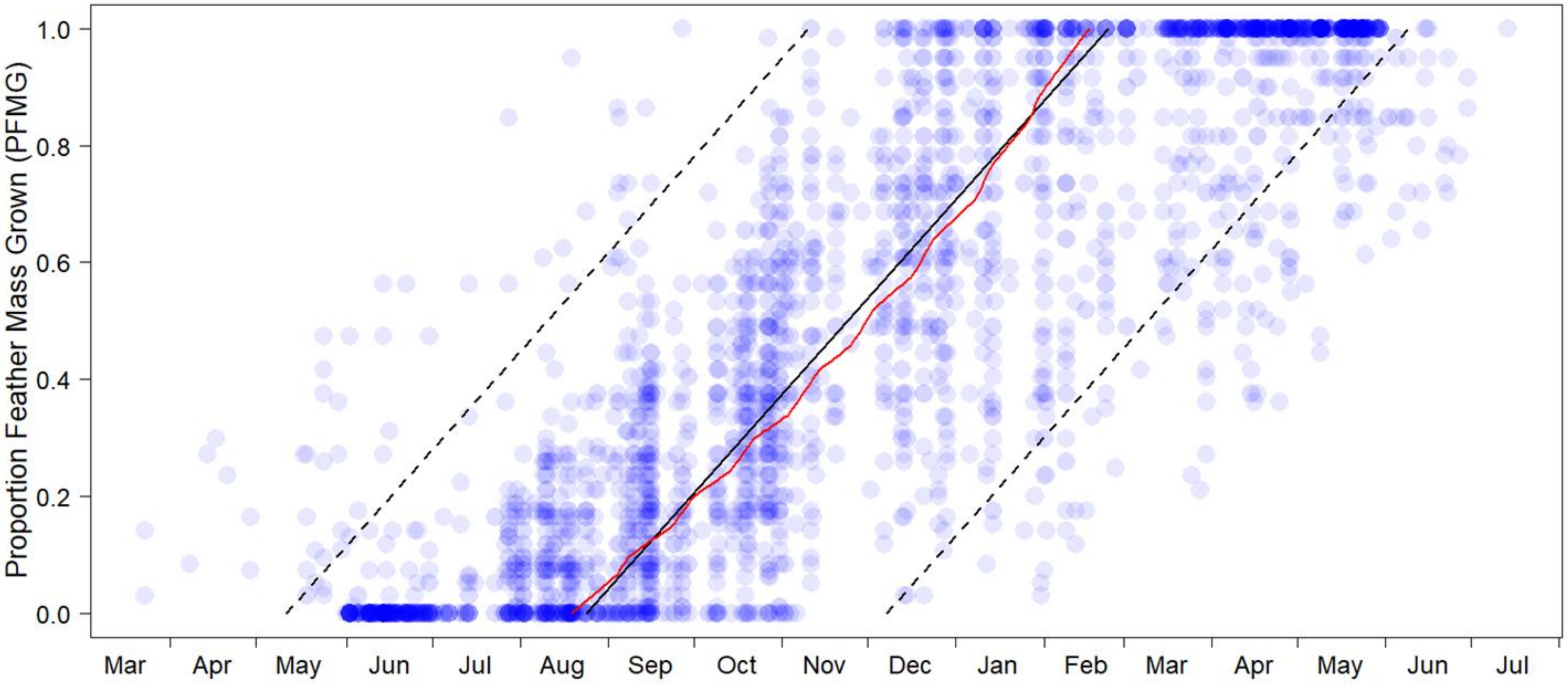

Figure 3. Modified scatter diagram of PFMG and adjusted day for adult Red-headed Finches. The straight line links the estimated starting date with the estimated end date using PFMG as the moult index. The dashed lines are the 95% intervals derived from the standard deviation of the start date. The red curved line was computed from the moult durations of the individual primaries giving each primary weight relative to its mass (see text). The modification to the scatter plot is described in the caption to Figure 1. The data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade refers to one data point and the darkest shade refers to 116 overlapping data points.

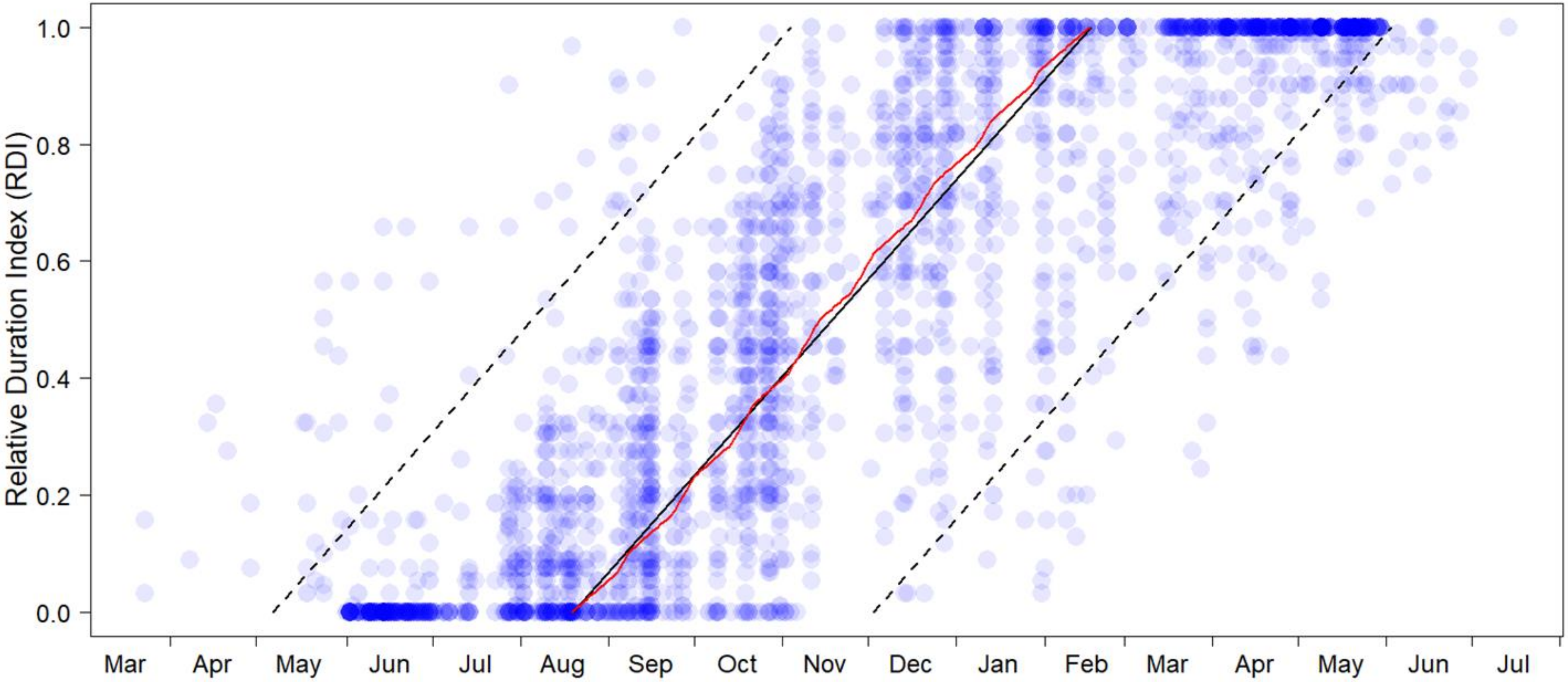

Figure 4. Modified scatter diagram of RDI and adjusted day for adult Red-headed Finches. The straight line links the estimated starting date with the estimated end date using RDI as the moult index. The dashed lines are the 95% intervals derived from the standard deviation of the start date. The red curved line was computed from the moult durations of the individual primaries giving each primary weight relative to its duration of moult (see text). The modification to the scatter plot is described in the caption to Figure 1. The data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade refers to one data point and the darkest shade refers to 116 overlapping data points.

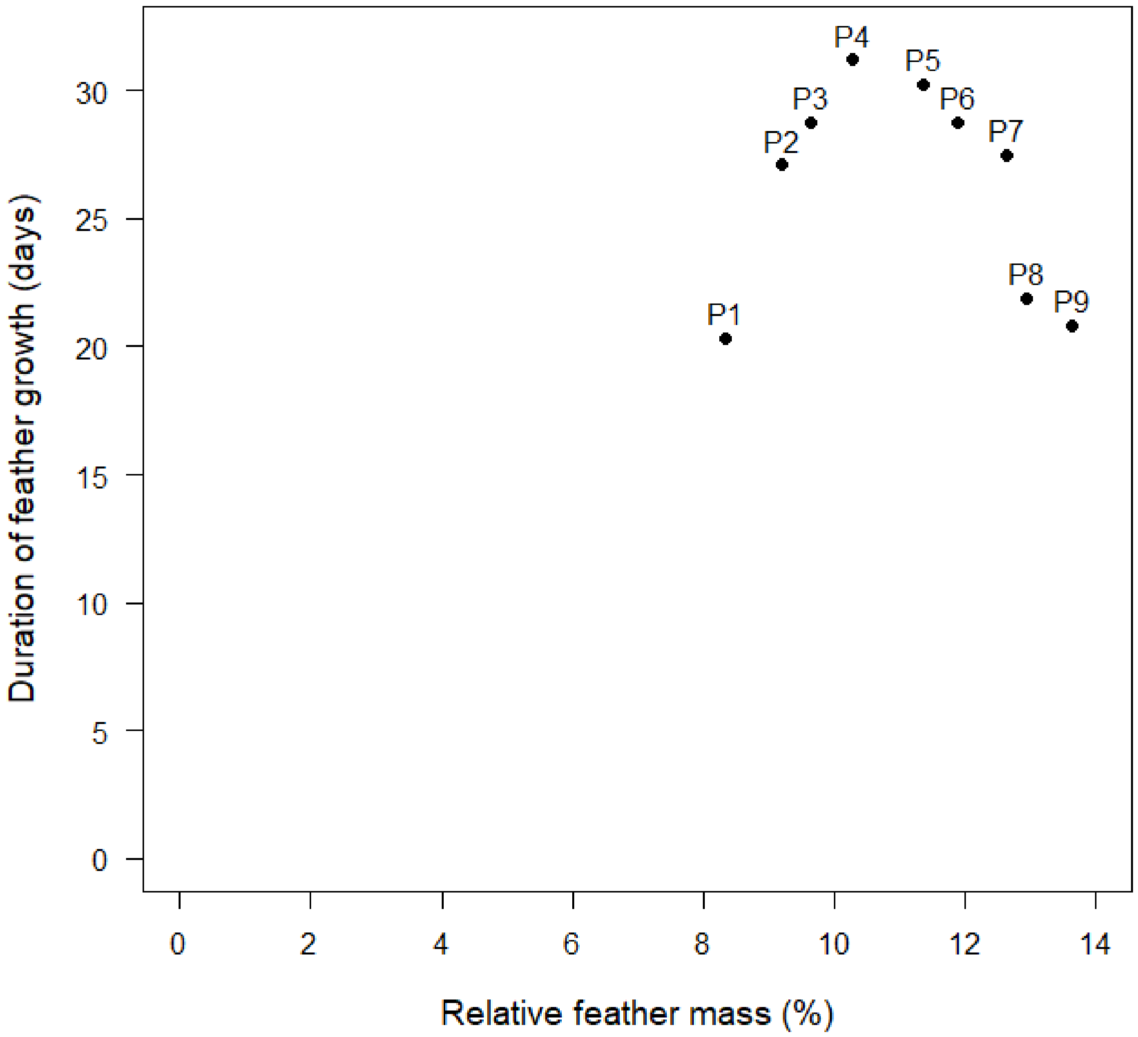

Figure 5. Plot of the duration of growth of each Red-headed Finch primary versus its relative mass.

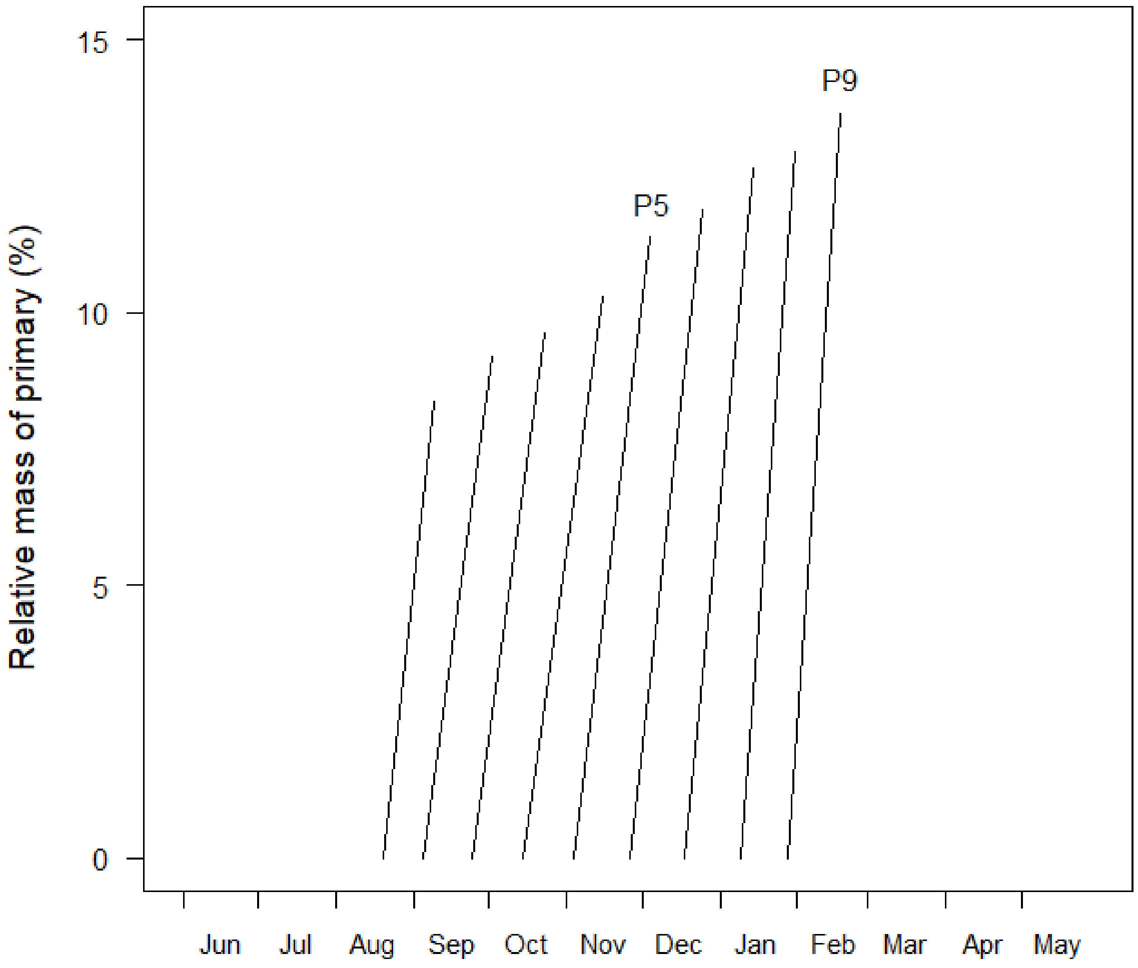

Figure 6. The progression of moult of individual primaries (P1–P9) of adult Red-headed Finches. The slope of the line of each primary represents the growth rate of the primary relative to its mass, so the unit of the slope is PFMG/day. The mean (and standard deviation) of the slopes of these nine lines was 0.435 (0.117) PFMG/day, yielding a coefficient of variation (CV) of 26.9%.

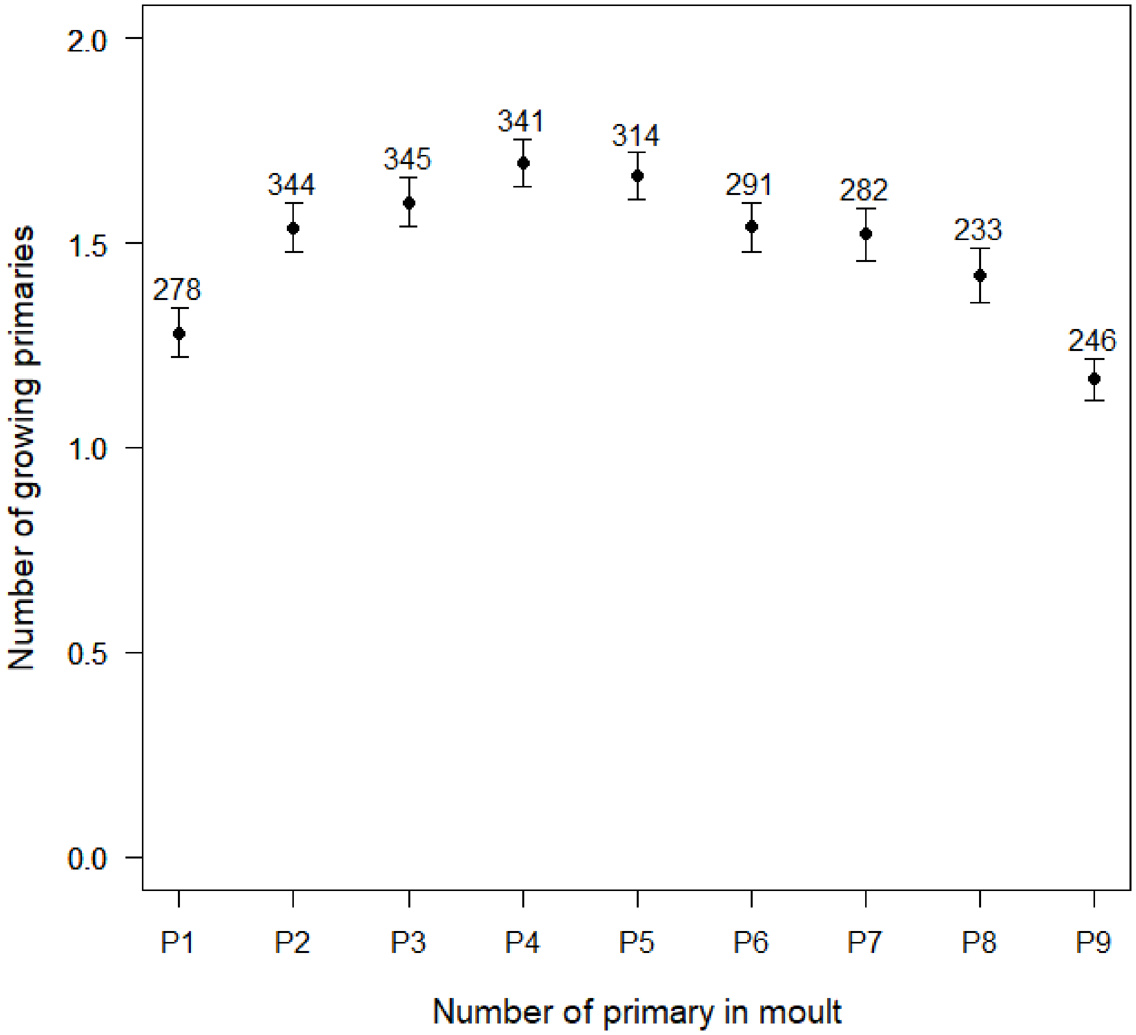

Figure 7. The mean number of primaries growing simultaneously while each of the nine primaries of adult Red-headed Finches was in moult. The 95% confidence intervals for the mean and the sample sizes are shown.

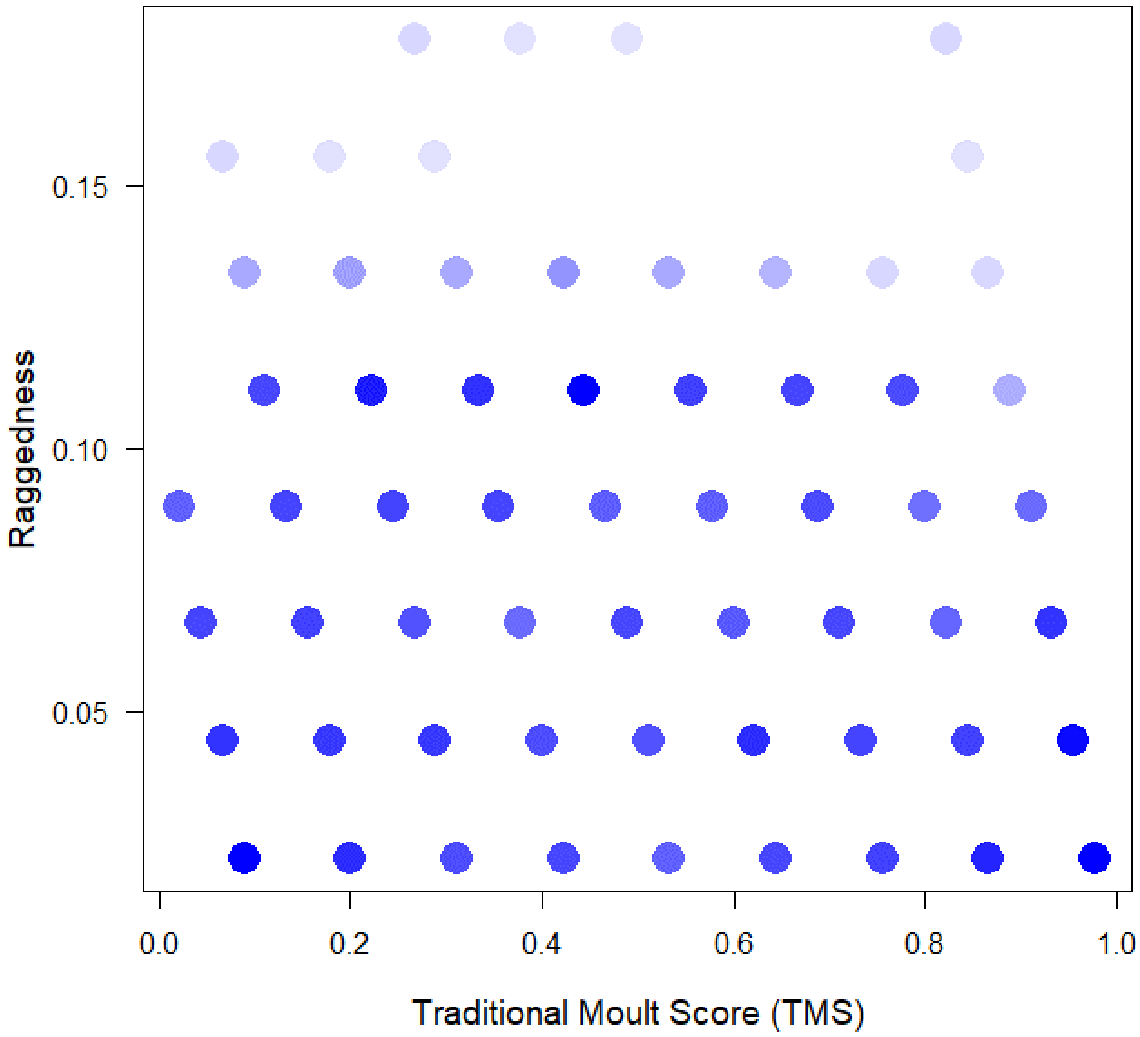

Figure 8. The relationship between raggedness and Traditional Moult Score (TMS) is shown by a modified scatter diagram for adult Red-headed Finches in active moult. The pattern of parallel lines occurs as a result of the in-field method used by bird ringers for recording primary moult scores as an integer between 0 and 5. The modification to the scatter plot is described in the caption to Figure 1. The data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade refers to one data point and the darkest shade refers to 80 overlapping data points.

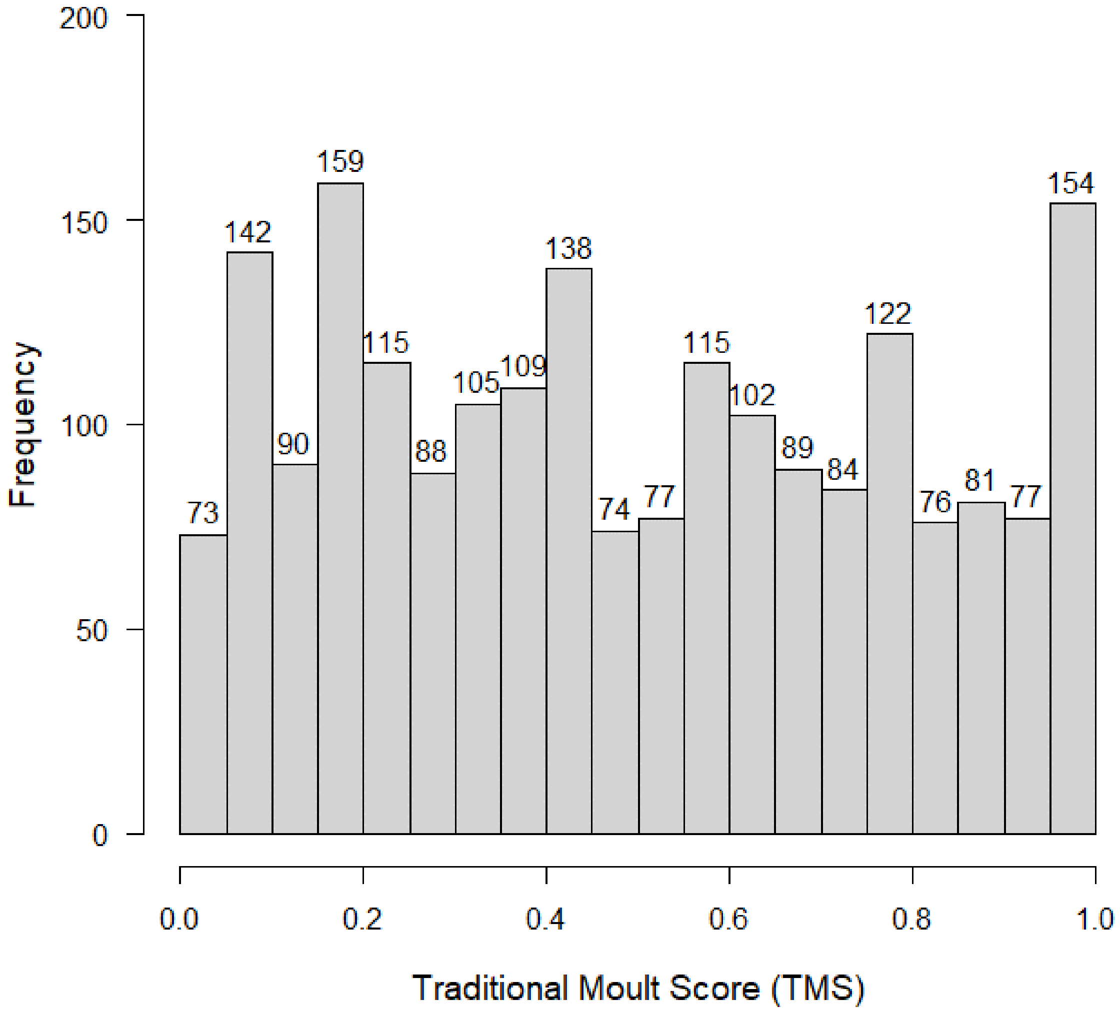

Figure 9. Histogram of Traditonal Moult Scores (TMS) of 2070 adult Red-headed Finches in active moult. The class interval was 0.05 TMS units. The histogram is approximately uniform which shows that the probability of trapping finches was independent of the moult stage.

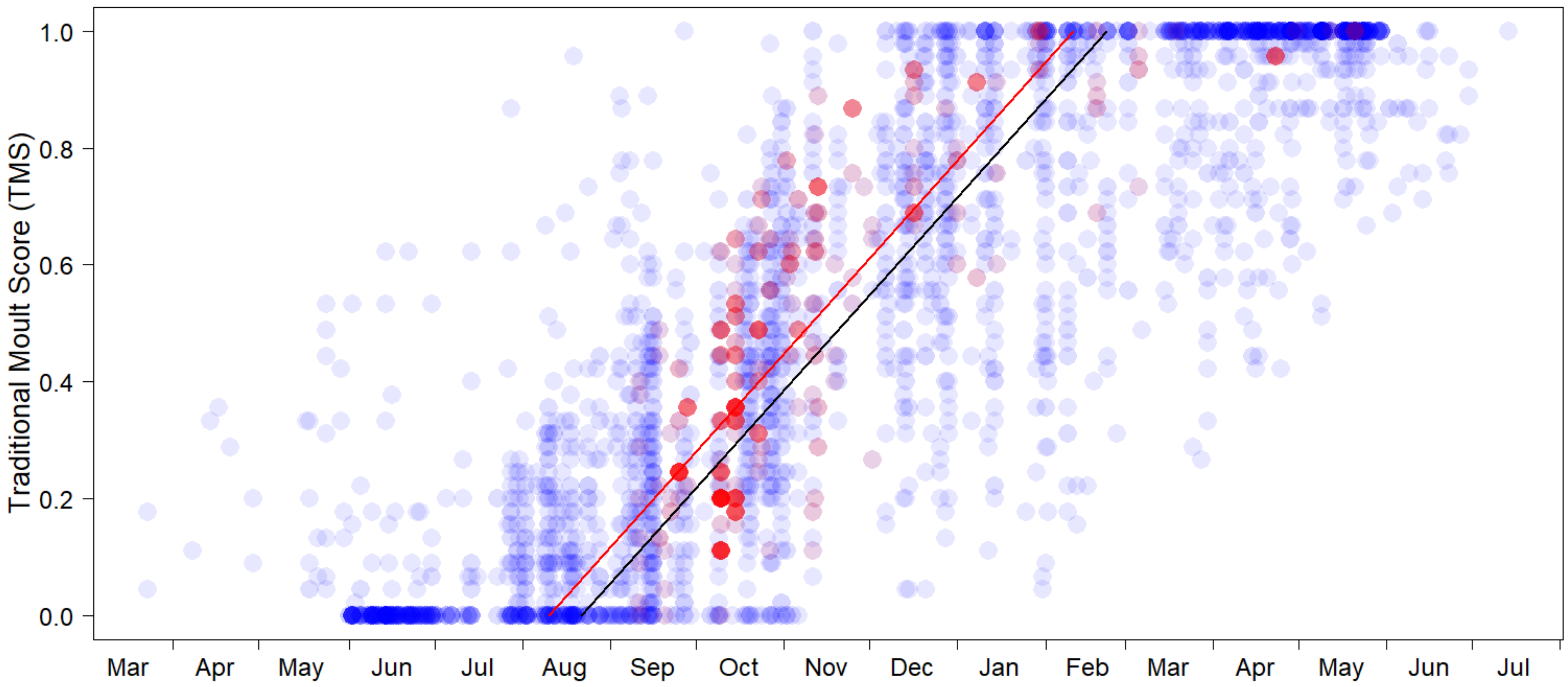

Figure 10. Modified scatter diagram of TMS for adult Red-headed Finches. This is the same plot as Figure 2, except that the data points for 1988 are shaded red. The black line shows the mean trajectory of primary moult for the years not identified as outliers by the modified Cook's distance algorithm (Tables 5 and 6). The red line shows the mean trajectory of moult for 1988. The modification to the scatter plot is described in the caption to Figure 1. The data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade refers to one data point. The darkest blue shade refers to 116 overlapping data points and the darkest red shade refers to 5 overlapping data points.

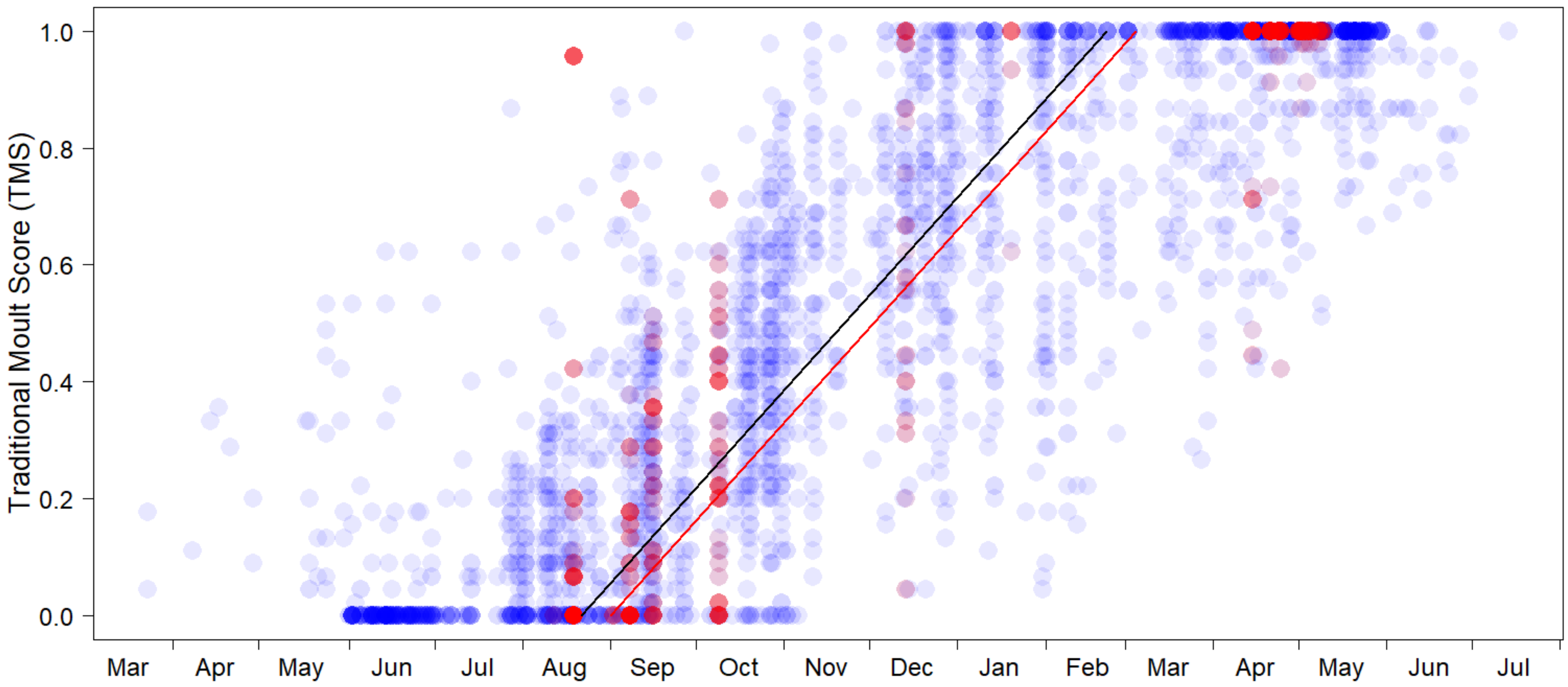

Figure 11. Modified scatter diagram of TMS for adult Red-headed Finches. This is the same plot as Figure 2, except that the data points for 2017 are shaded red. The black line shows the mean trajectory of primary moult for the years not identified as outliers by the modified Cook's distance algortihm (Tables 5 and 6). The red line shows the mean trajectory of moult for 2017. The modification to the scatter plot is described in the caption to Figure 1. The data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade refers to one data point. The darkest blue shade refers to 116 overlapping data points and the darkest red shade refers to 51 overlapping data points.

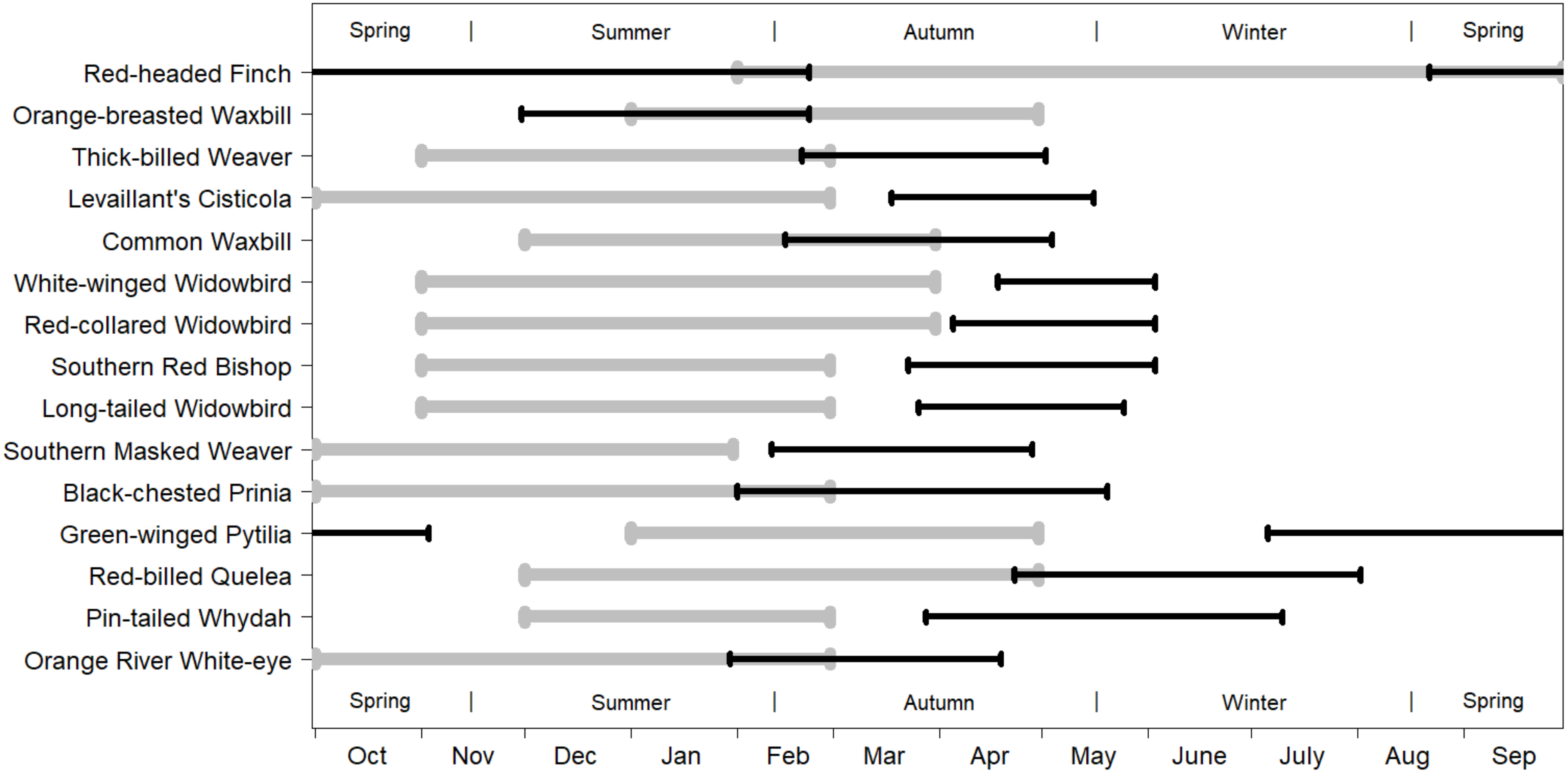

Figure 12. Representation of the relationship between the timing of breeding (grey bars) (Hockey et al. 2005) and the timing of moult (black bars) for 15 species of passerines in the Highveld regions of South Africa (Table 7).

CHAPTER 4

Primary moult of Silvereye *Zosterops lateralis* in New Zealand

Chapter 4

Primary moult of Silvereye *Zosterops lateralis* in New Zealand

Abstract: Little is known about the moult of New Zealand's endemic, native and introduced bird species. The focus of this study is the self-introduced Silvereye *Zosterops lateralis* in New Zealand. Moult data collected by bird banders between 1978 and 2022 were analysed using the Underhill-Zucchini moult model. The Silvereye population in New Zealand had an estimated primary moult duration of 74 days, with a mean population start date of 3 February and a mean completion date of 19 April. The standard deviation of the start date was 37 days. Post-breeding primary moult in adult Silvereyes starts soon after the breeding season and ends shortly before some of the more southern birds embark on their seasonal northward migratory movements. Post-juvenile primary moult is estimated to start approximately two weeks after the start of post-breeding moult in adults. Across all bird species, latitude plays an important role in determining patterns in timing, duration and synchronisation of primary moult but, apart from Africa, moult studies at the southernmost limits of the continents are lacking. A review of the literature suggested that primary moult durations for *Zosterops* species are similar regardless of latitude, but the timing of moult is variable and adjusted to local conditions. New Zealand has an important role to play in extending the latitudinal range of moult studies.

Keywords: White-eye, Zosteropidae, bird banding, Underhill-Zucchini moult model

INTRODUCTION

The first custom-built statistical model for the study of primary wing feather moult in birds was developed in the late 1980s (Underhill and Zucchini 1988, Underhill et al. 1990), however it was another 25 years before it could be utilised using widely accessible software (Erni et al. 2013). Subsequently, there have been many applications of the Underhill-Zucchini model and this has facilitated reviews of primary moult involving multiple species and many sites (e.g., Remisiewicz 2011, Dietz et al. 2015, Jackson and Underhill 2022, Chapter 7). Although there have been studies of primary moult in New Zealand birds (e.g., Gill 1983, Onley 1986, Rasmussen 1988, Sagar 1988, Davies 1997, Beauchamp 1998, Conklin and Battley 2011, Smith et al. 2015), no published studies include the application of moult specific statistical techniques, such as the Underhill-Zucchini moult model, to quantify the timing and extent of primary feather replacement.

The main conclusion of four reviews of primary moult (Remisiewicz 2011, Dietz et al. 2015, Jackson and Underhill 2022, Chapter 7) has been that latitude is a key variable in determining patterns of moult. Latitude, however, serves as a proxy variable, mainly related to seasonality and therefore climate, as well as a measure of how extreme climates become (during winter, especially at far northern and far southern latitudes) and therefore the need to migrate. However, latitude is a poor proxy for climate, especially in the tropics and subtropics (Chapter 7). Seasonal variability at latitudes near the equator is less pronounced than in temperate regions and, therefore, moult patterns in the tropics and subtropics show greater variation in timing and duration (Chapter 7). In temperate regions, latitude becomes a key driver of climate, through variables such as day length, seasonality and temperature. These place constraints on food availability and as a result primary moult patterns are increasingly synchronised, taking place at the same stage in the annual cycle of many bird species, namely after the spring breeding season and before the onset of harsh winter conditions (Jenni and Winkler 2020a, Jackson and Underhill 2022). However, our understanding of the relationship between latitude and moult is hampered by the latitudinal range of moult studies available. For example, the northernmost study to which the moult model has been applied was in Alaska at latitude 71°N (Taylor et al. 2018). In contrast, prior to this study, the southernmost analysis was in Australia, at latitude 39°S (Rogers et al. 2014). To extend the latitudinal range of moult studies, researchers need to target species found near the southern extremities of Australia (44°S), South America (56°S) and New Zealand (48°S).

This study, and Chapters 5 and 6, are based in New Zealand and extend the latitudinal range of quantitative primary moult studies southwards. Chapter 5 focuses on the primary moult of adult Wrybills *Anarhynchus frontalis*, a wader which breeds in the braided rivers of South Island and moults during the non-breeding season in North Island. Chapter 6 focuses on the primary moult of seven European passerines introduced to New Zealand from the United Kingdom and found that the duration of primary moult, and its timing relative to midsummer, was similar to that in the United Kingdom. The goal of this chapter is to quantify the timing and duration of primary moult of adult Silvereyes *Zosterops lateralis*, a self-introduced speciesin New Zealand. We also explore post-juvenile moult. The results are compared to those for other members of the genus *Zosterops* globally.

METHODS

Species

The genus *Zosterops* is large and its taxonomy is in a state of flux (Lim et al. 2019). BirdLife International (2022) recognised 101 species in the genus *Zosterops*, with 66 classified as Least Concern and the remaining 35 in threat categories: 14 are Near Threatened, nine Vulnerable, five Endangered, four Critically Endangered and three Extinct. Species of the genus *Zosterops* occur widely throughout southern and southeast Asia, Africa south of the Sahara, Australasia and New Zealand, with many species restricted to islands in the Indian and western Pacific Ocean (Oliver 1955, van Balen 2008, Gill et al. 2022). The Silvereye has one of the largest ranges of any *Zosterops* species occurring in southern and eastern Australia, New Zealand and islands of the southwestern Pacific Oceans (Higgins et al. 2006). It is also one of four species in the genus described as a migrant or partial migrant (van Balen 2008).

The Silvereye is a self-introduced species to New Zealand, arriving naturally from Australia and successfully establishing itself during the 19th century (Neuhäuser and Cuming 2007, Checklist Committee 2022). Silvereyes were first noticed at Milford Sound, South Island, in 1832 (Thomson 1922, Oliver 1955). By the 1850s they were sighted more frequently and appeared to be expanding northwards from Southland but were not observed north of Cook Strait until 1856. By 1858 Silvereyes were considered permanent residents in Wellington, North Island. They continued their northward expansion and had reached Hawke's Bay by 1861 and Auckland by 1865. By 1868, Silvereyes had reached the northern-most point of the North Island and were established successfully across the mainland (Buller 1888, Thomson 1922, Oliver 1955). By the 21st century, Silvereye was one of the most common and widespread bird species in New Zealand (Heather and Robertson 2005). They are considered valuable insectivores by fruit-growers and gardeners, despite causing some damage to orchards during the fruit season (Buller 1888, Thomson 1922, Oliver 1955, Wearing and McCarthy 1992, Heather and Robertson 2005).

Data collection

Moult data for Silvereyes were collected by bird banders throughout New Zealand between 1978 to 2022. The birds were aged as adult or juvenile based on the amount of wear and fading of the primaries, with juveniles having fresh primaries at the start of their post-juvenile moult (D.S. Melville *in litt.*). Additional cues, such as the presence of a gape, colouration of the base of the bill (pinkish-orange prior to post-juvenile moult, blueish-grey in adults) and eye colour (pale greyish-red-brown in younger birds, dark red-brown in adults) were also used to assist in separating age classes. These ageing criteria become less reliable as moult proceeds and it is likely that some juveniles were aged as adults towards the end of moult. Most juveniles would have been aged as adults after the completion of moult. The fact that the ageing of Silvereyes is imperfect impacts upon the analyses used to estimate the parameters of moult.

The location and co-ordinates of the banding sites were noted. Banders recorded the primary moult of captured birds using the standard protocol (Ginn and Melville 1983). This involves assigning a moult score to each primary feather (nine in the case of Silvereyes), ranging from zero to five (0=old feather, 5=new feather and 1–4 represent intermediate stages of feather growth).

Data analysis

Relative masses of the primary feathers of Silvereyes were obtained from a sample of two Silvereyes that had been processed as described by Underhill and Joubert (1995) (Table 1). For both the primary moult in adults and post-juvenile moult, the moult scores were converted to Proportion Feather Mass Grown (PFMG) using the relative feather masses. The Underhill and Zucchini (1988) moult model was used to analyse primary moult. The parameters of moult were estimated using the package "moult" (Erni et al. 2013) in R (R Core Team 2019). The estimated parameters were the duration of moult, the mean start date of moult and the standard deviation of the start date. Standard errors of each parameter were also estimated by the model. We estimated that 95% of birds start moult in the period given by the estimated mean start date ± 1.96 × estimated standard deviation parameter.

We used two of the five data types of the moult model, data type 2 and data type 5 (Underhill and Zucchini 1988, Underhill et al. 1990). Data type 2 assumes that the birds are sampled from a closed population which includes those that have not yet started moult, birds actively moulting and birds that have completed moult. Data type 5 assumes that the closed population consists of birds that have not yet started moult and birds actively moulting. A data type 5 analysis excludes birds which have completed moult. Where adequate data is available, it is preferable to use data type 2, because the moult model is then able to extract information from the birds which have completed moult. When this is done the standard errors of the estimates of the parameters are smaller with data type 2 than with data type 5. Because of the uncertainties with the ageing of Silvereyes, a series of moult models was tried using the two different data types and the results were compared and evaluated.

We applied data type 2 to birds aged as adults. However, because Silvereye undergo a complete post-juvenile moult, age classes are inseparable past this point in their annual cycle (D.S. Melville *in litt.*). Therefore, it is likely that a proportion of juveniles near the end of their moult cycle and all those having completed moult were aged as adults. To address the issue caused by the erroneous inclusion of the juveniles in the analysis of adult moult, we also applied data type 5 to the Silvereye adults to remove the overabundance of birds that had completed moult in the dataset. We applied data type 5 to the juveniles because the juveniles that had completed moult would have been aged as adults. We used data type 2 and data type 5 on the combined sample of Silvereyes aged as adults and juveniles. The moult model was first run with one mean start date estimated for both adults and juveniles combined using data type 2. It was then run a second time with two mean start dates estimated (one for adults and one for juveniles) using data type 5. In addition, we used data type 2 on a sample that included adult and juvenile birds as well as birds which were not aged. Our decision on the choice of model which best described the moult of Silvereyes in New Zealand was based partly on the biological insights provided by the models, rather than on statistical model selection techniques. We considered whether there were changes in the timing of moult, both latitudinally and temporally.

Two measures that relate to primary moult and provide insight into energetic costs of moult were computed. The first was the average number of simultaneously growing primaries, which is defined as moult intensity. This can serve as a proxy for the direct energetic costs of growing new feathers (Remisiewicz et al. 2009, Jenni and Winkler 2020a). For adult Silvereyes, the mean number of primary feathers growing simultaneously, along with its 95% confidence interval, was calculated and plotted for each of the nine primaries. The second measure was Proportion Feather Mass Missing (PFMM), as described by Remisiewicz et al. (2009). This quantifies the relative size of the wing gap created when primary feathers are being moulted, taking the relative mass of the primaries into account. The larger the wing gap, the greater the loss in flight performance (Jenni and Winkler 2020a, 2020b, Hedenström 2023) and therefore PFMM aids in quantifying this important component of the indirect costs of moult. PFMM was estimated for each bird in active moult using the method described by Remisiewicz et al. (2009): Primary feather moult scores of 1, 2, 3, 4 are converted to 0.875, 0.625, 0.375, 0.125 respectively and moult scores of 5 and 0 are taken as zero (i.e. no missing feather mass). These proportions are then multiplied by the relative mass of the corresponding primary and summed across all primaries.

RESULTS

We obtained data for 29 of the 44 years of the study period (1978 to 2022). There was a total of 1295 available moult records for Silvereyes in New Zealand: 310 for North Island and 985 for South Island. Latitudinal data were available for 1289 of the 1295 records. 84% of these 1289 moult records were between latitudes 41°S and 42°S. This range covers the northern part of the South Island and the southern part of the North Island. It was therefore not feasible to investigate whether there was a trend over the c. 12° latitudinal range of New Zealand (36.4°S to 48.0°S) for which moult data were recorded or whether there was a biologically meaningful difference between birds on the two islands. The mean latitude of the collected moult records was 42°S. Given the 44-year period for which data were available, we also wanted to test whether there was a long-term trend in the parameters of moult. However, 80% of the records were for the period 2002–2012 and 43% for the three years 2010, 2011 and 2012. It was therefore not possible to investigate temporal trends.

There were 693 moult records for adult Silvereyes: 162 were pre-moult, 301 were active moult and 230 were post-moult records (Table 2, Figure 1). Applying data type 2 to these data, the duration of moult was estimated as 73 days with a mean start date of 27 January and mean end date of 10 April. The start date was unchanged when data type 5 was applied but the duration was estimated to be 84 days, a change consistent with the reality that post-moult juveniles were included in the sample of adults. The standard error of the duration parameter was 3.9 days for data type 2 and 9.5 days for data type 5. The standard deviation parameters were estimated as 39 days and 41 days for data types 2 and 5 respectively (Table 2, Figure 1). For four adults (0.6 of the data) the moult scores had been recorded in ways suggestive of suspended moult (500000000 on 5 February, 555555500 on 6 February, 555555500 on 3 March, 555555000 on 24 April). All are inliers in relation to the scatter diagram in Figure 1. It is also possible that, within the natural variation in numbers of feathers actively moulting, a small proportion of birds have moult scores like this and therefore they were included in the analysis. When these four records are excluded, the estimated duration changes by 0.6 days, mean start date by 0.3 days and the standard deviation of start date by 0.1 days. The decision to include or exclude them has no biological impact.

There were 412 moult records for juveniles, of which 188 were pre-moult and 224 were in active post-juvenile primary moult (Table 2, Figure 2). The mean start date of post-juvenile moult was estimated by using data type 5 to be 5 February, the standard deviation parameter was 57 days and the estimated duration was 116 days. The duration, however, had a large standard error of 18 days, which points to it being unreliable (Table 2).

When the data for the birds aged as adults and those aged as juveniles were combined, and data type 2 was used, the duration of moult was estimated to be 78 days (standard error 3.4 days). The start date was estimated to be 2 February (standard error 1.8 days), which lies close to the middle of the estimated dates for adults (27 January) and juveniles (5 February) (Table 2). Start dates of 24 January and 7 February were estimated for adults and juveniles respectively when the same combined data were used in a moult model that predicted two mean start dates (one for each age class), one duration and one standard deviation. Data type 5 was used in this analysis because juveniles which had completed moult would have been classified as adults. It was therefore appropriate to omit the birds which had completed moult from the analysis. This analysis confirmed the delay of approximately two weeks between the start of primary moult in adults and the start in juveniles. The duration was estimated as 95 days (standard error 8.4 days) (Table 2). When the entire dataset (1295 records, including all unaged birds) was analysed using data type 2, the start date was estimated to be 3 February and the duration to be 74 days (standard error 2.9 days) (Table 2, Figure 3).

During the replacement of the first eight primaries there were, on average, 2.9 concurrently growing feathers (Figure 4). During the replacement of the outermost ninth primary this decreased to 2.2. The mean size of the gap in the primary feathers during active moult was 0.10 (SD=0.07). This means that, on average, adult Silvereyes were missing 10% of their primary feather mass during moult (Figure 5). The largest wing gap was 0.41, which corresponds to 41% of the total feather mass. This was for a bird replacing P4–P9 (moult formula 555443111 on 11 March).

DISCUSSION

Primary moult of the Silvereye

Regardless of choice of data type, the mean dates of the start of primary moult for Silvereyes were estimated to be 27 January for adults and 5 February for juveniles, a difference of 9 days (Table 2). Because of the difficulties of ageing juveniles at the end of moult, the duration of moult in adults, and therefore its average end date, are less reliably estimated. The impact on the Underhill-Zucchini moult model of having post-moult juvenile birds misclassified as adults is to bias the adult moult duration to be shorter when data type 2 is used. Thus, the estimated 73 days is most likely an underestimation of the duration of primary moult when only adults are considered (Table 2). However, when data type 5 is used, and accordingly 230 post-moult adult birds are omitted from the analysis, the standard error of the duration is too large for the result to be reliable.

Because of the concentration of records near the start of moult in juveniles (Figure 2), a reliable starting date for post-juvenile moult (5 February) was estimated but there is little information available for the estimation of the duration of their post-juvenile moult. This is confirmed by the large standard error of the estimate of the duration parameter (Table 2). The estimated duration of 116 days is deemed unreliable (Table 2).

When the data for adults and juveniles are combined the assumptions of data type 2 are satisfied because all birds are available for sampling throughout the moult period. The differences between the estimates using only the aged birds in a model with a single mean population start date and using all available data were relatively small and biologically meaningless. The estimated durations differed by 3.5 days. This should be seen in the context that the estimated 95% confidence interval for duration, when using all available data, was 74.3 ± 1.96 × 2.9 days or 69 to 80 days. The alternative estimate of 78 days, when using only aged birds, was within this interval.

Therefore, based on the reasoning set out above it is suggested that the most reliable estimates of the parameters of moult for the Silvereye in New Zealand are those for the entire Silvereye population given in the final line of Table 2; a duration of 74 days, a mean population start date of 3 February, and a standard deviation of start date of 37 days (Table 2, Figure 3).

Our understanding of post-juvenile primary moult is incomplete due to the inherent difficulties of ageing Silvereyes in the field towards the end and especially after the completion of primary moult (Higgins et al. 2006). However, it is evident from Table 2 that juveniles start moult, on average, about two weeks later than adults.

Juveniles that hatch early in the breeding season undergo a complete moult, similar to that seen in adults (Swanson 1971). Those that hatch slightly later are often found to be moulting in late April and May (Swanson 1971), while those hatched at the end of the breeding season undergo a partial post-juvenile moult (Swanson 1971, Higgins et al. 2006).

Primary moult within the genus *Zosterops*

In the era of climate change and given that 35 of 101 species of this large genus are threatened, improved knowledge of their biology, including moult, is a priority. Climate change has the potential to alter breeding seasons of species, resulting in shifts in the start of the post-breeding moult and possibly the speed at which it progresses (Morrison et al. 2015). However, it is unclear if changes in the timing and/or speed of moult can keep up with changes in breeding seasons (Jenni and Winkler 2020a).

Most *Zosterops* species are residents (van Balen 2008). Primary moult follows closely after the breeding season and it is a complete replacement of the primary feathers (Guest 1973, Greig-Smith 1979, Hulley et al. 2004). This is also true for Silvereyes (Swanson 1971, Kikkawa and Wilson 1982, Rooke 1984). The Silvereye is a multi-brooded species, usually laying two or three clutches in a breeding season (Fleming 1943, Gill 1994, Higgins et al. 2006). It undergoes a post-breeding moult annually (Fleming 1943, Mees 1969, Kikkawa and Wilson 1982). Multi-brooded species are expected to delay the start of post-breeding moult and possibly increase the speed of moult if the breeding season extends into autumn as a result of global warming (Jenni and Winkler 2020a). However, autumns and winters may also be milder and therefore there may not be a constraint on moult. Moult speed influences the quality of feathers grown and a rapid moult can produce poorer quality feathers (Serra 2001). Feathers have many vital functions, such as flight, insulation and signalling, and feather quality affects all these functions, thus impacting on the bird's chances of survival (Jenni and Winkler 2020a). Changes in the breeding season and a delayed post-breeding moult may also result in time constraints, causing birds to interrupt a moult which they would otherwise complete (Jenni and Winkler 2020a). It is therefore important to monitor species and the activities in their annual cycle. In the case of Silvereye, this includes breeding and moult, with moult being the easiest to monitor and quantify. Monitoring enables researchers to determine what effect climate change is having on the annual cycle and if birds are able to adapt or if conservation measures are appropriate.

Several studies have examined the primary moult of other *Zosterops* species (Table 3). When comparing moult results between studies it is preferable to use ones that used the Underhill and Zucchini (1988) moult model so that differences are due to biology and not analysis method (Dietz et al. 2015). Of the results presented in Table 3, only Hulley et al. (2004) used this model. Despite a latitudinal difference of c. 9° between South African and New Zealand populations, the durations of moult for Silvereyes in New Zealand (74 days) and two species of white-eyes in South Africa (69–78 days) were similar. Excluding the results obtained by Munro et al. (2006), which were based on captive birds with unlimited access to food, other methods of analysis have estimated moult durations between 83 and 90 days for wild white-eyes across a wide range of latitudes (Table 3). We suggest that it is likely that moult durations for *Zosterops* species are similar and independent of latitude (studies cover a latitudinal range of 65°). The timing of primary moult within the annual cycle is variable, adjusted to local conditions and follows breeding, which in turn is related to food availability.

In other genera there is large variability in moult durations, both between and within species, related to latitude, food availability, and migration patterns and distance. This is especially well documented for migrants of the genera *Calidris* and *Charadrius* (Remisiewicz 2011, Jackson and Underhill 2022). The passerine genus with the largest number of analyses using the Underhill-Zucchini moult model is *Ploceus*, with 14 analyses of seven species of weavers from 6°N to 33°S (see Appendix 1 of Chapter 7). Durations range between 67 days for the population of the Southern Masked Weaver *P. velatus* at 33°S (Craig et al. 2001) to 198 days for the Chestnut Weaver *P. rubiginosus* at 19°S (Oschadleus and Osborne 2005). The relatively short and consistent moult durations at different latitudes in the genus *Zosterops* are an apparent contrast to the varied patterns in other genera. This idea needs further investigation and confirmation. These observations emphasise our incomplete knowledge of moult, especially in the tropics and southern hemisphere.

Partial migration and moult

The nominate race of Silvereye *Z. lateralis lateralis* is the subspecies that colonised New Zealand (Oliver 1955, Heather and Robertson 2005) and this subspecies is a partial migrant in south-eastern Australia. In particular, a substantial proportion breed in Tasmania then migrate north to south-eastern continental Australia in winter (Griffioen and Clarke 2002, Chan 2005). In New South Wales, Australia it is an altitudinal migrant (Higgins et al. 2006). Mass movements of Silvereyes in New Zealand have been recorded from mid-April to June (Oliver 1955, Dawson 1961, Grant 1970, Stead 1952 in Dennison et al. 1981, Dennison et al. 1981). The timing of these would coincide with the period shortly after moult but before winter sets in. Flocks of birds have been seen travelling northwards, apparently from the South Island to the North Island (Oliver 1955, Grant 1970, Buller 1888, Dennison et al. 1981). As in Australia, this is a partial migration, because large populations remain on the South Island during winter (Stead 1930 in Fleming 1943, Kikkawa 1962, Grant 1970). Oliver (1955) and St Paul (1975) noted seasonal altitudinal movements with birds gathering in flocks in low-lying populated areas in winter. In contrast, in southern Africa, the Cape White-eye *Zosterops virens* is regarded as sedentary (Symes et al. 2001, Hulley et al. 2004). It is not an altitudinal migrant (Scott 2018, Craig and Hulley 2019), despite it being listed as such by Johnson and Maclean (1994). There are clearly interesting opportunities to study inter-relationships between timing of breeding, moult and movement patterns (partial migrant, altitudinal migrant and resident) between continents in these southernmost representatives of the genus *Zosterops*. Most comparable studies have been made in northern temperate zones (Jenni and Winkler 2020a, 2020b) and data from the temperate zones of the southern hemisphere is a priority (cf. Theuerkauf et al. 2022).

Moult intensity

The concept of moult intensity was introduced and developed by Haukioja (1971) and highlighted by Mumme et al. (2021). Mumme et al. (2021) measured moult intensity by the average number of simultaneously moulting primaries (Figure 4) and Proportion Feather Mass Missing (PFMM) (Figure 5). The relevant discussion point here is whether the gaps in the wings are large enough to impair flight to the extent that the birds become near-flightless and are therefore under-represented in mist-netted samples. One of the assumptions of the Underhill and Zucchini (1988) moult model is that the probability of being captured is independent of the state of moult.

Silvereyes consistently moulted an average of c. 2.9 primaries during moult (Figure 4). This contrasts with, for example, the Laughing Dove *Spilopelia senegalensis*, which tended to moult one or two primaries simultaneously (Chapter 2), but is similar to that of the Wood Sandpiper *Tringa glareola* (Remisiewicz et al. 2009). Both the Laughing Dove and the Wood Sandpiper are able to fly throughout moult. In contrast, Mumme et al. (2021) described the moult of 13 warbler species at 40°N in Pennsylvania, USA, which moulted, on average, between four and five primaries simultaneously through the central part of primary moult. These species were then reluctant to fly. The moult durations for these 13 species were between 39 and 53 days.

PFMM is likely to provide a more sensitive approach to assessing flightlessness than the numbers of simultaneously growing primaries. PFMM was first introduced by Ward et al. (2007) for the Kelp Gull *Larus dominicanus* and there are analyses for few species. PFMM refines the concept of "raggedness" developed by Haukioja (1971). PFMM takes into account the variation in the sizes of the primaries, which raggedness does not. The difference between PFMM and raggedness will get larger as the relative sizes of primaries change. It will reach an extreme with long-distance migrants, for which the outer primary is up to seven times larger than the innermost primary. An example is the Arctic Tern *Sterna paradisea* (Underhill and Joubert 1995).

Opportunities for the study of moult in New Zealand

Latitude plays an important role in determining moult patterns (Jackson and Underhill 2022). With an established community of citizen scientist bird banders, New Zealand has two distinct advantages as a country in which to study moult, both related to latitude. Firstly, it has a sufficient latitudinal range within the country, from 34.4°S to 46.7°S, to enable studies of the variation in timing of moult in relation to this variable. Secondly, its location enables the overall latitudinal range of moult studies to be extended further south than currently available, while at the same time overlapping latitudinally with Australia and Africa. Only South America stretches further south, but it lacks bird banding communities in the far south. Moult studies in New Zealand are therefore vitally important in aiding our understanding of the role latitude plays in moult.

We therefore recommend that the bird banding scheme in New Zealand encourages the routine and ongoing collection of moult data at a latitudinal spread of locations for four reasons: (1) It will help to fill a gap in knowledge because there are few quantitative moult studies in New Zealand prior to this one and Chapters 5 and 6; (2) the geographical configuration of New Zealand provides opportunities for studies along a latitudinal range; (3) the southern geographical location of New Zealand provides important opportunities to understand the timing of moult in relation to climate change; (4) the geographical location combined with a well-developed network of bird banders enables a unique contribution to be made to the global understanding of the biogeographical patterns of moult, breeding and migration.

For the Silvereye in particular, a good body of primary moult data is available for the period 2002 to 2012. A dedicated project to collect further data for this species would have the opportunity of using these historical data as a baseline from which to measure future change. This has been done, for example, by Taylor et al. (2018) for the Dunlin *Calidris alpina* in Alaska. They found a 43% increase in the duration of moult over six decades. Jackson and Underhill (2022) pointed out the need for further studies of this nature.

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Table 1. Relative masses of the nine primary feathers averaged for two adult Silvereyes *Zosterops lateralis*. The birds were roadkills in Hamilton, North Island, in June and July 2007 (Peter G. Ryan *in litt*.)

Primary	P1	P2	P3	P4	P5	P6	P7	P8	P9
Relative mass (%)	8.73	9.23	9.81	10.31	11.29	12.37	12.66	12.84	12.75

Table 2. Estimated moult parameters of the primary feather tract of Silvereyes in New Zealand using the Underhill-Zucchini moult model and PFMG as the moult index. Samples of birds using adult and juvenile age classes were selected and analysed using either data type 2 or data type 5 (see text). The penultimate analysis in the table is a four-parameter model that gave different start dates to adults and juveniles but kept the duration and standard deviation parameters common to both. Day 1 was 1 September.

Age class	Data type	Moult parameter					Sample sizes		
		Duration (SE)	Start day (SE)	Standard deviation of start day (SE)	Start date (SE)	End date (SE)	Pre-moult	In-moult	Post-moult
Adult	2	72.9 (3.9)	148.9 (2.6)	38.8 (2.0)	27 Jan (2.6)	10 Apr (2.7)	162	301	230
Adult	5	83.8 (9.5)	148.5 (3.0)	41.2 (3.5)	27 Jan (3.0)	20 Apr (8.4)	162	301	–
Juvenile	5	116.4 (17.9)	158.4 (3.8)	57.4 (8.0)	5 Feb (3.8)	2 Jun (16.7)	188	224	–
Adults and juveniles, one start date	2	77.8 (3.4)	155.0 (1.8)	39.6 (1.7)	2 Feb (1.8)	21 Apr (2.6)	350	525	230
Adults and juveniles, two start dates	5	95.2 (8.4)	Ad 145.8 (3.2), Juv 160.2 (2.9)	46.6 (3.4)	Ad 24 Jan (3.2), Juv 7 Feb (2.9)	Ad 29 Apr (7.4), Juv 13 May (8.2)	350	525	–
All data	2	74.3 (2.9)	156.4 (1.6)	37.3 (1.5)	3 Feb (1.6)	19 Apr (2.3)	429	605	261

Table 3. Results of moult studies in *Zosterops*. Species are arranged from north to south. Higgins *et al*. (2006) was a resource for moult studies of Silvereyes.

Species	Duration (days)	Latitude	Location	Moult period (estimated start date–end date)	Source
Warbling White-eye (*Z. japonicus*)	90	22.50°N	Hong Kong, China	Jun–Sep (23 Jun–21 Sep)	Melville 1989
Warbling White-eye (*Z. japonicus*)		21.44°N	Oahu, Hawaii	Jul–Oct	Guest 1973, Van Riper and van Balen 2020
Northern Yellow White-eyes (*Z. senegalensis*)	85	10–11°S	Nyika Plateau, Malawi/Zambia	Dec–Mar, peak Jan–Feb	Dowsett and Dowsett-Lemaire 1984
Canary White-eyes (*Z. luteus*)		17.88°S	Broome, Australia	Dec–Apr	Lewis and Macarthur 2011
Silvereye (*Z. lateralis*)		18.15°S	Fiji	Jan–May	Langham 1987
*Orange River White-eye (*Z. pallidus*)	78.0	28.39°S	Free State, South Africa	Feb to Apr/May (30 Jan–19 Apr)	Hulley et al. 2004
Cape White-eye (*Z. virens*)		28.53°S	KwaZulu-Natal, South Africa	Feb–Jun	Craig 1983
Cape White-eye (*Z. virens*)		29.83°S	Pietermaritzburg, KwaZulu-Natal, South Africa	Feb–Jun	Earlé 1981, Symes et al. 2001
*Cape White-eye (*Z. virens*)	76.7	33.31°S	Grahamstown, Eastern Cape, South Africa	Feb–Apr/May (7 Feb–25 Apr)	Hulley et al. 2004
*Cape White-eye (*Z. virens*)	75.5	33.83°S	Durbanville, Western Cape, South Africa	Dec–Mar/Apr (25 Dec–11 Mar)	Hulley et al. 2004
Silvereye (*Z. lateralis*)	83	33.87°S	Five Dock, New South Wales, Australia	Jan–Apr	Swanson 1971

Species	Duration (days)	Latitude	Location	Moult period (estimated start date–end date)	Source
Cape White-eye (*Z. virens*)		34.02°S	Sedgefield, Western Cape, South Africa	Jan–May	Dowsett 1985
**Silvereye (*Z. l. familiaris*)	52.5	34.07°S	Campbelltown, New South Wales, Australia	Jan/Feb–Apr (7 Feb–31 Apr)	Munro et al. 2006
*Cape White-eye (*Z. virens*)	69.7	34.07°S	Rondevlei, Western Cape, South Africa	Jan–Mar/Apr (12 Jan–23 Mar)	Hulley et al. 2004
Cape White-eye (*Z. virens*)		34.13°S	Sir Lowry's Pass, Western Cape, South Africa	Oct–Apr, peak Feb–Mar	Whitelaw 1985
*Cape White-eye (*Z. virens*)	68.9	34.37°S	Betty's Bay, Western Cape, South Africa	Dec/Jan–Mar (9 Jan–19 Mar)	Hulley et al. 2004
Silvereye (*Z. lateralis*)		36.88°S	Rumuera, Aukland, New Zealand	Jan–Mar/Apr	Fleming 1943
Silvereye (*Z. lateralis*)		36.98°S	Victoria, Australia	Jan–Apr	Rogers et al. 1986
*Silvereye (*Z. lateralis*)	74.3	41.70°S	New Zealand	Jan/Feb–Apr (3 Feb–19 Apr)	This study
**Silvereye (*Z. lateralis lateralis*)	49.0	42.53°S	Hobart, Tasmania	Jan–Mar (25 Jan–15 Mar)	Munro et al. 2006

* applied the Underhill-Zucchini moult model.

** captive birds, small sample

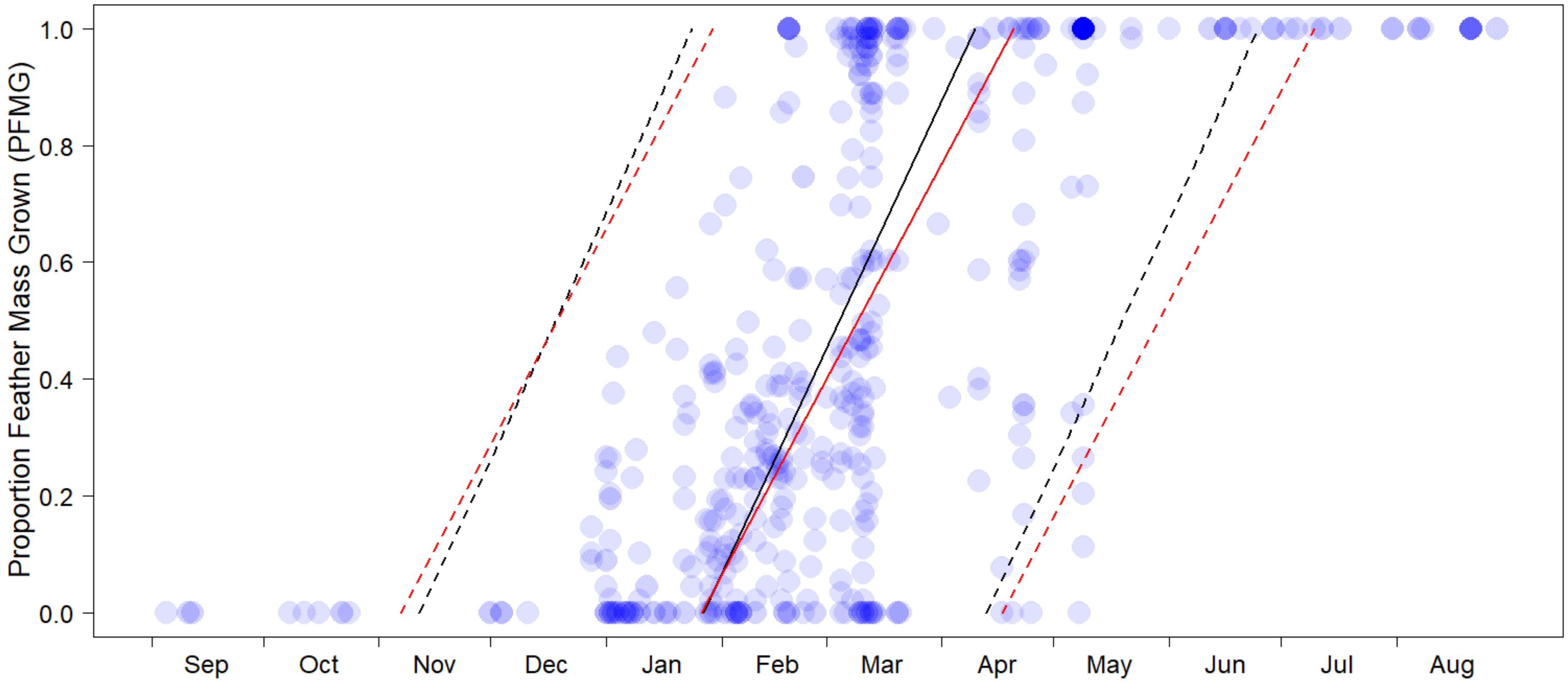

Figure 1. Modified scatter diagram* of the progression of primary moult for adult Silvereyes *Zosterops lateralis* in New Zealand using PFMG as the moult index. The solid straight lines represent the progression of moult for the average adult bird in the population using data type 2 (black line) and data type 5 (red line). The broken lines are the 95% intervals calculated from the standard deviation of the mean start date using data type 2 (black line) and data type 5 (red line).

* Moult scores are recorded on a discrete scale (each primary is allocated an integer score between 0 and 5). A consequence of this is that conventional scatter plots of moult scores in relation to dates are misleading because there is no representation of the number of records represented by a single symbol in the plot. In this modification of the scatter diagram, the data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade refers to one data point and the darkest shade refers to 69 overlapping data points.

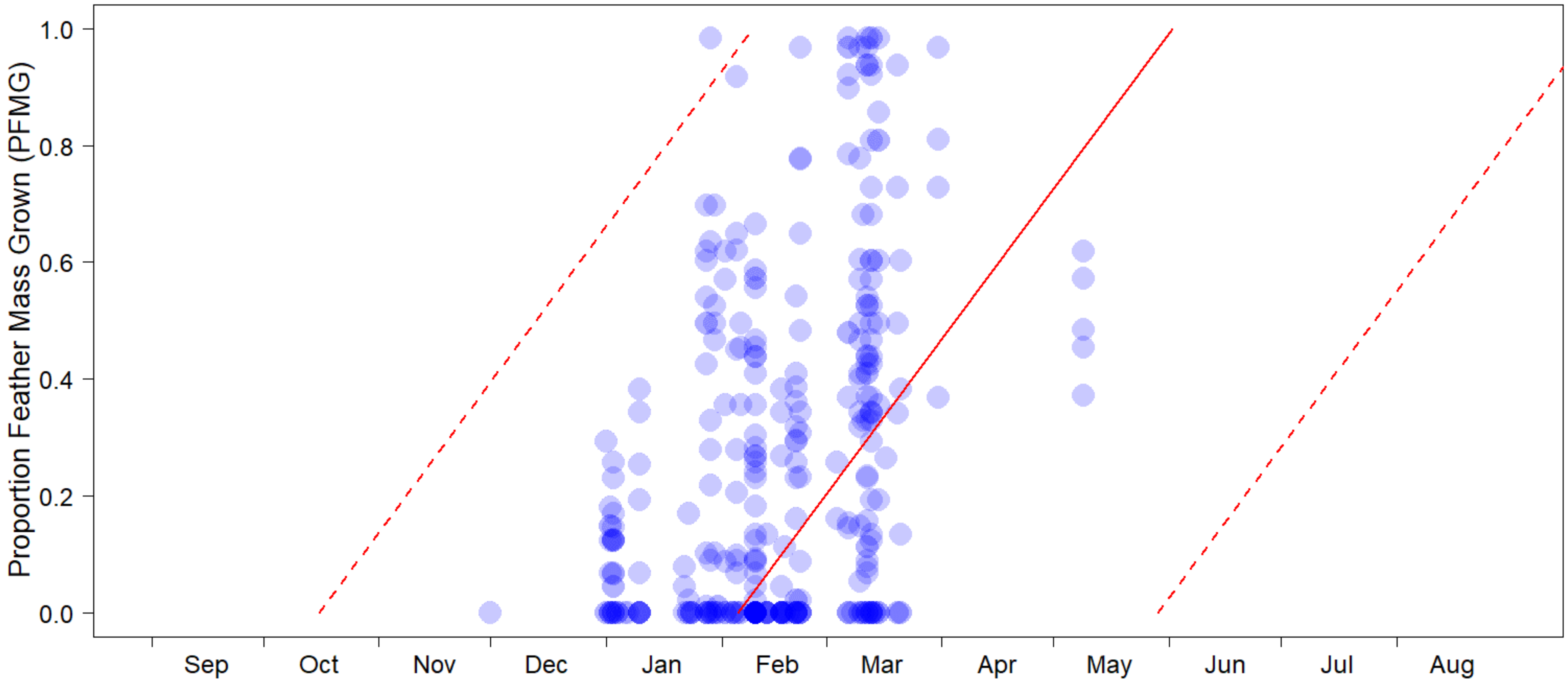

Figure 2. Modified scatter diagram* of the progression of post-juvenile primary moult in Silvereyes *Zosterops lateralis* in New Zealand using PFMG as the moult index and data type 5. The solid straight red line represents the progression of moult for the average juvenile bird in the population. The broken red lines are the 95% intervals calculated from the standard deviation of the mean start date.

* In this modification of the scatter diagram, the data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade refers to one data point and the darkest shade refers to 22 overlapping data points.

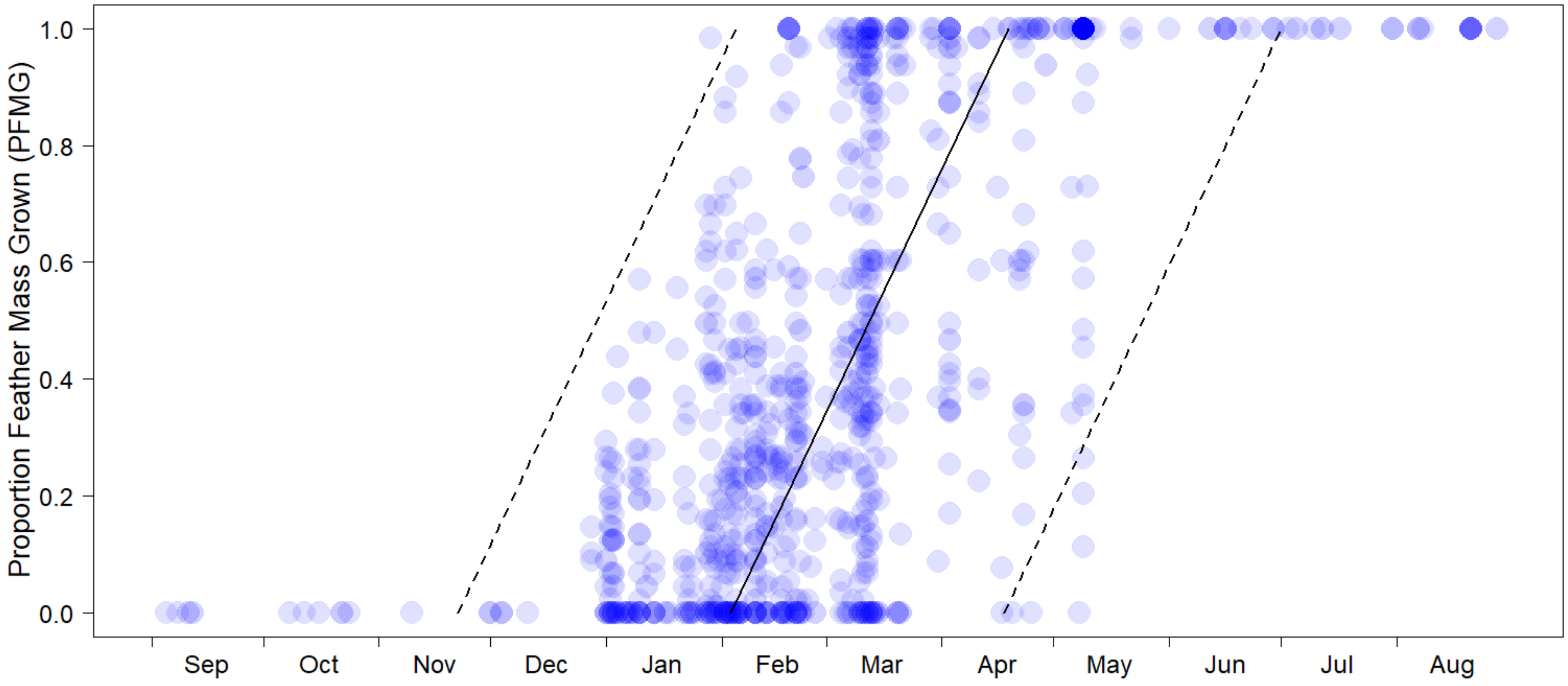

Figure 3. Modified scatter diagram* of the progression of primary moult in Silvereyes *Zosterops lateralis* in New Zealand using all available data (adults, juveniles and unaged birds), PFMG as the moult index and data type 2. The solid straight black line represents the progression of moult for the average juvenile bird in the population. The broken black lines are the 95% intervals caculated from the standard deviation of the mean start date.

* In this modification of the scatter diagram, the data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade refers to one data point and the darkest shade refers to 69 overlapping data points.

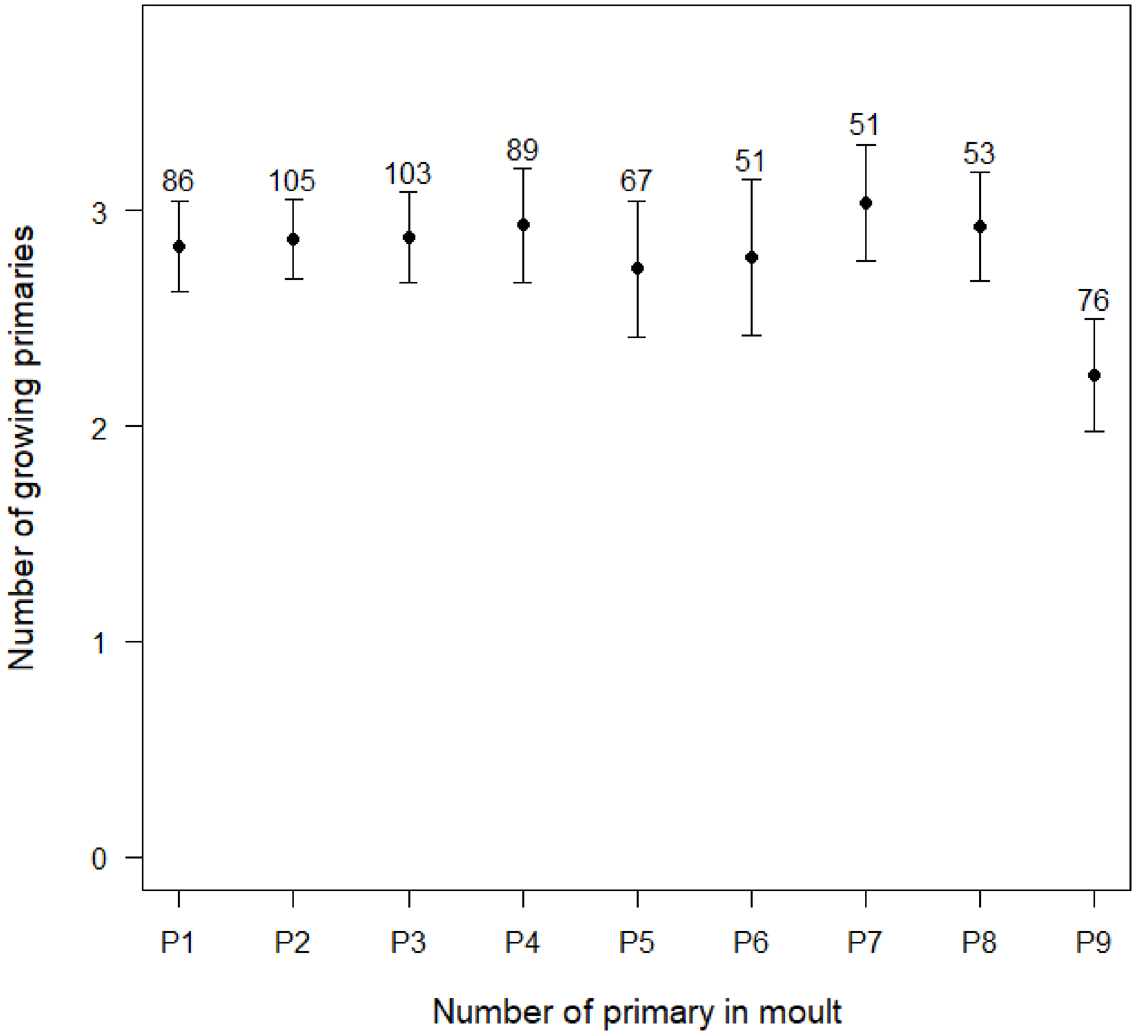

Figure 4. The mean number of primaries growing simultaneously while each of the nine primaries of adult Silvereyes was in moult. The 95% confidence intervals for the mean and the sample sizes are shown.

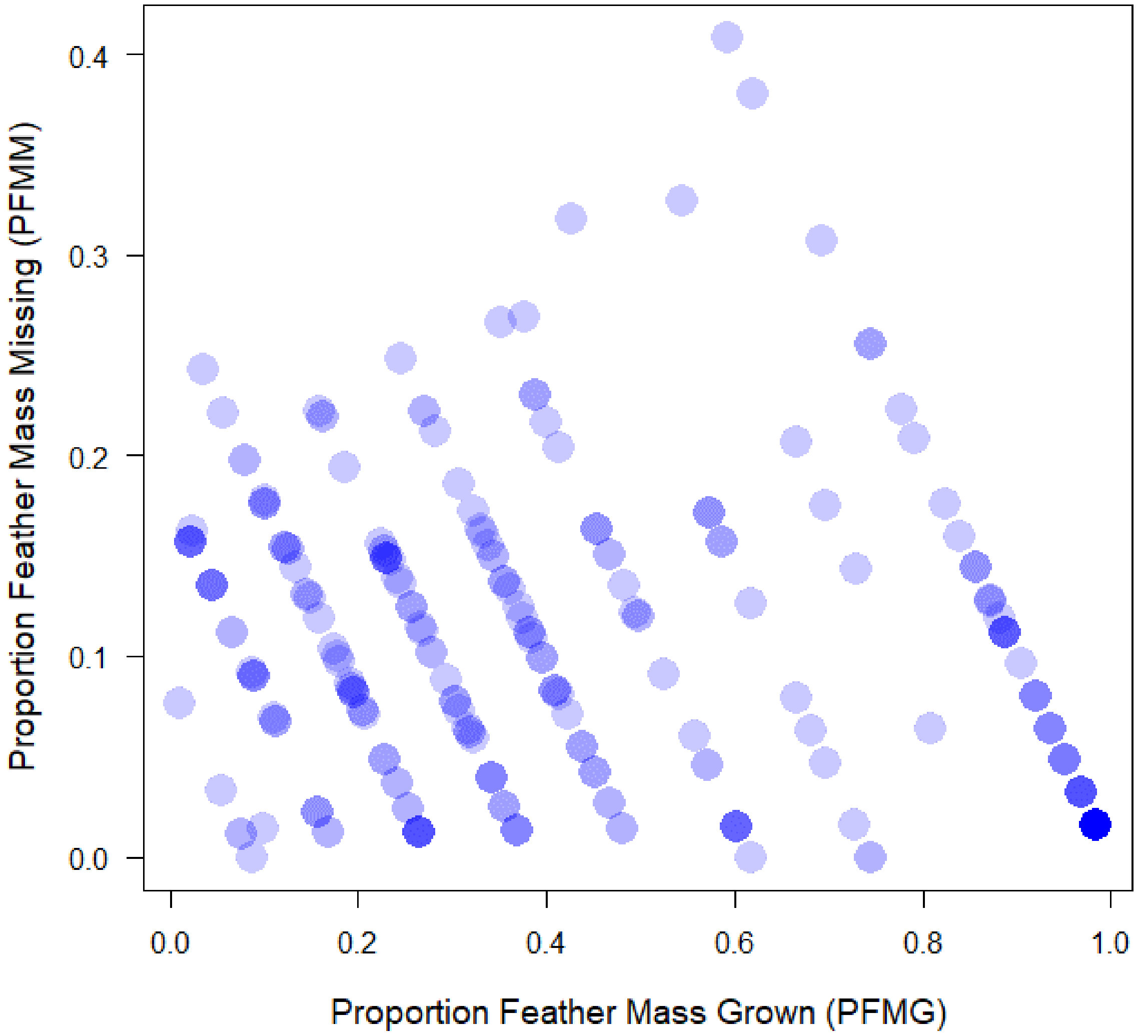

Figure 5. The relationship between Proportion Feather Mass Missing (PFMM) and Proportion Feather Mass Grown (PFMG) is represented by a modified scatter diagram* for adult Silvereyes in active moult. The pattern of parallel lines is an artefact of the protocol for the recording of the moult status of each primary as an integer between 0 and 5. Each point in this scatter diagram can represent multiple records.

* In this modification of the scatter diagram, the data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade refers to one data point and the darkest shade refers to 22 overlapping data points.

CHAPTER 5

Primary moult of Wrybills *Anarhynchus frontalis*

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Primary moult of Wrybills *Anarhynchus frontalis*

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

Keywords: Underhill-Zucchini moult model, plovers, *Charadrius*, Charadriinae, Charadriidae, New Zealand, braided river systems

INTRODUCTION

The Wrybill *Anarhynchus frontalis* is endemic to New Zealand and is unique among birds in having a laterally curved bill (Marchant and Higgins 1993, Conklin et al. 2019). Its IUCN threat classification is Vulnerable (BirdLife International 2022). It breeds during the austral spring and early summer on the braided river systems east of the Southern Alps on the South Island, between 43°S and 45°S (Heather and Robertson 2005). During the breeding season the curved bill is an adaptation for probing for insect larvae, mainly the larvae of mayflies *Deleatidium* spp., under stones in riffles (Pierce 1979). From midsummer it migrates north to non-breeding areas in the northern part of the North Island, especially to the large tidal bays, locally known as "harbours", east and west of Auckland (Riegen and Dowding 2003). In the non-breeding period the bill is used like a scythe, reminiscent of avocets (Turbott 1970, Conklin et al. 2019). Southward migration to the breeding areas takes place in August, during the late austral winter. The distance between the breeding and non-breeding areas averages c. 800 km. At an average flight speed of 65 km/hour for small plovers (Zwarts et al. 1990), the flying time between breeding and non-breeding areas is therefore c. 12 hours. Most Wrybills make the northward journey non-stop but some stop along the way for brief periods (Dowding and Moore 2006). Intermediate staging sites during the northward migration include sites along the east coast of South Island, particularly Lake Ellesmere (43.79°S, 172.50°E), and occasionally Farewell Spit (40.52°S, 172.87°E) in the northern part of South Island (Dowding and Moore 2006). On the return southward migration, it is unclear whether any Wrybills fly directly to their breeding grounds. Many migrate south via the estuaries on the east coast of South Island where they have brief stopovers (Dowding and Moore 2006).

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

The objective of this chapter is to estimate the timing of primary moult of Wrybills, using a larger sample than was available to Davies (1997) and using the moult model of Underhill and Zucchini (1988). We consider how moult fits into the annual cycle. Taxonomically, the Wrybill is placed in the monotypic genus *Anarhynchus*, but it is closely related to the genus *Charadrius* (Burton 1972, Conklin et al. 2019). We therefore compare the timing of moult of the Wrybill with that of species in the genus *Charadrius* for which estimates of timing and duration of moult obtained using the Underhill-Zucchini moult model are available. We also compare it with the timing of moult for other Charadrii which breed in the South Island in the austral spring and early summer and migrate to the North Island for the non-breeding season.

METHODS

Data collection

From the mid-1980s to early 2000s more than 500 Wrybill were caught at Jordan's Farm on the shores of the Kaipara Harbour, northwest of Auckland (36.57°S 174. 42°E). From 1991 to 2021 almost 7000 were caught on the western shores of the Firth of Thames (37.15°S 175.31°E). Both these locations were non-breeding sites. Small numbers were mist-netted at night, usually when targeting other species, and the rest were caught using cannon nets at high tide roosts particularly on shelly beaches. When large catches were made during cannon netting, processing was speeded up by ringing and releasing birds not in moult. Mensural data and primary moult details were obtained only for the birds which were actively moulting. Birds were aged as juveniles, second-year birds and adults. Juveniles show uniformly even fresh plumage on the non-breeding grounds, have more hints of pale brown and lack the black breast band.

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

Data analysis

For the conversion of moult score to Proportion Feather Mass Grown (PFMG), primary feather mass data were needed. Since feather mass data were unavailable for Wrybill, the averages of the relative masses of each of the 10 primaries of seven species in the closely related genus *Charadrius* were calculated (Table 1). Within the genus *Charadrius* there was little variation in the relative feather masses. These masses were used in the conversion of moult scores to PFMG. The date the bird was netted was recorded as the number of days since 1 August. Primary moult of adult and second-year Wrybills was modelled separately for the two age classes according to the Underhill and Zucchini (1988) moult model with PFMG as the moult index. The parameters of moult (duration, mean start date and standard deviation of mean start date) and their standard errors were estimated using the package “moult” (Erni et al. 2013) in R (R Core Team 2019). Data type 3 was used because moult score was mainly recorded for birds in active moult. It was estimated that 95% of birds start moult in the period given by the estimated mean start date ± 1.96 × estimated standard deviation parameter.

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

Terminology for seasonality

Unless otherwise stated, seasons are austral. When we compare the timing of breeding and primary moult between species in the southern and northern hemispheres, we make the comparison in terms of days since the midsummer solstice (20 December in the southern hemisphere, and 21 June in the northern). This approach brings the hemispheres into alignment.

RESULTS

During the sampling period, moult data was recorded for 2410 adult and second-year Wrybills captured during ringing operations on the shores of Kaipara Harbour and Firth of Thames.

There were 1999 moult records for adult Wrybills: 2% (37) had all old primaries, 87% (1737) were actively growing new primaries and 11% (225) had all new primaries (Table 2, Figure 1). Using data type 3 of the moult model, the primary moult of the average adult bird in the population was estimated to start on 20 January (standard error 1.0 days) and end on 3 April (standard error 1.0 days). The duration was estimated to be 73 days (standard error 1.9 days). The standard deviation of the start date was 13 days (Table 2, Figure 1). Consequently, the period during which 95% of the adult Wrybill population started moult was estimated to be 51 days, between 26 December and 15 February (Figure 1). Likewise, the interval during which 95% of Wrybills were expected to complete moult was 9 March to 29 April. There were four adult Wrybills (0.2% of adults in active moult) that had moult scores that suggested possible suspended moult (5550000000 on 14 January and 26 January, 5555550000 on 29 January and 5555555000 on 2 March). These moult scores all lie within the 95% confidence intervals of the mean moult line in the scatter diagram in Figure 1. It is also possible that within the natural variation of the number of actively moulting primaries a small proportion of the population could have moult scores such as these and therefore they were included in the analysis. When the four moult records are excluded from the analysis, the estimated duration decreases by 0.1 days, the mean start date increases by 0.1 days and the standard deviation of the start date remains the same. Therefore, including or excluding these four points has no biological impact.

There were 434 moult records for second-year Wrybills, of which 57% (247) had all old primaries, 37% (159) were actively moulting their primaries and 6% (28) had all new primaries (Table 2, Figure 2). Using only the records of active moult in the moult model (data type 3), the duration of primary moult in second-year Wrybills was 128 days (standard error 33.6 days) with a mean start date of 18 December (standard error 15.3 days) and an end date of 26 April (standard error 21.3 days). The standard deviation of the start date was 39 days (Figure 2).

There were insufficient data to fit the Underhill-Zucchini moult model to first-year Wrybills (a total of 10 records of birds in active primary moult).

Wrybills underwent a complete, continuous moult starting with the innermost primary (P1) and ending with the outermost (P10). Adult Wrybills initially moulted several inner primaries concurrently and then fewer as the longer, heavier outer primaries are grown. During the replacement of the first four primaries (P1 to P4), there was an average of 3.5 feathers growing simultaneously (Figure 3). This decreased to 3.1 and 2.7 for the P5 and P6 respectively and further decreased to an average of 2.1 for P7 to P9 (Figure 3). There were the fewest concurrently growing primaries, 1.6, during the moult of P10 (Figure 3). The mean size of the gap in primary feathers during primary moult was 0.126 (SD = 0.056) (Figure 4). This means that on average birds in active moult were missing 13% of their primary feather mass. The largest wing gap recorded was 0.384 for a bird moulting five of its 10 primary feathers simultaneously (moult formula 5555543122 on 27 February) (Figure 4). The correlation between PFMG and PFMM was −0.123, so that PFMG explained 1.5% of the variability of PFMM.

DISCUSSION

Primary moult in relation to the annual cycle of Wrybills

Adult Wrybills breed between late August and January on the shingle riverbeds of braided rivers in Canterbury and inland Otago, South Island (Heather and Robertson 2005). They typically lay two eggs per clutch and often have two clutches in one season (Marchant and Higgins 1993). First clutches are laid from late August and second clutches from late October to late December (Hay 1984). If the first clutch is lost, a replacement clutch is laid (Marchant and Higgins 1993). Adult Wrybills migrate northwards after breeding to winter in the large harbours and bays around Auckland on the North Island (Marchant and Higgins 1993, Davies 1997). They start arriving from the last week of December and their numbers quickly increase during January (Davies 1997). Juveniles hatched early in the season and non-breeding birds (second-year birds and failed breeders) migrate north earlier than the rest of the breeding population (Davies 1997). The majority of the population spends the non-breeding season in the Firth of Thames and Manukau Harbour north of 38°S, while a small proportion remains on the South Island (Davies 1997, Dowding and Moore 2006, Riegen and Sagar 2020). Adult Wrybills undergo a complete pre-basic post-breeding moult and start moulting their primaries soon after arriving on the North Island. Primary moult occurs on average between 20 January and 3 April. Second-year birds also undergo a complete moult starting in December, one month earlier than the adults, but finishing at approximately the same time. Both adults and second years appear to avoid moulting during the winter months, although these are relatively mild along the coastline of northern North Island. Adult wrybills generally depart the North Island and return south to their breeding grounds in August (Marchant and Higgins 1993). About half of the first-year birds return south to the breeding grounds, but do not breed, about a month after the adult departure, while the rest remain in the North Island (Davies 1997, Heather and Robertson 2005). Lowest numbers of Wrybill in the North Island occur from mid-November to late December.

The estimated mean start and end dates of primary moult in second-year Wrybills were 18 December and 26 April respectively, and the estimated duration was 128 days, all with relatively large standard errors (Table 2). The large standard errors can be attributed to small sample size and the lack of moult records late in the moult period (Figure 2). This in turn is related to the fact that second-year birds are not easily distinguished from adults once they are moulting their outer primaries (Davies 1997). Because most of the data are focused on the first half of the moult period, the estimated mean starting date of moult in second-year Wrybills is likely to be reliable. It is also likely that adults and second-years complete moult around the same time. However, the timing of primary moult of second-year Wrybills needs further investigation.

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

Moult of the Wrybill in relation to other species

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

Primary moult is the only activity in the annual cycle for which quantitative estimates are available for these waders (Rogers et al. 2014, Yang et al. 2020, Jackson and Underhill 2022, Table 2); the timing of breeding is more descriptive in nature, summarised by months (Marchant and Higgins 1993, Del Hoyo et al. 1996) (Figure 5). Based on the periods of moult estimated using the Underhill-Zucchini analyses and the described egg-laying periods for each species, four patterns are evident in Figure 5. Firstly, Wrybill breed in spring/early summer, migrate a short distance north and then undergo a fast primary moult (73 days) in late summer/early autumn. Due to the fast moult, Wrybills are able to separate breeding and moult and avoid moulting in winter. Secondly, the Hooded Dotterel undergoes a slow primary moult (203 days), so that it is energetically less expensive (Rogers et al. 2014). This enables the birds to breed and moult at the same time from spring to autumn and still avoid the winter period (Rogers et al. 2014). Thirdly, Greater Sand Plover, Lesser Sand Plover and Grey Plover breed over a short period on their northern hemisphere Palearctic breeding grounds in late spring/early-to-midsummer, and then migrate southwards to their wintering grounds, mostly on coastlines of the Indian and Atlantic Oceans, where they moult at variable rates (76–155 days) (Serra and Rusticali 1998, Serra et al. 1999, Balachandran et al. 2000, Minton and Serra 2001, Pearson et al. 2002, Serra et al. 2006, Jackson 2017, Yang et al. 2020, Jackson and Underhill 2022). Those that migrate a short distance and have northerly non-breeding grounds with harsh winters undertake a rapid primary moult, mainly in autumn, to avoid winter. Those that migrate further south to warmer wintering grounds with more benign climates in the southern hemisphere prolong moult through their non-breeding wintering period which occurs during the austral summer. Following moult, they migrate north back to the breeding grounds. Greater Sand Plover experiences warmer conditions on their breeding grounds than Lesser Plovers and Grey

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[1] Wei et al. (2022) proposed splitting Lesser Sand Plover *Charadrius mongolus* into two species: Siberian Sand Plover *C. mongolus* and Tibetan Sand Plover *C. atrifrons*. This proposal is currently under discussion (Gill et al. 2022).

Plovers and subsequently have an earlier breeding season. They also arrive in and depart from their breeding and wintering grounds earlier (Jackson 2017, Jackson and Underhill 2022).

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

Wrybills breed in spring through to early summer, whereas plovers breeding in the northern hemisphere (e.g. Greater Sand Plover, Lesser Sand Plover, Grey Plover) have shorter, more compact breeding seasons in early summer. Wrybill moult in late summer-early autumn, after its short-distance migration, as opposed to autumn through to winter in the northern-breeding plovers, which schedule moult differently in relation to their migration distance (Figure 5).

There are four other waders in New Zealand that, similar to Wrybill, have populations breeding in South Island that migrate to North Island where they spend the non-breeding season. However, not all individuals of each species breed on South Island and not all migrate north. The four waders are the South Island Pied Oystercatcher *Haematopus finschi*, Banded Dotterel *Charadrius bicinctus*, Pied Stilt *Himantopus leucocephalus* and Black Stilt *Himantopus novaezelandiae*.

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

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

The Pied Stilt is a common wader in New Zealand and usually breeds in colonies on riverbeds, lake shores and damp ground near water (Heather and Robertson 2005, Adams 2013). The breeding season extends from July to January (Heather and Robertson 2005) with egg-laying peaking August to October in lowland areas and October to November inland (Heather and Robertson 2005). After breeding, the stilts which breed on the riverbeds and ephemeral wetlands in southern North Island and South Island move to coastal locations between December and February and those in inland southern South Island migrate northwards to harbours in northern North Island (Heather and Robertson 2005). Birds breeding in coastal areas on both islands and those breeding in northern North Island do not usually migrate. Adults undergo a complete post-breeding moult which takes place between mid-December and early April. Most individuals are moulting their wing feathers by mid-January with primary feathers being the last feathers to be replaced (Pierce 1982). Pied Stilts return to lowland breeding grounds in June to July and inland breeding grounds August to October (Heather and Robertson 2005).

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

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

Suggestions for further research

This is the first quantitative moult study of a migratory wader which breeds in the southern hemisphere and migrates northwards within the same hemisphere after breeding. The Wrybill can be characterised by two features: Its breeding habitat becomes uninhabitable after the breeding season and it also migrates a relatively short distance, so that it spends the non-breeding season in winter. There is potential for several comparisons: (1) With the other waders breeding in the braided rivers of New Zealand; (2) with waders in southern South America, which migrate northwards after breeding (such as the Magellanic Oystercatcher); and (3) with populations of some short-distance migratory waders in the northern hemisphere (such as the population of Purple Sandpipers *Calidris maritima*, which migrates from Norway to Scotland (Summers et al. 2004)).

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

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

Table 2. Estimated moult parameters of the primary feather tract of Wrybills using data type 3 and PFMG as the moult index. Day 1 was 1 August.

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

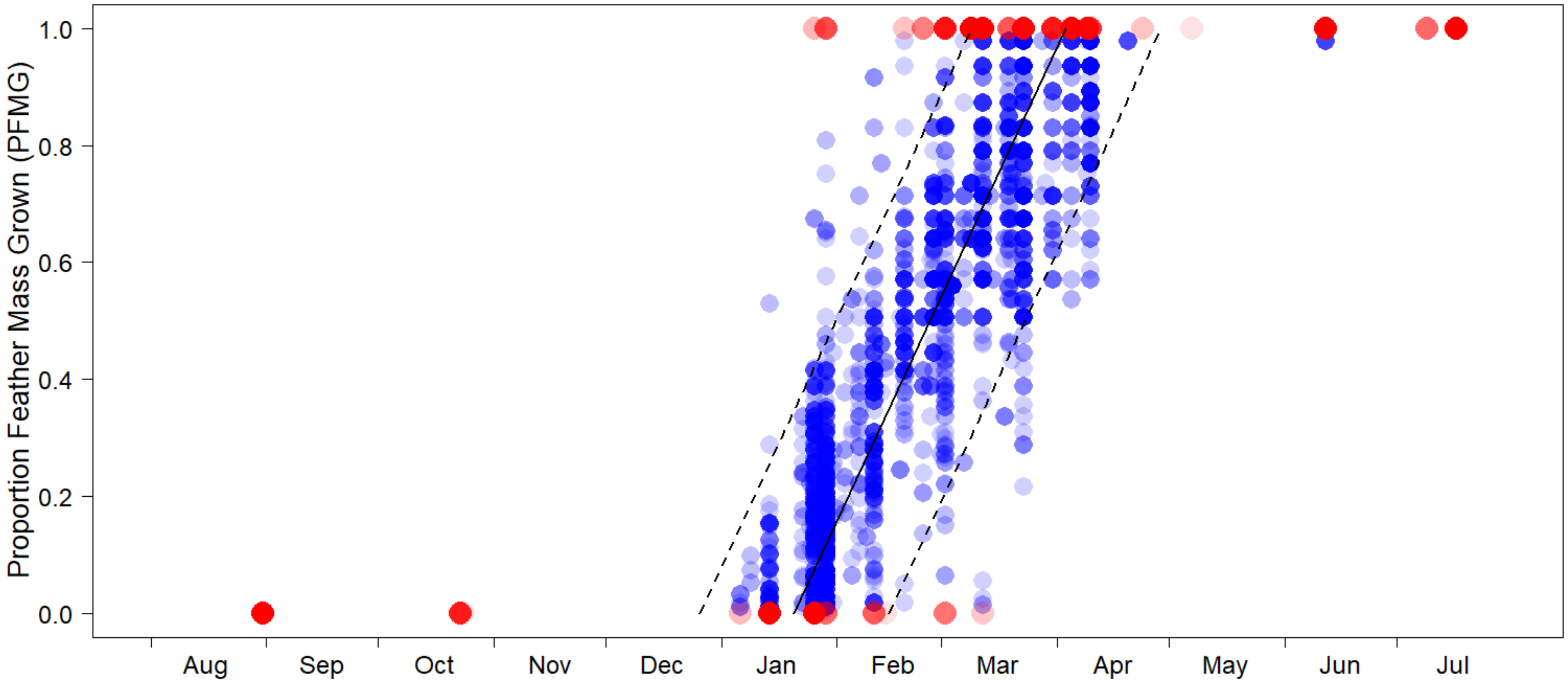

Figure 1. Modified scatter diagram* of PFMG for adult Wrybills. The solid line links the estimated start date with the estimated end date using PFMG as the moult index and data type 3. It shows the progression of primary moult for the average adult bird in the population. The dashed lines are the 95%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

* Moult scores are recorded on a discrete scale (each primary is given an integer score between 0 and 5). A consequence of this is that conventional scatter plots of moult scores in relation to dates are misleading because there is no representation of the number of records represented by a single symbol in the plot. In this modification of the scatter diagram, the data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade of blue and red refers to one data point, the darkest shade of blue refers to 31 overlapping data points and the darkest shade of red refers to 73 overlapping data points.

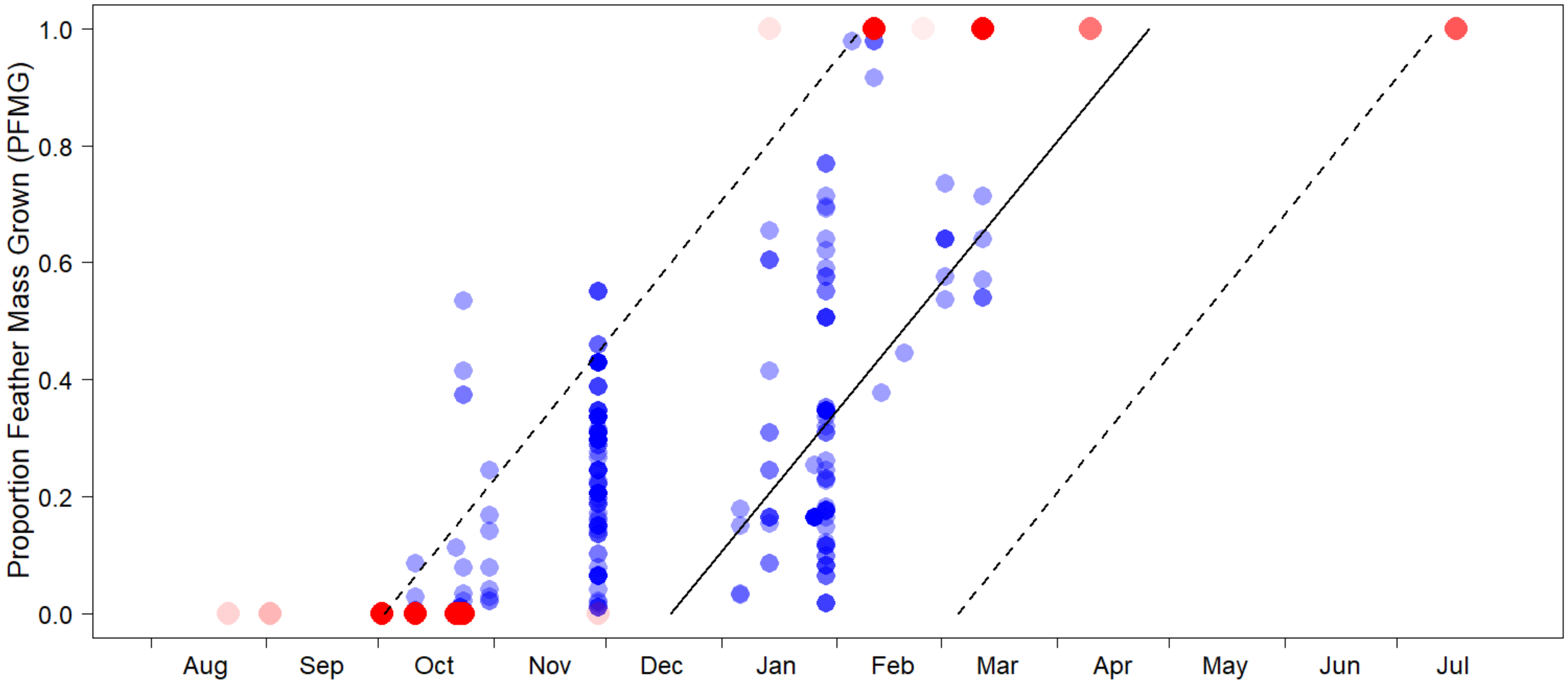

Figure 2. Modified scatter diagram* of PFMG for second-year Wrybills. The straight line links the estimated start date with the estimated end date using PFMG as the moult index and data type 3. It shows the progression of primary moult for the average second-year bird in the population. The dashed lines are the 95% intervals derived from the standard deviation of the mean start date and the parallelogram enclosed by them should contain 95% of second-year birds in active moult. The data points in blue are the birds in active primary moult which were used to estimate the parameters of the moult model. The red data points are pre- and post-moult birds that were not used in the model.

* In this modification of the scatter diagram, the data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade of blue and red refers to one data point, the darkest shade of blue refers to 7 overlapping data points and the darkest shade of red refers to 181 overlapping data points.

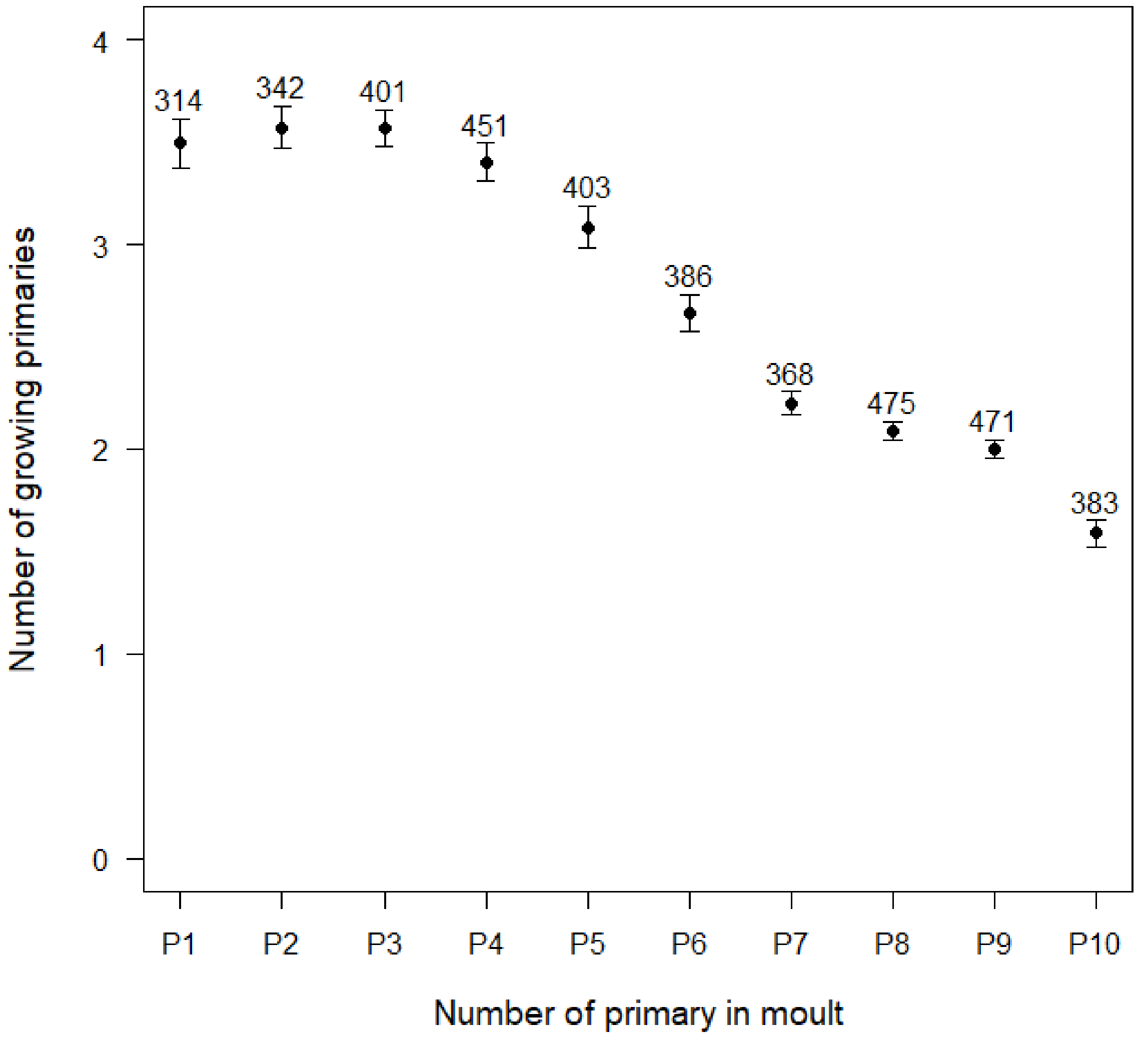

Figure 3. The mean number of primaries growing simultaneously while each of the 10 primaries of adult Wrybills was in moult. The 95% confidence intervals for the mean and the sample sizes are shown.

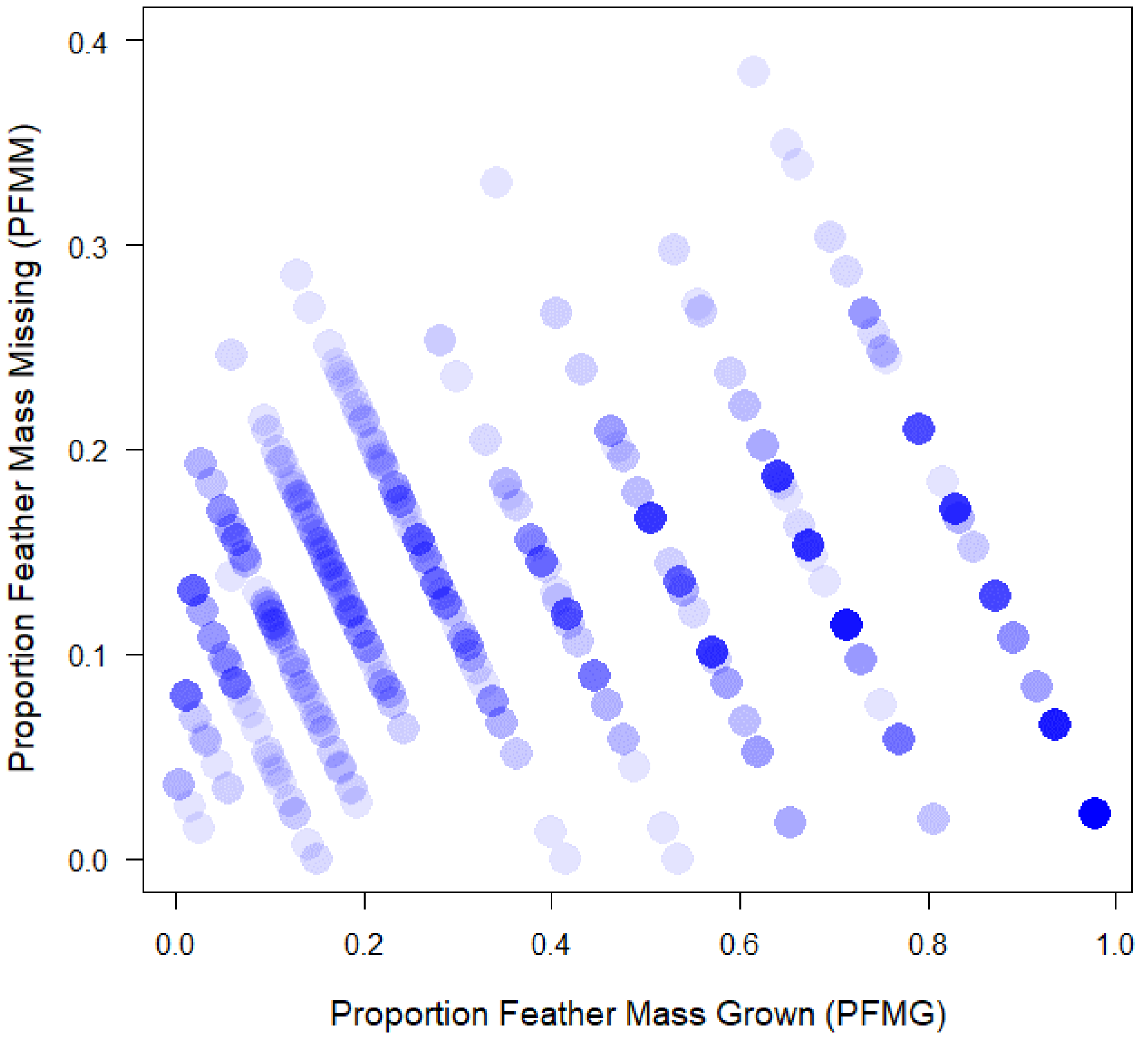

Figure 4. The relationship between Proportion Feather Mass Missing (PFMM) and Proportion Feather Mass Grown (PFMG) is shown by a modified scatter diagram* for adult Wrybills in active moult. The pattern of parallel lines occurs as a result of the in-field method used by bird ringers for recording primary moult scores as an integer between 0 and 5. Each point in this scatter diagram can represent multiple records.

* In this modification of the scatter diagram, the data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade refers to one data point and the darkest shade refers to 90 overlapping data points.

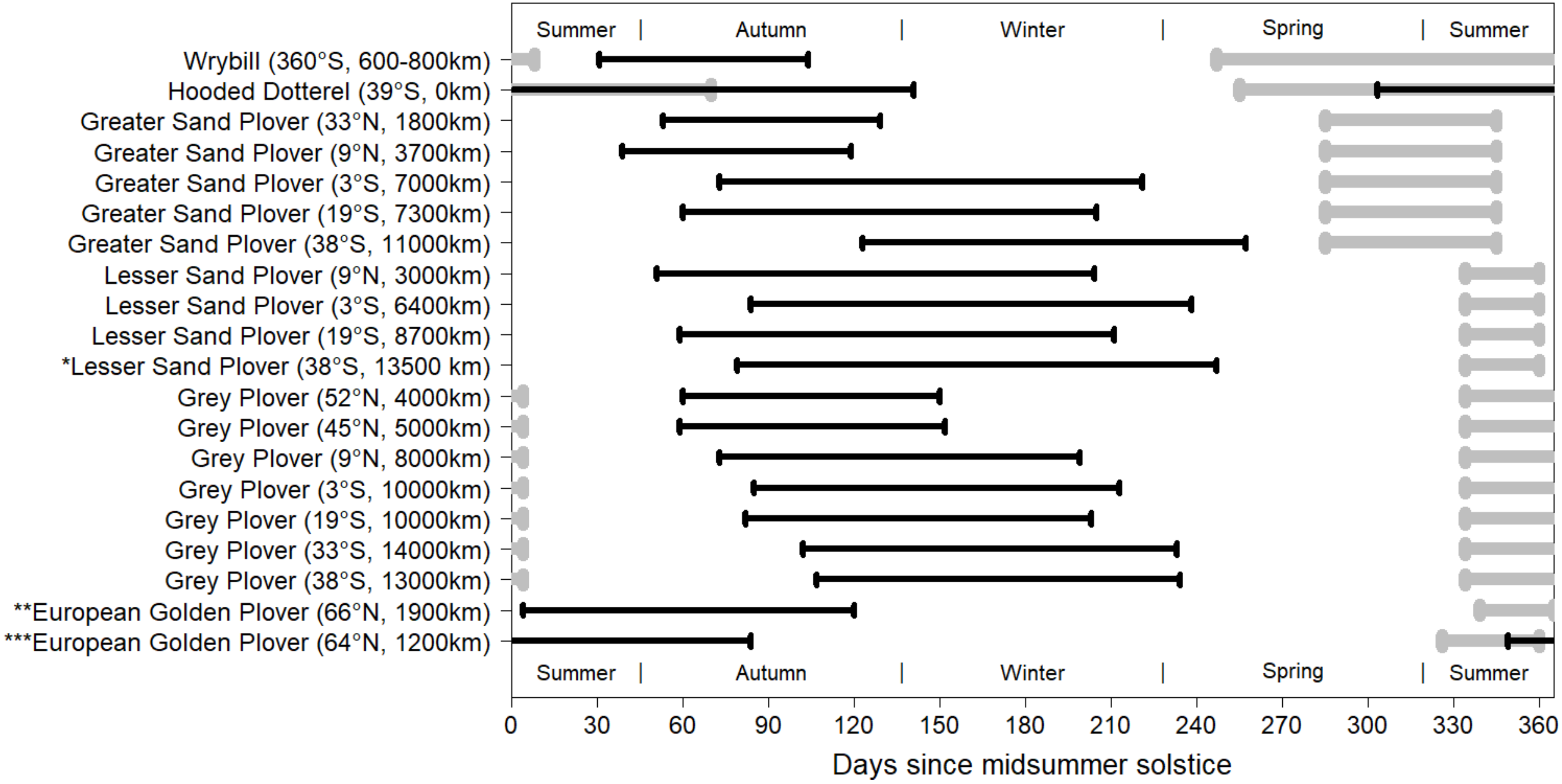

Figure 5. Representation of the relationship between the timing of breeding (grey bars) and the timing of moult (black bars) for 20 studies of six species in the subfamily Charadriinae. The species common name is followed by (a) the latitude at which moult took place and (b) the distance between the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

*Lesser Sand Plover (38N) estimated primary moult duration was considered unreliable by Jackson (2017).
**Starts primary moult on breeding grounds, then migrates to non-breeding grounds to complete moult.
***Starts and completes primary moult on breeding grounds, then migrates to non-breeding grounds.

CHAPTER 6

Primary moult of passerines introduced to New Zealand from source populations in the United Kingdom

Chapter 6

Primary moult of passerines introduced to New Zealand from source populations in the United Kingdom

Abstract: There have been numerous bird introductions worldwide throughout history, where birds have been taken from their natural range and introduced into new locations. Studies of introduced species are limited and tend to focus on their status as pests. There is minimal information on the moult patterns of resident species in their original range and in locations where they have been introduced, especially where they are in different hemispheres separated by c. 90 degrees of latitude. Of New Zealand's 429 bird species, 35 were introduced, mostly from the United Kingdom in the 1860s. We compared the primary moult of seven common passerine species in New Zealand with the same species in the United Kingdom, from where they originated. We are interested in how the change of hemispheres and 160 years of elapsed time since introduction have affected their moult patterns. The parameters of primary moult (duration, mean start date and standard deviation of mean start date) were estimated using the Underhill-Zucchini moult model. If the timing of moult relative to the summer solstice is the same in both hemispheres, the start dates of moult ought to differ by half a year. The timing of moult in the two locations relative to the summer solstice was the same for five of the seven species, meaning that they had shifted moult by half a year following introduction to the southern hemisphere. The other two species started moult nine and three days later relative to the summer solstice in New Zealand. There was no significant difference in moult duration between the two populations for four of the seven species. Two species had slightly shorter durations and one had a longer duration in New Zealand. Given the flexibility in the timing of moult, and how readily it adapts to local conditions, these are unexpected results. The findings of this study appear to suggest that, apart from the anticipated half-year shift in timing due to the change in hemispheres, these species made minor adjustments to their moult parameters. This is possibly due to the fact that both the source area of these seven species, the United Kingdom, and the release area, New Zealand, are in the same Köppen-Geiger climate classification zone. This similarity in climate might help explain why these species, and many others, were so successful when introduced to New Zealand.

Keywords: Underhill-Zucchini moult model, bird introductions, Common Chaffinch *Fringilla coelebs*, Dunnock *Prunella modularis*, European Goldfinch *Carduelis carduelis*, European Greenfinch *Chloris chloris*, House Sparrow *Passer domesticus*, Common Redpoll *Acanthis flammea*, Yellowhammer *Emberiza citronella*, Köppen-Geiger climate classification zone

INTRODUCTION

Moult is an important part of the annual cycle in birds. Research on the topic is lacking when compared to breeding and migration, thereby limiting our understanding of this vital process (Jenni and Winkler 2020a, 2020b). The lack of standardised approaches to the analysis of primary moult have hindered comparative studies in this field. The Underhill-Zucchini moult model provides such a standardised statistical approach to quantifying moult. There have been primary moult studies on populations of a single species at two or more locations over a wide range of latitudes for 28 species, 15 resident and 13 migrant, using the Underhill-Zucchini moult model (Table 1). These have demonstrated that moult strategies are flexible and that the timing and duration of moult are adapted to local conditions. Of the studies relating to resident species, only the studies of Cooper and Underhill 1991 and Rothery et al. 2001 (Common Starling *Sturnus vulgaris*) cover populations that are separated by a large latitudinal range (52°N (England) to 33°S (South Africa)). The rest have a maximum latitudinal range of 1°–10° between study sites. Cooper and Underhill 1991 and Rothery et al. 2001 are also the only studies that compare the moult patterns of an introduced resident species in its original range (England) versus introduced range (South Africa). Apart from this, there are no other studies comparing moult in introduced resident species where the original range and the introduced range are in separate hemispheres separated by c. 90 degrees of latitude. When populations of the same species are separated by such a large degree of latitude, we expect there might be a difference in moult patterns between these two populations due to differences in climatic, environmental and/or ecological conditions.

New Zealand currently has a total of 429 bird species, of which 35 are species that have been introduced by humans and have established self-sustaining populations in the region (Robertson et al. 2021). Most of these introduced species were obtained from source populations in the United Kingdom (55.38°N, 3.44°W) (Duncan 1997, Green 1997) and were released in New Zealand (40.90°S, 174.89°E) by European settlers around the 1860s, when “acclimatisation societies” were formed (Thomson 1922).

The goal of this chapter is to compare primary moult of European passerines introduced to New Zealand with birds of the same species in United Kingdom populations from where they originated. We are interested in how the change of hemispheres and 160 years of elapsed time since introduction have affected their moult patterns. We aim to investigate whether the timing of moult relative to the summer solstice is the same in both hemispheres and whether the duration of moult differs between the two populations.

METHODS

Seven common and widely-spread introduced passerine species in New Zealand were chosen for this investigation: Common Chaffinch *Fringilla coelebs*, Dunnock *Prunella modularis*, European Goldfinch *Carduelis carduelis*, European Greenfinch *Chloris chloris*, House Sparrow *Passer domesticus*, Common Redpoll *Acanthis flammea* and Yellowhammer *Emberiza citronella*. The choice was based on data availability. The taxonomy of redpolls has been in flux for several decades (e.g. Knox 1988, Fennell et al. 1985, Knox et al. 2001, Funk et al. 2021) and the official bird checklist committees of New Zealand and the United Kingdom have taken different viewpoints. The taxon of redpolls breeding in the United Kingdom are regarded as *Acanthis cabaret*. The New Zealand checklist committee did not accept this decision and retained *Acanthis flammea* (Colin Miskelly *in litt.*). There is no doubt that the source of the birds introduced to New Zealand were from the form now known as *Acanthis cabaret* in the United Kingdom (Robert Prŷs-Jones *in litt.*).

Primary moult data for each of the seven introduced European species in New Zealand were obtained from the New Zealand Moult Record Scheme and the New Zealand National Bird Banding Scheme. Moult data for United Kingdom populations of these same seven species were obtained from the British Trust for Ornithology. The datasets for each of the seven species from the two locations were combined and only adults were considered in the analyses.

The moult stage of the primary feathers of one wing was recorded as a moult formula consisting of a sequence of nine digits, one digit (moult score) for each primary, 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 intermediate stages of growth.

Proportion feather mass grown (PFMG), as defined by Underhill and Summers (1993) was used as the moult index. Moult scores observed were transformed into Proportion Feather Mass Grown, using the mean relative masses of the nine primary feathers obtained for five of the seven species: Common Chaffinch, European Goldfinch, European Greenfinch, House Sparrow and Yellowhammer (Table 2). For Dunnock and Common Redpoll, the recommendation of Bonnevie (2010) was followed and the index of relative feather mass constructed for passerines was used (Table 2). Bonnevie (2010) found that this feather mass index gives similar estimates for the parameters of moult to those parameter estimates obtained using known species-specific feather masses.

For each of the seven species, the Underhill-Zucchini moult model (Underhill and Zucchini 1988) was implemented in R (v. 3.6.2) (R Core Team 2019) using the package 'moult' which facilitates standard model selection procedures (Erni et al. 2013). PFMG was used as the moult index. "Location" (New Zealand or United Kingdom) was added as a binary covariate in the analysis. The parameters of primary moult (duration, mean start date and standard deviation of mean start date) were estimated allowing none, one, two or three of the moult parameters to vary according to location. We selected the best model using log-likelihood ratios within Erni et al. (2013). Because of the number of species being dealt with, we do not show the details of the model selection procedure. Additionally, we estimated that 95% of birds start moult in the period given by the estimated mean start date ± 1.96 × estimated standard deviation parameter. Data type 2 was used which uses data that classifies birds as either pre-moult (moult index = 0), post-moult (moult index = 1) or in-moult ($0 <$ moult index < 1). Birds actively moulting are assigned a moult index ranging between zero and one exclusive, based on the stage of moult of individual primaries. Data type 2 assumes that all birds had equal probability of capture on each sampling occasion regardless of their moult stage (Underhill and Zucchini 1988).

PFMG was plotted against date for each of the seven species with data from New Zealand (blue data points) and the United Kingdom (red data points) on the same set of axes.

If the timing of moult relative to the summer solstice is the same in both hemispheres (taken as 22 December in the south, and 21 June in the north), the difference between the start date of moult in New Zealand and the United Kingdom ought to be 182.5 days (half a year). To test the null hypothesis that the difference between the starting dates is 182.5, the z-score and its associated p-value were computed.

RESULTS

Sample sizes for New Zealand were smaller than for the United Kingdom. Sample sizes ranged between 98 moult records for Common Redpoll and 733 for House sparrow in New Zealand, and between 16879 for House sparrow and 62376 for European Goldfinch in the United Kingdom (Table 3). For all species, there was an adequate distribution of moult scores across the moult periods in both countries. This indicates that the moult model should perform satisfactorily (Figures 1 to 7). However, a consequence of the small sample sizes in New Zealand was that it was not feasible to investigate whether the standard deviation parameters in the moult models were different between the two countries.

The mean latitude of the moult records for all species was 41.54°S in New Zealand and 52.65°N in the United Kingdom. 80% of the records from New Zealand were between latitudes 40°S and 42°S. This latitudinal range includes the northern part of South Island and the southern part of North Island. Subsequently, it was not feasible to determine if there was a latitudinal trend shaping the moult patterns over the c. 12° latitudinal range of New Zealand (36.25°S to 48.02°S). Similarly, 92.5% of moult records from the United Kingdom were between the latitudes of 50°N and 56°N out of the possible c. 11° latitudinal range of 49°N to 60°N. The 6° latitudinal range encompasses England, Wales, Northern Ireland and the southern part of Scotland.

There was no significant difference in moult duration between the New Zealand and the United Kingdom populations for four of the seven species, namely Dunnock, European Goldfinch, Common Redpoll and Yellowhammer (Table 3). Common Chaffinch and European Greenfinch had estimated moult durations that were 11 days and 17 days shorter respectively in New Zealand than in the United Kingdom (Table 3). House Sparrow, however, took 13 days longer to complete moult in New Zealand than in the United Kingdom (Table 3).

The z-scores and the corresponding p-values of the differences in start dates of moult in New Zealand and the United Kingdom indicate that timing of moult in the two locations relative to the summer solstice was not statistically different for Dunnock, European Goldfinch, House sparrow, Common Redpoll and Yellowhammer (Table 4). This means that the shift in the starting dates of moult was not significantly different from half a year (182.5 days) in five out of the seven species which were introduced to the southern hemisphere. The difference in start dates for Common Chaffinch and European Greenfinch in New Zealand and the United Kingdom relative to the summer solstice were significantly different ($P<0.001$ and $P=0.05$ respectively) (Table 4). Common Chaffinch was estimated to start moult nine days later and European Greenfinch three days later in New Zealand relative to the start dates in the United Kingdom (Table 4, Table 5).

In summary Dunnock, European Goldfinch, Common Redpoll and Yellowhammer started moult at the same time relative to the summer solstice and moult progressed at the same rate in the New Zealand and United Kingdom populations (Table 4). House Sparrow populations started moult at the same time relative to the summer solstice, but moult progressed more slowly in New Zealand than in the United Kingdom, taking 13 days longer (Table 4). Common Chaffinch started moult nine days later in New Zealand relative to the United Kingdom start date (Table 5) but moult progressed faster, taking 11 days less than in the United Kingdom (Table 4). This means that, in effect, both Common Chaffinch populations completed moult by the same time relative to the summer solstice. European Greenfinch population in New Zealand started moult three days later (Table 5) but took 17 days less to complete moult than the population in the United Kingdom (Table 4).

DISCUSSION

Studies of introduced alien bird species are not often undertaken, but if they are, they tend to focus on their status as pests. For example, the Egyptian Goose *Alopochen aegyptiacus* was introduced to Europe mainly via private wildfowl collections from which they escaped, and rapidly spread eastwards across western Europe (Gyimesi and Lensink 2012). Research on this species focuses mainly on factors relating to the population dynamics enabling the range expansion and its perception as a “disgusting, polluting, and health-threatening” pest species (Kornherr and Pütz 2022).

Similarly, there is only a single study in South Africa of the biology of the Common Starling *Sturnus vulgaris*, where it was introduced at Cape Town in 1897 (Cooper and Underhill 1991). This paper included an analysis of primary moult using the moult model of Underhill and Zucchini (1988). It pointed out that it was the first study of moult of the Common Starling, apart from captive birds, in any part of its range, either in the natural range or in any of the many places where it has been introduced. Rothery et al. (2001) responded by doing an analysis of the primary moult of Common Starling in England.

In the same way as this chapter compares the timing of primary moult of introduced species across the hemispheres, Flux and Flux (2021) compared the timing of breeding of Common Starlings between New Zealand, where they are an introduced species, and Denmark, where they occur naturally. In New Zealand, it was found that there has been no significant increase in temperature in response to climate change over the past 50 years and the dates of egg laying have stayed constant. However, in Denmark, where there has been a significant increase in temperature, the laying dates were earlier.

For the seven species in this study, which were all introduced from the United Kingdom to New Zealand in the 1860s, the primary achievement of this chapter is a direct comparison of primary moult across the hemispheres. Both sets of data, from the natural and the introduced ranges, were included in a single statistical model. This facilitates comparisons through standard model selection approaches.

In the analyses it is striking that, for five of the seven species, the starting date of moult showed a shift of exactly six months following introduction to the southern hemisphere. Therefore, the timing of moult relative to the summer solstice had not changed. For the remaining two species, Common Chaffinch and European Greenfinch, the changes, relative to the summer solstice, were start dates that were nine days and three days later respectively in New Zealand compared to the United Kingdom. Given the flexibility in the timing of moult, and how readily it adapts to local conditions, this is an unexpected result. The findings of our paper appear to suggest that the five species, when they were naturalised in New Zealand, having been brought from the United Kingdom, only had to make a single adjustment from the northern hemisphere photoperiods to that of the southern hemisphere. No "fine-tuning" adjustments to the annual cycle were needed. This might help explain why these species, and many others, were so successful when introduced from the United Kingdom to New Zealand. This is further supported by the fact that both the source area of these seven species, the United Kingdom, and the release area, New Zealand, are in the same Köppen-Geiger climate classification zone (Kottek et al. 2006). There are 31 climate zones in the updated classification developed by Kottek et al. (2006).

In contrast, the comparison of primary moult results for the Common Starling in England and South Africa mentioned above, indicate that the hemispheric adjustment was not six months. The mean starting date was 4 June in England and 8 November at the South African study site near Cape Town (Cooper and Underhill 1991, Rothery et al. 2001). Relative to the summer solstice, primary moult was estimated to start 17 days prior to the solstice in the northern hemisphere and 44 days prior in the southern hemisphere. Using the standard errors of the estimates of the starting dates provided by Cooper and Underhill (1991) and Rothery et al. (2002) (1.7 days and 2.2 days respectively) in the two separate analyses, the difference of 27 days is statistically significant ($z=9.7$, $P<0.001$). For the Common Starlings introduced from England to the Western Cape, South Africa, the hemisphere adjustment of six months was supplemented with a fine-tuning adjustment to exploit local environmental conditions. The climate classification zones of the source and release areas are different (Kottek et al. 2006) and the change in relative timing of primary moult may in part be attributable to this.

Newton and Rothery (2005) and Newton and Rothery (2009) used the method of Underhill and Zucchini (1988) to investigate the timing and duration of primary moult in European Greenfinches and European Goldfinches, respectively, in east-central England. Newton and Rothery (2005) estimated that Greenfinches started moult on 24 July, on average, with a duration of 100 days. This start date is similar to the one estimated in this current study but the duration is 24 days longer. The data used in Newton and Rothery (2005), however, are from a single year and a substantial proportion of the moult records are from the beginning of the moult period. The difference between their results and ours might be attributable to these factors. Newton and Rothery (2009) estimated that Goldfinches started moult on 30 July, on average, with a duration of 77 days. These results are essentially identical to the ones in this current study.

For several of the species considered here, for example House Sparrow, there are introduced populations in many parts of the world: North America, South America, southern Africa, eastern Australia and New Zealand (Anderson 2006). The introductions cover a vast latitudinal range, from the equator to c. 55° north and south in both hemispheres, and in many cases the source populations are known (Anderson 2006). This represents an interesting opportunity to examine variation in the extent of fine-tuning of moult that House Sparrows have undertaken between the source and introduced populations. It is also possible that moult studies will provide insights into the limits of range expansion. It is likely that all three parameters of moult might be flexible. For example, if the standard deviation parameter is significantly larger in the introduced population than in the source population, it may indicate that the introduced population is still fine-tuning the optimal start date of moult or that different environmental constraints apply.

Explanatory note

During the analyses made for this chapter, errors were found in the results in Morrison et al. (2015). This is the reason why the results of Table 3 differ substantially with those of Morrison et al. (2015). A correction note is currently in press in Ibis. The results in the correction note are compatible with the results in this chapter.

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Table 1. Species with estimates of primary moult parameters at more than one location, separated by at least one degree of latitude and obtained using the Underhill-Zucchini moult model. This table is comprehensive.

	Species	**Latitudes of the two furthest study sites**	**Latitudinal range (°) between the two furthest study sites**	**Reference**
Migrants	Ruddy Turnstone *Arenaria interpres*	56°N–38°S	94°	Summers et al. 1989, Skewes et al. 2004
	Willow Warbler *Phylloscopus trochilus*	70°N–28°S	98°	Underhill et al. 1992
	Grey Plover *Pluvialis squatarola*	52°N–38°S	90°	Serra and Rusticali 1998, Serra et al. 1999, Minton and Serra 2001, Pearson et al. 2002, Serra et al. 2006
	European Storm Petrel *Hydrobates pelagicus*	44°N – 39°N	5°	Arroyo et al. 2004, Zuberogoitia et al. 2016
	Purple Sandpiper *Calidris maritima*	70°N–55°N	15°	Summers et al. 2004
	Red Knot *Calidris canutus*	56°N–33°S	89°	Summers et al. 2010
	Curlew Sandpiper *Calidris ferruginea*	9°N–38°S	47°	Barshep 2011
	Common Greenshank *Tringa nebularia*	18°S–34°S	16°	Remisiewicz et al. 2014
	Lesser Sand Plover *Charadrius mongolus*	9°N–38°S	47°	Jackson 2017, Jackson and Underhill 2022
	Greater Sand Plover *Charadrius leschenaultii*	9°N–38°S	47°	Jackson 2017, Jackson and Underhill 2022
	Terek Sandpiper *Xenus cinereus*	9°N–38°S	47°	Jackson 2017, Jackson and Underhill 2022
	Common Whitethroat *Curruca communis*	52°N–25°S	77°	Remisiewicz et al. 2019
	Little Stint *Calidris minuta*	0°–33°S	33°	Jackson and Underhill 2022
Residents	Common Starling *Sturnus vulgaris*	52°N–33°S*	85°	Cooper and Underhill 1991, Rothery et al. 2001
	Black-chested Prinia *Prinia flavicans*	17°S–24°S	7°	Herremans 1999
	Levaillant's Cisticola *Cisticola tinniens*	27°S–34°S	7°	Herremans et al. 1999
	Olive Thrush *Turdus olivaceus*	33°S–34°S	1°	Bonnevie et al. 2003

	Species	**Latitudes of the two furthest study sites**	**Latitudinal range (°) between the two furthest study sites**	**Reference**
	Cape Robin-Chat *Cossypha caffra*	33°S–34°S	1°	Bonnevie et al. 2003
	Cape White-eye *Zosterops virens*	33°S–34°S	1°	Hulley et al. 2004
	Sombre Greenbul *Andropadus importunus*	27°S–34°S	7°	Bonnevie 2014
	Common Waxbill *Estrilda astrild*	23°S–33°S	10°	Bonnevie and Oschadleus 2012
	Thick-billed Weaver *Amblyospiza albifrons*	26°S–30°S	4°	Oschadleus 2005, Oschadleus and Underhill 2006a
	Southern Red Bishop *Euplectes orix*	26°S–34°S	8°	Craig et al. 2001, Oschadleus 2005, Oschadleus and Underhill 2006b
	Social Weaver *Philetairus socius*	19°S–28°S	9°	Oschadleus 2004, Oschadleus 2005
	Cape Weaver *Ploceus capensis*	30°S–34°S	4°	Craig et al. 2001, Oschadleus 2005
	Village Weaver *Ploceus cucullatus*	30°S–33°S	3°	Craig et al. 2001, Oschadleus 2005, Oschadleus and Underhill 2006a
	Southern Masked Weaver *Ploceus velatus*	26°S–34°S	8°	Oschadleus et al. 2000, Craig et al. 2001, Oschadleus 2005
	Red-billed Quelea *Quelea quelea*	18°S–33°S	5°	Craig et al. 2001, Oschadleus 2005

* This species was introduced at 33°S.

Table 2. Relative masses (%) of primary feathers of five of the seven species considered in this chapter: Common Chaffinch, European Goldfinch, European Greenfinch, House sparrow and Yellowhammer. The relative masses are used for the calculation of Proportion Feather Mass Grown (PFMG). The sample size (number of birds) on which the relative masses are based is given as *n*.

Species		**Primary**									**Source**
	n	**P1**	**P2**	**P3**	**P4**	**P5**	**P6**	**P7**	**P8**	**P9**	
Common Chaffinch	1	8.00	8.44	8.96	9.67	11.95	13.53	13.53	13.18	12.74	Peter G. Ryan *in litt.*
European Goldfinch	7	7.33	8.15	8.80	9.30	10.71	13.00	13.58	14.32	14.82	Newton and Rothery 2009, Peter G. Ryan *in litt.*
European Greenfinch	10	7.13	7.74	8.35	9.05	10.55	12.97	14.13	14.61	15.46	Newton and Rothery 2005
House sparrow	2	8.94	9.71	10.27	10.62	11.35	11.94	12.18	12.30	12.69	Peter G. Ryan *in litt.*
Yellowhammer	3	8.14	8.31	8.65	9.50	11.30	12.88	13.30	13.78	14.14	Peter G. Ryan *in litt.*
General passerine		8.00	8.60	9.20	10.00	11.40	12.40	13.00	13.50	14.00	Bonnevie 2010

Table 3. Moult parameters, estimated using the Underhill-Zucchini moult model and data type 2, for adult birds of each of the seven species: Common Chaffinch, Dunnock, European Goldfinch, European Greenfinch, House Sparrow, Common Redpoll and Yellowhammer. Sample sizes of pre-moult, in-moult and post-moult birds are also given.

Species	Location	Moult parameters				Sample sizes (n)		
		Duration (SE)	Mean start date (SE)	Standard deviation of start date (SE)	End date	Pre-moult	In-moult	Post-moult
Common Chaffinch	New Zealand	50.7 (3.3)	19 Jan (2.4)	14.4 (0.1)	10 Mar (2.1)	37	61	52
Common Chaffinch	United Kingdom	61.4 (0.4)	10 Jul (0.3)	14.4 (0.1)	9 Sep (0.3)	39938	3647	7861
Dunnock	New Zealand	45.4 (0.5)	30 Jan (2.2)	13.0 (0.2)	16 Mar (2.2)	23	23	57
Dunnock	United Kingdom	45.4 (0.5)	31 Jul (0.3)	13.0 (0.2)	15 Sep (0.3)	29523	2294	3189
European Goldfinch	New Zealand	79.3 (0.3)	23 Jan (1.2)	13.2 (0.1)	13 Apr (1.2)	30	102	28
European Goldfinch	United Kingdom	79.3 (0.3)	25 Jul (0.2)	13.2 (0.1)	12 Oct (0.2)	47164	7892	7320
European Greenfinch	New Zealand	59.5 (3.2)	2 Feb (2.0)	16.3 (0.1)	2 Apr (2.2)	47	101	71
European Greenfinch	United Kingdom	76.0 (0.4)	30 Jul (0.2)	16.3 (0.1)	14 Oct (0.3)	34267	8015	7323
House sparrow	New Zealand	73.6 (1.8)	31 Jan (1.2)	16.4 (0.2)	15 Apr (1.2)	150	315	268
House sparrow	United Kingdom	61.1 (0.8)	2 Aug (0.4)	16.4 (0.2)	2 Oct (0.7)	14789	1656	434
Common Redpoll	New Zealand	43.0 (0.7)	6 Feb (1.4)	9.9 (0.2)	21 Mar (1.3)	36	41	21
Common Redpoll	United Kingdom	43.0 (0.7)	9 Aug (0.4)	9.9 (0.2)	21 Sep (0.5)	14265	685	6056
Yellowhammer	New Zealand	41.9 (1.7)	9 Feb (3.8)	13.7 (0.6)	23 Mar (3.9)	23	8	68
Yellowhammer	United Kingdom	41.9 (1.7)	18 Aug (1.1)	13.7 (0.6)	29 Sep (1.2)	19312	146	406

Table 4. Comparison of the parameters of moult of seven species in New Zealand (NZ) and the United Kingdom (UK), focusing on differences in timing of start dates, and the results of the test of the null hypothesis that the estimated mean starting dates were half a year (182.5 days) apart. Species with an estimated common duration in both countries are centred in the two duration columns.

<table>
<tr><th>Species</th><th>Duration NZ</th><th>Duration UK</th><th>Start date NZ</th><th>Start date UK</th><th>SD</th><th>Difference in start dates (days)</th><th>z-score</th><th>P-value</th></tr>
<tr><td>Common Chaffinch</td><td>50.7 (3.3)</td><td>61.4 (0.4)</td><td>19 Jan (2.4)</td><td>10 Jul (0.3)</td><td>14.4 (0.1)</td><td>172.4 (2.5)</td><td>−4.10</td><td><0.001</td></tr>
<tr><td>Dunnock</td><td colspan="2">45.4 (0.5)</td><td>30 Jan (2.2)</td><td>31 Jul (0.3)</td><td>13.0 (0.2)</td><td>182.9 (2.2)</td><td>0.17</td><td>0.86</td></tr>
<tr><td>European Goldfinch</td><td colspan="2">79.3 (0.3)</td><td>23 Jan (1.2)</td><td>25 Jul (0.2)</td><td>13.2 (0.1)</td><td>182.8 (1.2)</td><td>0.21</td><td>0.83</td></tr>
<tr><td>European Greenfinch</td><td>59.5 (3.2)</td><td>76.0 (0.4)</td><td>2 Feb (2.0)</td><td>30 Jul (0.2)</td><td>16.3 (0.1)</td><td>178.5 (2.0)</td><td>−1.97</td><td>0.05</td></tr>
<tr><td>House sparrow</td><td>73.6 (1.8)</td><td>61.1 (0.8)</td><td>3 Jan (1.2)</td><td>2 Aug (0.4)</td><td>16.4 (0.2)</td><td>183.1 (1.3)</td><td>0.48</td><td>0.63</td></tr>
<tr><td>Common Redpoll</td><td colspan="2">43.0 (0.7)</td><td>6 Feb (1.4)</td><td>9 Aug (0.4)</td><td>9.9 (0.2)</td><td>184.7 (1.4)</td><td>1.64</td><td>0.10</td></tr>
<tr><td>Yellowhammer</td><td colspan="2">41.9 (1.7)</td><td>9 Feb (3.8)</td><td>18 Aug (1.1)</td><td>13.7 (0.6)</td><td>189.5 (3.8)</td><td>1.85</td><td>0.06</td></tr>
</table>

Table 5. The number of days between the summer solstice and the start of primary moult in each of the seven species.

Species	**New Zealand**		**United Kingdom**	
	Start date	**Difference between summer solstice (22 Dec) and start date (days)**	**Start date**	**Difference between summer solstice and start date (21 Jun) (days)**
Chaffinch	19 Jan	28	10 Jul	19
Dunnock	30 Jan	39	31 Jul	40
Goldfinch	23 Jan	32	25 Jul	34
Greenfinch	2 Feb	42	30 Jul	39
House sparrow	31 Jan	40	2 Aug	42
Redpoll	6 Feb	46	9 Aug	49
Yellowhammer	9 Feb	49	18 Aug	58

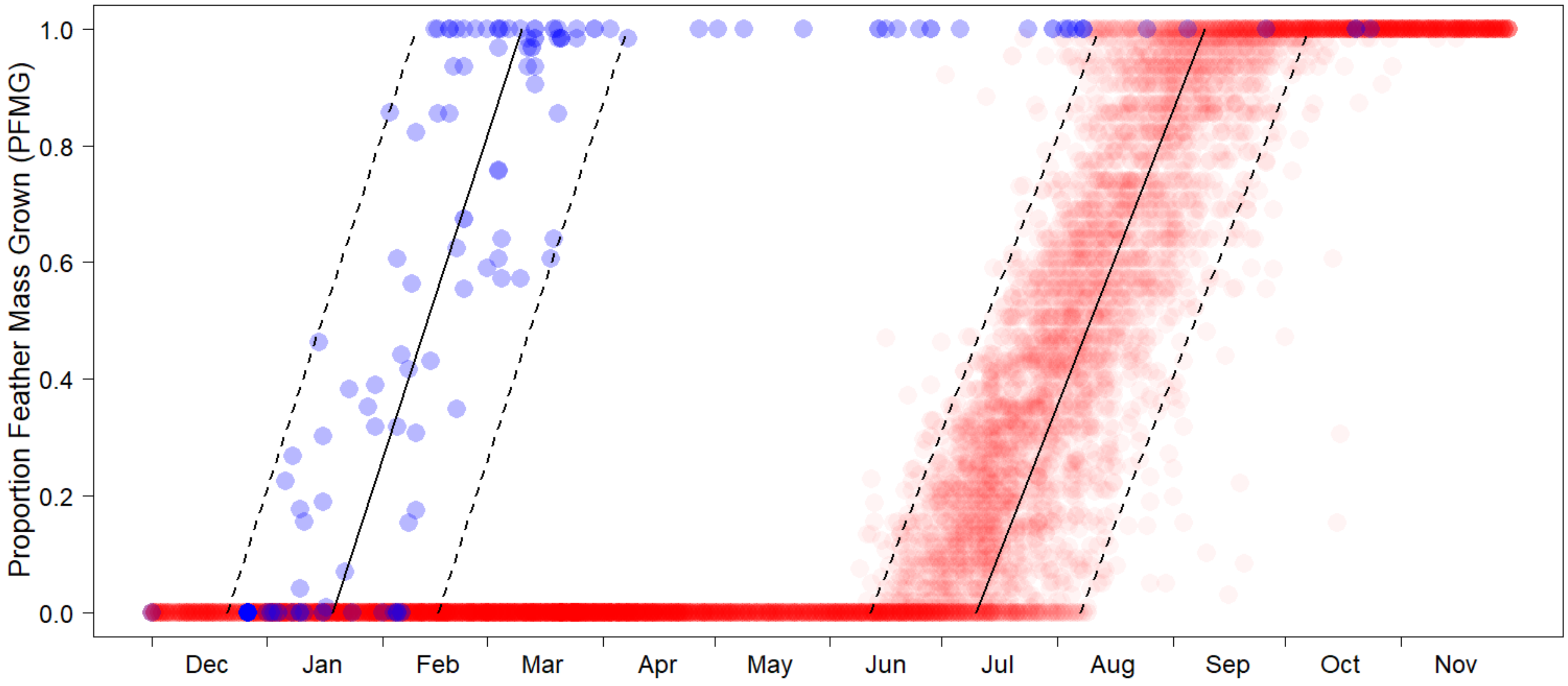


Figure 1. Modified scatter diagram* of PFMG against time (calendar date) for adult Common Chaffinches *Fringilla coelebs* in New Zealand (blue) and the United Kingdom (red). The two solid black lines are the mean moult lines and indicate the progression of moult for the average bird in the New Zealand and the United Kingdom populations respectively. The broken black lines on either side of the mean moult line are the 95% intervals within which 95% of birds in active moult ought to fall. These intervals were derived from the standard deviation of the mean start dates. The sample size was 150 for New Zealand and 51446 for the United Kingdom.

* Moult scores are recorded on a discrete scale (each primary is allocated an integer score between 0 and 5). As a result of this conventional scatter plots of moult scores against dates are misleading because there is no indication of the number of moult records represented by a single symbol in the plot. In this modification of the scatter diagram, the data points are represented by circles, and the intensity of the colour shading represents the relative number of records at each point. The lightest shade of blue and red refers to one data point, the darkest shade of blue refers to 13 overlapping data points and the darkest shade of red refers to 503 overlapping data points.

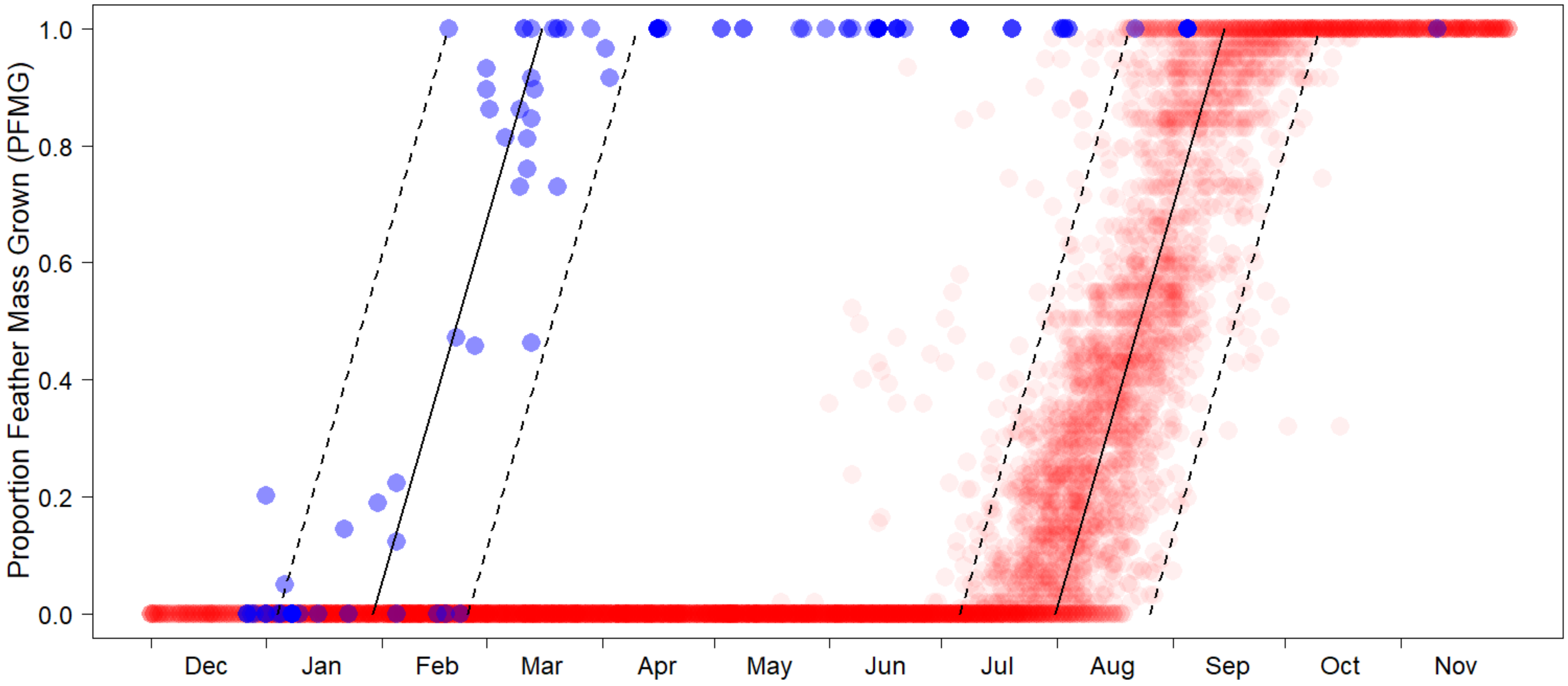


Figure 2. Modified scatter diagram* of PFMG against time (calendar date) for adult Dunnocks *Prunella modularis* in New Zealand (blue) and the United Kingdom (red). The two solid black lines are the mean moult lines and indicate the progression of moult for the average bird in the New Zealand and the United Kingdom populations respectively. The broken black lines on either side of the mean moult line are the 95% intervals within which 95% of birds in active moult ought to fall. These intervals were derived from the standard deviation of the mean start dates. The sample size was 103 for New Zealand and 35006 for the United Kingdom.

* In this modification of the scatter diagram, the data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade of blue and red refers to one data point, the darkest shade of blue refers to 5 overlapping data points and the darkest shade of red refers to 262 overlapping data points.

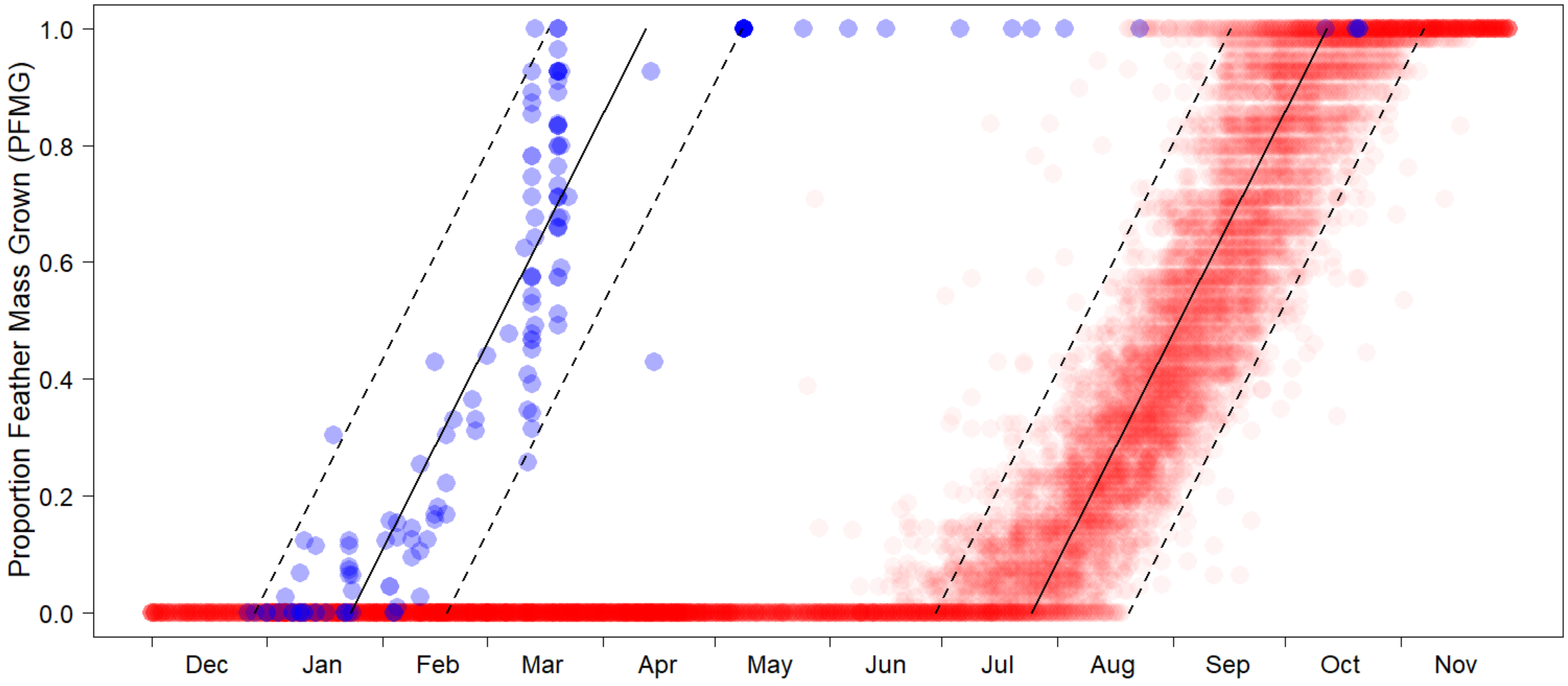


Figure 3. Modified scatter diagram * of PFMG against time (calendar date) for adult European Goldfinches *Carduelis carduelis* in New Zealand (blue) and the United Kingdom (red). The two solid black lines are the mean moult lines and indicate the progression of moult for the average bird in the New Zealand and the United Kingdom populations respectively. The broken black lines on either side of the mean moult line are the 95% intervals within which 95% of birds in active moult ought to fall. These intervals were derived from the standard deviation of the mean start dates. The sample size was 160 for New Zealand and 62376 for the United Kingdom.

* In this modification of the scatter diagram, the data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade of blue and red refers to one data point, the darkest shade of blue refers to 10 overlapping data points and the darkest shade of red refers to 566 overlapping data points.

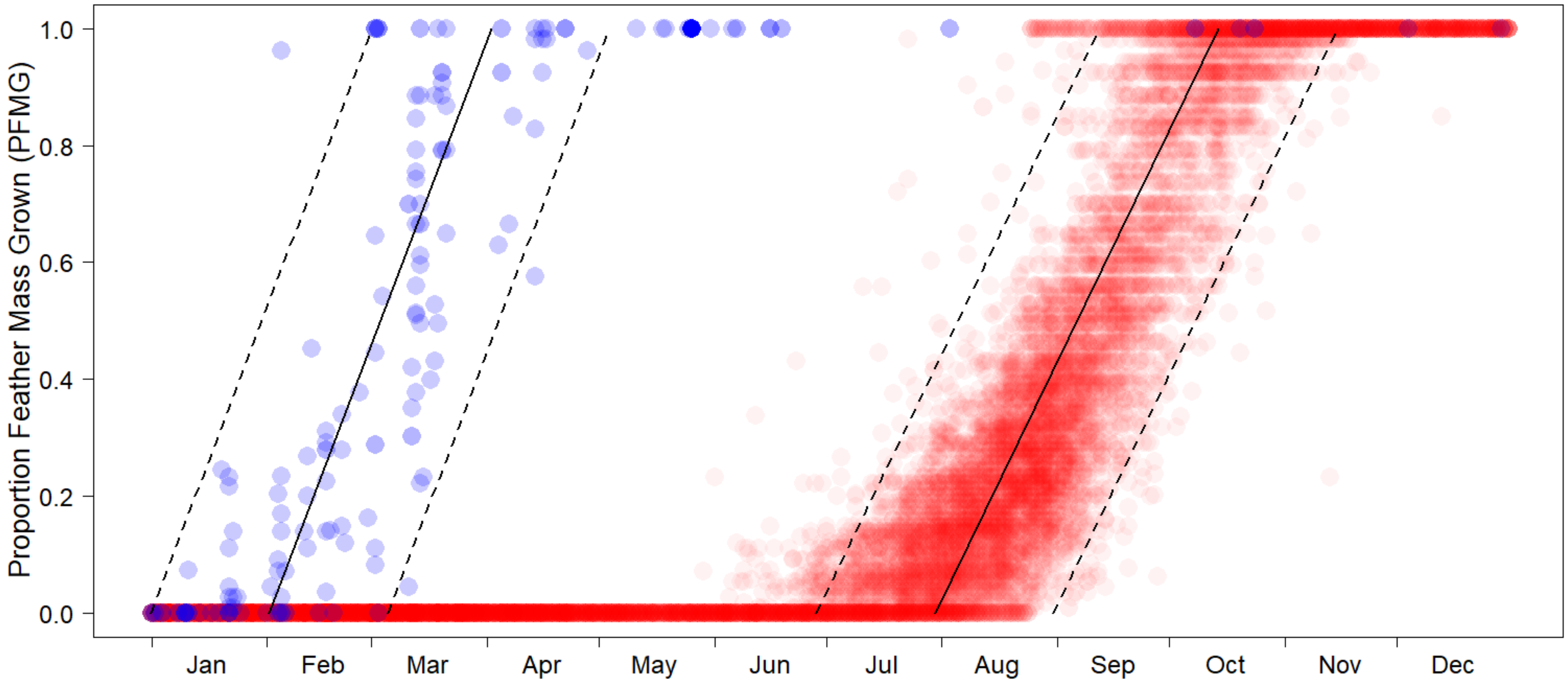


Figure 4. Modified scatter diagram* of PFMG against time (calendar date) for European Greenfinches *Chloris chloris* in New Zealand (blue) and the United Kingdom (red). The two solid black lines are the mean moult lines and indicate the progression of moult for the average bird in the New Zealand and the United Kingdom populations respectively. The broken black lines on either side of the mean moult line are the 95% intervals within which 95% of birds in active moult ought to fall. These intervals were derived from the standard deviation of the mean start dates. The sample size was 219 for New Zealand and 49605 for the United Kingdom.

* In this modification of the scatter diagram, the data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade of blue and red refers to one data point, the darkest shade of blue refers to 23 overlapping data points and the darkest shade of red refers to 364 overlapping data points.

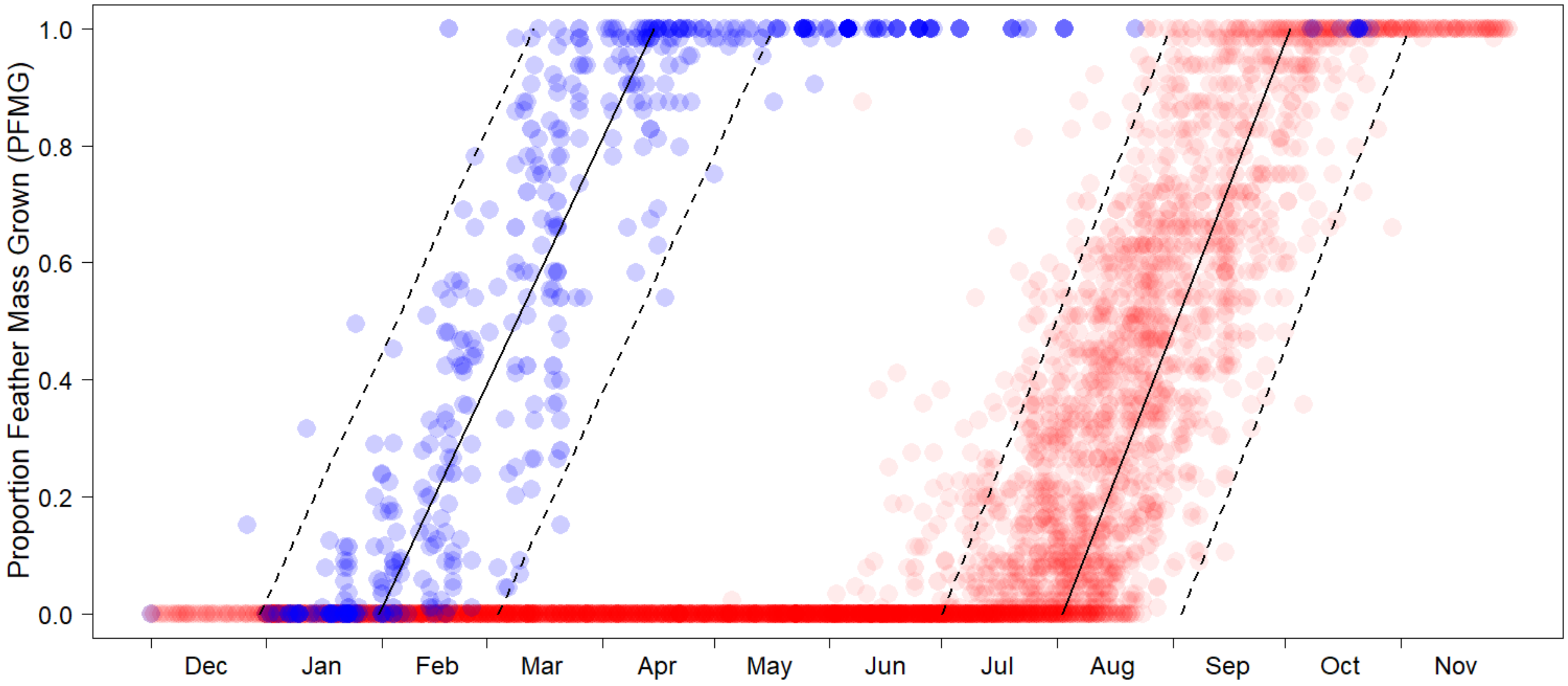


Figure 5. Modified scatter diagram* of PFMG against time (calendar date) for adult House sparrows *Passer domesticus* in New Zealand (blue) and the United Kingdom (red). The two solid black lines are the mean moult lines and indicate the progression of moult for the average bird in the New Zealand and the United Kingdom populations respectively. The broken black lines on either side of the mean moult line are the 95% intervals within which 95% of birds in active moult ought to fall. These intervals were derived from the standard deviation of the mean start dates. The sample size was 733 for New Zealand and 16879 for the United Kingdom.

* In this modification of the scatter diagram, the data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade of blue and red refers to one data point, the darkest shade of blue refers to 26 overlapping data points and the darkest shade of red refers to 169 overlapping data points.

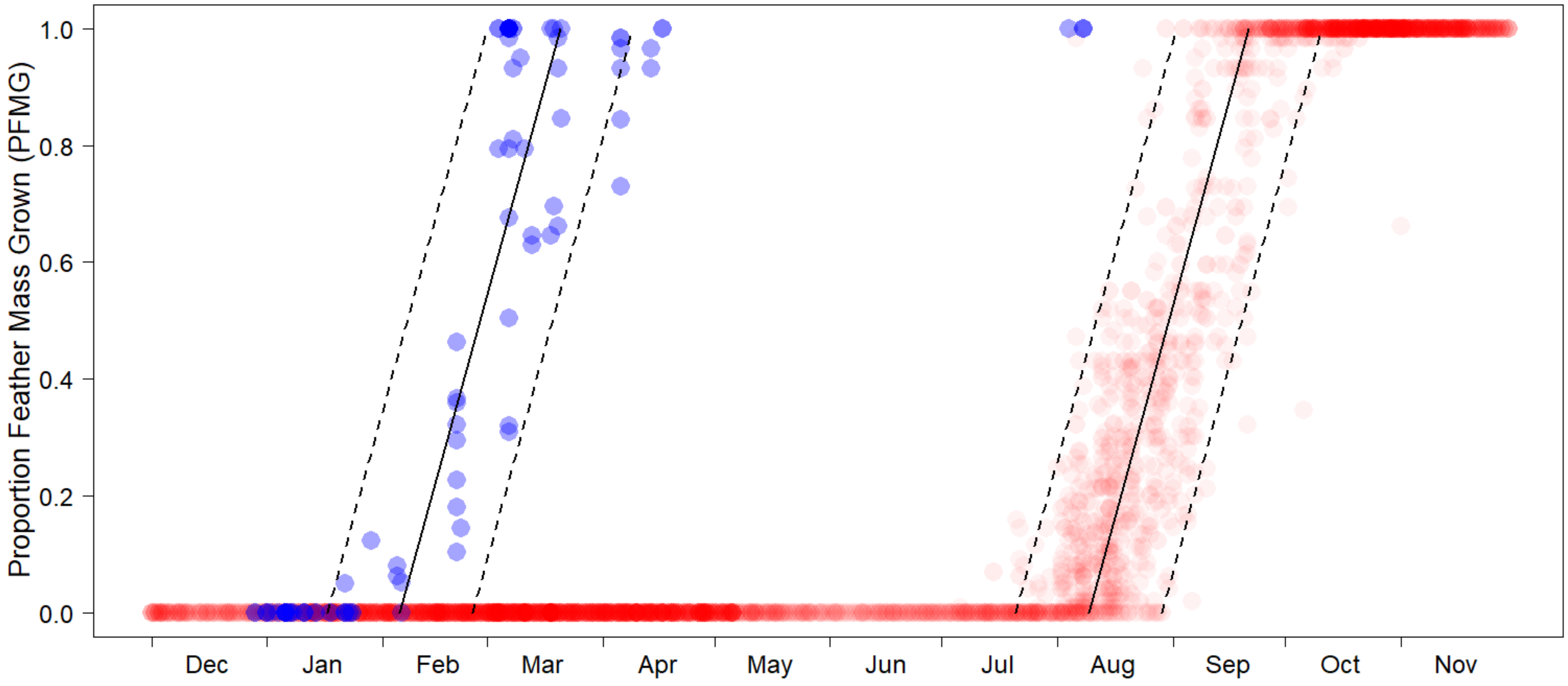


Figure 6. Modified scatter diagram* of PFMG against time (calendar date) for adult Common Redpolls *Acanthis flammea* in New Zealand (blue) and the United Kingdom (red). The two solid black lines are the mean moult lines and indicate the progression of moult for the average bird in the New Zealand and the United Kingdom populations respectively. The broken black lines on either side of the mean moult line are the 95% intervals within which 95% of birds in active moult ought to fall. These intervals were derived from the standard deviation of the mean start dates. The sample size was 98 for New Zealand and 21006 for the United Kingdom.

* In this modification of the scatter diagram, the data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade of blue and red refers to one data point, the darkest shade of blue refers to 8 overlapping data points and the darkest shade of red refers to 358 overlapping data points.

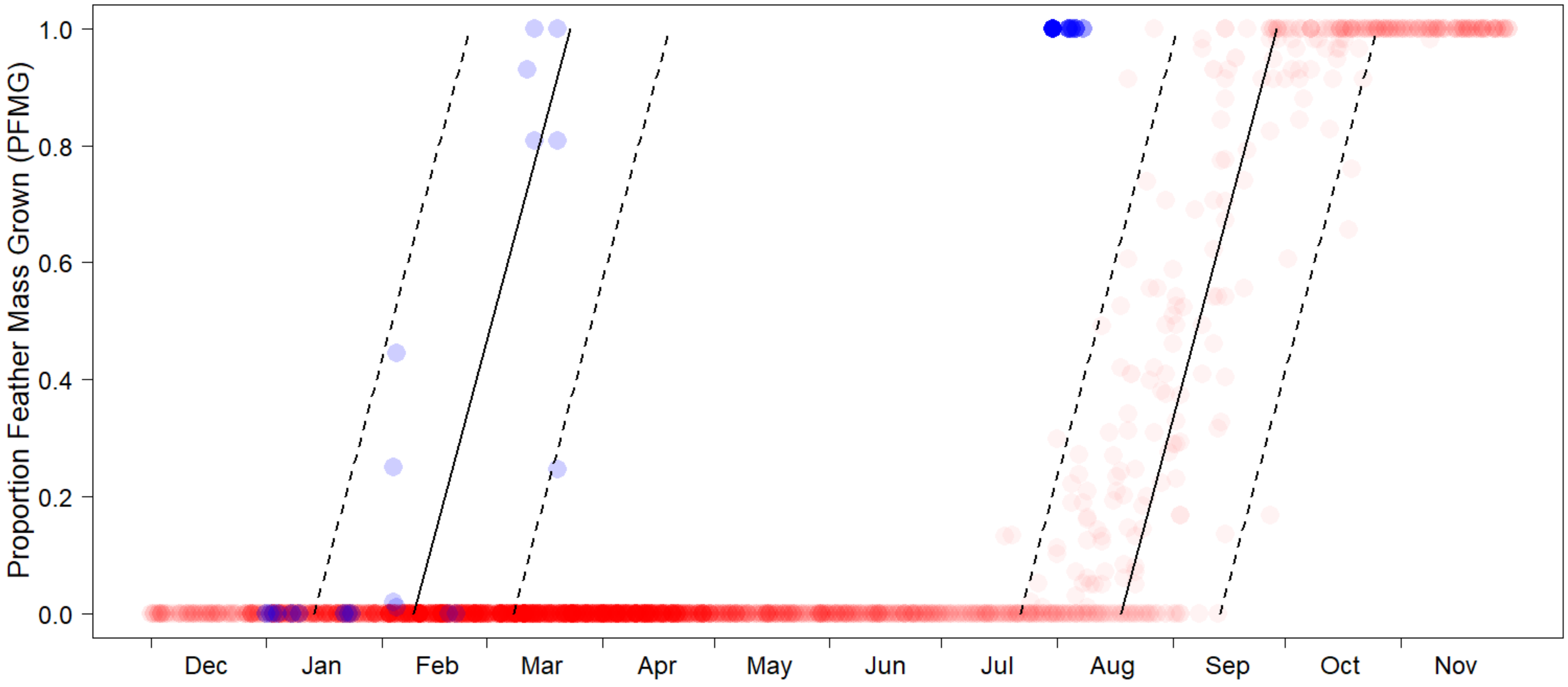


Figure 7. Modified scatter diagram* of PFMG against time (calendar date) for adult Yellowhammers *Emberiza citronella* in New Zealand (blue) and the United Kingdom (red). The two solid black lines are the mean moult lines and indicate the progression of moult for the average bird in the New Zealand and the United Kingdom populations respectively. The broken black lines on either side of the mean moult line are the 95% intervals within which 95% of birds in active moult ought to fall. These intervals were derived from the standard deviation of the mean start dates. The sample size was 99 for New Zealand and 19864 for the United Kingdom.

* In this modification of the scatter diagram, the data points are represented by circles and the intensity of the shading represents the number of records at each point. The lightest shade of blue and red refers to one data point, the darkest shade of blue refers to 27 overlapping data points and the darkest shade of red refers to 460 overlapping data points.

APPENDIX TO CHAPTER 6

Notes on the history of introductions to New Zealand of the seven species considered in this chapter.

The history of avian introductions in New Zealand was documented in a book by George Thomson in 1922, using records kept by acclimatisation societies and information from other sources. The first attempts to introduce new species to New Zealand began with the arrival of Captain Cook on his second voyage in 1773. He landed at Dusky Sound and the first animals that were purposely introduced were geese *Anser anser*. Bird introductions by European settlers, however, only started seriously around the 1860's, when acclimatisation societies were founded in New Zealand (Thomson 1992). The main aim of acclimatisation societies was to introduce, establish and domesticate species that appeared desirable, either for useful or aesthetic purposes (McDowall 1994). They introduced insectivorous birds to help farmers rid their crops of caterpillars (Thomson 1922) and gamebirds for hunting (Duncan et al. 2006). They also introduced birds as cage birds, especially canaries and other songbirds (Thomson 1922). These translocated birds originated from populations in Britain (Green 1997, Duncan 1997, Duncan et al. 2006).

Introductions were attempted for a total of 120 species identified in Duncan et al. 2006, of which 35 were successful (Robertson et al. 2021). Green (1997) considered that the key determinant of successful establishment in New Zealand was the number of birds released during the main period of introductions. There have also been several self-introductions. Silvereye *Zosterops lateralis* was the only bird that arrived naturally and successfully established itself in New Zealand in the 19th century. Since 1950, 10 additional self-introduced species have established permanent populations in the region (Neuhäuser and Cuming 2007, Robertson et al. 2021).

Seven of the most common and widely spread introduced species in New Zealand were chosen for this investigation: Common Chaffinch *Fringilla coelebs*, Dunnock *Prunella modularis*, European Goldfinch *Carduelis carduelis*, European Greenfinch *Chloris chloris*, House Sparrow *Passer domesticus*, Common Redpoll *Carduelis flammea* and Yellowhammer *Emberiza citronella*.

Common Chaffinch was first introduced near Nelson between 1862 and 1864 when 23 birds were released, but no further records of them were kept. There were several other introduction events in Canterbury, Auckland, Otago and Wellington between 1864–1877, when numerous birds were released by acclimatisation societies. Members of the public and dealers were also responsible for introductions in towns and cities. Once Chaffinch was naturalised in New Zealand there were still a few more introduction events (Thomson 1922). Chaffinches are self-introduced to many offshore islands (Angus 2013a). It is now the most abundant and widely spread of all finches introduced to New Zealand and is frequently seen in suburban gardens (Angus 2013a).

Dunnock was introduced from England between 1867 and 1882 in Auckland, Otago, Canterbury, Christchurch, Hawke's Bay and Wellington. First signs of nests were seen in 1873 and Dunnock established itself soon thereafter (Thomson 1922). Dunnock is commonly seen in urban gardens and open countryside and is common and widespread throughout New Zealand, except in northern North Island (Santos 2013).

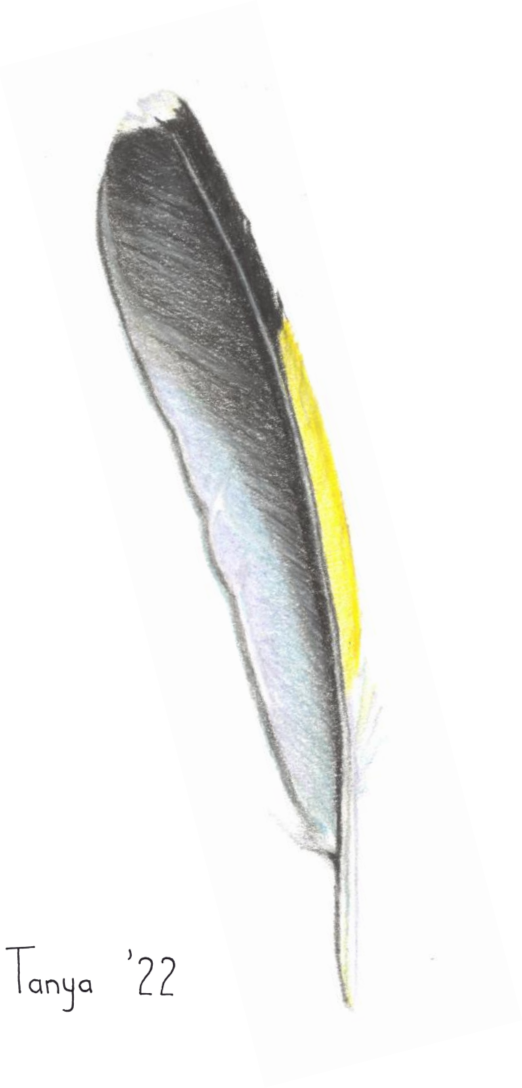
European Goldfinch was introduced from Britain in Nelson, Otago, Auckland, Canterbury and Wellington between 1862 and 1883. They established themselves quickly at their release sites and spread rapidly from there (Thomson 1922). They are common in open countryside throughout New Zealand (Miskelly 2013). These birds are resident on the Chatham Islands and vagrants on many other offshore islands (Miskelly 2013). They mainly consume seeds of weeds, such as thistle, and only occasionally feed on grain and seeds of other cultivated plants (Thomson 1922, Miskelly 2013).

European Greenfinch was introduced from Britain between 1862 and 1868 in Nelson, Auckland and Otago. By 1868 they were considered to have acclimatised to their new environment (Thomas 1922). These finches are widespread throughout the mainland and have small populations on offshore islands (Angus 2013b). They are destructive of ripening crops of grain and fruit. In winter they mainly feed on seeds they pick out of the cones of pine trees (*Pinus pinaster*) and seeds of weeds (Thomson 1922, Angus 2013b).

The Wanganui Acclimatisation Society on the North Island was the first to introduce House sparrows in 1866 and again in 1867. Other acclimatisation societies (Canterbury, Auckland, Nelson and Otago) on North and South Islands followed. The numbers of house sparrows increased very quickly in all parts of New Zealand and by 1871 this species was considered established and adapted in the region (Thomson 1922). They initially helped in combating hordes of agricultural pests, but they soon became a serious pest themselves. House sparrows are abundant and widespread throughout New Zealand, living in close association with human habitation. They are self-introduced to offshore Chatham Islands and are recorded as vagrants on a few other offshore islands (Thomson 1922, Dawson 2013).

Common Redpoll was introduced from Britain between 1862 and 1875 in Nelson, Otago, Canterbury, Auckland and Wellington. They tended to migrate away from their release sites to open hilly countryside (Thomson 1922). Redpoll is common throughout New Zealand but is generally more abundant on the South Island. They also occur on many offshore islands (Angus 2013c).

Yellowhammer was introduced from Britain by Acclimatisation Societies in Nelson, Auckland, Canterbury and Otago between 1862 to 1871. These birds spread rapidly throughout New Zealand (Thomson 1922). They commonly occur in open countryside throughout North and South Island and have been recorded on offshore islands (Angus 2013d).



CHAPTER 7

Global review of quantitative studies of primary moult of birds using the Underhill-Zucchini moult model

Chapter 7

Global review of quantitative studies of primary moult of birds using the Underhill-Zucchini moult model

Abstract: Knowledge about the timing of moult and how it fits into the annual cycle, along with breeding and, in some cases migration, is an important component of understanding the life history of birds. In comparison with breeding and migration, there is a lack of knowledge about the moult of birds. Primary moult can be quantified using models such as the moult model of Underhill and Zucchini. Studies that included estimates of primary moult parameters (duration, mean start date and standard deviation of mean start date) obtained using the Underhill-Zucchini moult model were compiled to generate a moult analysis database. These parameters provide information about the timing of moult, how it fits into the annual cycle and how synchronised moult is in the population. Relationships between the estimated moult parameters and a series of explanatory variables were explored. Critical gaps in our understanding of primary moult were revealed. The available data are taxonomically biased towards Charadriiformes and Passeriformes and there are substantial gaps in coverage across the phylogenetic tree. There are severe biases in the global distribution of moult studies across continents, with Africa having almost half of all applications of the Underhill-Zucchini moult model. Latitude emerged as an important explanatory variable but there are latitudinal gaps in the data, especially from the tropics extending to 40°N and in the far northern and far southern hemispheres. Citizen scientists, both bird ringers and photographers, have a key role to play in helping to fill these data gaps. An emerging pattern in the available data is that the timing of primary moult is more synchronised in populations in far northern and far southern latitudes than in temperate or tropical zones, but more data in the far south is needed to confirm this. Timing of moult shows great variability in the tropics and sub-tropical regions of the southern hemisphere. In species that undertake an annual sequential moult, larger birds take longer to moult than smaller birds, but the allometric relationship is not tight. Migrants appear to be more synchronised in their moult than residents.

Keywords: bird ringing, citizen science, latitudinal studies, annual sequential moult

INTRODUCTION

Newton (2009) highlighted the overall lack of knowledge of the primary moult of birds and the importance of this information in understanding their annual cycles. He pointed out that the quantitative study of moult "can be used to throw light on aspects of bird ecology that are otherwise hard to study." He stated that these gaps in knowledge, filled by moult studies, would improve conservation recommendations for birds. Both explicitly, within the paper, and implicitly, by publishing this important paper in the journal *Ringing & Migration*, Newton (2009) recognised the key role of citizen scientists in the study of avian moult. In Newton's (2009) thinking, the citizen scientists were bird ringers. Subsequently, a second category of citizen scientists has also made a contribution. These are photographers whose passion includes the challenge of taking photographs of open wings in such a way that moult status can be recorded in the same way as a bird ringer does with a bird in the hand (de Beer et al. 2000). The first quantitative study of primary moult using digital photographs as the data source was on the Black Skimmer *Rynchops niger* (Vieira et al. 2017); this has been followed up by a study of the moult of the African Oystercatcher *Haematopus moquini* (Bate et al. submitted).

Newton (2009) also highlighted the existence of custom-built models for the quantitative analysis of primary moult, referring in particular to the moult model of Underhill and Zucchini (1988). Other statistical approaches have been shown to introduce bias into the estimates of the parameters of moult (Underhill and Zucchini 1988). An important milestone since Newton's paper was the development, by Erni et al. (2013), of a universally available algorithm to implement the moult model in the R environment (R Core Team 2019).

Remisiewicz (2011) and Dietz et al. (2015) recognised that moult analyses which used the Underhill-Zucchini moult model provided results which were comparable between species and that the sample size of primary moult studies of migrant waders had grown to a size that inter-species analyses were feasible. Remisiewicz (2011) showed how wing length, latitude of the moulting grounds and migration distance affect the timing and duration of primary moult of waders. Dietz et al. (2015) explored the effect of body mass and latitude on moult duration using data from studies on 27 wader populations of 11 different species. They found that larger and smaller waders had different latitudinal relationships with moult duration and that the moult duration for waders moulting in the northern hemisphere increased allometrically with body mass, whereas there was no correlation between moult duration and body mass for waders moulting in the southern hemisphere. Jackson and Underhill (2022) extended these investigations of moult strategies in waders by compiling data from 57 populations of 24 species. The variables explored were moult duration, timing of moult, body mass and moulting latitude. It was found that adult waders that moult at far northern latitudes (>30°N) undergo a consistently early, short moult; those that moult in the zone centred on the equator undergo a more variable moult in terms of timing and duration; and those moulting at more southern latitudes (>30°S) have a consistently late, long moult. In terms of the relationship between body mass and moult duration, smaller waders showed more variability in moult duration than larger waders (Jackson and Underhill 2022).

Hedenström (2006), Rohwer et al. (2009) and Dietz et al. (2015) found an allometric relationship between body mass and moult duration. However, most of the species assessed by Hedenström (2006) and Rohwer et al. (2009) moult in the northern hemisphere and Dietz et al. (2015) only investigated moult in migrant waders breeding in the northern hemisphere. Dietz et al. (2015) realised that the moult differed between the hemispheres and suggested investigating whether moult duration differs between the northern and southern hemispheres in birds generally.

The original aim of this paper was to undertake a comprehensive review, on a global scale, of primary moult in populations of adult birds, both resident and migrant species, and both passerine and non-passerine species. However, preliminary analyses demonstrated that, in 2022, the available data had major shortcomings, so that the envisaged analyses were premature. The revised aims of the paper are thus to create a database of reliable Underhill-Zucchini moult parameter estimates and possible explanatory variables, such as moulting latitude, body mass and taxonomic classification, and to point out the deficiencies in the available information, which consists mainly of critical gaps in knowledge. The paper describes priorities for fieldwork and analysis, in order that key gaps are filled and a global review of primary moult can be undertaken. The focus in this paper is on the substantial majority of bird species for which primary moult is sequential over a single year. We exclude species such as ducks, which moult all their flight feathers simultaneously, and species such as many of the large raptors, which take several years to replace all their primaries.

METHODS

Data assembly

We followed the precedent set by Remisiewicz (2011), Dietz et al. (2015) and Jackson and Underhill (2022) to restrict this database to analyses which had followed the method of Underhill and Zucchini (1988). The reason for doing so is because analyses using alternative statistical approaches have been demonstrated to show biases (Underhill and Zucchini 1988).

All available literature was searched for studies of primary moult in birds that cited Erni et al. (2013) and/or Underhill and Zucchini (1988). Studies that included estimates of primary moult parameters obtained using the Underhill-Zucchini moult model (Underhill and Zucchini 1988) were compiled to generate a moult analysis database. Some species have results for multiple populations at different study sites, which are sometimes reported in a single publication. We treated each population as a single study. Scientific and English common names of species are those used by Gill et al. (2022). To eliminate the potential for bias between adults and juveniles and free-living and captive birds, only results from studies of populations of adult free-living birds were used. The duration of moult, the start date of moult and the standard deviation of the start date were recorded where given. Mid-date of moult was calculated from the sum of the start date and half the duration. We used the mid-date of moult, rather than the starting date estimated by the Underhill-Zucchini moult model, because it can be more reliably estimated (Jackson and Underhill 2022).

Jenni and Winkler (2020) generally defined "moult intensity" as the number of simultaneously growing primaries during moult. This number varies as moult progresses (Chapters 2, 3, 4 and 5, Remisiewicz et al. 2009) and this is therefore not an entirely satisfactory definition. However, Jenni and Winkler (2020, p. 114) also defined moult intensity as the "rate of feather mass production", which is calculated as feather mass/duration. In other words, moult intensity is proportional to the reciprocal of duration, so that as duration increases the number of simultaneously moulting primaries decreases. Morrison et al. (2015) found a strong relationship between duration and number of simultaneously growing feathers of 15 passerine species. However, the relationship plotted in Morrison et al. (2015) is distinctly curvilinear but when it is transformed to the reciprocal of moult duration plotted against the number of simultaneously growing primaries, it becomes linear (pers. obs.). We therefore created the variable moult intensity by taking the reciprocal of duration.

At each study site, each population of each species was classified according to migratory status (resident or migrant, taken from the regional handbooks) and grouped according to the order and family to which it belonged. Body mass was taken from the published study where possible. Where body mass was not given, it was taken from Dunning (2008). We acknowledge that published estimates of body mass for a species often show considerable variation. In this paper, body mass is transformed to a logarithmic scale. Because of this, in the plots in this paper the different available body mass values for a species would almost invariably produce visually equivalent results.

Coordinates of localities for studies were mostly provided in the published papers. Where data were accumulated over a region, we chose a central position. If the coordinates of the study were not given, we used the coordinates of the place name given as the location of the sampling site. Latitudes in the northern hemisphere were given a positive sign whereas southern latitudes were given a negative sign.

We created a rate-of-change-in-day-length explanatory variable by calculating the difference in day length between the day on which moult started and the following day using package "geosphere" (v. 1.5-18) (Hijmans et al. 2022) in R.

Exploratory data analysis methods

Guided by the approaches pioneered by Remisiewicz (2011), Dietz et al. (2015) and Jackson and Underhill (2022), we explored relationships between the moult parameters and a series of explanatory variables. All analyses were performed in R (v. 3.6.2) (R Core Team 2019) and should be treated as having the status of exploratory data analyses (Tukey 1977).

We have sought to determine how representative the data are and if there is bias in the distribution of Underhill-Zucchini analyses across taxonomic orders, continents and latitudes. We are interested in how the timing of moult, synchronicity of moult and the duration of moult vary with latitude. How the intensity of moult varies with the rate of change in day length measured at the start of moult will be investigated. When day length is rapidly decreasing at the start of moult, it is expected that the birds might have a shorter, more intense moult so that they can complete moult before harsh winter conditions set in. We will look at how duration and intensity of moult vary with species mass and if there is there is a physiological limit as to the how intensely birds of given mass can moult. This chapter further examines how moult duration and synchronicity of moult within a population varies between migratory and resident species, the idea being that migratory species should have a shorter, more synchronous moult than residents because of time constraints imposed by their annual cycles.

In most studies, the scatter plots generated by plotting pairs of variables are a means to an end. They are used to infer relationships and to justify the fitting of particular statistical models. In this chapter, the scatter plots are an end in their own right. Our focus is on examining the patterns they display. Following Jackson and Underhill (2022), we make extensive use of quantile regression (Koenker and Bassett 1978, Cade and Noon 2003, Koenker 2005) as an objective framework for examining patterns in the scatter plots, assisting with interpretation of plots and providing visual summaries of the data. Quantile regression was implemented in R using the rq() function from the "quantreg" package (v. 5.95) (Koenker 2023). We used both linear and quadratic relationships in the quantile regressions, and only plotted lines and curves that were statistically significant. Quantile regression was used solely for interpretation of patterns.

In a least squares regression, the objective is to find the line which minimises the sum of the squares of the vertical distance between the line and the points in the scatter diagram. It is a line which, in some sense, passes through the "middle" of the points in the scatter diagram. In contrast, with a quantile regression it is possible to fit a line that goes through any quantile of the data in the scatter diagram (Koenker and Bassett 1978). The 50% quantile regression line has half the points above it and half below it, and of all possible lines that achieve this, the objective is to fit the line which minimises the sum of the absolute differences between the line and the points in the scatter diagram. We also make extensive use of the 10% and 90% quantile regressions. The former has 10% of the points below the line and 90% above it, and vice versa for the latter. In other words, the 10% quantile regression helps define the shape of the "bottom" of the scatter diagram, and the 90% quantile regression helps define the shape of the "top" of the scatter diagram. All quantiles are feasible in the algorithm used to fit the lines. The 10%, 50% and 90% quantiles were chosen because of the size of our database made this a sensible option. The same algorithm is used for fitting all quantile regression lines. For lines other than 50%, the description is more complex than the 50% quantile regression but the algorithm uses the same concept, namely sums of absolute residuals. The 50% quantile regression (or median regression) is not the same as a least squares regression, because the former has an objective function minimising the sums of absolute residuals, whereas the latter is minimising the sums of squared residuals. This difference results in quantile regression being more robust than least squares regression, in the sense that it is less likely to be influenced by outliers. Jackson and Underhill (2022) provide further insights into quantile regression and its applications.

We summarised the analyses taxonomically by order and geographically by continent. We plotted the study sites on a world map. The number of Underhill-Zucchini moult analyses per taxonomic order was calculated. In the Passeriformes, the number of families covered by these analyses was tabulated. The number of analyses per continent as well as the distribution of these analyses across 5° bands of latitude was determined.

The mid-date of moult, the standard deviation parameter and the duration of moult were plotted separately against latitude and the 10%, 50% and 90% quantile regression lines were drawn. We also plotted moult intensity against the rate of change of day length.

To explore the allometric relationship between primary moult duration and body mass, we plotted the logarithm of duration against logarithm of body mass. Maintaining the consistency of using quantile regression, we used the 50% quantile regression as a robust approach to the estimation of the allometry. In this case, we also estimated the least squares regression line, to enable direct comparison with other results. We also explored the relationships between the logarithm of mass and both the reciprocal of duration and the logarithm of the reciprocal of duration.

Migrant species have to allocate time for two migratory journeys (and time for preparation for migration) into their annual cycles. Because moult and breeding rarely overlap, we anticipated that the time available for moult might be shorter for migrants than for residents. Likewise, due to the same constraints, we anticipated that primary moult would be more synchronised for migrants than residents. We tested these hypotheses for duration and standard deviation of start date of moult using the Mann-Whitney test.

RESULTS

A total of 260 studies were found which had used the Underhill-Zucchini moult model (Appendix 1). These included 143 species, of which 49 had moult data recorded for more than one population. All studies reported the estimate of the parameter for the mean starting date, 256 studies reported the estimate of the duration parameter and 214 reported the estimate of the standard deviation parameter.

The species were distributed across eight taxonomic orders and 40 families. The majority of moult analyses (94%) focused on species in two orders: Passeriformes (60%) and Charadriiformes (34%) (Table 1). Within the Passeriformes moult analyses have been undertaken for 25 families, with the largest number of analyses in the Ploceidae (31 studies on 16 species) (Table 2).

Geographically, Africa was the continent with the most moult analyses (128, 49%), followed by Europe (68, 26%) (Figure 1). Together, North and South America had 15 analyses. The spatial bias in the studies is further emphasised in the global map of study sites (Figure 2). Several studies were frequently made at single sites. Therefore, although South America had eight studies (Figure 1), they were located at two sites (Figure 2).

More primary moult analyses using the Underhill-Zucchini model have been done in the southern hemisphere (159, 61%) than in the northern hemisphere (101, 39%) (Figure 3). There was a substantial gap in latitudinal coverage between 40°N and 15°S, with a total of 40 studies (15% of the total) between these latitudes, despite this zone containing a large fraction of the available terrestrial habitat. In the northern hemisphere the continents stretch to c. 75°N and there were 16 studies north of 55°N. In the southern hemisphere, both South America and Oceania stretch south of 35°S, with the former stretching to 56°S. There were 24 studies south of 35°S and none south of 45°S (Figure 3).

Figure 4 relates the timing of moult, expressed as the mid-date of primary moult, to latitude. The three quantile regression lines (10%, 50% and 90%) summarise the underlying pattern of the available data. In the northern hemisphere, at latitudes from 30°N and northwards, moult took place towards the end of the boreal summer and into autumn (July–September). Variability in the timing of primary moult appeared to increase southwards towards the tropics and the southern hemisphere. With the available data, the greatest variability occurred between 15°S–30°S, when the mid-date of primary moult occurred throughout the year (Figure 4). Note that the Discussion will argue that these results are misleading.

The standard deviation of start date provides a measure for how synchronised moult is within the population of a species at a site (Figures 5, 6 and 7). Overall, based on the available data, there was a clear trend for smaller standard deviations (and therefore greater synchronicity) at far northern latitudes than in the southern hemisphere (Figure 5). Figure 6 shows the pattern for the northern hemisphere only. There was greater synchronicity of moult in the far north than in the northern tropics. Closer inspection of Figure 5 suggests that the overall pattern of larger standard deviations was not maintained at the most southerly latitudes for which data were currently available. This is evident in Figure 7, which demonstrates greater synchronicity at the southernmost latitudes for which data were available.

The duration of primary moult appeared to be relatively short in the northern hemisphere and longer and more variable in the southern hemisphere (Figure 8). The form of the 10% quantile regression is quadratic, suggesting that the duration of primary moult was shorter at high latitudes, for at least some species, than it was in the tropics. As with Figure 4, the Discussion will point out that, once additional data are available for the tropics, the overall pattern displayed by these results might be misleading.

When day length was decreasing rapidly at the start of primary moult, the available data suggested that the duration of moult was short and birds underwent a moult of high intensity. However, moults of short durations and high intensity also occurred when the rate of change of day length was close to zero (Figure 9). The longest moult durations occurred when day length was increasing. The quadratic relationship for the 10% quantile regression suggests that there were no exceptionally rapid durations for primary moult when day length was increasing by two or more minutes per day at the start of moult (Figure 9).

There was an allometric relationship between mass and duration (Figure 10). The relationship suggested by the 50% quantile regression line fitted to the logarithms of both variables was $\text{duration}=52.79\ \text{mass}^{0.149}$. However, the 10% and 90% quantile regression lines were far apart, suggesting that the allometric relationship was not tight. For completeness, the allometric relationship obtained using conventional least squares regression was $\text{duration}=53.76\ \text{mass}^{0.144}$ (the standard error of the exponent of mass was 0.017, $t_{251}=8.2$, $P<0.0001$) and that obtained from reduced major axis regression was $\text{duration}=51.43\ \text{mass}^{0.155}$.

Figures 11 and 12 explore the relationships between the inverse of duration and mass. The inverse of duration is proportional to the daily increase in the moult index and therefore to moult intensity. From the quantile regression, the allometric relationship between these two variables was $\text{intensity}=0.0189\ \text{mass}^{-0.0149}$ (Figure 12). From the least squares regression the relationship was $\text{intensity}=0.0186\ \text{mass}^{-0.0144}$ (the standard error of the exponent of mass was 0.017, $t_{251}=-8.2$, $P<0.0001$) and from the reduced major axis regression it was $\text{intensity}=0.0169\ \text{mass}^{-0.0155}$. The relationships between the pairs of models in this paragraph and the one above are a mathematical consequence of the properties of logarithms.

The median durations of moult for migrants and residents were 95 days ($n=115$) and 99 days ($n=136$) respectively and were not significantly different (Mann-Whitney $U = 7074.5$, $P = 0.19$) (Figure 13). If the standard deviation parameter in the moult model is small, it indicates that moult is synchronised and the stage of moult for birds in the population are all close to the moult trajectory of the average bird. The medians of the estimated standard deviation parameters for migrants and residents were 16 days (n=87) and 24 days (n=126) respectively. Thus, the primary moult of migrants was more synchronised than that of residents (Mann-Whitney U = 3698, P<0.001) (Figure 14).

DISCUSSION

Quantile regression

As in Jackson and Underhill (2022), quantile regression (Koenker and Bassett 1978, Cade and Noon 2003, Koenker 2005) was used in the role of exploratory data analysis (Tukey 1977). In least squares regression analysis, the focus is on the mean of the response variable in relation to the explanatory variable. If prediction intervals are included in a plot showing a least squares regression line these are essentially parallel to the regression line (Figure 15). Their calculation involves an assumption of homoscedasticity, in other words that the distribution of "errors" along the regression line is identical. Quantile regression enables the nature of the heteroscedasticity to be revealed. These points are illustrated in Figure 15. Note that the 50% quantile regression line, effectively the median regression line, is similar to, but not identical to, the least squares regression line, i.e. the "mean" line (Figure 15).

Gaps in knowledge

The most notable outcome of this review is the fact that it exposes the gaps in our understanding of primary moult in quantitative terms. This is true in relation to every fundamental measure of the representativeness of the data: for example, by taxonomy (Tables 1 and 2), continent (Figures 1 and 2) and latitude (Figure 3).

The available data are taxonomically biased. Only eight of the 38 orders of flying birds (Gill et al. 2022) have at least one species with its primary moult parameters estimated using the Underhill-Zucchini model, with most of the analyses attributed to two orders (Charadriiformes and Passeriformes) (Table 1). Likewise, within the Passeriformes, the analyses are not well distributed across the families (Table 2). This highlights a substantial gap in coverage across the phylogenetic tree.

Furthermore, a major shortcoming of the available results is their geographical bias. The most serious shortfall is the lack of data from the tropics and extending north to 40°N (Figures 2 and 3). There are also severe biases in relation to the global distribution across the continents (Figures 1 and 2). Once these gaps are addressed it will be feasible to do a comprehensive review of primary moult.

Suggestions for further investigation

From Figures 4 to 8, it is clear that latitude is an important explanatory variable in relation to the parameters of primary moult. But it is possible, and probably likely, that the patterns exhibited in these figures are somewhere between incomplete and misleading. It is probable that these plots capture the variability of timing of primary moult (Figure 4), its standard deviation (Figures 5 to 7) and its duration (Figure 8) at latitudes 55°N to 40°N and from 15°S to

35°S, but not in the far north, the far south and a broad band of latitudes north and south of the equator. In particular, it is likely that the biggest shortfall in data is the last-mentioned zone, between latitudes 40°N and 15°S. Once more results from this zone are available it is likely that the patterns in Figure 4 to 8 will change radically.

The relationship which the available data are suggesting is that in far northern latitudes the mid-date of moult lies in the boreal late summer and autumn, after the spring-early summer breeding season, and avoiding the harsh winter period (Figure 4). At the southernmost latitudes for which data are available, especially south of 40°S, the complementary pattern appears to be emerging, with the mid-date of moult in the austral autumn (Figure 4), consistent with a predominant breeding season in the austral spring. Between 15°S and 25°S there are a total of 40 moult studies (Figure 2); the mid-dates of moult are scattered throughout the calendar year (Figure 4). In this latitudinal band, temperatures are relatively warm throughout the year but seasonality and regularity of rainfall, and therefore food availability, vary considerably. The timing of breeding and moult is therefore variable depending on local conditions (e.g. Jackson and Underhill 2022). Once more data become available for latitudes between 40°N and 15°S it is likely that the pattern shown between these latitudes will change dramatically and that the mid-dates of moult will be shown to occur throughout the year. The lack of cold conditions continues as far north as c. 30°N. It is therefore likely that this lack of seasonal pattern in the timing of primary moult might extend as far north as this, beyond which the tendency for the mid-date of moult to be in the boreal autumn will start to predominate. Based on the above discussion, we hypothesise that the actual pattern will be like Figure 16.

Likewise, the current pattern between latitude and the standard deviation parameter (Figure 5) is likely to prove misleading once additional data become available. We anticipate that there will be a lot more species with large standard deviations in the tropics (i.e. unsynchronised moult). We anticipate small standard deviations (i.e. synchronised moult) when additional analyses become available from places such as the South Island of New Zealand and southern South America (Figure 7 hints at this). We predict that the 90% quantile regression (currently a straight line in Figure 5) will show a quadratic pattern, with a maximum value in the tropics and decreases towards high latitudes in both the southern and northern hemispheres.

Although the parameters of primary moult are clearly related to latitude (Figures 4 to 8), it is an explanatory variable implying relationship and not causation. It is a proxy for the real causal explanatory variables, which would include temperature, seasonality, day length, and many others. In northern latitudes, north of c. 45°N, primary moult mainly takes place after breeding and ahead of harsh winter weather (Figure 4). A similar pattern is developing in the southern hemisphere (Figure 4), but more studies south of 35°S are needed to confirm this. It is clear that in the north and south, explanatory variables such as temperature and seasonality, for which latitude is a proxy, dominate the parameters of moult. However, in the tropics, it is likely that species-specific factors and local conditions dominate in determining the timing of moult. For example, in Thailand (13°N), Long-toed Stints *Calidris subminuta* moult rapidly near the end of the wet season when food is most abundant (Round et al. 2012). In Kenya (3°S), Greater Sand Plovers *Charadrius leschenaultii* moult slowly because the only constraint is to complete moult prior to fattening for migration in February/March (Jackson 2017).

Given that latitude is not, in itself, a causal variable, we searched for alternatives. We tried to relate rate of change in day length measured at the start of moult to duration (Figure 9). Rate of change in day length is a complex variable, an interaction of both latitude and calendar date. The underlying hypothesis was that the duration of moult should be short when day length is decreasing rapidly, because large negative values for this variable can be interpreted by the bird as an indication that harsh winter conditions are approaching and that a rapid moult rate is needed, with the outcome that duration would then be short. This variable showed promise, with short moult durations when day length was decreasing rapidly and no short durations when day length was increasing rapidly. However, when day length was stable there was a large variation in moult durations (Figure 9).

We explored the allometric relationship between the duration of primary moult and bird mass, where the focus is on the exponent of mass (Figure 10). There have been three studies which have examined this allometric relationship (Hedenström 2006, Rohwer et al. 2009, Dietz et al. 2015). Hedenström (2006) used a sample of 60 European passerines with durations fitted "by eye" in Ginn and Melville (1983) and derived the allometric relationship: duration=34.4 mass$^{0.19}$. He considered this result preliminary. Rohwer et al. (2009), based on primary moult durations for 43 species obtained using a variety of methods, claimed that the exponent of mass was 0.14. Dietz et al. (2015) found the exponent of mass to be 0.17 for 13 species of northern hemisphere waders with durations estimated using the Underhill-Zucchini moult model. Using least squares regression (the recommended method for finding allometric relationships, Kilmer and Rodríguez 2016) we found the relationship: duration=53.76 mass$^{0.144}$. Our relationship estimates durations longer than that of Hedenström (2006). For example, for a bird with a mass of 100 g, the predicted durations are 104 days and 83 days, respectively. The direction of the difference is unsurprising, given that Hedenström's (2006) results were based on European species moulting either under the constraint of impending migration or the advent of cold weather.

Figures 11 and 12 present the same underlying information as Figure 10, but with a different visual emphasis. In Figure 11, increases along the y axis, for birds of a given mass, can be interpreted as measuring increasing moult intensity. The striking feature of Figure 11 is that the upper right corner contains no values. This is not a consequence of data limitations but a physiological reality. There appears to be a physiological frontier of moult intensity for birds at a certain mass. This frontier must lie above the 90% quantile regression line in Figure 11. Species moulting close to this frontier are probably producing poor quality primaries. In contrast, species which lie below the 50% quantile regression line are probably producing high quality primaries. It remains to be seen whether the bottom left corner of Figure 11 remains empty once additional data are available. Species in this corner would consist of birds with small mass and long moult durations; these are potentially species from the tropics, which is the region with the largest data deficiency (Figures 2 and 3). Based on this discussion, and the insights on moult intensity in relation to feather quality in Jenni and Winkler (2020), Figure 17 encapsulates the hypotheses proposed in this paragraph. The concepts presented here should be investigated further. In particular, the relationship between the traditional definition of moult intensity as average number of growing primaries and the definition suggested here, the reciprocal of moult duration, needs attention.

Figure 12, with logarithms on both axes, lays the foundation for the allometric relationships between the proposed new definition of moult intensity and mass. However, as a straightforward property of logarithms, the allometric relation in Figure 12 is the inverse of the relationship in Figure 10 between mass and duration. From a visual communication perspective, Figure 11 is more successful than Figure 12 therefore we do not consider Figure 12 further.

De la Hera et al. (2009) analysed moult durations in 48 European passerine species, also using moult durations fitted “by eye” in Ginn and Melville (1983). They found that larger species took longer to moult than smaller species. After controlling for body mass, moult duration was found to be longer in residents (and short distance migrants) than in long distance migrants. These results are likely to be improved by the use of durations estimated statistically by a quantitative moult model. This also applies to the results of Silveira and Marini (2012) who focused on the primary moult of passerine and non-passerine tropical birds in South America. They found that the duration of moult was longer than in similar temperate-zone species and an increase in body mass was associated with an increase in moult duration. The one migratory species in their study had the shortest moult duration out of the eight studied.

In this study we reported only one result per species per locality. Newton (2009) envisaged annual studies which would reveal long terms trends in each of the parameters of moult and which could be related to environmental conditions in each year. Newton (2009) was thinking in a European, mainly British, context where seasonal variation is relatively small. In many parts of the world, and especially in arid areas in the tropics and near-tropics, there is large variability in the timing and annual amount of rainfall (Underhill 1999). This impacts annual environmental productivity, which in turn impacts the timing of moult (Nwaogu and Cresswell 2021). Thus, consideration needs to be given to the possibility that studies pooling primary moult data across multiple years generate estimated standard deviation parameters which are larger than they would be if only individual years were considered.

In an era of global climate change, there is also a need for repeat studies of moult at, for example, decadal intervals. Even if data volumes are inadequate to undertake annual studies, it might be feasible to accumulate available data over long enough periods, possibly a decade, to ensure that the impact of individual outlying years is relatively small. The only study of this nature that we are aware of is that of Taylor et al. (2018), who found an increase in moult duration of 46% over six decades in Alaska. This is a such a dramatic change that it needs to be compared to the results of further studies of this nature.

As noted in the Introduction, citizen scientists have a crucial role to play in the study of primary moult. Bird ringers have the opportunity to collect moult data while they have the bird in the hand. These fieldwork methods are described by de Beer et al. (2000). Bird ringing schemes need to curate these data. Digital photography (Vieira et al. 2017, Bate et al. submitted) represents an additional source of primary moult data, especially for species that are seldom handled by ringers. Systems need to be devised to curate these images. Remarkably, the protocol for moult data collection by ringers has remained unaltered since it was first developed (Ashmole 1962, Ginn and Melville 1983). A large proportion of primary moult data accumulated by ringers in the early decades of recording moult was not curated by ringing schemes and remains in notebooks. These historical data are of particular value because they will enable the quantification of trends in primary moult parameters through time.

CONCLUSIONS

It is noteworthy that Africa is the leader of quantitative studies of primary moult. Almost half of all applications of the moult model of Underhill and Zucchini (1988) have been undertaken on birds on this continent.

However, this is also a symptom of the major shortcomings of the current database. In every aspect considered there are unfortunate data gaps. The fact that half the analyses are African is a consequence of many other continents having little data. Citizen scientists, both bird ringers and photographers, have a key role to play in helping to fill the data gaps.

Latitude emerged as the dominant explanatory variable. But there are latitudinal gaps in the data, especially in the tropics, in the far northern hemisphere and at the southern limits of the continents of South America and Oceania, especially the South Island of New Zealand.

The main pattern that appears to be emerging is that primary moult is more synchronised across populations of all species at far northern latitudes than in temperate or tropical zones. Individuals within populations moulting in the far north all tend to moult at the same time to ensure that moult is finished before the harsh winter conditions set in. This pattern is clear in the northern hemisphere and is an emerging trend in the southern hemisphere. The available data for the tropics and for sub-tropical climates of the southern hemisphere display a great deal of variability in the timing of moult.

In these analyses, latitude is acting as a proxy for the true explanatory variables. In the far north and far south, latitude, combined with calendar date, is a satisfactory proxy for variables such as temperature, day length, seasonality, and ultimately food availability. Across the tropics and sub-tropics, the true factors that determine timing of moult are much less related to latitude but more to species-specific factors and local conditions. A single latitude can straddle habitats ranging from deserts to tropical rainforests. Thus, the lack of any consistent pattern with regard to moult is thus the anticipated result in the tropics and sub-tropics. The challenge in these areas is going to be finding the actual variables explaining the parameters of primary moult.

In broad terms, among species that undertake an annual sequential moult, larger birds take longer to moult than smaller birds. But the allometric relationship is not tight. Migrants appear to be more synchronised in their moult than residents. This is expected for migrants because they must fit migration into their annual cycles along with breeding and moult.

The objective of this paper was to describe the statistical patterns that are emerging as the number of quantitative analyses using the moult model of Underhill and Zucchini (1988) increases. Moult, however, is a physiological process, controlled by endogenous and exogenous factors (Jenni and Winkler 2020). A next step would be to explore these patterns of moult in relation to these factors.

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Table 1. Taxonomic orders of birds with studies using the moult model of Underhill and Zucchini (1988). The number of species in each taxonomic order was obtained from Gill et al. (2022). The number of analyses and the number of species with analyses were derived from Appendix 1.

Taxonomic order	Number of species in each taxonomic order	Number of Underhill-Zucchini moult analyses	Number of species with Underhill-Zucchini moult analyses
Accipitriformes	266	1	1
Apodiformes	497	1	1
Charadriiformes	390	89	46
Columbiformes	351	4	4
Passeriformes	6533	156	85
Piciformes	449	2	2
Procellariiformes	147	5	3
Suliformes	61	2	1

Table 2. Taxonomic families of passerine birds with studies using the moult model of Underhill and Zucchini (1988). The number of species in each taxonomic family was obtained from Gill et al. (2022). The number of analyses and the number of species with analyses were derived from Appendix 1.

Taxonomic family	Number of Underhill-Zucchini moult analyses	Number of species with Underhill-Zucchini moult analyses
Acrocephalidae	1	1
Aegithalidae	2	1
Cisticolidae	6	2
Corvidae	1	1
Emberizidae	3	2
Estrildidae	14	9
Fringillidae	18	10
Furnariidae	1	1
Hirundinidae	1	1
Motacillidae	1	1
Muscicapidae	7	6
Paridae	3	3
Passerellidae	2	2
Passeridae	4	2
Phylloscopidae	15	2
Ploceidae	31	16
Prunellidae	3	1
Pycnonotidae	7	2
Sturnidae	9	4
Sylviidae	6	3
Thraupidae	2	2
Turdidae	3	2
Tyrannidae	2	2
Viduidae	8	6
Zosteropidae	6	3

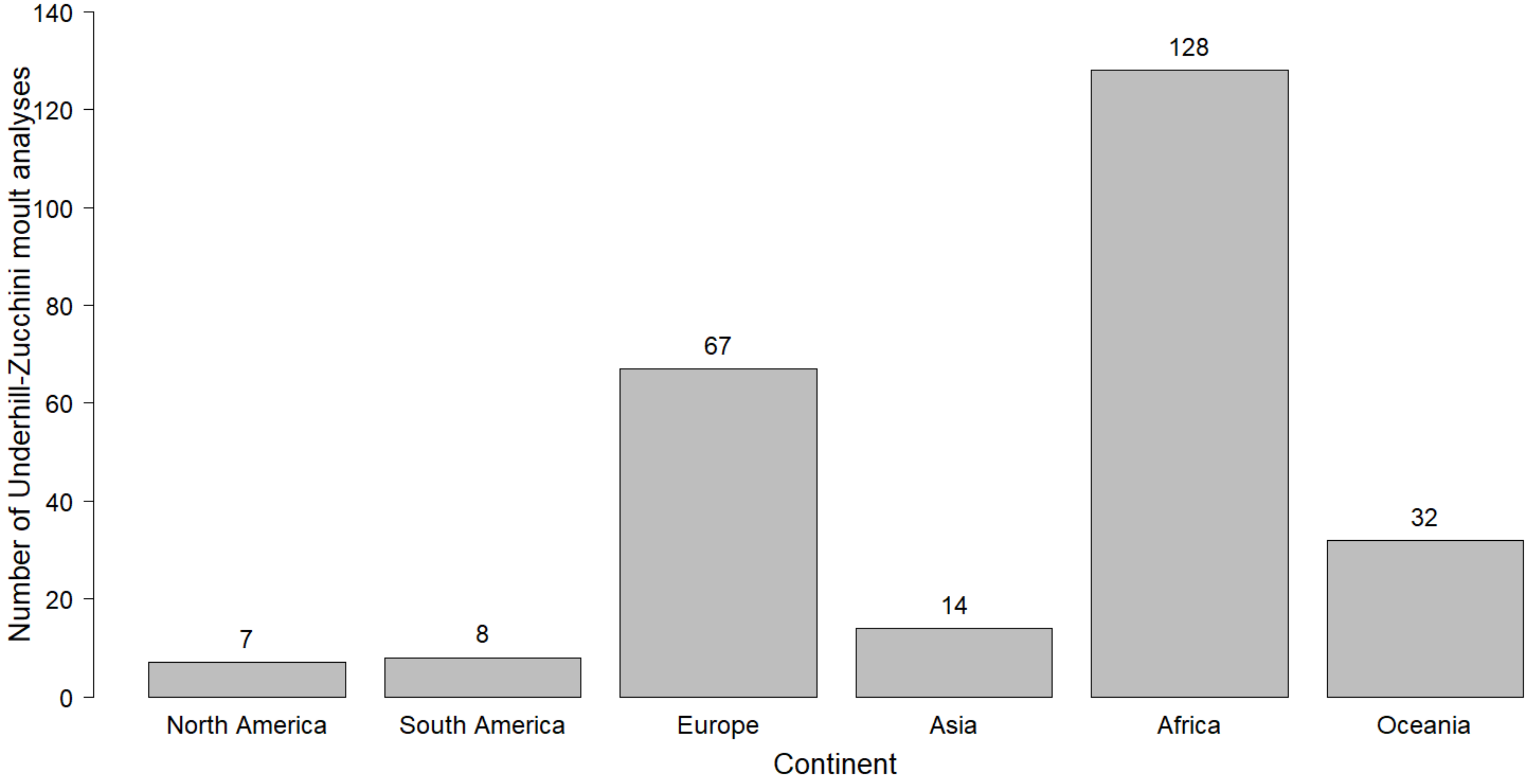

Figure 1. Histogram summarising the number of Underhill-Zucchini analyses by continent. See Figure 2.

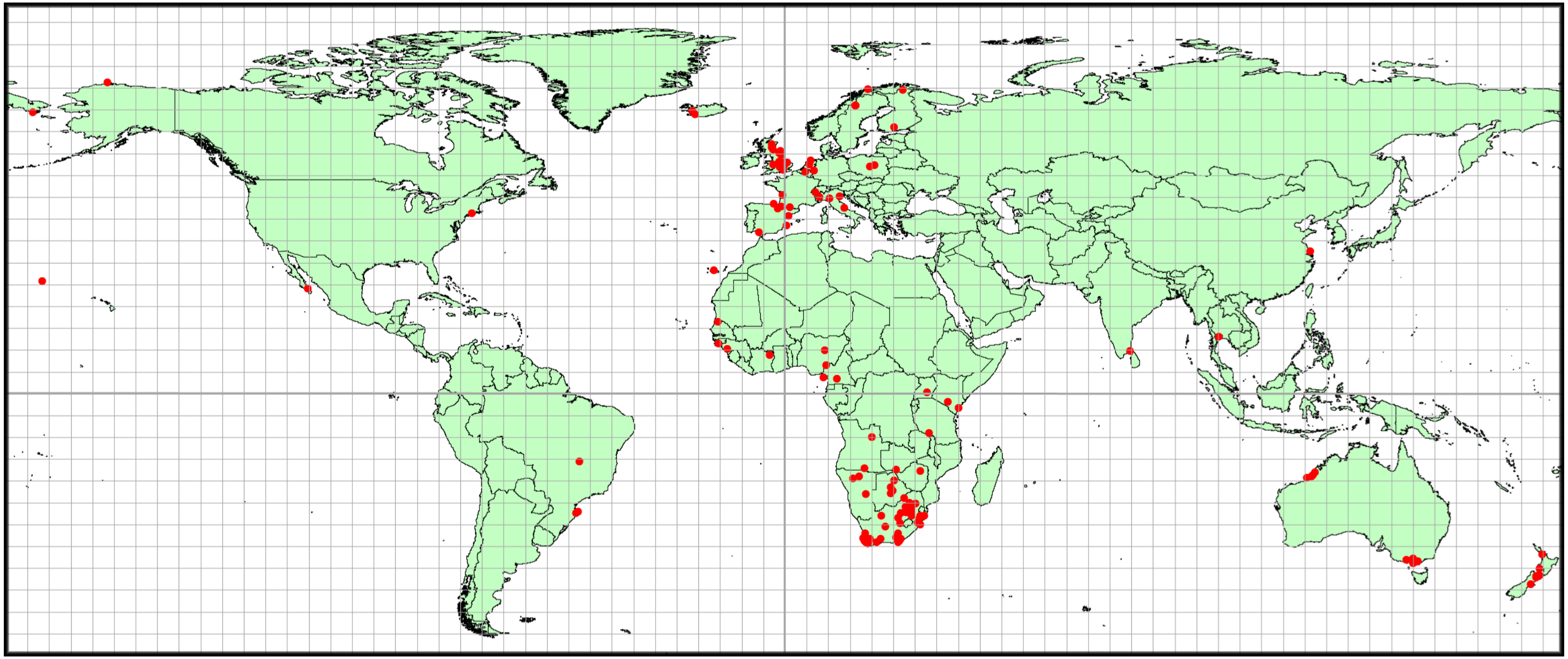

Figure 2. Map of the world showing the locations of bird populations where the Underhill-Zucchini analyses of primary moult have been done (red dots). Some sites have more than one study. Coordinates for the study sites are contained in Appendix 1.

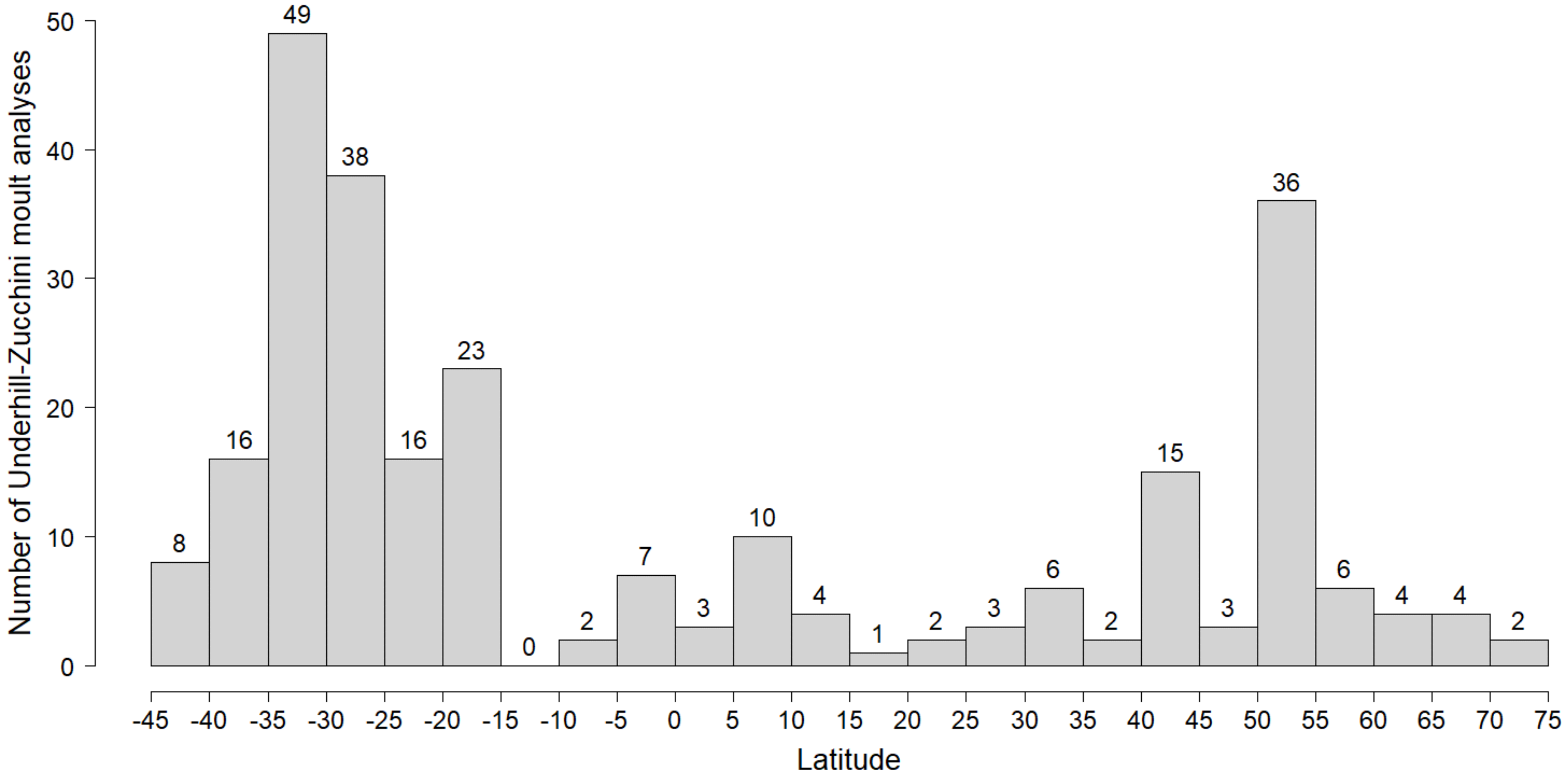

Figure 3. The distribution of Underhill-Zucchini analyses of primary moult in latitudinal bands of 5° widths. Latitudes in the southern hemisphere are negative.

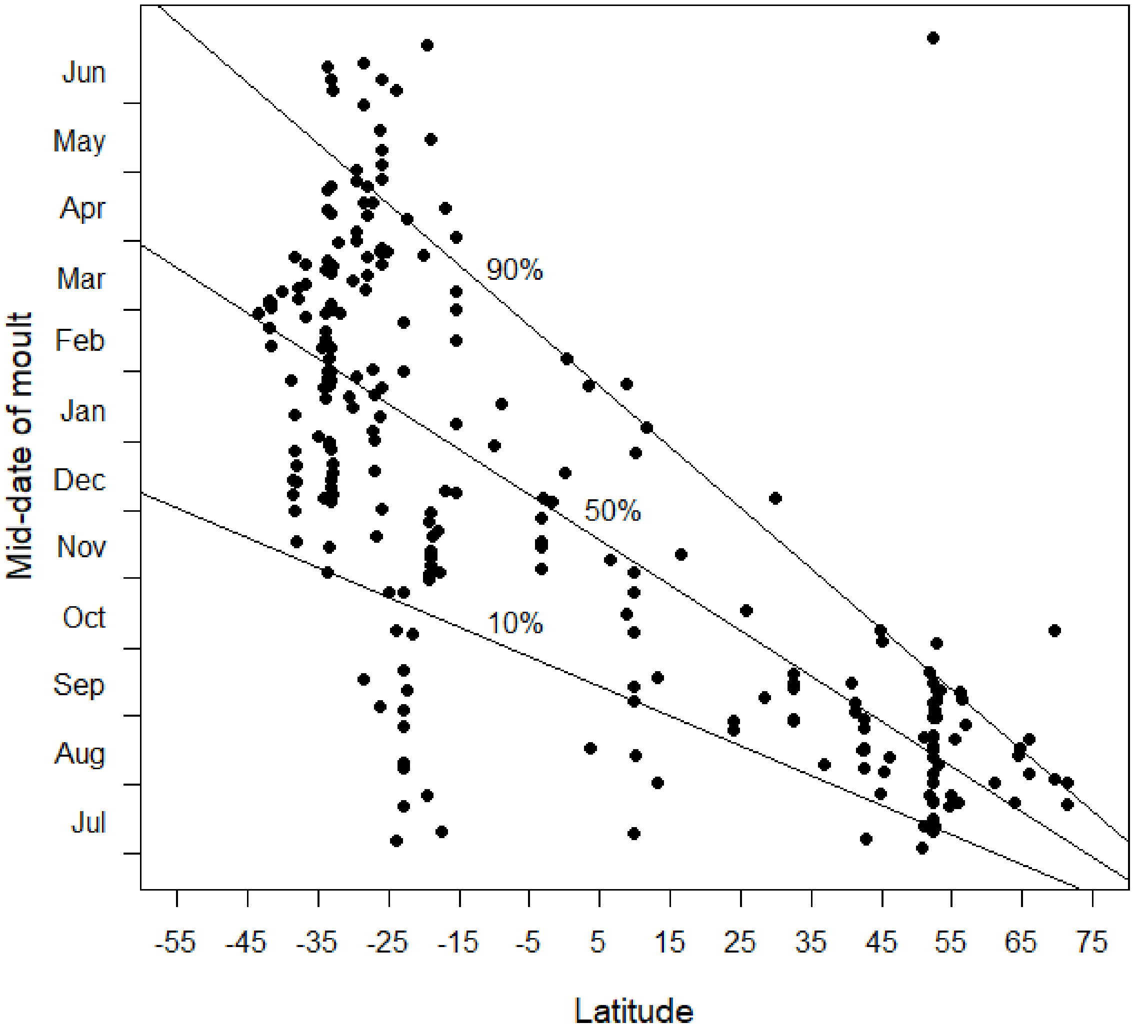

Figure 4. The mid-date of moult (see text) plotted against latitude. Latitudes in the southern hemisphere are negative. The 10%, 50% and 90% quantile regression lines (see text) are shown. The sample size was 257. This plot is criticised in the Discussion.

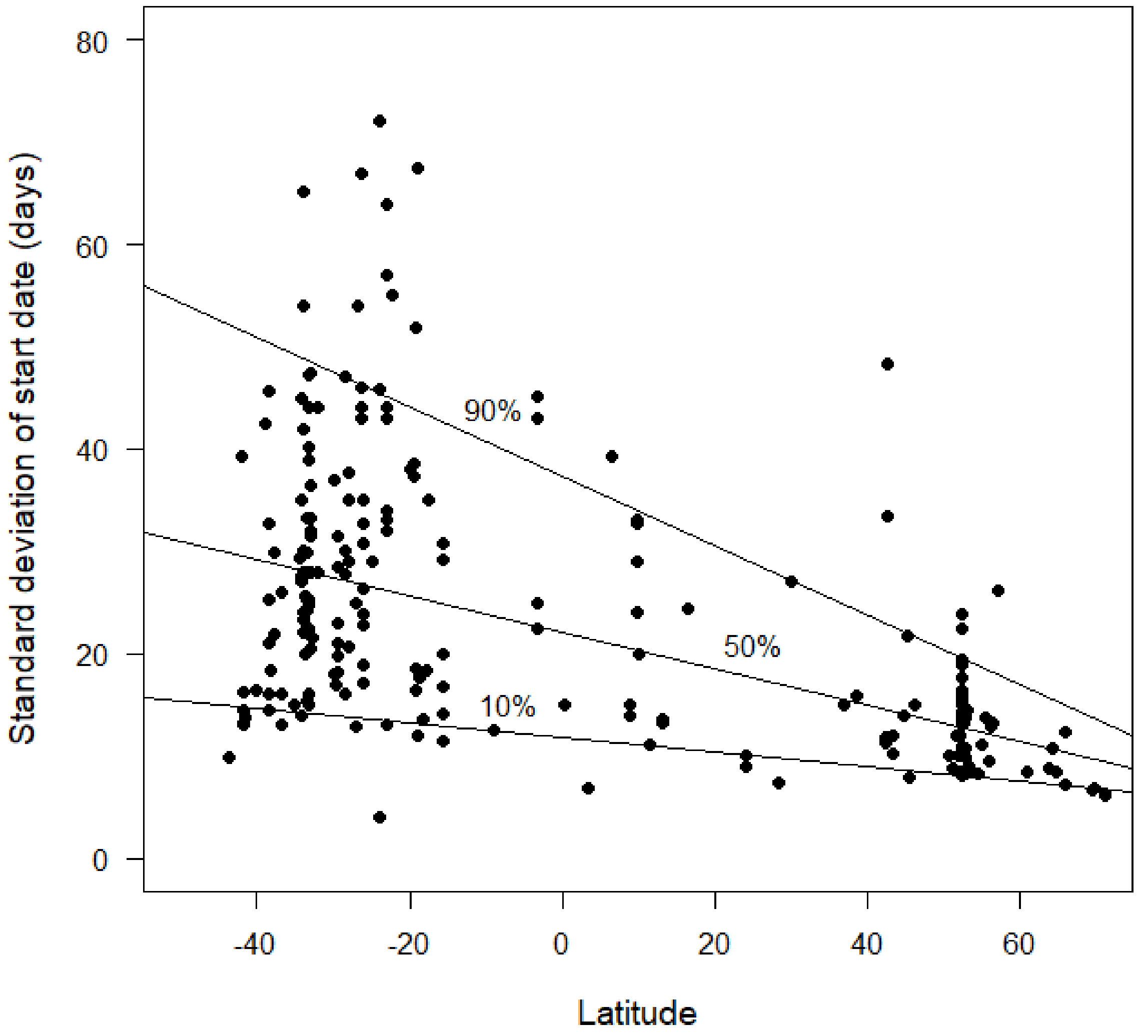

Figure 5. The standard deviation in start date of moult (days), as estimated by the Underhill-Zucchini moult model, plotted against latitude. Latitudes in the southern hemisphere are negative. The 10%, 50% and 90% quantile regression lines (see text) are shown. The sample size was 214.

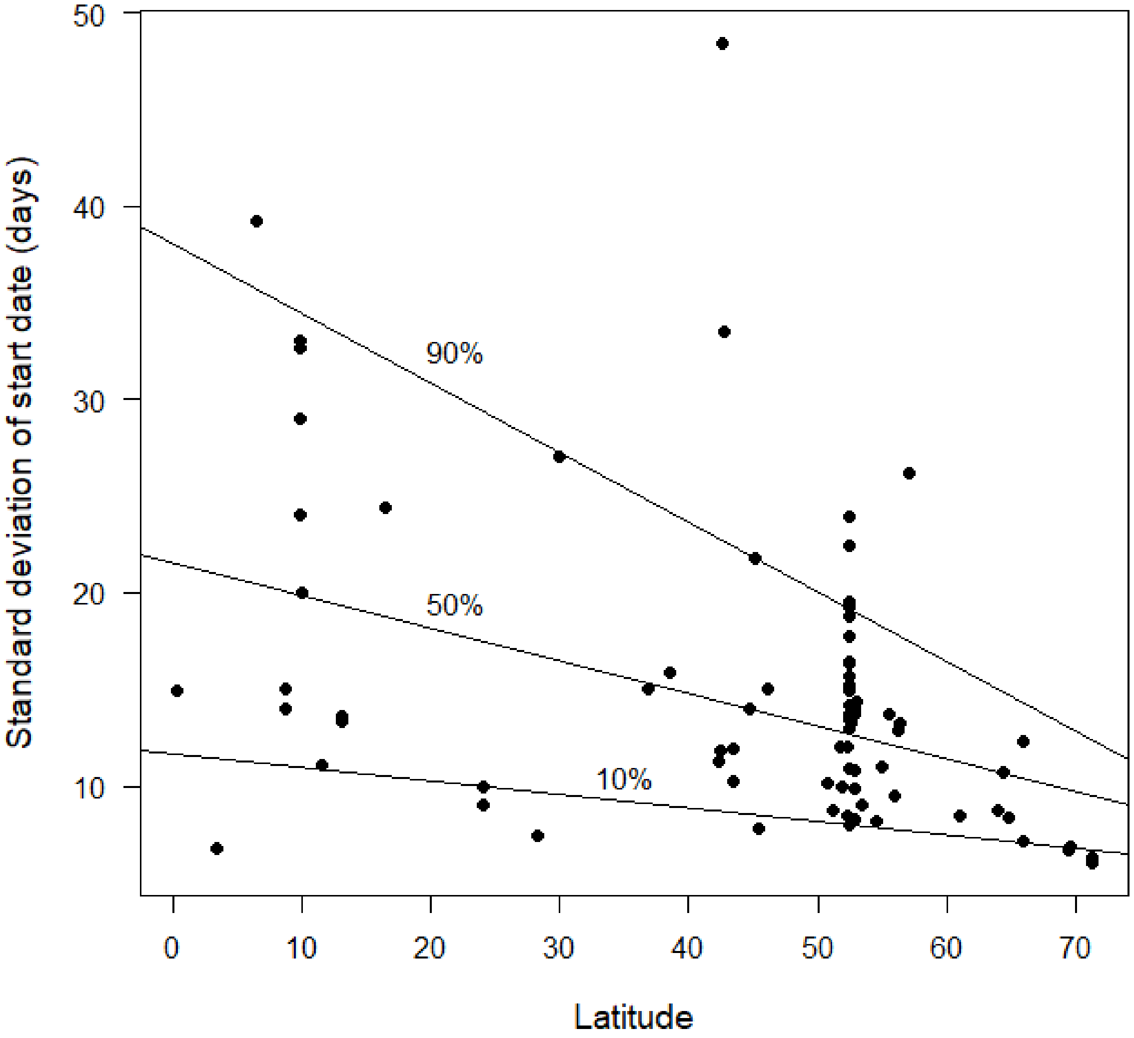

Figure 6. The standard deviation in start date of moult (days), as estimated by the Underhill-Zucchini moult model, plotted against latitude. The plot is restricted to studies in the northern hemisphere. The 10%, 50% and 90% quantile regression lines (see text) are shown. Sample size was 80.

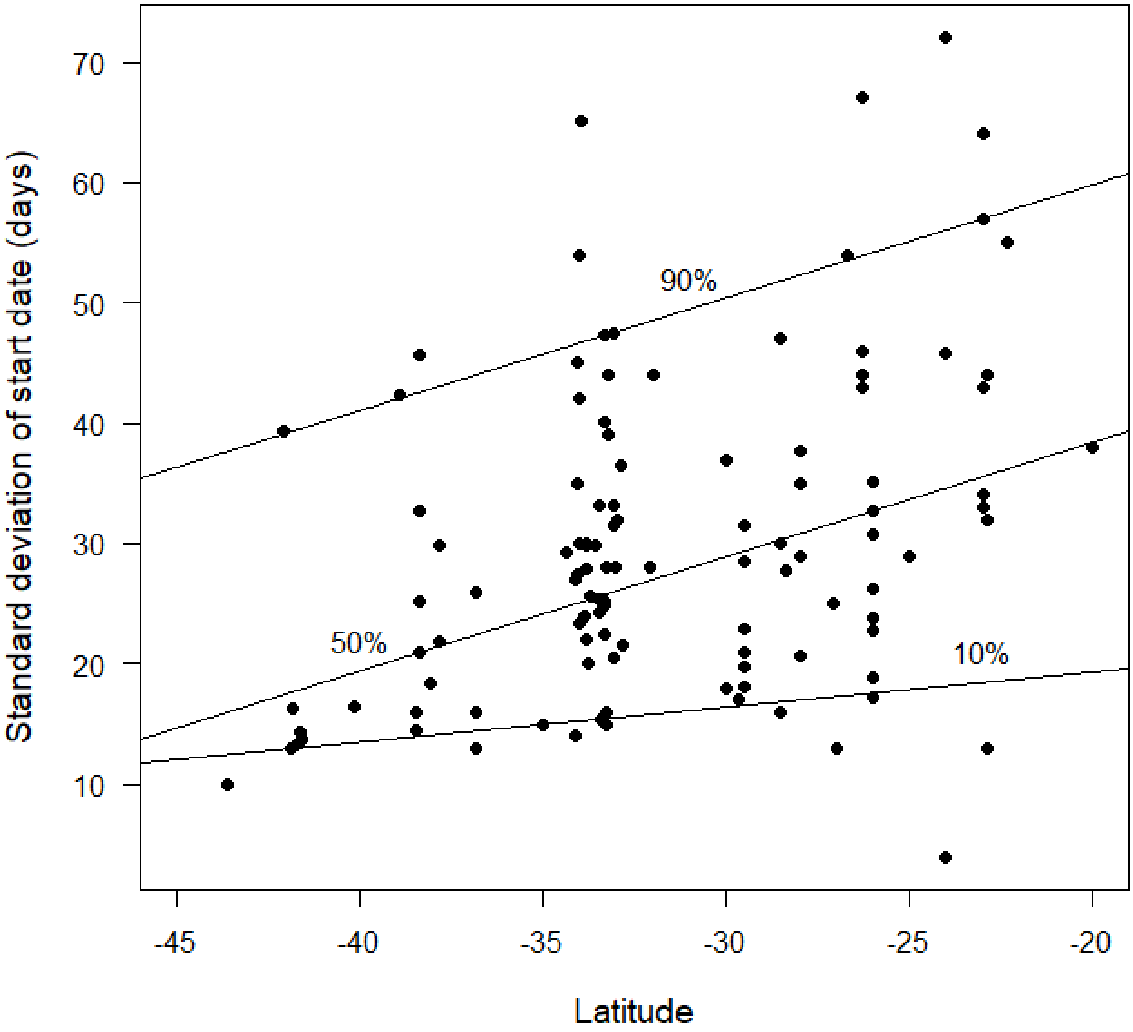

Figure 7. The standard deviation in start date of moult (days), as estimated by the Underhill-Zucchini moult model, plotted against latitude. The plot is restricted to studies in the southern hemisphere, south of 20°S. The 10%, 50% and 90% quantile regression lines (see text) are shown. The sample size was 112.

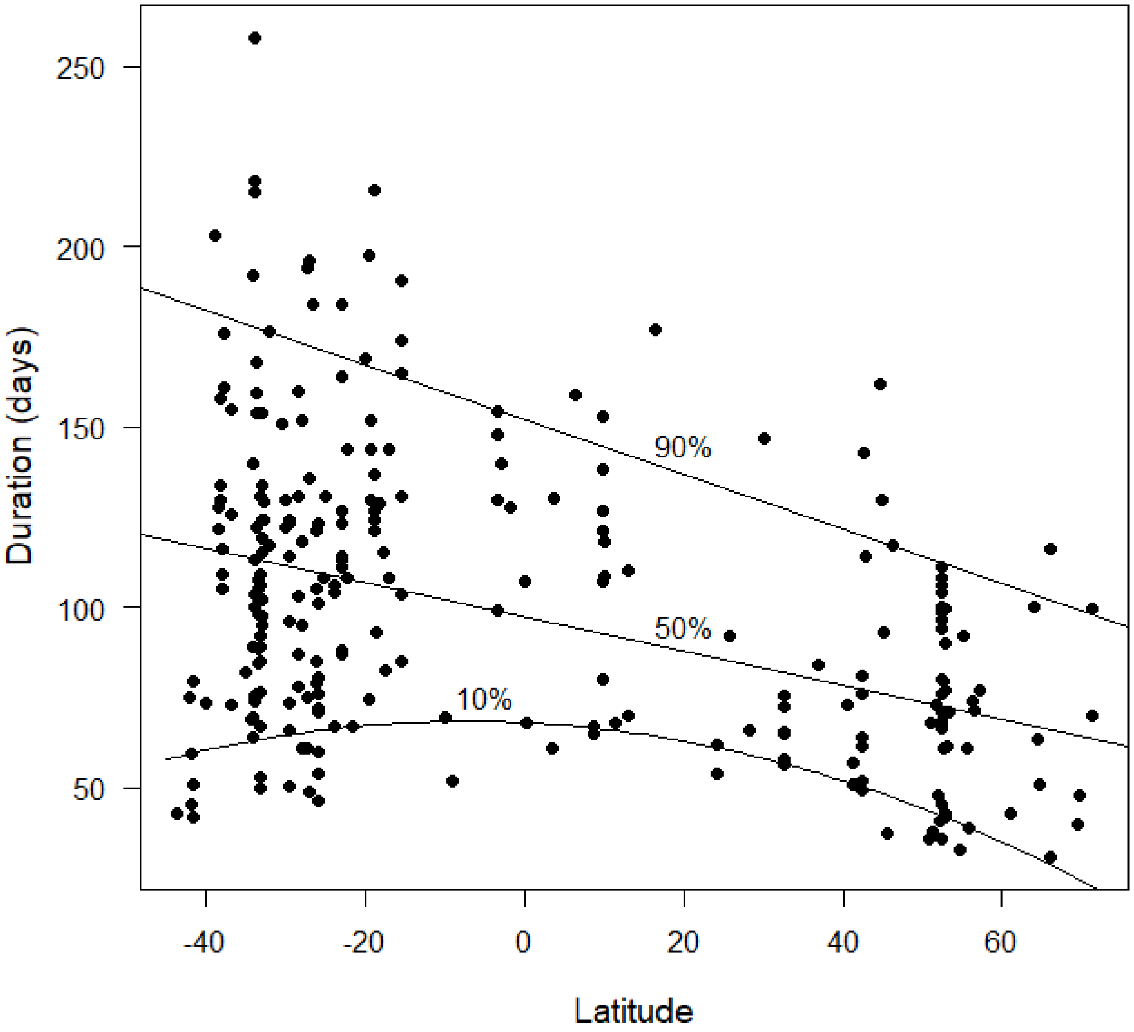

Figure 8. The duration of primary moult (days), as estimated by the Underhill-Zucchini moult model, plotted against latitude. Latitudes in the southern hemisphere are negative. The 10%, 50% and 90% quantile regression lines (see text) are shown. For the 10% quantile regression, the quadratic term was statistically significant but for the 50% and 90% quantile regression lines only the linear term was significant. The sample size was 256.

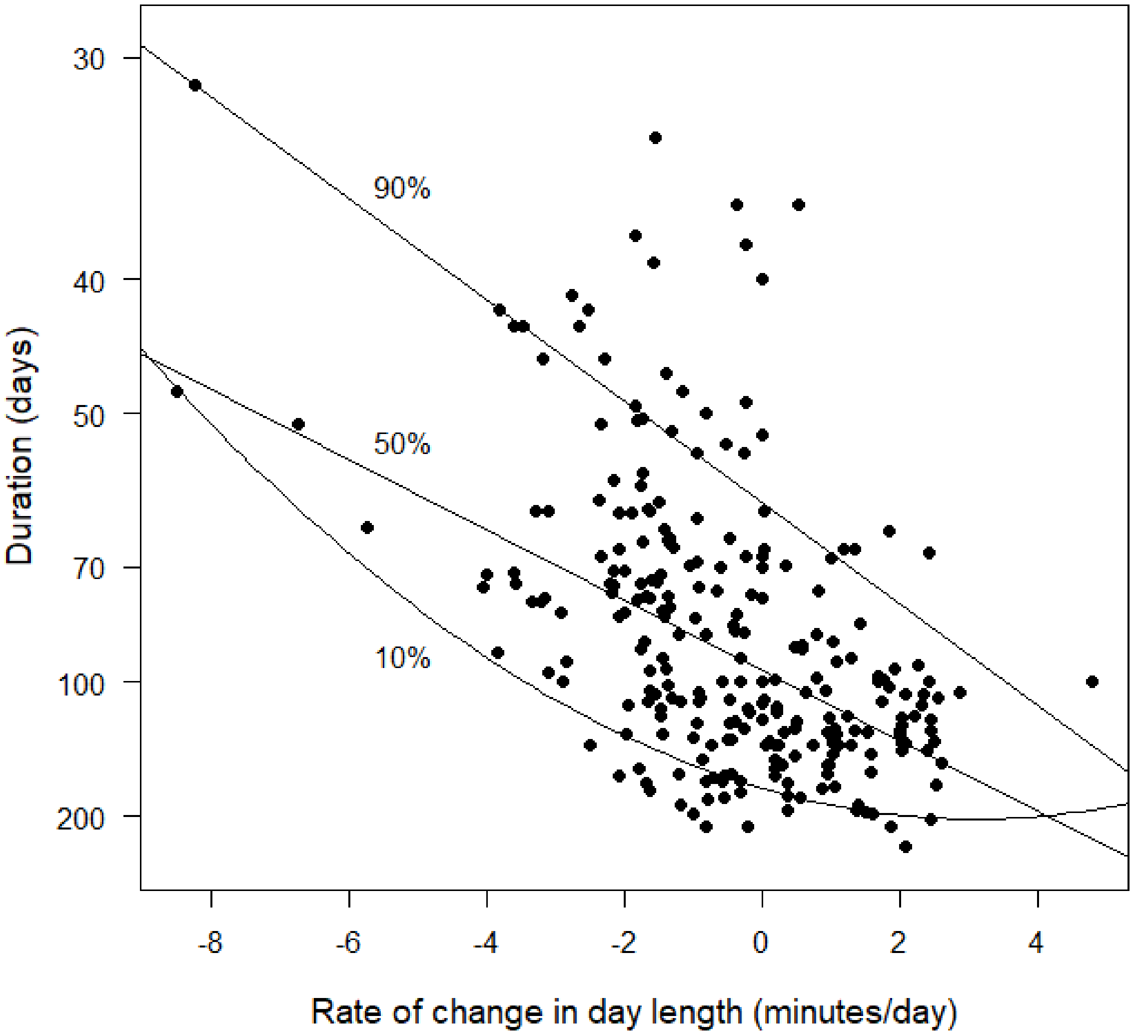

Figure 9. The duration of primary moult (days), as estimated by the Underhill-Zucchini moult model, plotted against rate of change in day length (minutes/day) at the date of start of moult. The values plotted on the y-axis are the reciprocals of the durations. Because 1/30 > 1/200, the species with durations of 30 days are plotted higher on the graph than species with durations of 200 days. This strategy results in the y-axis being interpretable as "moult intensity", with greater intensity associated with shorter durations (see text). The 10%, 50% and 90% quantile regression lines are shown. The sample size was 256.

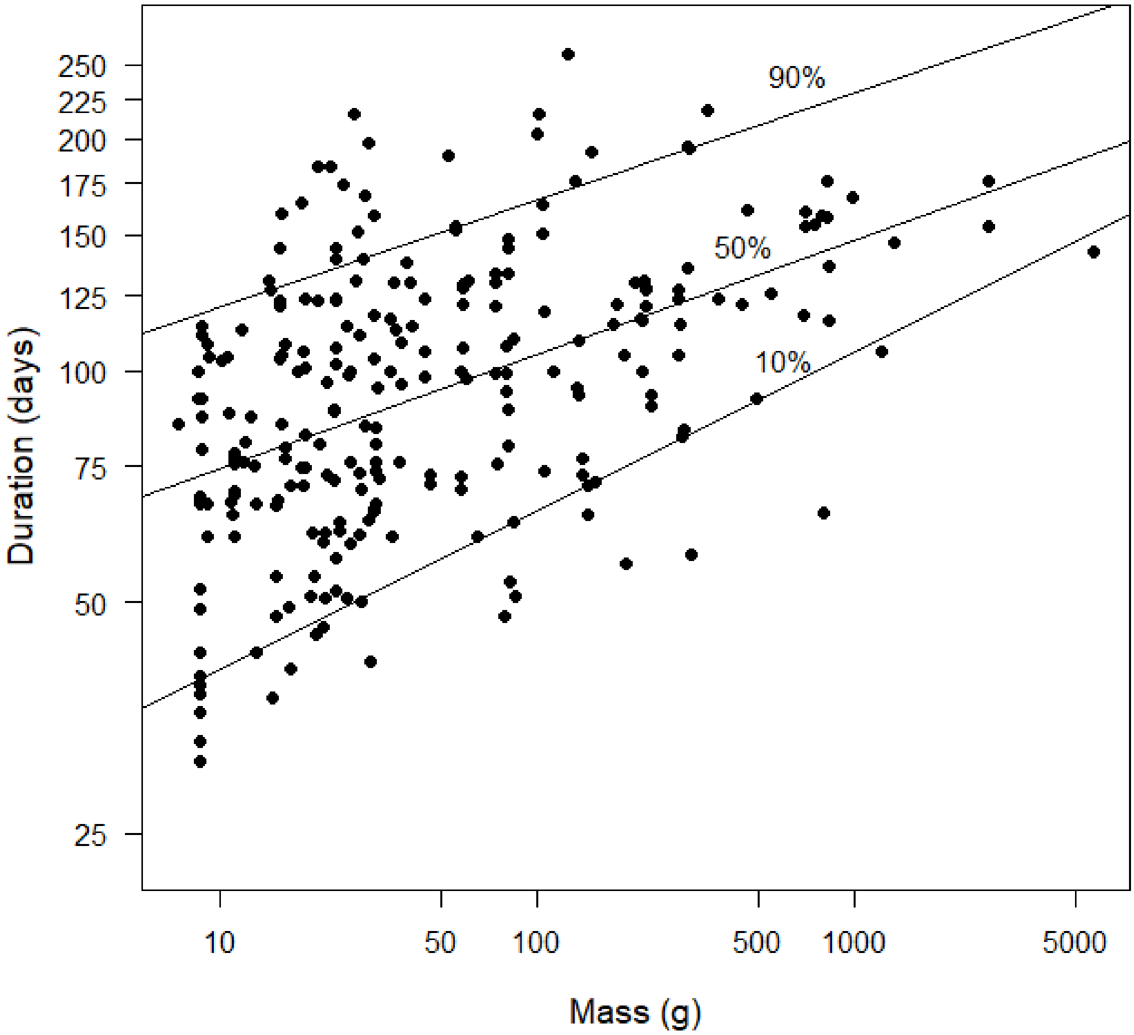

Figure 10. The duration (days) of primary moult, as estimated by the Underhill-Zucchini moult model, plotted against mass (g). The x-axis and y-axis are plotted on a logarithmic scale. The 10%, 50% and 90% quantile regression lines (see text) are shown. The sample size was 253.

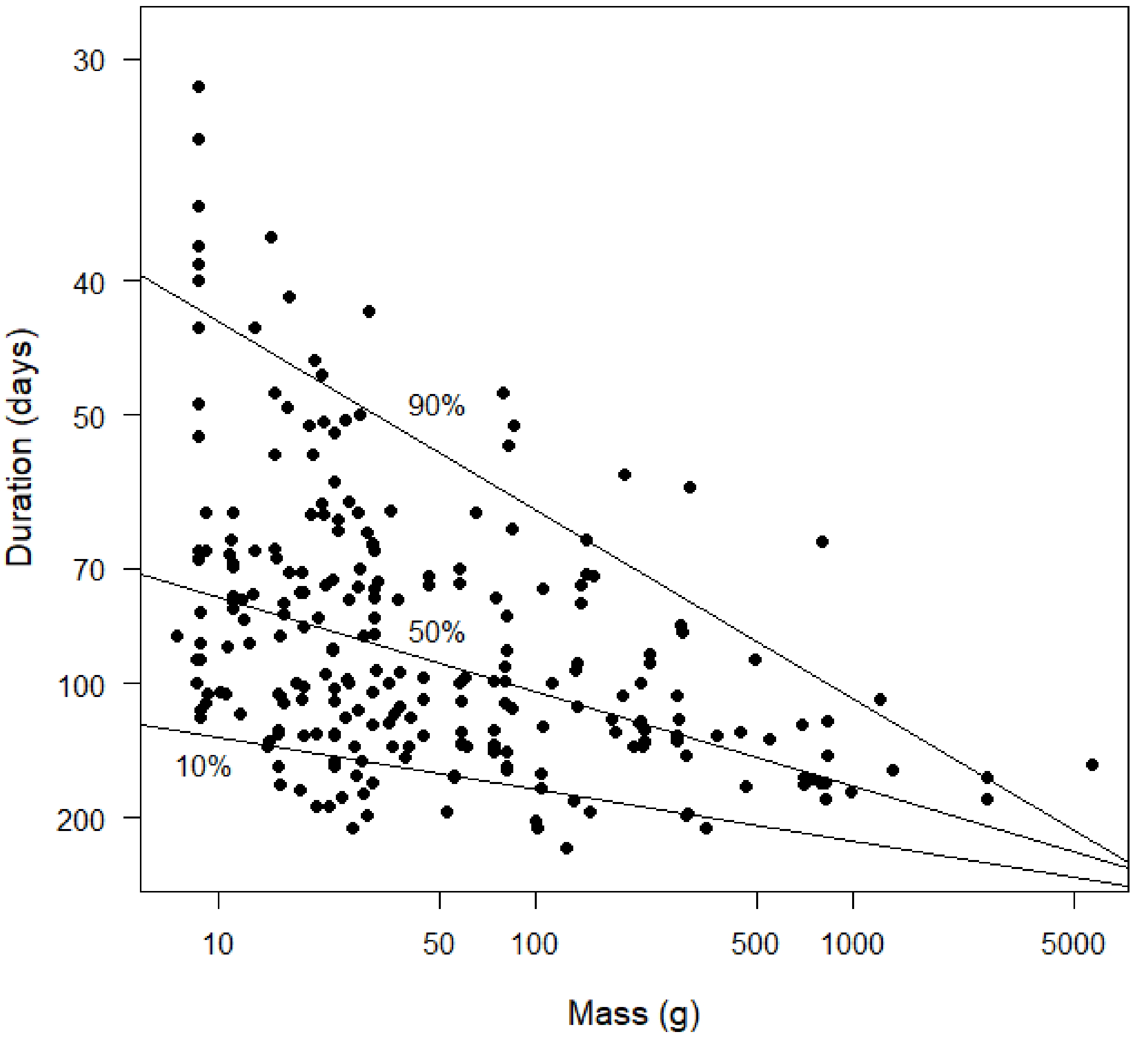

Figure 11. Scatter diagram duration (days), plotted against mass (g). Note that the x-axis is plotted on a logarithmic scale and the values plotted on the y-axis are the reciprocals of the durations. Because 1/30 > 1/200, the species with durations of 30 days are plotted higher on the graph than species with durations of 200 days. This strategy results in the y-axis being interpretable as "moult intensity", with greater intensity associated with shorter durations (see text). Duration was estimated using the Underhill-Zucchini moult model. The 10%, 50% and 90% quantile regression lines are shown. The sample size was 253.

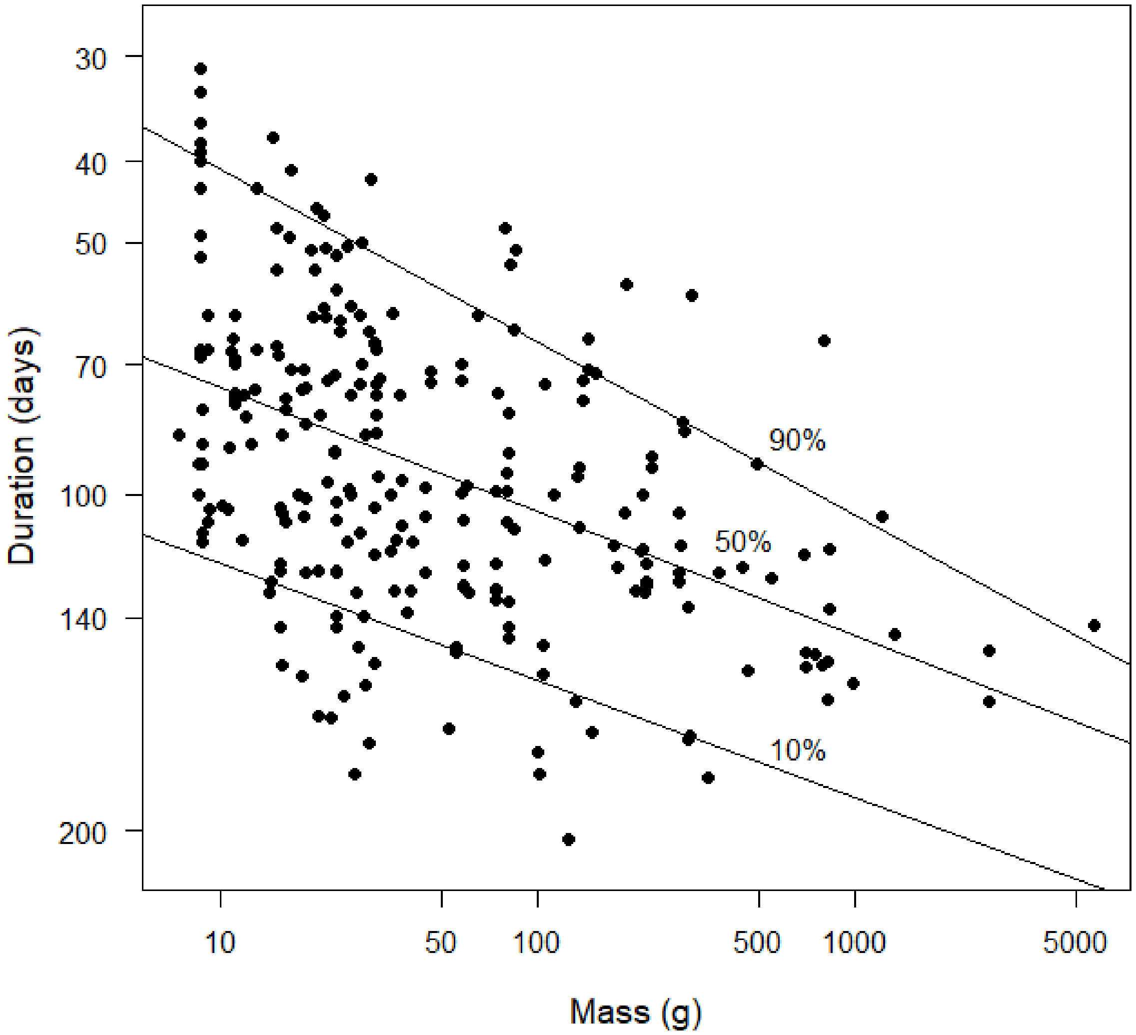

Figure 12. Scatter diagram duration (days), plotted against mass (g). Note that the x-axis is plotted on a logarithmic scale. The values plotted on the y-axis are the logarithms of the reciprocals of the durations. Because log(1/30) > log(1/200), the species with durations of 30 days are plotted higher on the graph than species with durations of 200 days. This strategy results in the y-axis being interpretable as "moult intensity", with greater intensity associated with shorter durations (see text). Duration was estimated using the Underhill-Zucchini moult model. The 10%, 50% and 90% quantile regression lines are shown. The sample size was 253.

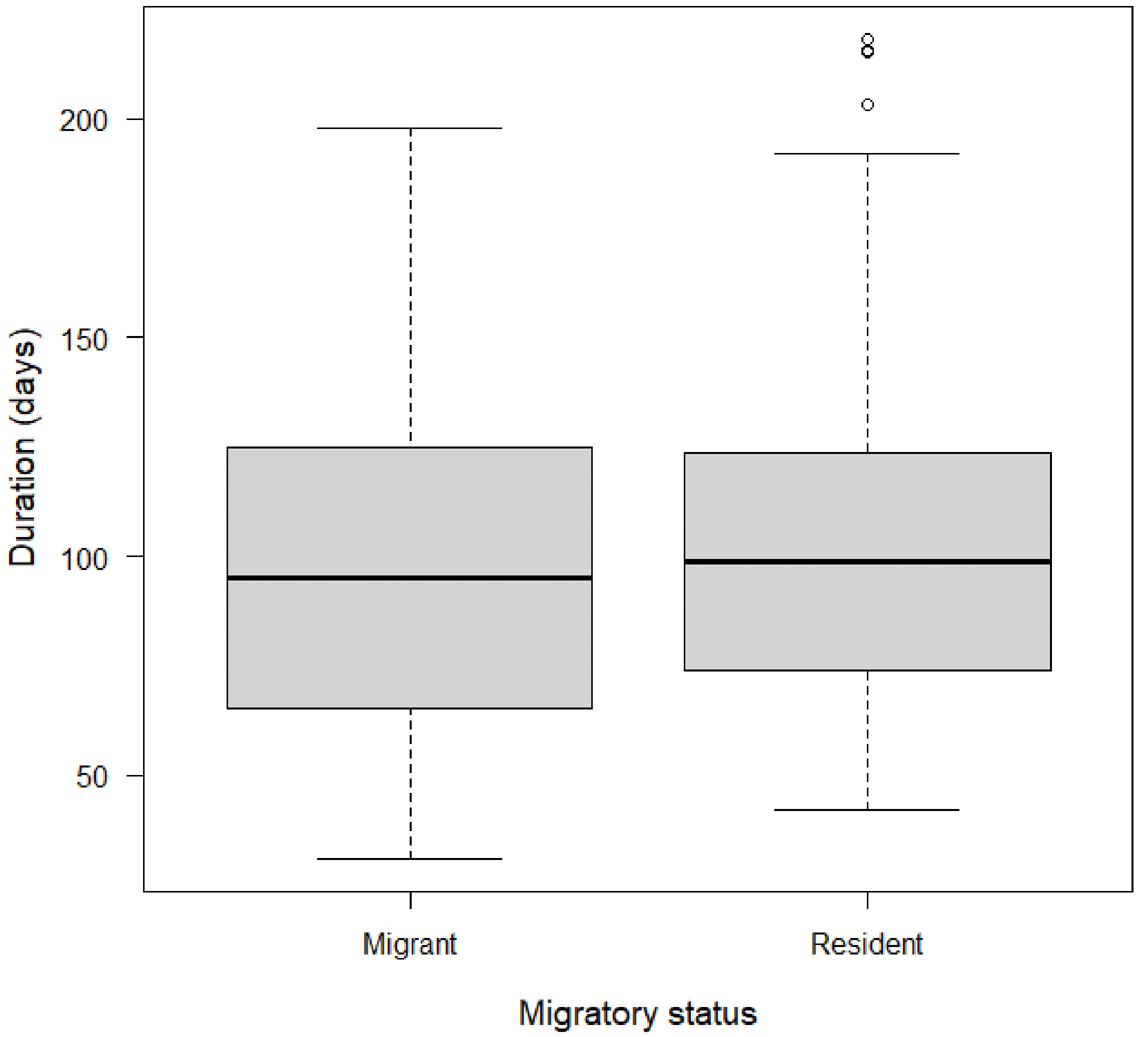

Figure 13. Box-and-whisker plots of the estimated duration parameter of the Underhill-Zucchini moult model for species classified as migrant or resident. The medians and their sample sizes for migrants and residents were 95 (n=115) and 99 (n=136) respectively.

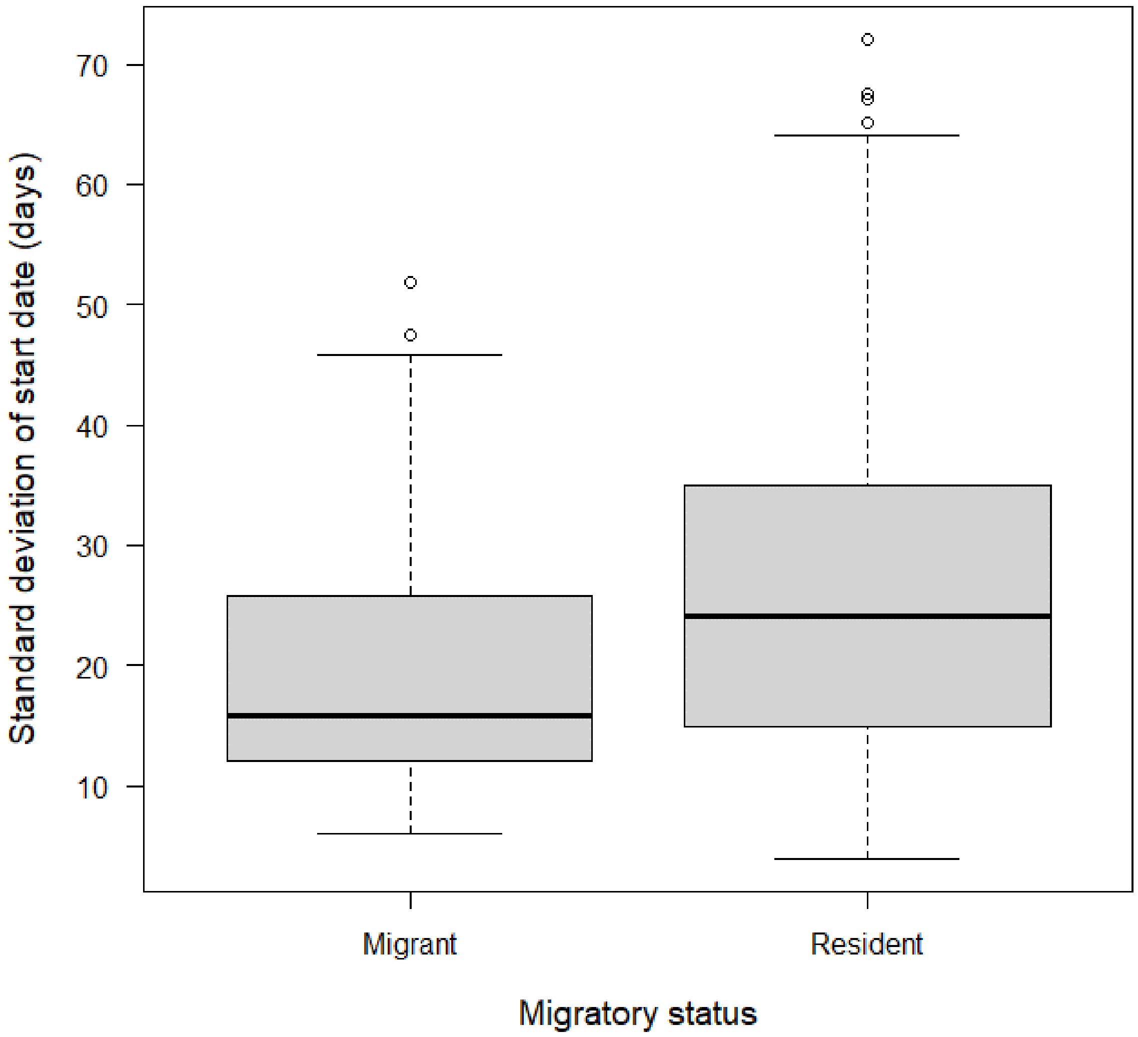

Figure 14. Box-and-whisker plots of the estimated standard deviation parameter of the Underhill-Zucchini moult model for species classified as migrant or resident. The medians and their sample sizes for migrants and residents were 16 (n=87) and 24 (n=126) respectively.

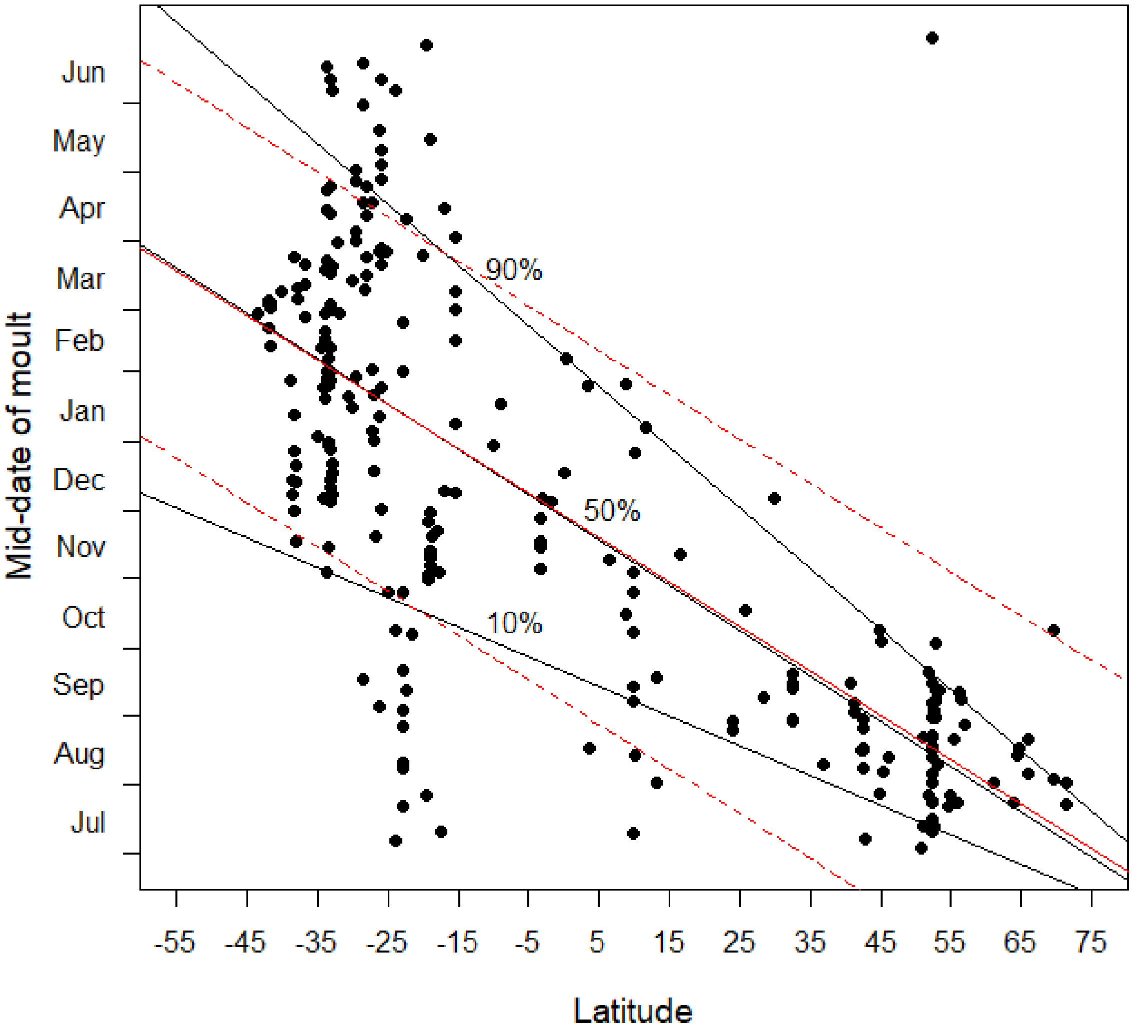

Figure 15. This graphic illustrates a key difference between ordinary least squares regression and quantile regression. In the scatter diagram the mid-date of moult is plotted against latitude. The black lines are the 10%, 50% and 90% quantile regression lines, as in Figure 4. The red line is the least squares regression line, and the dotted lines are the lines for the regular 80% prediction intervals for linear regression.

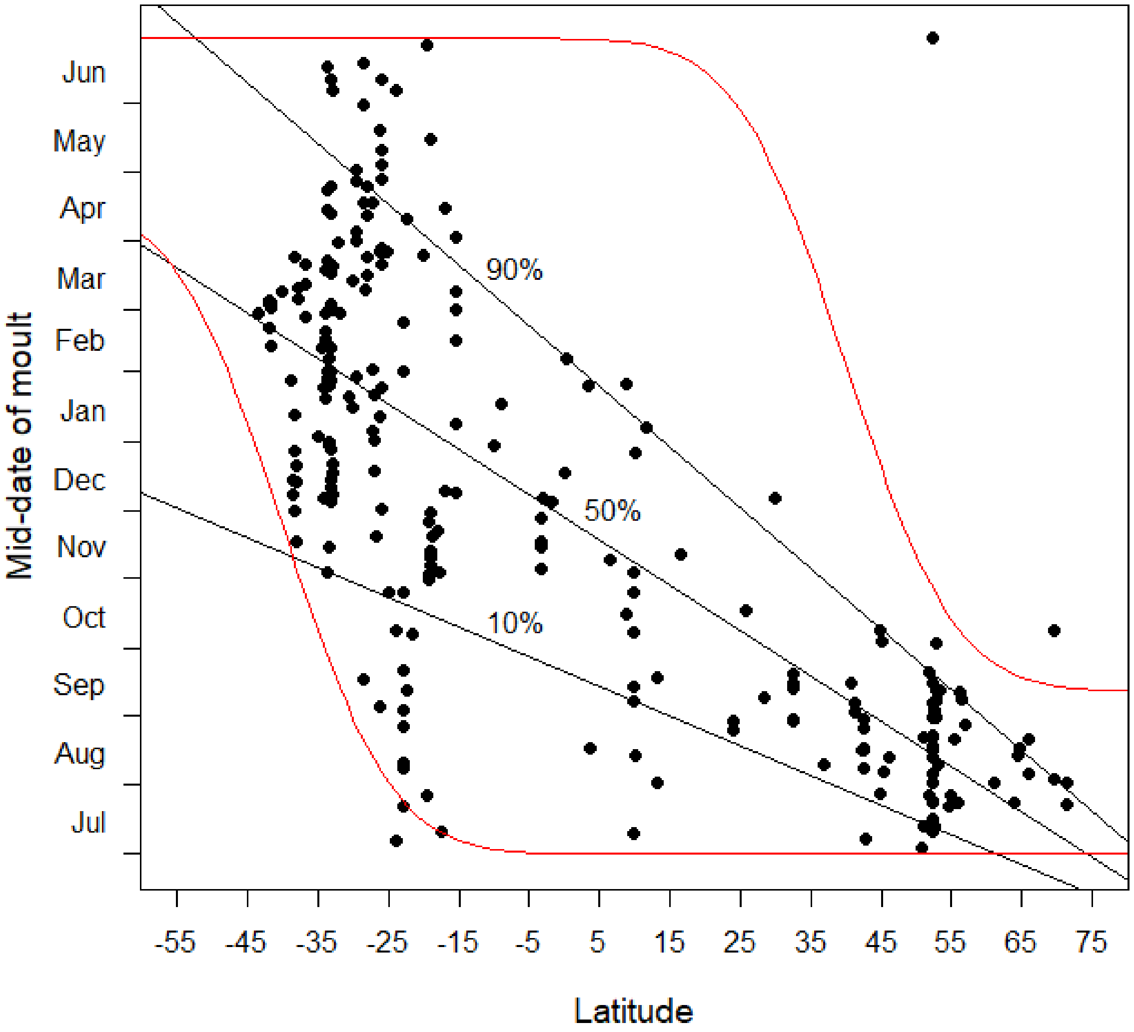

Figure 16. The mid-date of moult (see text) plotted against latitude. Latitudes in the southern hemisphere are negative. Our working hypothesis (see text) is that the area between the two red lines will be occupied with results when there is a more representative sample of analyses from the latitudes between about 40°N and 15°S than currently available (Figure 3). The quantile regression lines in this plot, based on currently available data, and copied from Figure 4, are then likely to prove misleading.

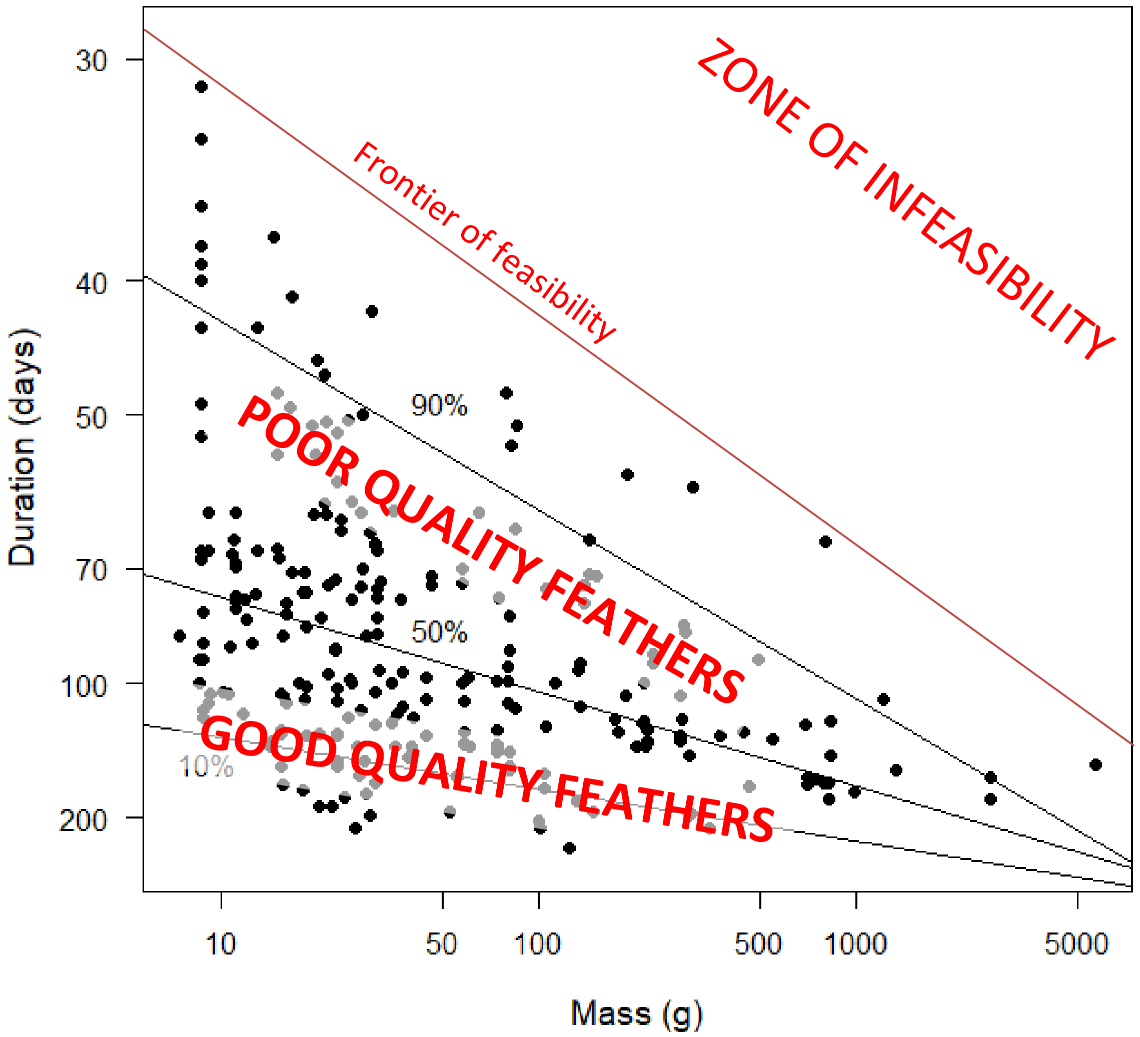

Figure 17. Hypothesised interpretation of Figure 11 in relation to quality of primary feathers. The y-axis represents "moult intensity" (see text), calculated as the increase in the moult index per day of primary moult, which is the inverse of duration.

Appendix 1

Estimates of primary moult parameters using the Underhill-Zucchini moult model

This appendix contains the database that was used for analysis in Chapter 7. The methods used to compile the database are described in the chapter. In brief, it contains the results of analyses which used the moult model of Underhill and Zucchini (1988) to estimate the parameters of primary moult. All literature was searched for studies which cited Erni et al. (2013) and/or Underhill and Zucchini (1988) and which contained estimates of the primary moult parameters using this model. A total of 260 studies were found to have used the Underhill-Zucchini moult model to estimate the parameters of primary moult (duration, starting date and standard deviation of starting date). These studies focussed on 143 different species, of which 49 had moult data recorded for more than one population. Since some species have results for multiple populations at different study sites, which are sometimes reported in a single publication, each population is treated as a single study. The database contains studies from a total of 91 publications. The studies contained in this thesis have been included in these totals.

For each study, the English and scientific name of the study species was recorded, as well as its taxonomic order and family. Scientific and English common names of species are those used by Gill et al. (2022). The species was classified as either migrant or resident. The location of the study site was noted along with its coordinates of latitude and longitude. Coordinates of localities for studies were mostly provided in the published papers. Where data were accumulated over a region, we chose a central position. If the coordinates of the study were not given, we used the coordinates of the place name given as the location of the sampling site. Latitudes in the northern hemisphere were given a positive sign whereas southern latitudes were given a negative sign. The study was assigned to the continent on which it was based. The three parameters of moult were recorded as well as the mid-date and end date of moult. Mid-date of moult was calculated from the sum of the start date and half the duration. The species body mass was taken from the published study where possible. Where body mass was not given, it was taken from Dunning (2008). The source of the data recorded for each study was noted.

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English name	Scientific name	Order	Family	Migratory status	Continent	Study site location	Latitude	Longitude	Duration	Start date	SD of start date	Mid-date	End date	Mass (g)	Source	Notes
Bearded Vulture	*Gypaetus barbatus*	Accipitriformes	Accipitridae	Resident	Europe	Central Pyrenees, Spain	42,7	1,0	143	27-Apr	48	08-Jul	17-Sep	5680	Zuberogoitia et al. 2016	
Pallid Swift	*Apus pallidus*	Apodiformes	Apodidae	Migrant	Europe	Carmagnola and Torino, North-West Italy	45,0	7,7	130	05-Aug		09-Oct	13-Dec	40	Boano et al. 2015	Longitude recorded as west in Boano et al. 2015. Mass=average of female and male values
Least Auklet	*Aethia pusilla*	Charadriiformes	Alcidae	Resident	Asia	Cape Ulyakhpen, Chukotka Peninsula, Russia	64,4	-173,9	63	13-Jul	11	14-Aug	15-Sep	84	Bond et al. 2013	Weighted averages of three years for duration, start day, SD of start day
Eurasian Stone-curlew	*Burhinus oedicnemus*	Charadriiformes	Burhinidae	Migrant	Europe	Taro River Regional Park, Parma, Italy	44,7	10,2	162	08-May	14	28-Jul	17-Oct	459	Giunchi et al. 2008	
Wrybill	*Anarhynchus frontalis*	Charadriiformes	Charadriidae	Migrant	Oceania	Auckland, New Zealand	-36,8	174,8	73	20-Jan	13	26-Feb	03-Apr	58	This study	
Greater Sand Plover	*Charadrius leschenaultii*	Charadriiformes	Charadriidae	Migrant	Asia	Southern Jiangsu coast, China	32,5	121,2	76	12-Aug		19-Sep	27-Oct	75	Yang et al. 2020	
Greater Sand Plover	*Charadrius leschenaultii*	Charadriiformes	Charadriidae	Migrant	Asia	South-East India	9,8	79,5	80	29-Jul	24	07-Sep	17-Oct	82	Jackson 2017	Full-tract moult model
Greater Sand Plover	*Charadrius leschenaultii*	Charadriiformes	Charadriidae	Migrant	Africa	Kenya (coast)	-3,3	40,0	148	01-Sep	45	15-Nov	27-Jan	82	Jackson 2017	Per primary moult model; P1 SD of start date
Greater Sand Plover	*Charadrius leschenaultii*	Charadriiformes	Charadriidae	Migrant	Oceania	North-West Australia	-19,3	120,3	144	19-Aug	19	31-Oct	11-Jan	82	Jackson 2017	Per primary moult model; P1 SD of start date
Greater Sand Plover	*Charadrius leschenaultii*	Charadriiformes	Charadriidae	Migrant	Oceania	South-East Australia	-38,4	145,5	134	21-Oct	25	28-Dec	04-Mar	82	Jackson 2017	Full-tract moult model
Lesser Sand Plover	*Charadrius mongolus*	Charadriiformes	Charadriidae	Migrant	Asia	South-East India	9,8	79,5	153	10-Aug	33	26-Oct	10-Jan	55	Jackson 2017	Per primary moult model; P1 SD of start date
Lesser Sand Plover	*Charadrius mongolus*	Charadriiformes	Charadriidae	Migrant	Africa	Kenya (coast)	-3,3	40,0	154	12-Sep	43	28-Nov	13-Feb	55	Jackson 2017	Per primary moult model; P1 SD of start date

English name	**Scientific name**	**Order**	**Family**	**Migratory status**	**Continent**	**Study site location**	**Latitude**	**Longitude**	**Duration**	**Start date**	**SD of start date**	**Mid-date**	**End date**	**Mass (g)**	**Source**	**Notes**
Lesser Sand Plover	*Charadrius mongolus*	Charadriiformes	Charadriidae	Migrant	Oceania	North-West Australia	-19,3	120,3	152	18-Aug	52	03-Nov	17-Jan	55	Jackson 2017	Per primary moult model; P1 SD of start date
Lesser Sand Plover	*Charadrius mongolus*	Charadriiformes	Charadriidae	Migrant	Oceania	South-East Australia	-38,4	145,5		07-Sep	46	01-Dec	22-Feb	55	Jackson 2017	Per primary moult model; P1 SD of start date; Duration unreliably estimated
European Golden Plover	*Pluvialis apricaria*	Charadriiformes	Charadriidae	Migrant	Europe	Vindelfjällen Nature Reserve, Ammarnas, Northern Sweden; Russia; Lund, Southern Sweden; The Netherlands (Russia, Sweden, The Netherlands)	66,0	16,0	116	24-Jun	12	21-Aug	18-Oct	214	Machin et al. 2018	Latitude of breeding ground
European Golden Plover	*Pluvialis apricaria*	Charadriiformes	Charadriidae	Migrant	Europe	Selfoss, Iceland	63,9	-21,0	100	04-Jun	9	24-Jul	12-Sep	214	Machin et al. 2018	Start date: 22-Jul females, 16-Jul males. Start date was average of the two dates
Grey Plover	*Pluvialis squatarola*	Charadriiformes	Charadriidae	Migrant	Europe	The Wash, England, United Kingdom	52,8	0,3	90	19-Aug	14	03-Oct	17-Nov	230	Serra et al. 2006	
Grey Plover	*Pluvialis squatarola*	Charadriiformes	Charadriidae	Migrant	Europe	North-East Italy	45,2	12,4	93	18-Aug	22	04-Oct	19-Nov	230	Serra and Rusticali 1998	
Grey Plover	*Pluvialis squatarola*	Charadriiformes	Charadriidae	Migrant	Asia	South-East India	9,8	79,5	127	01-Sep	29	04-Nov	05-Jan	220	Balachandran et al. 2000	
Grey Plover	*Pluvialis squatarola*	Charadriiformes	Charadriidae	Migrant	Africa	Kenya (coast)	-3,3	39,9	130	13-Sep	25	17-Nov	19-Jan	205	Pearson et al. 2002	
Grey Plover	*Pluvialis squatarola*	Charadriiformes	Charadriidae	Migrant	Oceania	North-West Australia	-19,0	121,5	121	10-Sep	12	10-Nov	09-Jan	220	Minton and Serra 2001	
Grey Plover	*Pluvialis squatarola*	Charadriiformes	Charadriidae	Migrant	Africa	South Africa	-33,3	19,4	131	30-Sep	28	05-Dec	08-Feb	219	Serra et al. 1999	
Grey Plover	*Pluvialis squatarola*	Charadriiformes	Charadriidae	Migrant	Oceania	South-East Australia	-38,5	145,5	128	05-Oct	16	08-Dec	09-Feb	220	Minton and Serra 2001	

English name	Scientific name	Order	Family	Migratory status	Continent	Study site location	Latitude	Longitude	Duration	Start date	SD of start date	Mid-date	End date	Mass (g)	Source	Notes
Hooded Dotterel	*Thinornis cucullatus*	Charadriiformes	Charadriidae	Resident	Oceania	South-East Australia, between Cape Otway and Wilson's Promontory	-38,9	144,9	203	19-Oct	42	28-Jan	10-May	100	Rogers et al. 2014	
South Island Pied Oystercatcher	*Haematopus finschi*	Charadriiformes	Haematopodidae	Migrant	Oceania	Auckland, New Zealand	-36,9	174,8	126	08-Jan	16	12-Mar	14-May	545	TC Bate (in examination)	
Sooty Oystercatcher	*Haematopus fuliginosus*	Charadriiformes	Haematopodidae	Resident	Oceania	Melbourne, Australia	-37,8	145,0	176	13-Dec	30	11-Mar	07-Jun	827	TC Bate (in examination)	
Sooty Oystercatcher	*Haematopus fuliginosus fuliginosus*	Charadriiformes	Haematopodidae	Resident	Africa	South-East Australia	-38,4	146,0	158	04-Jan	21	24-Mar	11-Jun	817	Hansen et al. 2009	
Pied Oystercatcher	*Haematopus longirostris*	Charadriiformes	Haematopodidae	Resident	Oceania	Melbourne, Australia	-37,8	145,0	161	16-Dec	22	06-Mar	26-May	703	TC Bate (in examination)	
African Oystercatcher	*Haematopus moquini*	Charadriiformes	Haematopodidae	Resident	Africa	Cape Peninsula, Cape Town, Western Cape, South Africa	-33,8	18,4	154	01-Apr	28	17-Jun	02-Sep	701	TC Bate (in examination)	
Variable Oystercatcher	*Haematopus unicolor*	Charadriiformes	Haematopodidae	Migrant	Oceania	Auckland, New Zealand	-36,9	174,8	155	03-Jan	26	21-Mar	07-Jun	751	TC Bate (in examination)	
Grey-headed Gull	*Chroicocephalus cirrocephalus*	Charadriiformes	Laridae	Resident	Africa	Gauteng and Durban, KwaZulu Natal, South Africa	-27,1	29,1	136	12-Oct	25	19-Dec	25-Feb	300,3	McInnes 2006	
Hartlaub's Gull	*Chroicocephalus hartlaubii*	Charadriiformes	Laridae	Resident	Africa	Western Cape, South Africa: Lambert's Bay, Malgas Island, Robben Island	-33,0	18,2	115	11-Oct	32	08-Dec	03-Feb	284	Crawford and Underhill 2003	
Kelp Gull	*Larus dominicanus vetula*	Charadriiformes	Laridae	Resident	Africa	Robben Island, Western Cape, South Africa	-33,8	18,4	168	29-Jan	22	23-Apr	16-Jul	989	Ward et al. 2007	
Black Skimmer	*Rynchops niger*	Charadriiformes	Laridae	Nomadic	South America	Island of Santa Catarina, Southern Brazil	-27,4	-48,4	194	28-Oct		02-Feb	10-May	302	Vieira et al. 2017	

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(South American) Black Skimmer	*Rynchops niger intercedens*	Charadriiformes	Laridae	Nomadic	South America	Brazil	-27,0	-48,0	196	26-Sep		02-Jan	10-Apr	298	Vieira 2017	Female and male duration and start day averaged; female and male masses averaged (small sample sizes for mass); photographic data
Roseate Tern	*Sterna dougallii*	Charadriiformes	Laridae	Nomadic	Africa	Eastern Cape, South Africa	-34,0	26,0	258	13-Sep	30	20-Jan	29-May	125	Tree et al. 2019	Parameters for first series moult, there was also a second series moult (only few inner primaries moulted)
Ruddy Turnstone	*Arenaria interpres*	Charadriiformes	Scolopacidae	Migrant	Europe	Scotland, United Kingdom	56,3	-3,2	74	05-Aug	13	11-Sep	19-Oct	105	Summers et al. 1989	
Ruddy Turnstone	*Arenaria interpres*	Charadriiformes	Scolopacidae	Migrant	Oceania	North-West Australia	-18,8	121,8	93	05-Oct	18	20-Nov	06-Jan	136	Skewes et al. 2004	
Ruddy Turnstone	*Arenaria interpres*	Charadriiformes	Scolopacidae	Migrant	Africa	Southern Africa	-33,1	18,1	119	09-Oct	32	08-Dec	05-Feb	105	Summers et al. 1989	
Ruddy Turnstone	*Arenaria interpres*	Charadriiformes	Scolopacidae	Migrant	Oceania	South-East Australia	-38,1	143,3	109	27-Oct	18	21-Dec	13-Feb	136	Skewes et al. 2004	
Sanderling	*Calidris alba*	Charadriiformes	Scolopacidae	Migrant	Africa	Langebaan Lagoon, Southern Africa	-33,1	18,0	98	09-Nov	21	29-Dec	15-Feb	60	Underhill 2003	
Dunlin	*Calidris alpina arcticola*	Charadriiformes	Scolopacidae	Migrant	North America	Utqiaġvik, Alaska, USA	71,3	-156,7	70	17-Jun	6	23-Jul	27-Aug	58	Taylor et al. 2018	Moult parameter estimates for three consecutive years in the early 1960's
Dunlin	*Calidris alpina arcticola*	Charadriiformes	Scolopacidae	Migrant	North America	Utqiaġvik, Alaska, USA	71,3	-156,7	100	13-Jun	6	02-Aug	21-Sep	58	Taylor et al. 2018	Moult parameter estimates for three randomly selected years

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																between 2003 and 2012
Red Knot	*Calidris canutus canutus*	Charadriiformes	Scolopacidae	Migrant	Africa	South Africa	-33,1	18,0	95	25-Oct	33	12-Dec	28-Jan	133	Summers et al. 2010	
Red Knot	*Calidris canutus islandica*	Charadriiformes	Scolopacidae	Migrant	Europe	Eastern Scotland, United Kingdom	57,1	-3,3	77	20-Jul	26	28-Aug	05-Oct	139	Summers et al. 2010	
Red Knot	*Calidris canutus islandica*	Charadriiformes	Scolopacidae	Migrant	Europe	Netherlands	53,4	5,8	71	07-Aug	9	12-Sep	17-Oct	145	Dietz. et al 2013, Dietz et al. 2015	Average of male and female
Curlew Sandpiper	*Calidris ferruginea*	Charadriiformes	Scolopacidae	Migrant	Europe	Salines de la Trinitat, Ebro Delta, North-East Spain	40,6	0,6	73	09-Aug		15-Sep	21-Oct	140	Figuerola and Bertolero 1995	
Curlew Sandpiper	*Calidris ferruginea*	Charadriiformes	Scolopacidae	Migrant	Asia	India	9,8	79,5	107	15-Aug		08-Oct	30-Nov	58	Barshep 2011	
Curlew Sandpiper	*Calidris ferruginea*	Charadriiformes	Scolopacidae	Migrant	Africa	Kenya (inland)	-1,9	37,5	128	02-Oct		05-Dec	07-Feb	58	Barshep 2011	
Curlew Sandpiper	*Calidris ferruginea*	Charadriiformes	Scolopacidae	Migrant	Oceania	North-West Australia	-18,1	122,3	129	18-Sep	14	22-Nov	25-Jan	58	Barshep 2011	
Curlew Sandpiper	*Calidris ferruginea*	Charadriiformes	Scolopacidae	Migrant	Africa	South Africa	-32,9	18,3	129	04-Oct	22	08-Dec	10-Feb	58	Barshep 2011	
Curlew Sandpiper	*Calidris ferruginea*	Charadriiformes	Scolopacidae	Migrant	Oceania	South-East Australia	-38,5	145,5	122	15-Oct	15	15-Dec	14-Feb	58	Barshep 2011	
Purple Sandpiper	*Calidris maritima*	Charadriiformes	Scolopacidae	Migrant	Europe	Tromsø, Northern Norway	69,6	19,0	48	15-Sep	7	09-Oct	02-Nov	79	Summers et al. 1990, Summers et al. 2004	
Purple Sandpiper	*Calidris maritima*	Charadriiformes	Scolopacidae	Resident	Europe	West Iceland	64,8	-21,5	51	22-Jul	8	17-Aug	11-Sep	85	Summers et al. 1988, Summers et al. 2004	
Purple Sandpiper	*Calidris maritima*	Charadriiformes	Scolopacidae	Migrant	Europe	East Britain, United Kingdom	55,5	-1,3	61	21-Jul	14	21-Aug	20-Sep	65	Summers et al. 1988, Summers et al. 2004	
Western Sandpiper	*Calidris mauri*	Charadriiformes	Scolopacidae	Migrant	North America	Mexico	24,1	-110,4	62	29-Jul	10	29-Aug	29-Sep	24	Galindo-Espinosa et al. 2013	

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Little Stint	*Calidris minuta*	Charadriiformes	Scolopacidae	Migrant	Africa	Kenya (inland)	0,0		107	25-Oct		18-Dec	09-Feb	23	CHW Jackson, DJ Pearson and M Remisiewicz (unpubl. data)	
Little Stint	*Calidris minuta*	Charadriiformes	Scolopacidae	Migrant	Africa	Kenya (coast)	-3,0		140	28-Sep		07-Dec	15-Feb	23	CHW Jackson, DJ Pearson and M Remisiewicz (unpubl. data)	
Little Stint	*Calidris minuta*	Charadriiformes	Scolopacidae	Migrant	Africa	Zimbabwe	-17,0		144	29-Sep		10-Dec	20-Feb	23	M Remisiewicz and AJ Tree (unpubl. data)	
Little Stint	*Calidris minuta*	Charadriiformes	Scolopacidae	Migrant	Africa	North-West South Africa	-26,0		123	01-Oct		02-Dec	01-Feb	23	M Remisiewicz and AJ Tree (unpubl. data)	
Little Stint	*Calidris minuta*	Charadriiformes	Scolopacidae	Migrant	Africa	Eastern Cape, South Africa	-33,0		124	17-Oct		18-Dec	18-Feb	23	M Remisiewicz and AJ Tree (unpubl. data)	
Little Stint	*Calidris minuta*	Charadriiformes	Scolopacidae	Migrant	Africa	Western Cape, South Africa	-33,0		102	01-Nov		22-Dec	11-Feb	23	M Remisiewicz and AJ Tree (unpubl. data)	
Least Sandpiper	*Calidris minutilla*	Charadriiformes	Scolopacidae	Migrant	North America	Mexico	24,1	-110,4	54	29-Jul	9	25-Aug	21-Sep	20	Galindo-Espinosa et al. 2013	
Spoon-billed Sandpiper	*Calidris pygmaea*	Charadriiformes	Scolopacidae	Migrant	Asia	Southern Jiangsu coast, China	32,5	121,2	73	08-Aug		13-Sep	20-Oct	32	Yang et al. 2020	
Long-toed Stint	*Calidris subminuta*	Charadriiformes	Scolopacidae	Migrant	Asia	Thailand	13,1	100,1	70	14-Aug	13	18-Sep	23-Oct	28	Round et al. 2012	
Great Knot	*Calidris tenuirostris*	Charadriiformes	Scolopacidae	Migrant	Asia	Southern Jiangsu coast, China	32,5	121,2	56	16-Aug		13-Sep	11-Oct	192	Yang et al. 2020	

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Bar-tailed Godwit	*Limosa lapponica*	Charadriiformes	Scolopacidae	Migrant	Asia	Southern Jiangsu coast, China	32,5	121,2	58	17-Aug		15-Sep	14-Oct	307	Yang et al. 2020	
Bar-tailed Godwit	*Limosa lapponica*	Charadriiformes	Scolopacidae	Migrant	Oceania	North-West Australia	-19,0		124	10-Sep		11-Nov	12-Jan	278	M Remisiewicz, H Sitters and CMD Minton (unpubl. data)	
Bar-tailed Godwit	*Limosa lapponica*	Charadriiformes	Scolopacidae	Migrant	Oceania	South-East Australia	-38,0		105	22-Oct		14-Dec	04-Feb	278	M Remisiewicz, H Sitters and CMD Minton (unpubl. data)	
Black-tailed Godwit	*Limosa limosa*	Charadriiformes	Scolopacidae	Migrant	Oceania	North-West Australia	-19,0		127	04-Sep		07-Nov	09-Jan	278	M Remisiewicz, H Sitters and CMD Minton (unpubl. data)	
Black-tailed Godwit	*Limosa limosa limosa*	Charadriiformes	Scolopacidae	Migrant	Europe	Donana National Park, Southern Spain	36,9	-6,2	84	29-Jun	15	10-Aug	21-Sep	291	Marquez-Ferrando et al. 2018	
Eurasian Curlew	*Numenius arquata*	Charadriiformes	Scolopacidae	Migrant	Asia	Southern Jiangsu coast, China	32,5	121,2	65	28-Jul		30-Aug	01-Oct	806	Yang et al. 2020	
Far Eastern Curlew	*Numenius madagascariensis*	Charadriiformes	Scolopacidae	Migrant	Oceania	North-West Australia	-19,0		137	05-Sep		13-Nov	20-Jan	834	M Remisiewicz, H Sitters and CMD Minton (unpubl. data)	
Far Eastern Curlew	*Numenius madagascariensis*	Charadriiformes	Scolopacidae	Migrant	Oceania	South-East Australia	-38,0		116	20-Sep		17-Nov	14-Jan	834	M Remisiewicz, H Sitters and CMD Minton (unpubl. data)	
Eurasian Whimbrel	*Numenius phaeopus*	Charadriiformes	Scolopacidae	Migrant	Oceania	North-West Australia	-19,0		124	29-Sep		30-Nov	31-Jan	375	M Remisiewicz, H Sitters and CMD Minton (unpubl. data)	

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Bristle-thighed Curlew	*Numenius tahitiensis*	Charadriiformes	Scolopacidae	Migrant	North America	Laysan Island, North-Western Hawaiian Islands	25,8	-171,7	92	02-Sep		18-Oct	03-Dec	493	Marks 1993	
Wood Sandpiper	*Tringa glareola*	Charadriiformes	Scolopacidae	Migrant	Africa	South Africa & Zimbabwe	-25,0	28,5	131	21-Aug	29	26-Oct	30-Dec	60,7	Remisiewicz et al. 2009	
Nordmann's Greenshank	*Tringa guttifer*	Charadriiformes	Scolopacidae	Migrant	Asia	Southern Jiangsu coast, China	32,5	121,2	65	27-Jul		29-Aug	30-Sep	145	Yang et al. 2020	
Common Greenshank	*Tringa nebularia*	Charadriiformes	Scolopacidae	Migrant	Africa	Harare, Zimbabwe	-17,8	31,0	115	07-Sep	18	04-Nov	31-Dec	175	Remisiewicz et al. 2014	
Common Greenshank	*Tringa nebularia*	Charadriiformes	Scolopacidae	Migrant	Africa	South Africa: West coast between Berg River and Betty's Bay	-33,6	18,5	105	23-Sep	30	15-Nov	06-Jan	188	Remisiewicz et al. 2014	
Common Greenshank	*Tringa nebularia*	Charadriiformes	Scolopacidae	Migrant	Africa	South Africa: East coast between Port Alfred and Port Elizabeth	-33,8	26,2	122	04-Sep	20	04-Nov	03-Jan	179	Remisiewicz et al. 2014	
Common Redshank	*Tringa totanus*	Charadriiformes	Scolopacidae	Migrant	Europe	Firth of Tay and Eden Estuary, Scotland, United Kingdom	56,4	-3,1	72	03-Aug	13	08-Sep	14-Oct	152	Underhill et al. 1990	
Terek Sandpiper	*Xenus cinereus*	Charadriiformes	Scolopacidae	Migrant	Asia	South-East India	9,8	79,5	121	15-Jul		14-Sep	13-Nov	74	Jackson 2017	Per primary moult model; only a derived start date for P1, no other info for P1-P3
Terek Sandpiper	*Xenus cinereus*	Charadriiformes	Scolopacidae	Migrant	Africa	Kenya (coast)	-3,3	40,0	99	16-Sep	22	05-Nov	23-Dec	74	Jackson 2017	Per primary moult model; P1 SD of start date
Terek Sandpiper	*Xenus cinereus*	Charadriiformes	Scolopacidae	Migrant	Oceania	North-West Australia	-19,3	120,3	130	22-Sep	16	26-Nov	29-Jan	74	Jackson 2017	Per primary moult model; P1 SD of start date
Terek Sandpiper	*Xenus cinereus*	Charadriiformes	Scolopacidae	Migrant	Africa	South Africa	-33,1	18,3	134	06-Oct	48	15-Dec	17-Feb	74	Jackson 2017	Full-tract moult model
Terek Sandpiper	*Xenus cinereus*	Charadriiformes	Scolopacidae	Migrant	Oceania	South-East Australia	-38,4	145,5	130	09-Nov	33	13-Jan	19-Mar	74	Jackson 2017	Full-tract moult model
Long-tailed Jaeger	*Stercorarius longicaudus*	Charadriiformes	Stercorariidae	Migrant		Atlantic Ocean	-35,0		82	23-Nov	15	03-Jan	13-Feb	289	Van Bemmelen et al. 2018	

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Parasitic Jaeger	*Stercorarius parasiticus*	Charadriiformes	Stercorariidae	Migrant		Atlantic Ocean	-30,0		122	16-Nov	18	16-Jan	18-Mar	446	Van Bemmelen et al. 2018	
Pomarine Jaeger	*Stercorarius pomarinus*	Charadriiformes	Stercorariidae	Migrant		Atlantic Ocean	10,0		118	29-Oct	20	27-Dec	24-Feb	694	Van Bemmelen et al. 2018	
Great Skua	*Stercorarius skua*	Charadriiformes	Stercorariidae	Migrant		Atlantic Ocean	30,0		147	24-Sep	27	07-Dec	18-Feb	1340	Van Bemmelen et al. 2018	
Speckled Pigeon	*Columba guinea*	Columbiformes	Columbidae	Resident	Africa	Western Cape, South Africa	-33,8	18,5	218	26-Dec	30	14-Apr	02-Aug	344	Underhill and Underhill 1997	
Laughing Dove	*Spilopelia senegalensis*	Columbiformes	Columbidae	Resident	Africa	Cape Town, Western Cape, South Africa	-33,9	18,5	215	03-Nov	66	19-Feb	06-Jun	101	This study	
Ring-necked Dove	*Streptopelia capicola*	Columbiformes	Columbidae	Resident	Africa	Western Cape, South Africa	-34,1	18,5	192	23-Nov	45	27-Feb	02-Jun	148	Underhill et al. 1999	
European Turtle Dove	*Streptopelia turtur*	Columbiformes	Columbidae	Migrant	Africa	Richard Toll, Northern Senegal	16,4	-15,7	177	16-Aug	24	12-Nov	09-Feb	132	Underhill and Scott 2021	
Melodious Warbler	*Hippolais polyglotta*	Passeriformes	Acrocephalidae	Migrant	Africa	Ivory Coast, West Africa	8,8	-3,8	65	13-Sep	15	16-Oct	17-Nov	11	Salewski et al. 2004	
Long-tailed Tit	*Aegithalos caudatus*	Passeriformes	Aegithalidae	Resident	Europe	Gosforth Park Nature Reserve, Newcastle, North-East England, United Kingdom	55,0	-1,6	92	11-Jun	11	27-Jul	11-Sep	8,6	Frater and Redfern 2012	
Long-tailed Tit	*Aegithalos caudatus*	Passeriformes	Aegithalidae	Resident	Europe	United Kingdom	52,4	-3,0	100	27-May	11	16-Jul	04-Sep	8,6	Morrison et al. 2015	
Levaillant's Cisticola	*Cisticola tinniens elegans (brookei)*	Passeriformes	Cisticolidae	Resident	Africa	Western Cape, South Africa	-33,6	18,6	76	22-Dec		29-Jan	06-Mar	11,9	Herremans et al. 1999	
Levaillant's Cisticola	*Cisticola tinniens tinniens*	Passeriformes	Cisticolidae	Resident	Africa	South Africa: Vanderbijlpark, Potchefstroom, Kimberley	-27,3	26,5	61	18-Mar		18-Apr	16-May	11,1	Herremans et al. 1999	
Black-chested Prinia	*Prinia flavicans*	Passeriformes	Cisticolidae	Resident	Africa	Western Southern Africa (Namibia, Angola)	-17,1	18,2	108	20-Feb		15-Apr	08-Jun	9,1	Herremans 1999	

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Black-chested Prinia	*Prinia flavicans*	Passeriformes	Cisticolidae	Resident	Africa	Eastern, Central and Western Southern Africa (South Africa, Swaziland, Mozambique; Botswana; Namibia, Angola)	-21,6	24,3	67	03-Sep		07-Oct	09-Nov	9,1	Herremans 1999	
Black-chested Prinia	*Prinia flavicans*	Passeriformes	Cisticolidae	Resident	Africa	Central Southern Africa (Botswana)	-22,3	24,7	108	15-Feb		10-Apr	03-Jun	9,1	Herremans 1999	
Black-chested Prinia	*Prinia flavicans*	Passeriformes	Cisticolidae	Resident	Africa	Eastern Southern Africa (South Africa, Swaziland, Mozambique)	-25,2	30,0	108	01-Feb		27-Mar	20-May	9,1	Herremans 1999	
Alpine Chough	*Pyrrhocorax graculus*	Passeriformes	Corvidae	Resident	Europe	Col de Bretolet, South-West Switzerland	46,1	6,8	117	15-Jun	15	13-Aug	10-Oct	212	Winkler et al. 1988	
Yellowhammer	*Emberiza citrinella*	Passeriformes	Emberizidae	Resident	Europe	United Kingdom	52,8	-0,3	42	18-Aug	14	08-Sep	29-Sep	30	This study	
Yellowhammer	*Emberiza citrinella*	Passeriformes	Emberizidae	Resident	Oceania	New Zealand	-41,6	174,1	42	09-Feb	14	02-Mar	23-Mar	30	This study	
Common Reed Bunting	*Emberiza schoeniclus*	Passeriformes	Emberizidae	Resident	Europe	United Kingdom	52,4	-3,0	71	14-Jul	14	18-Aug	23-Sep	18,5	Morrison et al. 2015	
Red-headed Finch	*Amadina erythrocephala*	Passeriformes	Estrildidae	Resident	Africa	Mpumalanga and Gauteng, South Africa	-26,7	28,3	185	19-Aug	54	19-Nov	19-Feb	23	This study	
Orange-breasted Waxbill	*Amandava subflava*	Passeriformes	Estrildidae	Resident	Africa	Gauteng, South Africa	-26,3	28,1	85	30-Nov	46	12-Jan	22-Feb	7,5	Bonnevie and Oschadleus 2012	
Common Waxbill	*Estrilda astrild*	Passeriformes	Estrildidae	Resident	Africa	Namibia	-23,0	18,5	111	29-Dec	43	23-Feb	18-Apr	8,8	Bonnevie and Oschadleus 2012	
Common Waxbill	*Estrilda astrild*	Passeriformes	Estrildidae	Resident	Africa	Gauteng, South Africa	-26,3	28,1	79	15-Feb	44	27-Mar	04-May	8,8	Bonnevie and Oschadleus 2012	
Common Waxbill	*Estrilda astrild*	Passeriformes	Estrildidae	Resident	Africa	KwaZulu-Natal, South Africa	-28,5	30,9	87	05-Mar	30	18-Apr	30-May	8,8	Bonnevie and Oschadleus 2012	
Common Waxbill	*Estrilda astrild*	Passeriformes	Estrildidae	Resident	Africa	Western Cape, South Africa	-33,2	21,9	92	28-Dec	39	12-Feb	30-Mar	8,8	Bonnevie and Oschadleus 2012	

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Violet-eared Waxbill	*Granatina granatina*	Passeriformes	Estrildidae	Resident	Africa	Namibia	-23,0	18,5	113	15-Jun	57	11-Aug	06-Oct	11,8	Bonnevie and Oschadleus 2012	
Brown Firefinch	*Lagonosticta nitidula*	Passeriformes	Estrildidae	Resident	Africa	Botswana; Namibia; Northern Province, South Africa	-22,9	24,2	88	14-Jul	32	27-Aug	10-Oct	10,7	Bonnevie and Oschadleus 2012	
Jameson's Firefinch	*Lagonosticta rhodopareia*	Passeriformes	Estrildidae	Resident	Africa	Botswana; Northern Province, South Africa; Gauteng, South Africa	-24,0	27,4	104	16-May	72	07-Jul	28-Aug	9,3	Bonnevie and Oschadleus 2012	
African Firefinch	*Lagonosticta rubricata*	Passeriformes	Estrildidae	Resident	Africa	KwaZulu-Natal, South Africa	-28,5	30,9	103	09-Apr	47	31-May	20-Jul	10,2	Bonnevie and Oschadleus 2012	
Red-billed Firefinch	*Lagonosticta senegala*	Passeriformes	Estrildidae	Resident	Africa	Botswana; Namibia; Northern Province, South Africa	-22,9	24,2	114	30-Aug	44	26-Oct	21-Dec	8,8	Bonnevie and Oschadleus 2012	
Green-winged Pytilia	*Pytilia melba*	Passeriformes	Estrildidae	Resident	Africa	Botswana	-22,3	24,7	144	02-Jul	55	12-Sep	23-Nov	15,4	Bonnevie and Oschadleus 2012	
Green-winged Pytilia	*Pytilia melba*	Passeriformes	Estrildidae	Resident	Africa	Namibia	-23,0	18,5	123	03-Jul	64	03-Sep	02-Nov	15,4	Bonnevie and Oschadleus 2012	
Green-winged Pytilia	*Pytilia melba*	Passeriformes	Estrildidae	Resident	Africa	Gauteng, South Africa	-26,3	28,1	121	06-Jul	67	05-Sep	03-Nov	15,4	Bonnevie and Oschadleus 2012	
Common Redpoll	*Acanthis flammea*	Passeriformes	Fringillidae	Resident	Europe	United Kingdom	52,8	-1,4	43	09-Aug	10	31-Aug	21-Sep	13	This study	
Common Redpoll	*Acanthis flammea*	Passeriformes	Fringillidae	Resident	Oceania	New Zealand	-43,6	172,0	43	06-Feb	10	27-Feb	21-Mar	13	This study	
European Goldfinch	*Carduelis carduelis*	Passeriformes	Fringillidae	Resident	Europe	Pickworth, Lincolnshire, United Kingdom	52,9	-0,4	77	30-Jul	8	07-Sep	15-Oct	16	Newton and Rothery 2009	
European Goldfinch	*Carduelis carduelis*	Passeriformes	Fringillidae	Resident	Europe	United Kingdom	52,6	-1,6	79	25-Jul	13	03-Sep	12-Oct	16	This study	
European Goldfinch	*Carduelis carduelis*	Passeriformes	Fringillidae	Resident	Europe	United Kingdom	52,4	-3,0	108	08-Jul	16	31-Aug	24-Oct	16	Morrison et al. 2015	
European Goldfinch	*Carduelis carduelis*	Passeriformes	Fringillidae	Resident	Oceania	New Zealand	-41,8	174,0	79	23-Jan	13	04-Mar	13-Apr	16	This study	

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Citril Finch	*Carduelis citrinella*	Passeriformes	Fringillidae	Resident	Europe	Biguezal and Uztarroz, Western Pyrenees, Northern Spain; El Royo and Villoslada de Cameros, Spain	42,4	-1,9	81	07-Jul	11	16-Aug	25-Sep	12	Fernández-Eslava et al. 2020	
European Greenfinch	*Chloris chloris*	Passeriformes	Fringillidae	Resident	Europe	East-Central England, United Kingdom	52,9	-0,4	100	24-Jul	11	12-Sep	01-Nov	26	Newton and Rothery 2005	
European Greenfinch	*Chloris chloris*	Passeriformes	Fringillidae	Resident	Europe	United Kingdom	52,4	-1,3	76	30-Jul	16	06-Sep	14-Oct	26	This study	
European Greenfinch	*Chloris chloris*	Passeriformes	Fringillidae	Resident	Oceania	New Zealand	-41,9	173,9	60	02-Feb	16	03-Mar	02-Apr	26	This study	
Common Chaffinch	*Fringilla coelebs*	Passeriformes	Fringillidae	Resident	Europe	United Kingdom	53,0	-1,6	61	10-Jul	14	10-Aug	09-Sep	21	This study	
Common Chaffinch	*Fringilla coelebs*	Passeriformes	Fringillidae	Resident	Europe	United Kingdom	52,4	-3,0	98	14-Jun	16	02-Aug	20-Sep	26	Morrison et al. 2015	
Common Chaffinch	*Fringilla coelebs*	Passeriformes	Fringillidae	Resident	Oceania	New Zealand	-41,7	173,8	51	19-Jan	14	13-Feb	10-Mar	21	This study	
Tenerife Blue Chaffinch	*Fringilla teydea (teydea)*	Passeriformes	Fringillidae	Resident	Africa	Tenerife, Canary Islands	28,3	-16,6	66	07-Aug	7	09-Sep	12-Oct	31	Garcia-Del-Ray and Gosler 2005	Small sample, only 19 adults
Common Linnet	*Linaria cannabina*	Passeriformes	Fringillidae	Migrant	Europe	National Park Gran Sasso Monti della Laga, Central Italy	42,5	13,6	61	30-Jul		30-Aug	30-Sep	19,6	Strinella et al. 2015	Female and male duration and start day were averaged
Red Crossbill	*Loxia curvirostra*	Passeriformes	Fringillidae	Resident	Europe	Biguezal and Uztarroz, Western Pyrenees, Northern Spain	42,8	-1,1	114	12-May	34	08-Jul	26-Sep	41	Fernández-Eslava et al. 2020	Full duration=136.8 (136.8-23(days of suspended moult)=113.8)
Eurasian Bullfinch	*Pyrrhula pyrrhula*	Passeriformes	Fringillidae	Resident	Europe	United Kingdom	52,4	-3,0	96	29-Jul	18	15-Sep	02-Nov	22	Morrison et al. 2015	
Eurasian Bullfinch	*Pyrrhula pyrrhula*	Passeriformes	Fringillidae	Resident	Europe	Southern England, United Kingdom	51,8	-1,3	73	14-Aug	12	20-Sep	26-Oct	22	Newton and Rothery 2000	

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Rufous-fronted Thornbird	*Phacellodomus rufifrons*	Passeriformes	Furnariidae	Resident	South America	Distrito Federal, Brazil	-15,5	-47,6	174	04-Dec	29	01-Mar	27-May	25	Silveira and Marini 2012	U-Z moult model was not used in the original paper (Silveira & Marini 2012). Used their data (primary feather moult scores) and ran my own full-tract moult model in R
Barn Swallow	*Hirundo rustica*	Passeriformes	Hirundinidae	Migrant	Africa	South Africa	-29,7	26,3	123	29-Nov	17	30-Jan	01-Apr	20	Burman 2016	
Water Pipit	*Anthus spinoletta*	Passeriformes	Motacillidae	Migrant	Europe	National Park Gran Sasso Monti della Laga, Central Italy	42,5	13,6	64	15-Jul		16-Aug	17-Sep	24	Strinella et al. 2015	
Cape Robin-Chat	*Cossypha caffra*	Passeriformes	Muscicapidae	Resident	Africa	Grahamstown, Eastern Cape, South Africa	-33,3	26,5	50	07-Jan	15	01-Feb	26-Feb	28	Bonnevie et al. 2003	
Cape Robin-Chat	*Cossypha caffra*	Passeriformes	Muscicapidae	Resident	Africa	Western Cape, South Africa	-34,1	18,6	64	05-Nov	14	07-Dec	08-Jan	30	Bonnevie et al. 2003	
European Robin	*Erithacus rubecula*	Passeriformes	Muscicapidae	Resident	Europe	United Kingdom	52,4	-3,0	100	05-Jun	24	25-Jul	13-Sep	17,7	Morrison et al. 2015	
Bluethroat	*Luscinia svecica namnetum*	Passeriformes	Muscicapidae	Migrant	Europe	Conchemarche Marsh, France	45,5	-0,8	37	19-Jul	8	07-Aug	25-Aug	14,7	Musseau et al. 2017	Start date: 22-Jul females, 16-Jul males. Start date was average of the two dates
Northern Wheatear	*Oenanthe oenanthe*	Passeriformes	Muscicapidae	Migrant	Europe	National Park Gran Sasso Monti della Laga, Central Italy	42,5	13,6	52	13-Jul		08-Aug	03-Sep	23	Strinella et al. 2015	average of male and female start day
Black Redstart	*Phoenicurus ochruros*	Passeriformes	Muscicapidae	Migrant	Europe	National Park Gran Sasso Monti della Laga, Central Italy	42,5	13,6	49	24-Jul		17-Aug	11-Sep	16,5	Strinella et al. 2015	average of male and female start day
European Stonechat	*Saxicola rubicola*	Passeriformes	Muscicapidae	Migrant	Europe	Cologne, North-West Germany	51,0	6,5	68	19-Jul		22-Aug	25-Sep	15,3	Flinks et al. 2008	
Eurasian Blue Tit	*Cyanistes caeruleus*	Passeriformes	Paridae	Resident	Europe	United Kingdom	52,4	-3,0	104	20-May	19	11-Jul	01-Sep	10,6	Morrison et al. 2015	

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Great Tit	*Parus major*	Passeriformes	Paridae	Resident	Europe	United Kingdom	52,4	-3,0	106	25-May	19	17-Jul	08-Sep	18,3	Morrison et al. 2015	
Marsh Tit	*Poecile palustris*	Passeriformes	Paridae	Resident	Europe	Monks Wood, Cambridgeshire, Eastern England, United Kingdom	52,4	-0,2	67	27-May		30-Jun	02-Aug	10,9	Broughton et al. 2008	
Saltmarsh Sparrow	*Ammospiza caudacuta*	Passeriformes	Passerellidae	Migrant	North America	Connecticut, USA	41,3	-72,5	51	12-Aug		06-Sep	02-Oct	19,3	Borowske et al. 2017	Female and male duration and start day were averaged
Seaside Sparrows	*Ammospiza maritima*	Passeriformes	Passerellidae	Migrant	North America	Connecticut, USA	41,3	-72,5	57	05-Aug		02-Sep	01-Oct	23	Borowske et al. 2017	Female and male duration and start day were averaged
White-winged Snowfinch	*Montifringilla nivalis*	Passeriformes	Passeridae	Resident	Europe	Campo Imperatore, National Park Gran Sasso Monti della Laga, Central Italy	42,5	13,6	76	19-Jul	12	26-Aug	03-Oct	37	Strinella et al. 2011	
House Sparrow	*Passer domesticus*	Passeriformes	Passeridae	Resident	Europe	United Kingdom	52,5	-1,7	61	02-Aug	16	02-Sep	02-Oct	28	This study	
House Sparrow	*Passer domesticus*	Passeriformes	Passeridae	Resident	Europe	United Kingdom	52,4	-3,0	111	06-Jul	22	31-Aug	25-Oct	28	Morrison et al. 2015	
House Sparrow	*Passer domesticus*	Passeriformes	Passeridae	Resident	Oceania	New Zealand	-40,2	174,1	74	31-Jan	16	09-Mar	15-Apr	28	This study	
Wood Warbler	*Phylloscopus sibilatrix*	Passeriformes	Phylloscopidae	Migrant	Africa	Southern Cameroon	3,3	11,8	61	26-Dec	7	26-Jan	25-Feb	9,1	Jarrett et al. 2021	
Willow Warbler	*Phylloscopus trochilus*	Passeriformes	Phylloscopidae	Migrant	Europe	United Kingdom	52,4	-3,0	69	12-Jun	15	16-Jul	20-Aug	8,7	Morrison et al. 2015	
Willow Warbler	*Phylloscopus trochilus*	Passeriformes	Phylloscopidae	Migrant	Africa	Coastal mangrove swamps, Guinea-Bissau	11,5	-15,5	68	04-Dec	11	07-Jan	10-Feb	8,7	Underhill et al. 1992	
Willow Warbler	*Phylloscopus trochilus*	Passeriformes	Phylloscopidae	Migrant	Africa	Ivory Coast, West Africa	8,8	-3,8	67	24-Dec	14	27-Jan	01-Mar	8,7	Salewski et al. 2004	
Willow Warbler	*Phylloscopus trochilus*	Passeriformes	Phylloscopidae	Migrant	Africa	Kampala, Southern Uganda	0,3	32,7	68	04-Jan	15	07-Feb	13-Mar	8,7	Underhill et al. 1992	
Willow Warbler	*Phylloscopus trochilus*	Passeriformes	Phylloscopidae	Migrant	Africa	South-Central Africa	-9,0	33,0	52	23-Dec	13	18-Jan	13-Feb	8,7	Underhill et al. 1992	
Willow Warbler	*Phylloscopus trochilus*	Passeriformes	Phylloscopidae	Migrant	Africa	South Africa: Transvaal, Orange Free State, KwaZulu-Natal	-27,0	28,0	49	28-Dec	13	22-Jan	15-Feb	8,7	Underhill et al. 1992	

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Willow Warbler	*Phylloscopus trochilus acredula*	Passeriformes	Phylloscopidae	Migrant	Europe	Kevo, Finnish Lappland	69,5	27,0	40	14-Jul	7	03-Aug	23-Aug	8,7	Underhill et al. 1992	
Willow Warbler	*Phylloscopus trochilus acredula*	Passeriformes	Phylloscopidae	Migrant	Europe	Ammarnäs, Northern Sweden	66,0	16,1	31	21-Jul	7	06-Aug	21-Aug	8,7	Underhill et al. 1992	
Willow Warbler	*Phylloscopus trochilus acredula*	Passeriformes	Phylloscopidae	Migrant	Europe	Lammi, Southern Finland	61,1	25,1	43	11-Jul	9	02-Aug	23-Aug	8,7	Underhill et al. 1992	
Willow Warbler	*Phylloscopus trochilus trochilus*	Passeriformes	Phylloscopidae	Migrant	Europe	Hadfast, Lothian Region, South-East Scotland, United Kingdom	55,9	-3,0	39	04-Jul	10	24-Jul	12-Aug	8,7	Underhill et al. 1992	
Willow Warbler	*Phylloscopus trochilus trochilus*	Passeriformes	Phylloscopidae	Migrant	Europe	Wilton, Cleveland, North-Eastern England, United Kingdom	54,6	-1,1	33	05-Jul	8	22-Jul	07-Aug	8,7	Underhill et al. 1992	
Willow Warbler	*Phylloscopus trochilus trochilus*	Passeriformes	Phylloscopidae	Migrant	Europe	Oostrvaardersplassen, Zuidelijk Flevoland, the Netherlands	52,5	5,4	36	25-Jun	8	13-Jul	31-Jul	8,7	Underhill et al. 1992	
Willow Warbler	*Phylloscopus trochilus trochilus*	Passeriformes	Phylloscopidae	Migrant	Europe	Witley Common, Surrey, Southern England, United Kingdom	51,2	-0,7	38	24-Jun	9	13-Jul	01-Aug	8,7	Underhill et al. 1992	
Willow Warbler	*Phylloscopus trochilus trochilus*	Passeriformes	Phylloscopidae	Migrant	Europe	Brabant Province, Belgium	50,8	4,5	36	16-Jun	10	04-Jul	22-Jul	8,7	Underhill et al. 1992	
Thick-billed Weaver	*Amblyospiza albifrons*	Passeriformes	Ploceidae	Resident	Africa	Gauteng, South Africa	-26,0	28,0	71	20-Feb	24	28-Mar	02-May	46	Oschadleus 2005, Oschadleus and Underhill 2006	
Thick-billed Weaver	*Amblyospiza albifrons*	Passeriformes	Ploceidae	Resident	Africa	KwaZulu-Natal, South Africa	-29,5	30,5	73	26-Mar	23	02-May	07-Jun	46	Oschadleus 2005, Oschadleus and Underhill 2006	

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White-winged Widowbird	*Euplectes albonotatus*	Passeriformes	Ploceidae	Resident	Africa	Gauteng, South Africa	-26,0	29,0	47	18-Apr	26	11-May	03-Jun	21	Oschadleus 2005, Oschadleus and Underhill 2006	
Red-collared Widowbird	*Euplectes ardens*	Passeriformes	Ploceidae	Resident	Africa	Gauteng, South Africa	-26,0	29,0	60	05-Apr	31	05-May	03-Jun	21	Oschadleus 2005, Oschadleus and Underhill 2006	
Fan-tailed Widowbird	*Euplectes axillaris*	Passeriformes	Ploceidae	Resident	Africa	KwaZulu-Natal, South Africa	-29,5	30,5	51	02-Apr	18	27-Apr	23-May	25	Oschadleus 2005, Oschadleus and Underhill 2006	
Yellow Bishop	*Euplectes capensis*	Passeriformes	Ploceidae	Resident	Africa	Western Cape, South Africa	-34,0	18,5	103	04-Dec	23	25-Jan	17-Mar	31	Oschadleus 2005, Oschadleus and Underhill 2006	
Southern Red Bishop	*Euplectes orix*	Passeriformes	Ploceidae	Resident	Africa	Gauteng, South Africa	-26,0	28,0	72	23-Mar	35	28-Apr	03-Jun	23	Oschadleus 2005, Oschadleus and Underhill 2006	
Southern Red Bishop	*Euplectes orix*	Passeriformes	Ploceidae	Resident	Africa	Grahamstown, Eastern Cape, South Africa	-33,3	26,5	89	28-Apr	47	12-Jun	26-Jul	23	Craig et al. 2001, Oschadleus and Underhill 2006	
Southern Red Bishop	*Euplectes orix*	Passeriformes	Ploceidae	Resident	Africa	Western Cape, South Africa	-33,5	18,5	89	13-Dec	25	26-Jan	12-Mar	23	Oschadleus 2005, Oschadleus and Underhill 2006	
Long-tailed Widowbird	*Euplectes progne*	Passeriformes	Ploceidae	Resident	Africa	South Africa: Gauteng, Free State, KwaZulu-Natal	-28,0	29,0	61	26-Mar	21	25-Apr	25-May	35	Oschadleus 2005, Oschadleus and Underhill 2006	

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Sociable Weaver	*Philetairus socius eremnus*	Passeriformes	Ploceidae	Resident	Africa	Northern Cape, South Africa	-20,0	25,0	169	31-Dec	38	25-Mar	17-Jun	29	Oschadleus 2004, Oschadleus 2005	
Sociable Weaver	*Philetairus socius geminus*	Passeriformes	Ploceidae	Resident	Africa	Northern Namibia	-19,0	17,0	216	28-Jan	68	16-May	31-Aug	27	Oschadleus 2004, Oschadleus 2005	
Sociable Weaver	*Philetairus socius socius*	Passeriformes	Ploceidae	Resident	Africa	Northern Cape, South Africa	-28,0	22,0	152	26-Jan	38	12-Apr	26-Jun	27	Oschadleus 2004, Oschadleus 2005	
Bannerman's Weaver	*Ploceus bannermani*	Passeriformes	Ploceidae	Resident	Africa	Obudu Plateau, South-Eastern Nigeria	6,4	9,4	159	21-Aug	39	09-Nov	27-Feb	31	Barshepand Manu 2013	
Cape Weaver	*Ploceus capensis*	Passeriformes	Ploceidae	Resident	Africa	KwaZulu-Natal, South Africa	-29,5	30,5	124	02-Feb	32	05-Apr	06-Jun	44	Oschadleus 2005	
Cape Weaver	*Ploceus capensis*	Passeriformes	Ploceidae	Resident	Africa	Grahamstown, Eastern Cape, South Africa	-33,3	26,5	106	09-Jan	25	03-Mar	25-Apr	44	Craig et al. 2001	
Cape Weaver	*Ploceus capensis*	Passeriformes	Ploceidae	Resident	Africa	Western Cape, South Africa	-33,5	18,5	98	11-Nov	24	30-Dec	17-Feb	44	Oschadleus 2005	
Village Weaver	*Ploceus cucullatus*	Passeriformes	Ploceidae	Resident	Africa	KwaZulu-Natal, South Africa	-29,5	30,5	96	12-Feb	29	01-Apr	19-May	37	Oschadleus 2005, Oschadleus and Underhill 2006	
Village Weaver	*Ploceus cucullatus*	Passeriformes	Ploceidae	Resident	Africa	Grahamstown, Eastern Cape, South Africa	-33,3	26,5	109	17-Feb	40	13-Apr	06-Jun	37	Craig et al. 2001	
Spectacled Weaver	*Ploceus ocularis*	Passeriformes	Ploceidae	Resident	Africa	KwaZulu-Natal, South Africa	-29,5	30,5	114	03-Feb	21	01-Apr	28-May	25	Oschadleus 2005	
Chestnut Weaver	*Ploceus rubiginosus*	Passeriformes	Ploceidae	Migrant	Africa	Northern Namibia	-19,5	15,5	198	20-Apr	39	27-Jul	03-Nov	29	Oschadleus 2005, Oschadleus and Osborne 2005	Male and female duration, start day & SD of start day were averaged

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Eastern Golden Weaver	*Ploceus subaureus*	Passeriformes	Ploceidae	Resident	Africa	KwaZulu-Natal, South Africa	-29,5	30,5	66	27-Feb	20	01-Apr	04-May	31	Oschadleus 2005, Oschadleus and Underhill 2006	
Southern Masked Weaver	*Ploceus velatus*	Passeriformes	Ploceidae	Resident	Africa	Gauteng, South Africa	-26,0	28,0	76	11-Feb	19	21-Mar	28-Apr	31	Oschadleus 2005	
Southern Masked Weaver	*Ploceus velatus*	Passeriformes	Ploceidae	Resident	Africa	North-West Province/North-West Gauteng (Transvaal) Staffordtuin Farm near Rustenburg and Johannesburg, South Africa	-26,0	27,7	80	15-Feb	23	27-Mar	07-May	31	Oschadleus et al. 2000	
Southern Masked Weaver	*Ploceus velatus*	Passeriformes	Ploceidae	Resident	Africa	Grahamstown, Eastern Cape, South Africa	-33,3	26,5	67	22-Mar	25	25-Apr	28-May	31	Craig et al. 2001	
Southern Masked Weaver	*Ploceus velatus*	Passeriformes	Ploceidae	Resident	Africa	Western Cape, South Africa	-33,5	18,5	84	27-Dec	33	07-Feb	22-Mar	31	Oschadleus 2005	
Southern Masked Weaver	*Ploceus velatus*	Passeriformes	Ploceidae	Resident	Africa	Western Cape, South Africa	-33,9	18,6	74	09-Jan	24	15-Feb	24-Mar	31	Oschadleus et al. 2000	
Red-billed Quelea	*Quelea quelea*	Passeriformes	Ploceidae	Migrant	Africa	Northern Botswana	-17,5	25,5	83	31-May	35	11-Jul	22-Aug	18,6	Oschadleus 2005	
Red-billed Quelea	*Quelea quelea*	Passeriformes	Ploceidae	Migrant	Africa	Windpoort Farm, Namibia	-19,5	15,5	75	21-May	37	27-Jun	04-Aug	18,6	Oschadleus 2005	
Red-billed Quelea	*Quelea quelea*	Passeriformes	Ploceidae	Migrant	Africa	Gauteng, South Africa	-26,0	28,0	101	23-Apr	33	12-Jun	02-Aug	18,6	Oschadleus 2005	
Red-billed Quelea	*Quelea quelea*	Passeriformes	Ploceidae	Migrant	Africa	Eastern Cape, South Africa	-32,9	25,5	124	06-Apr	37	07-Jun	08-Aug	18,6	Craig et al. 2001	
Dunnock	*Prunella modularis*	Passeriformes	Prunellidae	Resident	Europe	United Kingdom	52,4	-1,1	45	31-Jul	13	23-Aug	15-Sep	20	This study	
Dunnock	*Prunella modularis*	Passeriformes	Prunellidae	Resident	Europe	United Kingdom	52,4	-3,0	80	13-Jul	15	22-Aug	01-Oct	21	Morrison et al. 2015	
Dunnock	*Prunella modularis*	Passeriformes	Prunellidae	Resident	Oceania	New Zealand	-41,9	173,3	45	30-Jan	13	21-Feb	16-Mar	20	This study	
Sombre Greenbul	*Andropadus importunus importunus*	Passeriformes	Pycnonotidae	Resident	Africa	Mpumalanga & Limpopo, South Africa	-28,0	31,0	118	16-Jan	29	16-Mar	14-May	31	Bonnevie 2014	

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Sombre Greenbul	*Andropadus importunus importunus*	Passeriformes	Pycnonotidae	Resident	Africa	KwaZulu-Natal, South Africa	-30,0	31,0	130	08-Jan	37	14-Mar	18-May	35	Bonnevie 2014	
Sombre Greenbul	*Andropadus importunus importunus*	Passeriformes	Pycnonotidae	Resident	Africa	South Africa	-32,0	26,0	117	30-Dec	44	27-Feb	26-Apr	35	Bonnevie 2014	Moult parameters of all SA regions combined
Sombre Greenbul	*Andropadus importunus importunus*	Passeriformes	Pycnonotidae	Resident	Africa	Western Cape, South Africa	-34,0	21,0	113	18-Dec	54	13-Feb	10-Apr	36	Bonnevie 2014	
Sombre Greenbul	*Andropadus importunus importunus*	Passeriformes	Pycnonotidae	Resident	Africa	Eastern Cape, South Africa	-34,0	26,0	100	28-Dec	42	16-Feb	07-Apr	35	Bonnevie 2014	
Sombre Greenbul	*Andropadus importunus oleaginus*	Passeriformes	Pycnonotidae	Resident	Africa	South Africa	-28,0	32,0	95	04-Feb	35	24-Mar	09-May	32	Bonnevie 2014	
Common Bulbul	*Pycnonotus barbatus*	Passeriformes	Pycnonotidae	Resident	Africa	Amurum Forest Reserve, Jos Plateau, Nigeria	9,9	9,0	138	02-May	33	10-Jul	17-Sep	39	Nwaogu et al. 2019	
Siamese Pied Myna	*Gracupica floweri*	Passeriformes	Sturnidae	Resident	Asia	Phetchaburi province, Thailand	13,1	100,1	110	08-Jun	14	02-Aug	26-Sep	84	Round et al. 2014	
Splendid Starling	*Lamprotornis splendidus chrysonotis*	Passeriformes	Sturnidae	Nomadic	Africa	Guinea-Bissau; Sierra Leone	10,1	-13,5	109	21-Jun		14-Aug	08-Oct		Craig 2012a	
Splendid Starling	*Lamprotornis splendidus lessoni*	Passeriformes	Sturnidae	Resident	Africa	Bioko, Equatorial Guinea	3,6	8,7	130	13-Jun		17-Aug	21-Oct		Craig 2012a	
Splendid Starling	*Lamprotornis splendidus splendidus*	Passeriformes	Sturnidae	Nomadic	Africa	Southern Congo Basin: Angola, Demographic Republic of Congo south of 4 degrees south	-9,9	19,8	70	25-Nov		30-Dec	03-Feb		Craig 2012a	
Pale-winged Starling	*Onychognathus nabouroup*	Passeriformes	Sturnidae	Resident	Africa	Namibia	-23,0	18,5	164	11-Nov		01-Feb	24-Apr	104	Craig 2012b	
Pale-winged Starling	*Onychognathus nabouroup*	Passeriformes	Sturnidae	Resident	Africa	South Africa	-30,6	22,9	151	06-Nov		21-Jan	06-Apr	104	Craig 2012b	
Common Starling	*Sturnus vulgaris*	Passeriformes	Sturnidae	Resident	Europe	United Kingdom	52,4	-3,0	94	29-May	13	15-Jul	31-Aug	80	Morrison et al. 2015	

English name	Scientific name	Order	Family	Migratory status	Continent	Study site location	Latitude	Longitude	Duration	Start date	SD of start date	Mid-date	End date	Mass (g)	Source	Notes
Common Starling	*Sturnus vulgaris*	Passeriformes	Sturnidae	Resident	Europe	Monks Wood, Cambridgeshire, Eastern England, United Kingdom	52,3	-0,3	99	04-Jun	9	24-Jul	11-Sep	80	Rothery et al. 2001	1977 and 1978 duration, startday and SD of start day paramters averaged
Common Starling	*Sturnus vulgaris*	Passeriformes	Sturnidae	Resident	Africa	Dassen Island, South Africa	-33,4	18,1	108	08-Nov	15	01-Jan	24-Feb	80	Cooper and Underhill 1991	
Common Whitethroat	*Curruca communis*	Passeriformes	Sylviidae	Migrant	Europe	United Kingdom	52,4	-3,0	67	04-Jul	14	06-Aug	09-Sep	15,1	Morrison et al. 2015	
Common Whitethroat	*Curruca communis*	Passeriformes	Sylviidae	Migrant	Europe	Poland	51,9	19,4	48	03-Jul	10	27-Jul	20-Aug	15,1	Remisiewicz et al. 2019	
Common Whitethroat	*Curruca communis*	Passeriformes	Sylviidae	Migrant	Africa	North-Eastern South Africa (North-West, Gauteng, Mpumalanga, Limpopo provinces)	-26,0	28,0	54	29-Dec	17	25-Jan	21-Feb	15,1	Remisiewicz et al. 2019	
Eurasian Blackcap	*Sylvia atricapilla*	Passeriformes	Sylviidae	Migrant	Europe	United Kingdom	52,4	-3,0	71	12-Jul	15	16-Aug	21-Sep	16,7	Morrison et al. 2015	
Eurasian Blackcap	*Sylvia atricapilla*	Passeriformes	Sylviidae	Migrant	Europe	Poland	52,3	20,6	41	23-Jul	12	13-Aug	02-Sep	16,7	Misztal 2015	
Garden Warbler	*Sylvia borin*	Passeriformes	Sylviidae	Migrant	Africa	Southern Africa	-27,2	27,8	75	30-Nov		06-Jan	13-Feb	18,2	Krawczyk 2016	
Wedge-tailed Grass Finch	*Emberizoides herbicola*	Passeriformes	Thraupidae	Resident	South America	Distrito Federal, Brazil	-15,5	-47,6	85	18-Feb	14	02-Apr	14-May	29	Silveira and Marini 2012; moult model applied to data supplied by authors	U-Z moult model was not used in the original paper (Silveira & Marini 2012). Used their data (primary feather moult scores) and ran my own full-tract moult model in R

English name	Scientific name	Order	Family	Migratory status	Continent	Study site location	Latitude	Longitude	Duration	Start date	SD of start date	Mid-date	End date	Mass (g)	Source	Notes
Shrike-like Tanager	*Neothraupis fasciata*	Passeriformes	Thraupidae	Resident	South America	Distrito Federal, Brazil	-15,5	-47,6	131	11-Dec	20	15-Feb	21-Apr	27	Silveira and Marini 2012; moult model applied to data supplied by authors	U-Z moult model was not used in the original paper (Silveira & Marini 2012). Used their data (primary feather moult scores) and ran my own full-tract moult model in R
Common Blackbird	*Turdus merula*	Passeriformes	Turdidae	Resident	Europe	United Kingdom	52,4	-3,0	100	27-Jun	20	16-Aug	05-Oct	113	Morrison et al. 2015	
Olive Thrush	*Turdus olivaceus*	Passeriformes	Turdidae	Resident	Africa	Grahamstown, Eastern Cape, South Africa	-33,3	26,5	53	01-Jan	16	28-Jan	23-Feb	83	Bonnevie et al. 2003	
Olive Thrush	*Turdus olivaceus*	Passeriformes	Turdidae	Resident	Africa	Western Cape, South Africa	-34,1	18,6	89	11-Dec	27	25-Jan	10-Mar	81	Bonnevie et al. 2003	
Lesser Elaenia	*Elaenia chiriquensis*	Passeriformes	Tyrannidae	Resident	South America	Distrito Federal, Brazil	-15,5	-47,6	104	18-Nov	11	09-Jan	01-Mar	15,4	Silveira and Marini 2012; moult model applied to data supplied by authors	U-Z moult model was not used in the original paper (Silveira & Marini 2012). Used their data (primary feather moult scores) and ran my own full-tract moult model in R
Plain-crested Elaenia	*Elaenia cristata*	Passeriformes	Tyrannidae	Resident	South America	Distrito Federal, Brazil	-15,5	-47,6	165	17-Sep	31	09-Dec	01-Mar	18,2	Silveira and Marini 2012; moult model applied to data supplied by authors	U-Z moult model was not used in the original paper (Silveira & Marini 2012). Used their data (primary feather moult scores) and ran my own full-

English name	Scientific name	Order	Family	Migratory status	Continent	Study site location	Latitude	Longitude	Duration	Start date	SD of start date	Mid-date	End date	Mass (g)	Source	Notes
																tract moult model in R
Village Indigobird	*Vidua chalybeata*	Passeriformes	Viduidae	Resident	Africa	Botswana; Namibia; Northern Province, South Africa	-22,9	24,2	87	08-Aug	13	21-Sep	03-Nov	12,5	Bonnevie and Oschadleus 2012	
Dusky Indigobird	*Vidua funerea*	Passeriformes	Viduidae	Resident	Africa	KwaZulu-Natal, South Africa	-28,5	30,9	131	13-Jul	16	17-Sep	21-Nov	14,4	Bonnevie and Oschadleus 2012	
Pin-tailed Whydah	*Vidua macroura*	Passeriformes	Viduidae	Resident	Africa	Gauteng, South Africa	-26,3	28,1	105	28-Mar	43	20-May	10-Jul	15,8	Bonnevie and Oschadleus 2012	
Pin-tailed Whydah	*Vidua macroura*	Passeriformes	Viduidae	Resident	Africa	KwaZulu-Natal, South Africa	-28,5	30,9	160	31-Mar	47	19-Jun	07-Sep	15,8	Bonnevie and Oschadleus 2012	
Pin-tailed Whydah	*Vidua macroura*	Passeriformes	Viduidae	Resident	Africa	Western Cape, South Africa	-33,2	21,9	85	17-Jan	44	01-Mar	12-Apr	15,8	Bonnevie and Oschadleus 2012	
Long-tailed Paradise-Whydah	*Vidua paradisaea*	Passeriformes	Viduidae	Resident	Africa	Namibia	-23,0	18,5	184	21-Apr	33	22-Jul	22-Oct	20	Bonnevie and Oschadleus 2012	
Purple Indigobird	*Vidua purpurascens*	Passeriformes	Viduidae	Resident	Africa	Botswana; Northern Province, South Africa; Gauteng, South Africa	-24,0	27,4	67	05-Sep	4	09-Oct	11-Nov	13,1	Bonnevie and Oschadleus 2012	
Shaft-tailed Whydah	*Vidua regia*	Passeriformes	Viduidae	Resident	Africa	Namibia	-23,0	18,5	127	05-Jun	34	08-Aug	09-Oct	14,4	Bonnevie and Oschadleus 2012	
Silvereye	*Zosterops lateralis*	Passeriformes	Zosteropidae	Resident	Oceania	New Zealand	-41,7	173,6	74	03-Feb	37	13-Mar	19-Apr	12,9	This study	
Orange River White-eye	*Zosterops pallidus*	Passeriformes	Zosteropidae	Resident	Africa	Bloemfontein and Sandveld Nature Reserve, Free State, South Africa	-28,4	26,0	78	30-Jan	28	10-Mar	19-Apr	11,1	Hulley et al. 2004	
Cape White-eye	*Zosterops virens*	Passeriformes	Zosteropidae	Resident	Africa	Grahamstown, Eastern Cape, South Africa	-33,3	26,5	77	07-Feb	23	17-Mar	25-Apr	11,1	Hulley et al. 2004	
Cape White-eye	*Zosterops virens*	Passeriformes	Zosteropidae	Resident	Africa	Durbanville, Western Cape, South Africa	-33,8	18,7	76	25-Dec	30	01-Feb	11-Mar	11,1	Hulley et al. 2004	

English name	Scientific name	Order	Family	Migratory status	Continent	Study site location	Latitude	Longitude	Duration	Start date	SD of start date	Mid-date	End date	Mass (g)	Source	Notes
Cape White-eye	*Zosterops virens*	Passeriformes	Zosteropidae	Resident	Africa	Rondevlei Nature Reserve, Cape Town, Western Cape, South Africa	-34,1	18,5	70	12-Jan	28	16-Feb	23-Mar	11,1	Hulley et al. 2004	
Cape White-eye	*Zosterops virens*	Passeriformes	Zosteropidae	Resident	Africa	Betty's Bay, Western Cape, South Africa	-34,4	18,9	69	09-Jan	29	12-Feb	19-Mar	11,1	Hulley et al. 2004	
White-eared Puffbird	*Nystalus chacuru*	Piciformes	Bucconidae	Resident	South America	Distrito Federal, Brazil	-15,5	-47,6	191	04-Dec	17	09-Mar	12-Jun	52	Silveira and Marini 2012; moult model applied to data supplied by authors	U-Z moult model was not used in the original paper (Silveira & Marini 2012). Used their data (primary feather moult scores) and ran my own full-tract moult model in R
Lesser Honeyguide	*Indicator minor*	Piciformes	Indicatoridae	Resident	Africa	Rondevlei Nature Reserve, Cape Town, Western Cape, South Africa	-34,1	18,5	140	08-Jan	35	19-Mar	28-May	28	Underhill et al. 1995	
European Storm Petrel	*Hydrobates pelagicus*	Procellariiformes	Hydrobatidae	Migrant	Europe	Aketx islet, Biscay, Northern Spain	43,5	-2,8		21-Jul	12			25	Zuberogoitia et al. 2016	They studied the moult of European storm petrels during the breeding season and they only moult some of their first primaries during this period. Thus they analysed the onset of moult but could not analyse the duration.
European Storm Petrel	*Hydrobates pelagicus*	Procellariiformes	Hydrobatidae	Migrant	Europe	Vizcaya, Basque country, Northern Spain	43,4	-2,8		22-Jul	10			25	Arroyo et al. 2004	

English name	Scientific name	Order	Family	Migratory status	Continent	Study site location	Latitude	Longitude	Duration	Start date	SD of start date	Mid-date	End date	Mass (g)	Source	Notes
European Storm Petrel	*Hydrobates pelagicus*	Procellariiformes	Hydrobatidae	Migrant	Europe	Benidorm Island, Eastern Spain	38,5	0,1		25-Jun	16			25	Arroyo et al. 2004	
Sooty Shearwater	*Ardenna grisea*	Procellariiformes	Procellariidae	Migrant	Africa	South-Western Cape, South Africa	-33,7	18,2	159	02-Jan	26	23-Mar	10-Jun	787	Cooper et al. 1991	
White-chinned Petrel	*Procellaria aequinoctialis*	Procellariiformes	Procellariidae	Migrant	Africa	Southern Africa	-24,0		106	15-Apr	46	07-Jun	30-Jul	1213	OE Adekola and PG Ryan (unpubl. data)	
Cape Gannet	*Morus capensis*	Suliformes	Sulidae	Resident	Africa	Lambert's Bay, South Africa	-32,1	18,3	177	02-Jan	28	31-Mar	27-Jun	2644	Adekola et al. 2021	
Cape Gannet	*Morus capensis*	Suliformes	Sulidae	Resident	Africa	Malgas Island, South Africa	-33,1	17,9	154	02-Jan	28	20-Mar	05-Jun	2644	Adekola et al. 2021	

Appendix 2

The method described in this appendix was applied in Chapter 3. The statistical method was developed by the first author, the supervisor of this thesis, and extensive data analysis to test the method, and potential alternatives, was done by the second author, the PhD student. This appendix is therefore not part of this thesis but is presented here because it is the only source of the method applied in Chapter 3. The paper has been submitted to a journal and is deliberately presented in the style of the journal, rather than the style of the thesis.

Influence of groups of points on estimates of the parameters of moult

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The Underhill-Zucchini moult model is a statistical simplification for the analysis of avian primary moult, a complex biological system. As with all such models, conclusions can be biased if a subset of the data used to fit the model is strongly influential on the results. In the analysis of primary moult of a species, it is standard practice to assemble as many records as possible, frequently from different years or localities. In this note we develop an approach, based on the concepts underpinning Cook's distance in regression, to evaluate the influence on the estimated moult parameters of groups of records which differ from the bulk of the data. The method is applied to a simulated dataset.

Keywords: bias, primary moult, statistical models, leverage, case deletion strategies, Cook's distance, Mahalanobis distance, Underhill-Zucchini moult model,

As pointed out by Cook (1986) statistical models are almost invariably simplifications of complex systems and "therefore are nearly always wrong". A model which has been successful at improving our understanding of the key features of a biological process is the moult model of Underhill and Zucchini (1988). One standard approach to assessing the quality of a model is to check whether the model is robust against modest changes to the dataset that is used to fit the model; one family of such perturbations consists of case-deletion strategies (Cook 1986). The early approach was to delete one case at a time (e.g. Cook 1977, 1979); in the context discussed here, the strategy is to delete groups of related cases. The aim is to avoid the situation where conclusions are strongly influenced or biased by a subset of the database.

A standard strategy in the quantitative description of primary moult is to combine available moult records across multiple years, and then to apply the moult model developed by Underhill and Zucchini (1988) to estimate the parameters of moult. Frequently, blocks of data are collected by bird ringers on one or more days in different years. A potential source of bias occurs if the timing of moult for some years differs from the average and is "influential" (in the statistical sense described by Cook and Weisberg (1992)) in the estimation of the parameters. A similar concern applies when data from many locations are pooled; if the parameters of moult at one of the locations differ from the others, it may have a large influence on the analysis, so that the final results are misleading.

As a theoretical example, suppose that we have primary moult data collected for a species over seven years (Figure 1). Suppose that in the first five of these seven years the parameters of moult are identical, but that in the sixth- and seventh-year moult is early or delayed relative to the previous five, respectively. Suppose that a small number of opportunistic samples of primary moult are made in each of the first five years; in the sixth year, the sample is made in the middle of the moult period and that, in the seventh year, the sample was made near the end of the moult period. The data are pooled and plotted (Figure 1). Regardless of method of analysis, the sample from year seven will result in the duration of moult appearing to be longer than it ought to be, and the finishing date of moult later than it ought to be. So, the data in this sample are "influential" in terms of the statistical definition and will bias the results of the analysis. How that date from year six will influence the results is less clear cut. The purpose of this short note is to provide an algorithm that can detect influential subsets of data in the moult model of Underhill and Zucchini (1988).

The statistic we propose works on the same principles as Cook's distance in multiple regression (Cook 1977); it is a measure of the change in parameters taking account of the correlations between the estimates of the parameters. We therefore propose calling it the "modified Cook's distance".

In regression, Cook's distance is calculated by successively omitting each of the *n* data points used in the least squares analysis and the statistic measures how much the regression line is changed by omitting the data point. This is defined as the "influence" of the data point. Each of the influential data points are evaluated. In this process, numerical errors may be located and corrected. Alternatively, it might be decided that a particular point is an outlier and should be excluded from the final analysis.

Suppose the estimates of duration, starting date and standard deviation of starting date with the full dataset are t, d and s respectively. Suppose, using a standard notation for this concept, the estimates of the parameters of moult with n_i values in group i removed from the dataset are $t_{(-i)}$, $d_{(-i)}$ and $s_{(-i)}$. The intuitive approach to calculating the influence of the data for group i, in this example, the data for a single year, is calculating the differences between the estimates for each parameter, squaring the differences and adding them: $C_1 = (t - t_{(-i)})^2 + (d - d_{(-i)})^2 + (s - s_{(-i)})^2$. However, Cook (1977) showed that the correct way to do the calculation is to take account of the correlations between the estimates. In this context, the appropriate measure of distance is that developed by Mahalanobis (1930); in matrix-vector notation this is:

$$M = (b - b_{(-i)})^T V^{-1} (b - b_{(-i)})$$

where b and $b_{(-i)}$ are the two sets of parameter estimates arranged as vectors and V is the so-called variance-covariance matrix, available as an optional output from Erni et al. (2013). The matrix V is the variance-covariance matrix from the complete dataset.

The approach of Cook (1977) was to deal with one point at a time. With the primary moult data, we are dealing with groups of points of different sizes, and each of the n_i points in group i is contributing to the Mahalanobis distance M. Thus our final step is to divide by the group size, so that the modified Cook's distance for group i is $C_{(-i)}=M/n_i$. The quantity $C_{(-i)}$ may be interpreted as the average influence of the observations in group i on the estimates of the parameters of moult. It is, in essence, a measure of the magnitude of the change in the estimates of the parameters when group i is removed from the dataset, taking into account the correlations between the parameter estimates.

An appropriate decision strategy about whether to include or exclude a group of observations is to calculate $C_{(-i)}$ for each group. Find the largest value of $C_{(-i)}$. Examine the estimates of the parameters of moult with this group removed. If the change is substantial, then serious consideration should be given to removing this group from the dataset. Alternatively, the possibility of a gross error should also be considered; for example, the observation in a group might have the date wrong, and this can be corrected. As emphasized by Cook (1977) and by Cook and Weisberg (1992), the decision-making process needs to depend on context.

Five of the seven years of the simulated data of Figure 1 were constructed to fit the assumptions of the moult model of Underhill and Zucchini (1988), with starting date 60 days, duration 120 days and standard deviation 20 days. Imaginary samples of birds were collected on 20 dates over seven years. 18 of the samples were obtained in the first five years. The one sample for year 6 was collected on the mid-date of the assumed moult period, day 120; the data for this year were simulated assuming that moult was 30 days early in this year. Likewise, the only sample for year 7 was collected on day 180, the day when half the birds should have completed moult. Moult was simulated to have started 30 days late in this year. The data for year 7 is designed to be influential; because it is late in the moult period it clearly ought to have considerable leverage on the results and be detected as data to be considered for enquiry and possible deletion. The data for year 6, collected on the mid-date of moult, seems unlikely to have much impact on the results and it is not at all obvious that the approach will detect that this year is an outlier.

For the 664 simulated data points for the seven years, the estimated starting date was on day 58 (in place of 60), duration was 125 (120) days, end date was on day 183 (180), and the estimated standard deviation was 25 (20) days (Table 1). The calculations for the modified Cook's distances make use of the variance-covariance matrix (Table 2). For years 1 to 5, these distances lay between 0.016 and 0.113 (Table 1). Year 7 was clearly an outlier, with a distance of 2.275, and the distance for year 6 was 0.313, an outlier when compared with the values for years 1 to 5, but very much smaller than value for year 7 (Table 1). These results confirm the expected outcomes.

Year 7 is clearly influential on the results and there is no hesitation in the decision to remove the 60 data points in this sample. The verdict for year 6 is less clear cut and if we did not know that by design this sample is an outlier, the decision to leave it in or remove it would be subjective. But in relation to years 1 to 5 its modified Cook's distance does flag it as different and the decision to remove it can be taken. With years 6 and 7 removed, and based on the remaining 544 data points, the 95% confidence intervals for the moult parameters (i.e. estimate plus/minus 1.96 x SE) contain their “true” values (Table 1).

The differences between the “true” values of the moult parameters for start date, duration and end date and the estimated values in all the rows of Table 1 are relatively small, less than 8%. The standard deviation parameter is, however, inflated by up to 33% (Table 1). In general, timing and duration of primary moult are the most used parameters in studies relating moult to explanatory variables and to other components of the annual schedule; it is encouraging that they are least impacted by perturbations of the data (Chapter 7).

Bonnevie (2010) devised a strategy to deal with what must have been essentially the same problem as described here, that of influential sets of observations. He recommended a form of case-deletion of moult records to obtain what he subjectively described as the “best estimates of moult”. The approach described here is likely to provide a reasonably objective way of estimating the relative influence of data from a variety of sources in the situations he was describing.

The algorithm devised here is applied to a moult dataset with records over 30 years by Scott et al. (Chapter 3). The species for which moult is analysed in that paper is the Red-headed Finch *Amadina erythrocephala*. In that case, five years were found to be influential.

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Table 1: Estimates of the parameters of moult of the simulated data are provided in row labelled "All". The following seven rows provide the estimates with each successive year missing. The sample sizes are given with negative numbers to indicate the number of data points removed. The final column provides the "Modified Cook's distance" (see text). The final row provides the estimates of moult when years 6 and 7, identified as influential years, are removed. Standard errors are provided in brackets for the first and final rows. The data for years 1 to 5 were simulated to have a start date of day 60, a duration of 120 days and a standard deviation of 20 days (see text).

Year	Start date	duration	Standard deviation	End date	Sample size	Modified Cook's distance
All	57.95 (3.04)	125.19 (1.60)	25.04 (0.92)	183.14 (2.05)	664	–
–1	56.60	126.79	25.67	183.38	–85	0.026
–2	58.71	125.91	26.47	184.61	–115	0.031
–3	55.47	128.13	26.24	183.59	–127	0.059
–4	55.38	130.21	26.17	185.59	–168	0.113
–5	57.68	125.86	25.57	183.54	–49	0.016
–6	60.28	127.43	23.24	187.71	–60	0.313
–7	60.21	113.45	21.28	173.66	–60	2.275
– 6, –7	61.65 (2.71)	117.27 (1.46)	19.93 (0.77)	178.89 (1.87)	544	–

Table 2: The variance-covariance matrix for the simulated moult data. The matrix is symmetric and only the lower triangular section is shown. The diagonal elements are the estimated variances of the three parameters of moult, so their standard deviations are the square roots of the values shown. The matrix is calculated within the R package "moult" (Erni et al. 2013, R Core Team 2019).

	Duration	Starting date	Standard deviation
Duration	9.255		
Starting date	-3.803	2.560	
Standard deviation	1.291	-0.480	0.843

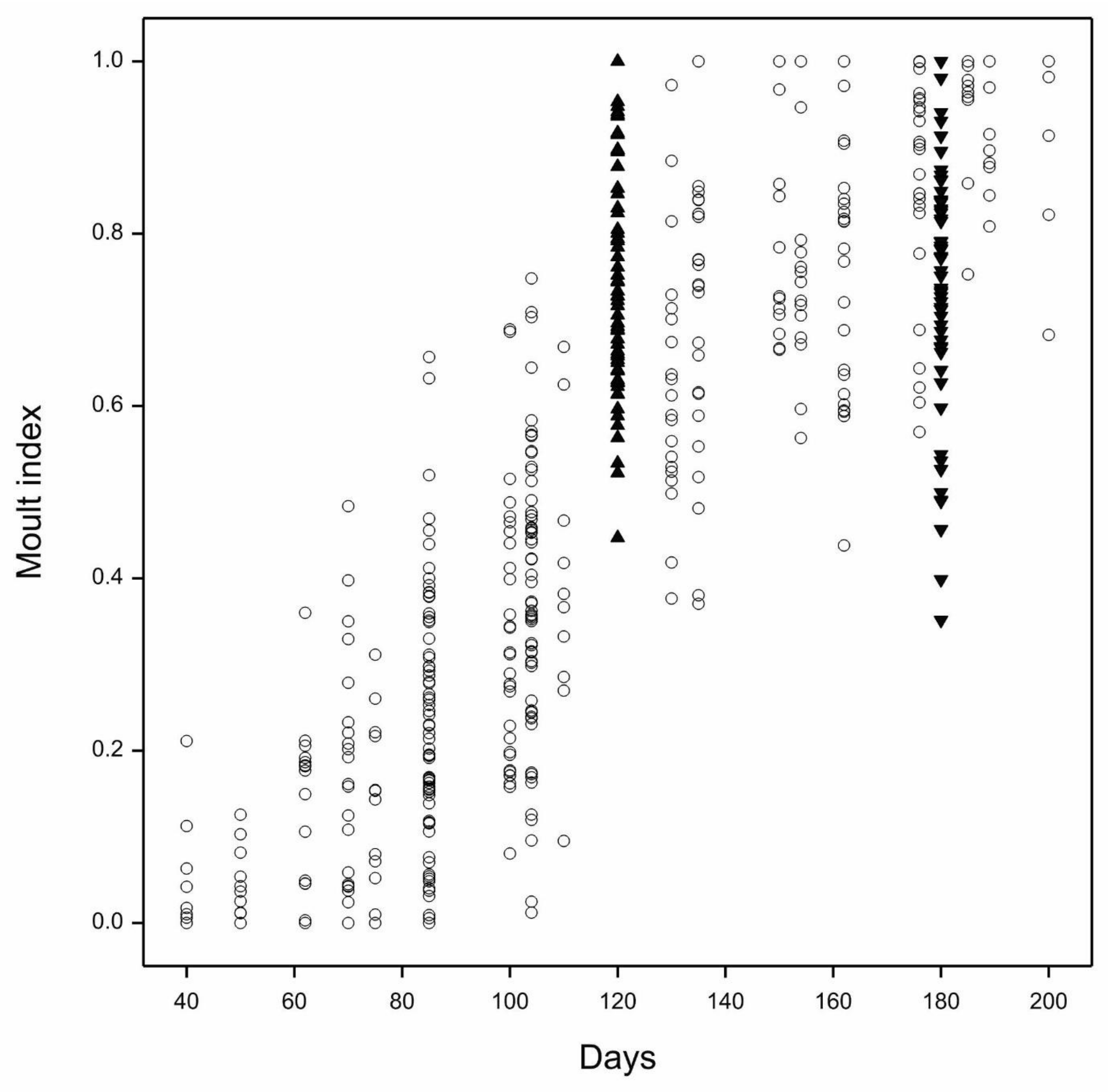

Figure 1: Simulated moult data with 20 mistnetting days over seven years. In years 1 to 5, the parameters of moult were duration 120 days, starting date on day 60, and standard deviation 20 days. These data are displayed with open circles. In year 6, one sample was obtained on day 120, in which the simulated starting date was day 30, shown with triangles. In year 7 the sample was obtained on day 180, and this had a simulated starting date of day 90, shown with inverted triangles.